The effect of fire regime on tropical savannas of north-eastern Australia: interpreting floristic patterns through critical life events.

Thesis submitted by
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Paul Williams

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Abstract.

The degree to which fire influences plant species composition and abundance (referred to in this thesis as floristic patterns) in Australian tropical savannas has been the subject of debate. Available information emphasises floristic patterns rather than the mechanisms that determine patterns. The assessment of critical events in a plant's life cycle (referred to in this thesis as critical life events) is necessary to understand population dynamics and therefore the processes that determine floristic patterns. Fire may affect population size through its influence on one or more critical life events including seed dormancy release, seed bank dynamics, seedling emergence, seedling survival and the survival and growth of juvenile and mature plants.

This thesis presents data on floristic patterns in response to fire regimes in savannas of north-eastern Australia, a region with limited quantitative information on fire response at a community level; and contributes to the broader understanding of savanna function, through an examination of life cycle processes. The aims of the research were to examine the effect of fire regime on:

a) floristic patterns in eucalypt savannas in the vicinity of Townsville, north-eastern Australia; and
b) critical life events, to investigate mechanisms determining floristic patterns.

To achieve these objectives, laboratory and shadehouse experiments were carried out and surveys of seedling emergence and vegetative post-fire regeneration were undertaken at four sites in the Townsville region. At one of these sites, Cape Cleveland, floristic patterns and critical life events were studied in detail using a manipulative fire experiment which examined three fire regimes between 1997 and 2001:

1. Control: savanna burnt in the mid dry season (July) 1997 only.
2. Early burnt: savanna burnt in the mid dry season 1997 and early dry season (May) 1999.
3. Late burnt: savanna burnt in the mid dry season 1997 and late dry season (Oct) 1999.

Five annual surveys of permanent plots at Cape Cleveland demonstrated a high degree of stability in species composition, however the abundance of several species was affected by fire regime. A significant increase in the abundance of various subshrubs, ephemeral and twining perennial forbs, and grasses was detected in the first year after fire, particularly following late dry season burning. The abundance of these species declined towards pre-fire levels in the second year after fire. The dominant grass *Heteropogon triticeus* significantly declined in abundance, and tree density increased, with fire intervals of four years.

Investigations of critical life events detected mechanisms that determine floristic patterns. A pulse of seedling emergence of subshrubs and herbaceous species occurred in the post-fire wet season, with greatest seedling density following late dry season fires. This pulse of seedling emergence explained the increase in plant abundance documented in the year following fire. It resulted from seed dormancy release, triggered by multiple fire-related agents, including the removal of herbaceous cover, which increased germination of a range of species; and the exposure to: heat-shock, which increased the germination of a range of forbs; smoke, which promoted the germination of upright perennial forbs and grasses; and nitrate, which interacted with heat shock to increase germination of at least two forbs.

The germinable soil seed bank was dominated by grasses and forbs, and seed banks of trees and shrubs were scarce and short-lived. Seasonal fluctuations were evident in the seed bank, which increased through the dry season to a maximum density in the late dry season, and declined to a minimum by the mid wet season. The high intensity late dry season fires reduced seed production by the dominant tree *Corymbia clarksoniana* in the year following burning, however the effect of fire on soil seed bank dynamics was limited due to the annual wet season decline in seed reserves that occurred irrespective of fire. These data indicate that late dry season fires promoted the emergence of a greater density of herb seedlings, compared with early dry season fires, by stimulating seed dormancy release in a higher proportion of seeds, and because more soil seed reserves were available in the late dry season to be affected by fire.

Seedling survival of herbaceous species was higher for those that emerged from recently burnt rather than unburnt savanna. High rates of seedling mortality of perennial species, and the short lifespan of ephemeral forbs, explained the decline in plant abundance documented in the second year following fire. A moderate proportion of seedlings of common sprouter species developed the capacity to survive fire within one year of germination. Only five percent of *C. clarksoniana* seedlings survived in unburnt, and fewer in burnt savanna, three years after germination.

In savanna that remained unburnt for four years, growth of juvenile trees above 2 m in height accounted for the observed increase in tree density. The capacity of the majority of species to sprout after fire, and rapid seed production of non-sprouter species, explained the stability in species composition documented in the annual floristic surveys at Cape Cleveland. Fire-promoted stem reproduction via root-suckering explained the increase in abundance detected in the subshrub *Breynia oblongifolia* following burning.

This thesis provides important information on the processes that drive tropical savanna function. It indicates that seedling recruitment is a process that limits population growth. Seedling recruitment of trees and shrubs is scarce and episodic, apparently linked to high rainfall years. The seedling recruitment of subshrubs and herbaceous species is driven by opportunities for seed dormancy release, which are primarily restricted to fire events, and limited by the low to moderate soil seed bank density and poor levels of seedling survival. Growth of juvenile trees beyond 2 m in height, and hence to reproductive maturity, requires fire-free intervals of at least four years and is therefore an event that is restricted by fire and limits population growth. The high proportion of sprouting species enables plant persistence, so that juvenile and mature plant survival are life events that provide population resilience. For ephemeral species, the soil seed bank provides a storage mechanism that provides population resilience.

This thesis provides practical information to improve the management of this widespread and important ecosystem. Conservation management of these savannas will need to balance the role of regular fires in maintaining the diversity of herbaceous species with the requirement of fire intervals of at least four years for allowing recruitment, and therefore population maintenance, of trees. While late dry season fires may cause some tree mortality, the use of occasional late fires will promote dense seedling recruitment of herbaceous species, which may be necessary to maintain sustainable populations of many grasses and forbs.

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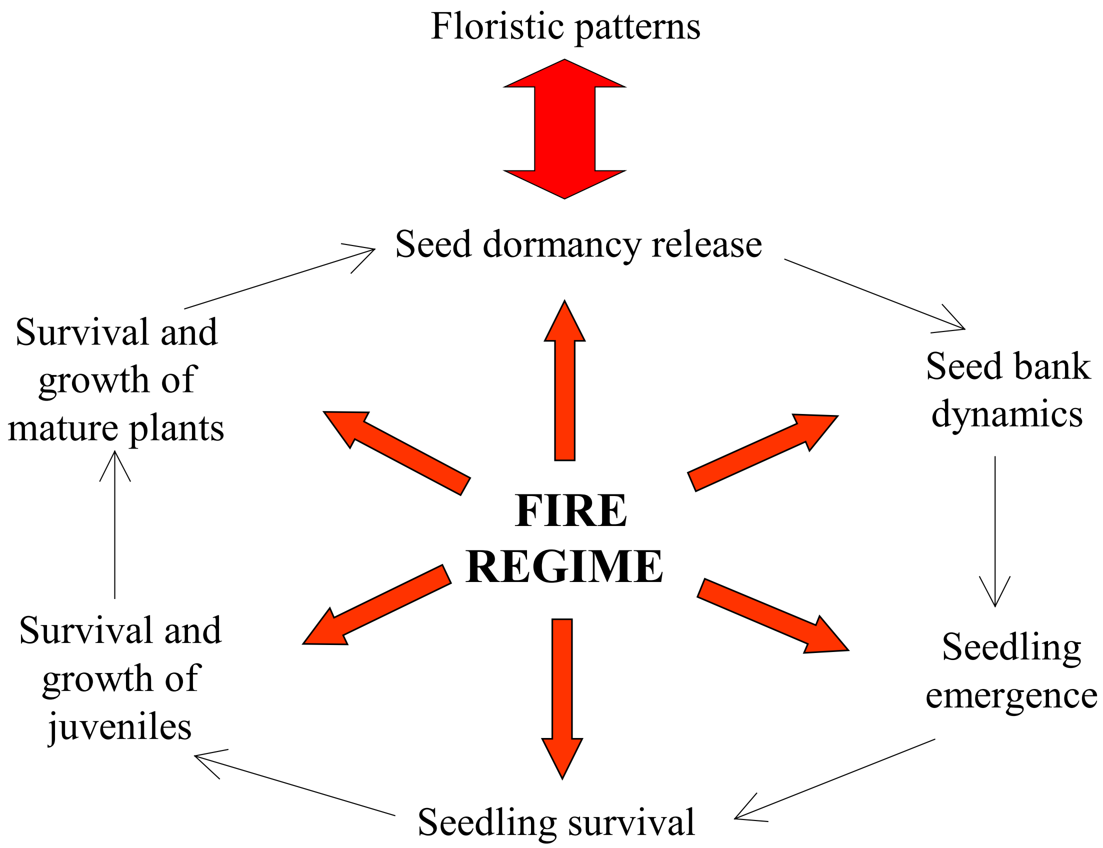


1.1 Context

This thesis examines the influence of fire regime on plant species composition and abundance (referred to as floristic patterns) within tropical eucalypt savannas of north-eastern Australia. The mechanisms determining floristic patterns are investigated through an assessment of critical events in a plant's life cycle (referred to as critical life events). These include seed dormancy release, soil seed bank dynamics, seedling emergence, seedling survival and the survival and growth of juvenile and mature plants.

The relative importance of key factors that drive savanna function, including climate, soils, biological interactions and fire, is debated (Scholes and Archer 1997; Higgins *et al*. 2000). An examination of life cycle processes that produce floristic patterns is critical for understanding how savannas function and allows predictions of how savannas will respond to fire regimes, and forecast climate change (Whelan *et al*. 2002).

There has been only limited research into the influence of fire regimes on floristic patterns in savannas of north-eastern Australia. Therefore floristic patterns within eucalypt savannas of this region were examined using manipulative field and laboratory experiments, coupled with surveys of seedling and vegetative regeneration after a range of fires in several locations in the vicinity of Townsville, north-east Queensland (19° 15'S, 146° 46'E; Figure 1.1). These data contribute to our broader understanding of how tropical savannas function and provide essential information to aid the management of this widespread ecosystem.

1.2 The effect of fire regime on floristic patterns in Australian tropical savannas

1.2.1 Australian tropical savannas

Tropical savannas cover approximately 13% of the world's land surface (Scholes and Archer 1997). The "dual significance" of herbaceous and woody species is a characteristic feature of these savannas, which possess a sparse to moderate tree canopy and an abundance of grasses and forbs (Mott *et al*. 1985; Walker 1985; Higgins *et al*. 2000).

Figure 1.1. The distribution of Australian tropical savannas (courtesy of the Tropical Savannas CRC).

Australian tropical savannas are dominated by eucalypts (*Eucalyptus* and *Corymbia*, Myrtaceae) and cover a large proportion of northern Australia (Mott *et al*. 1985; Williams *et al*. 2002*a*; Figure 1.1). They experience intense summer wet seasons (December to March) and prolonged winter dry seasons (Mott *et al*. 1985; Williams *et al*. in press). The strong seasonal variation in rainfall is a critical factor influencing ecological processes within these communities (Williams *et al*. 1999*a*; Woinarski 1999). Long-term climatic fluctuations, including irregular severe droughts, also influence savanna structure and composition (Fensham and Holman 1999).

1.2.2 Fire in Australian tropical savannas

The intense summer wet seasons in Australian tropical savannas yield a large biomass of grass, which cures during the subsequent dry season (Walker 1981). The consistency of this cycle leads to frequent and extensive fires (Wilson and Bowman 1987; Gill *et al*. 1996). Grasses rapidly regenerate after fire in northern Australia, re-establishing fuel loads and creating the potential for fire intervals as low as one or two years (Walker 1981; Gill *et al*. 2000). Contemporary fire intervals typically range from one to three years in the high rainfall region of the Northern Territory and Kimberley, and two to five years in the north and central coast of Queensland (Burrows and Burrows 1992; Crowley 1995; Craig 1997; Russell-Smith *et al*. 1997; Crowley and Garnett 2000).

As a consequence of progressive grass curing through the dry season, the timing of fire has a strong influence on intensity (Bowman 1988). Low intensity, patchy fires are typical of the early dry season, with higher intensity and extensive fires produced by later dry season burning (Gill *et al*. 1990). Fire intensity in Australian tropical savannas is typically lower than in southern Australia and crown fires are rare (Craig 1997). Annual early dry season fire intensities can be in the order of < 1000 to 2200 kWm^{-1} and annual mid to late dry season fires from 1000 to 7700 kWm^{-1} (Williams *et al*. 1999b; Russell-Smith *et al*. in press). A single late dry season fire in a savanna unburnt for seven years was estimated to have an intensity of approximately 20 000 kWm^{-1} (Williams *et al*. 1999*b*).

Soils of many Australian tropical savannas are low in nutrients (Mordelet *et al*. 1996; Morgan *et al*. 2000; Jackson and Ash 2001). Volatilization of nutrients occurs during fire, although most are returned via rain and ash redistribution (Cook 1994). Repeated annual burning may be too frequent to allow the replacement of lost nitrogen in savannas of the Northern Territory (Cook 1994; Russell-Smith *et al*. in press). However the dynamics of soil nutrition may vary significantly between fires and communities, as the nitrogen content of a south-eastern Queensland eucalypt forest burnt annually for thirty years was similar to that of adjacent unburnt forest (Lamb *et al*. 1989).

1.2.3 Structural and floristic patterns

The high fire frequency experienced in tropical savannas may be expected to impact on community structure and composition. Indeed, frequent fire is often linked with reduced tree densities in tropical savannas throughout the world, including southern Africa (Trollope 1982; Skowno *et al*. 1999), India (Puyravaud *et al.* 1995) South America (Hoffman 1996) and Australia (Sandercoe 1988; Williams *et al*. 1999*b*). The season and intensity of fire can be as important in affecting floristic patterns as fire frequency. Annual late dry season fires can lead to reduced tree densities, while early annual fires can promote tree density (Trapnell 1959).

Increases in tree density typically result from the growth of stunted juvenile trees (< 2 m in height) with fire intervals of greater than two or three years (Bowman and Panton 1995; Russell-Smith *et al*. in press). The release of stunted juveniles following fire protection may be most rapid for non-eucalypts, such as *Acacia* spp., *Melaleuca viridiflora* and other broad-leaved species (Bowman *et al*. 1988; Fensham 1990; Crowley and Garnett 1998). The release of eucalypt juveniles in the absence of fire is often slow and in some species not apparent after a fire interval of 21 years (Russell-Smith *et al*. in press).

Charcoal and pollen records indicate the distributions of rainforest and eucalypt-dominated communities in northern Australia has been dynamic over thousands of years (Kershaw *et al*. 1991; Hopkins *et al*. 1993). Rainforest invasion into eucalypt forests has occurred in the Wet Tropics region of north-eastern Australia (Harrington and Sanderson 1994) and parts of Cape York Peninsula (Stanton and Roeger 2001). However, the establishment of rainforest, or vine thicket, species in savannas away from the east coast is generally limited, or at least slow (Bowman *et al*. 1988; Fensham 1990; Bowman 1993; Bowman 1994; Williams *et al*. in press; Russell-Smith *et al*. in press). In fact, across much of northern Australia, many rainforests and stands of *Callitris intratropica* and *Acacia shirleyi*, have declined in distribution as a result of damage from repeated high intensity fires that spread from adjacent eucalypt savannas (Price and Bowman 1994; Woinarski and Fisher 1995; Bowman 2000; Russell-Smith and Stanton 2002).

The herbaceous component of tropical savannas is a diverse and important feature, yet assessment of fire effects has been largely confined to the dominant grasses. Many of these perennial and annual grasses maintain high densities with fire intervals of one to three years, although a few grasses are favoured by less frequent burning (Shaw 1957; Mott and Andrew 1985; Mott *et al*. 1985; Russell-Smith *et al*. in press). The season of fire may have a significant impact, with early and late dry season fires promoting different grasses, and wet season burning reducing the abundance of both perennial and annual species (Stocker and Sturtz 1966; Walker *et al*. 1989; Williams and Lane 1999).

Although there has been limited research into the effects of fire on forbs in Australian tropical savannas, it is apparent that fire can affect their abundance. Many are most abundant with high fire frequency or in recently burnt savanna (Hoare *et al*. 1980; Sandercoe 1988; Fensham 1990; Williams *et al*. 2002*b*). Forb composition can also be affected by the season of fire (Bowman *et al*. 1988; Williams and Lane 1999).

1.3 The assessment of critical life events for interpreting floristic patterns

1.3.1 The value of examining critical life events

To understand how a community functions in response to fire, details are required of the mechanisms that drive floristic patterns. The assessment of critical events in a plant's life cycle provides an understanding of population, and therefore community, dynamics (Harper 1977; Whelan *et al*. 2002). Population changes can be driven by the variation in fire intervals, the unique characteristics of each fire event, and/or density-dependent processes (Bond and van Wilgen 1996). Fire can influence the persistence of standing plants and seeds; the density of seed germination; the establishment of seedlings; the progression from seedling to mature plant; and seed production (Whelan 1995; Keith 1996; Whelan *et al*. 2002).

There is currently very little data on the effect of fire on the demographics of Australian tropical savanna species. The most detailed information has been collected for *Sorghum intrans*, which dominates some savannas of the Northern Territory and Western Australia, and highlights the value of a demographic assessment. Knowledge of the mass recruitment of this annual grass at the onset of the wet season, the fire-sensitivity of seedlings, and the transient nature of the soil seed bank provide an insight into the mechanisms that cause a decline in this species after wet season burning (Stocker and Sturtz 1966; Andrew and Mott 1983; Andrew 1986).

Further work is needed to assess the influence of fire on critical life events in the life cycle of a wider range of savanna species, to provide data on seed production, seed dispersal, seed dormancy, seed bank dynamics, seedling emergence, and the survival and growth of seedlings, juveniles and mature plants. Hence this thesis aims to investigate fire effects on critical life events of a range of savanna species, which will improve the current understanding of processes that govern savanna function. The following discussion introduces the current knowledge of fire effects on these life events.

1.3.2 The effect of fire regime on seed production and dispersal

Plants in Australian tropical savanna are pollinated by a wide range of vectors including bats, gliders, birds, insects and wind (House 1997; Franklin and Noske 2000; Hansman 2001). Their reproductive phenology reflects the annual wet-dry cycle (Burrows and Burrows 1992; Setterfield and Williams 1996; Williams *et al*. 1999*a*). Peak seed fall of grasses occurs from the middle of the wet to the early dry season (Tothill 1977a; Andrew and Mott 1983; Mott and Andrew 1985). Forb seed fall peaks in the late wet to mid dry season, while the late dry season and onset of the wet season is the major period of seed fall for woody species (Brennan 1996; Setterfield and Williams 1996; Williams *et al*. 1999*a*).

Fire influences seed production of tropical savanna plants by promoting flowering, affecting pollinator abundance and by damaging reproductive structures before seed set (Woinarski 1990; Brennan 1996; Setterfield 1997*a*). The pattern of seed production can vary with fire response, as vegetative regenerating “sprouter” species tend to put fewer resources into seed production compared with fire-killed, “obligate seeder” species (Pate *et al*. 1990; Bond and van Wilgen 1996; Bond and Midgley 2001).

Seed of savanna plants are dispersed by non-biotic agents, including gravity, wind and water (Grice 1996; Pettit and Froend 2001). Biotic seed dispersers (and predators) include ants, cattle, birds, feral pigs and wallabies (Andersen 1991; Grice 1996;

Setterfield 1997*b*). Explosive capsules can also increase the distance of seed dispersal (Auld 1996). Fire can influence seed dispersal and predation. For instance, seed harvesting ants in the Northern Territory, which both consume seed and disperse seed undamaged, can be most abundant with high fire frequency (Andersen 1991).

Several dominant grasses of tropical savannas possess awns with a hygroscopic mechanism that buries seed into the topsoil, so that they are insulated from lethal temperatures during the passage of fire (Tothill 1969; Andrew and Mott 1983).

1.3.3 The effect of fire regime on seed dormancy release

Viable, fresh seeds are considered to possess a primary, or “innate”, dormancy if they will not germinate without a further stimulus when provided with moisture and temperatures suitable for germination (Harper 1977; Bell 1999). A secondary dormancy may develop if environmental conditions are inappropriate for germination (Bell 1999). Secondary dormancy may be induced in buried seed by darkness or temperature regime and may explain why viable seeds that lack an innate dormancy remain stored in the soil seed bank (Bell *et al*. 1999; Auld *et al*. 2000).

Seed dormancy can allow a seed to persist through unfavourable environmental conditions until climatic and micro-site factors favour seedling establishment (Bell 1999). Cues for releasing seeds from a state of dormancy are often linked with seasonal conditions, including day length and exposure to high or low temperatures (Beardsell and Mullett 1984; Bell *et al*. 1993; Battaglia 1996; Clarke *et al*. 2000).

Fire can improve micro-site conditions that influence seedling survival and growth, such as increased nutrient and light availability (Whelan 1995). It is not surprising then that many plants of fire-prone environments have dormancy mechanisms that cue seeds to germinate after fire. Fire-related cues found to break seed dormancy include exposure to heat shock (i.e. a short duration of elevated temperature), smoke, charcoal and nitrate (Bell *et al*. 1987*a*; Auld and O’Connell 1991; Dixon *et al*. 1995; Bell *et al*. 1999; Clarke *et al*. 2000).

Some species show enhanced germination after exposure to multiple germination cues, such as heat shock and smoke (Keith 1997; Kenny 2000; Morris 2000). Several different factors may be required to cue the germination of co-existing species and a germination trigger for one species may inhibit the recruitment of an adjacent species (Clarke *et al*. 2000; McIvor and Howden 2000). Such variation in germination requirements may help explain levels of species diversity (Grubb 1977).

Several grasses of northern Australia show an after-ripening requirement, whereby the embryo of fresh seed requires further time to mature before the seed will germinate (Bell 1999). The after-ripening dormancy in these species expires during the dry season allowing dense germination with the onset of the wet season (Andrew and Mott 1983; McIvor and Howden 2000). Some tropical eucalypts and grasses have no apparent innate seed dormancy, being capable of germination immediately after seed fall (Setterfield 1997*b*; Crowley and Garnett 2001).

Few studies have quantified the link between fire and seed dormancy of tropical savanna plants. Smoke-triggered germination has been documented for several tropical species including *Themeda triandra* (Baxter *et al*. 1994), *Callitris intratropica* (Roche *et al*. 1997) and *Heteropogon contortus* (Campbell *et al*. 1996). Heat shock has been shown to promote several semi-arid shrubs, including *Acacia aneura* and *Senna nemophila* (Hogkinson and Oxley 1990). Clearly fire plays a role in seed dormancy release of some tropical savanna species, and therefore savanna function, and further research is required to examine additional species.

1.3.4 The effect of fire regime on soil seed bank dynamics

Seed dormancy allows the development of seed storage, typically referred to as “seed banks” (Harper 1977). Seed banks bridge the temporal gap between seed production and seed germination, provide a storage mechanism for regeneration after disturbance and can be essential where limited seed dispersal distances result in little seed immigration from adjacent areas (Whelan 1986; Lunt 1997).

Seed can be stored on the plant or in the soil (Whelan 1995). The storage of seed in the canopy is generally referred to as “serotiny” or “bradyspory” (Lamont *et al*. 1991;

Whelan 1995). Seed storage on or below the soil surface is referred to as the “soil seed bank” and is the principal means of seed storage in Australian tropical savanna species (Shaw 1957; Mott and Andrew 1985; Andrew 1986; McIvor 1987; Williams *et al*. in press).

Many species do not produce a seed bank, as their seeds either germinate, rot or are eaten by predators soon after seed fall (Crowley and Garnett 2001; Pettit and Froend 2001). Species whose seeds remain viable in the seed bank for less than a year are referred to as possessing a “transient” seed bank (Thompson and Grime 1979). To remain within a community, these species rely on the persistence of standing plants or annual recruitment and seed production, or seed dispersal from outside the community. Some species produce seeds that remain viable within a seed bank for many years. This is referred to as a “persistent” seed bank and is an important storage mechanism, especially for annual species that do not germinate every year (Thompson and Grime 1979; Bond and van Wilgen 1996).

Research into the seed banks of Australian tropical savanna species has primarily focused on dominant grasses. While some, such as *Alloteropsis semialata* and *Dichanthium fecundum*, produce no apparent seed bank, many annual and perennial grasses produce a transient seed bank that expires just prior to further seed input during the wet season (Andrew and Mott 1983; Mott and Andrew 1985; Crowley and Garnett 2001). Soil seed banks of tropical savanna trees and shrubs are rarely detected, and when present, tend to be transient (McIvor 1987; Higgins *et al*. 2000; Rogers 2000; Pettit and Froend 2001).

Fire can affect seed bank dynamics by influencing seed input, killing stored seed, or promoting germination (Keith 1996). While the bradysporous seed banks tend to increase with fire interval (e.g. Witkowski *et al*. 1991; Pannell and Myerscough 1993), the effect of fire on soil seed banks is more variable. Zammit and Zedler (1988) found fire interval influenced soil seed banks of one shrub and nine herbs in California chaparral. The soil seed bank of several South African fynbos shrubs decline immediately after fire, but do not show annual increases with time since fire (Pierce and Cowling 1991).

Research in tropical savannas has indicated that, in addition to affecting seed production (Setterfield 1997*a*), fire can affect soil seed banks through direct mortality of surface seeds and enhanced seed predation (Crowley and Garnett 1999). Further research is required to address the influence of fire on soil seed bank dynamics at a community level in Australian tropical savannas.

1.3.5 The effect of fire regime on seedling emergence

The term "seedling emergence" is used throughout this thesis to signify the emergence of seedlings above the soil surface, following seed germination. Micro-site, seed dispersers and predators, seed dormancy triggers, and seasonal conditions influence the density and rate of seedling emergence (Ashton 1979; McIvor and Gardener 1985; Wellington 1989; Stoneman and Dell 1994; Clarke and Davidson 2001).

Seedling emergence may be cued to seasonal cycles, irregular climatic events or disturbance. Many Australian tropical savanna trees and shrubs, including the dominant eucalypts, are known to recruit seedlings episodically (Lacey 1974; Fensham 1992). The emergence of many annual grass and forb seedlings occurs at the start of each wet season, irrespective of fire (Andrew and Mott 1983; Brennan 1996; Crowley and Garnett 1999; Crowley and Garnett 2001).

The influence of fire on seedling emergence varies, depending on many factors. These include the size of the seed bank at the time of fire; the level of seed mortality during fire; the proportion of the seed bank released from dormancy; and the loss of seed due to predation, disease and desiccation before germination (Whelan 1995; Bond and van Wilgen 1996; Keith 1996). While seedling emergence of some Australian tropical trees may be greater in unburnt rather than burnt savanna (Setterfield 1997*b*), seedling density of several perennial grasses, most notably *Heteropogon contortus*, is increased by fire (Shaw 1957; Tothill 1969).

There are limited data on the complex factors promoting seedling emergence of savanna species (Higgins *et al*. 2000) and more information is required on the influence of fire on seedling emergence in northern Australia. Fire frequency and season affect seedling emergence through their influence on seed bank size and fire intensity. Fire intensity affects seed mortality and the release from seed dormancy.

1.3.6 The effect of fire regime on seedling survival

Seedling survival is an important process that can limit population growth (Keith 1996). Conditions that promote seedling survival may differ from those that increase the density of seedling emergence (Lamont *et al*. 1993; Stoneman and Dell 1994; Stoneman *et al*. 1994; Keith 2002). Seedling mortality can result from desiccation, herbivory, insufficient nutrients, disease, shading, and disturbance (Lacey 1974; Hoffman 1998; Facelli *et al*. 1999). Both inter- and intra-specific competition for resources can be high for seedlings (Morgan 1998). Conversely, the establishment of seedlings may be facilitated by adjacent plants (Kellman 1985). Resource competition, herbivory and disease can lead to density-dependent mortality of seedlings (Andrew 1986; Whelan 1995; Bond and van Wilgen 1996).

Seedling survival can be strongly influenced by fire (Pate *et al*. 1990; Keith 1996). Seedlings recruited into the immediate post-fire environment can benefit from reduced competition and enhanced nutrient and light availability (Ashton and Chinner 1999). Herbivore pressure may be either magnified or diminished, depending on species and fire characteristics (Whelan and Main 1979; Keith 1996).

Percentage seedling survival in Australian tropical savannas varies between species, sites and seasons (Andrew and Mott 1983; Setterfield 1997*b*; Crowley and Garnett 1999). Further information is required on the interaction of burning with other factors that limit survival and the time required for seedlings to develop the capacity to survive fire and to produce seed (i.e. the primary juvenile period, Gill 1975).

1.3.7 The effect of fire regime on the survival and growth of juvenile and mature plants

The persistence of standing plants provides stability to a community (Bond and Midgley 2001). Longevity of Australian tropical savanna species ranges from annuals that survive as standing plants for less than one year, to trees that can survive for more than one hundred years (Mucha 1979; Watkinson *et al*. 1989). Growth rates are related to environmental factors, especially temperature, rainfall, and soil fertility (Barbour 1987). Both soil moisture and nutrients have been found to limit plant growth in tropical savannas (Cook and Andrew 1991; Jackson and Ash 1998).

Fire can have a significant impact on the survival and longevity of plants. The mode of post-fire regeneration forms the basis of several life history classifications (e.g. Noble and Slatyer 1980; Gill 1981; Bond and van Wilgen 1996). Species that survive and vegetatively regrow after complete canopy scorch are described as “sprouters” or “resprouters” (Gill 1981; Whelan 1995; Bond and van Wilgen 1996; Keith 1996). Vegetative regrowth can result from subterranean buds, located in rhizomes, roots and the base of stems, which are insulated from lethal temperatures by the soil (Gill 1981). Post-fire regeneration from subterranean buds can result in the proliferation of stems (Lacey 1974; Hoffman 1998).

Sprouting may also originate from aerial buds, located on the trunk or branches. This is described as “epicormic” sprouting and the insulation of aerial buds is provided by the bark (Gill 1975; Burrows 2002). An additional sprouting mechanism, most notably found in *Xanthorrhoea* spp., involves bud protection within the stem apex (Gill 1981).

Plants that are killed by fire when completely scorched are often described as “non-sprouters” or “obligate seeders”, in reference to their reliance on regeneration via seedlings (Gill 1981; Whelan 1995; Bond and van Wilgen 1996). The term “fire ephemerals” is also used, in reference to plants that germinate in response to fire and complete their life cycle within a few years (Pate *et al*. 1985; Whelan 1995).

Both plant survival and growth are affected by fire regime. High fire frequencies can stunt juvenile plant growth by repeated top kill (Midgley and Bond 2001). Suppression of juveniles through regular burning in savannas in high rainfall regions may be an important factor limiting tree density and allowing the coexistence of grasses and trees (Higgins *et al*. 2000). In the absence of fire, the growth of juveniles of tropical eucalypts may be slower than that of other trees and may also require release from overstorey competition (Bowman *et al*. 1988; Fensham 1990; Fensham and Bowman 1992; Russell-Smith *et al*. in press).

Frequent fire can cause mortality of sprouters if they are unable to replenish the necessary bud or carbohydrate reserves, or protective tissue, within fire intervals (Whelan 1995; Keith 1996). Perennial grasses, such as *Heteropogon contortus* and *Themeda triandra*, may senesce during long fire intervals (e.g. more than five years), and their populations decline due to an absence of fire-promoted seedling recruitment to replace senesced individuals (Mott and Andrew 1985; Mott *et al.* 1985; Morgan and Lunt 1999).

The intensity of a fire can affect plant mortality. Obligate seeders may survive low intensity fires, when their canopy is not completely scorched (Gill 1981). Percentage stem and whole-plant mortality of sprouter species is proportional to fire intensity (Williams *et al.* 1999b). Fire season can also influence survival and re-growth (Bond and van Wilgen 1996). The higher intensity, late dry season fires tend to produce greater plant mortality than early fires in tropical savannas (Williams *et al.* 1999b). Soil moisture at the time of burning and the period before post-fire rain can be critical for plant survival. Up to 50% mortality of the perennial grass, *Aristida latifolia*, can result from burning during the mid dry season, when there is no follow-up rain for two or three months (Phelps 2001). Burning during a period of rapid growth may also cause greater damage than when the plant is in a state of dormancy (Whelan 1995), and the season of fire that causes the least damage to standing plants may be the very season that produces the lowest density of seedling emergence and establishment (Keith 1996).

Further research is required to examine processes governing survival and growth in tropical savannas. Variation in survival after different fire events may result from differences in the survival of regenerative buds and/or the quantity of stored carbon reserves (Bond and van Wilgen 1996). The dominance of sprouting species may provide stability to savanna composition and therefore the survival of the passage of fire by juveniles and mature plants may be a critical life event that maintains savanna function.

1.4 This study

1.4.1 Aims of this study

The degree to which fire influences floristic patterns in Australian tropical savannas is debated (Duff and Braithwaite 1989; Williams *et al*. 2002*a*). It has been argued that the long history of frequent fire has lead to savanna communities that are resilient to fire regimes and driven by edaphic and climatic factors (Wilson and Bowman 1987; Bowman *et al*. 1988). While a high level of stability in floristic composition has been demonstrated in response to a range of fire regimes, fire effects on species abundance and savanna structure are apparent (Bowman and Panton 1995; Williams and Lane 1999; Russell-Smith *et al*. in press). Research into the influence of fire on floristic patterns has primarily been carried out in the monsoonal regions of the Northern Territory and Cape York Peninsula, so that less is known about the savannas of north-eastern Australia, south of Cape York Peninsula.

Available information emphasises floristic patterns rather than the mechanisms that determine patterns in Australian tropical savannas. Fire may limit population growth, and therefore affect floristic patterns, through its influence on one or more life cycle processes, including plant survival during the fire event and intervals between fires, seed production and seedling recruitment (Whelan *et al*. 2002). Higgins *et al*. (2000) proposed that the seedling emergence of trees, governed by rainfall, and the release of stunted juvenile trees to the canopy, controlled by fire, may be critical events limiting tree density in savannas and allowing the coexistence of grasses and trees. This hypothesis requires testing in a range of savannas and further information is required on the factors driving seedling recruitment of grasses and forbs. The ability of established plants to sprout after fire may be a critical process that provides population stability (Bond and Midgley 2001) and may explain reports of resilience in species composition in frequently burnt savannas (e.g. Bowman *et al*. 1988; Williams *et al*. in press).

Given this theoretic context, this thesis focuses on patterns and processes in Australian tropical savannas to:

1. determine the effect of a series of fires on floristic patterns in a tropical savanna in north-eastern Australia; and

2. investigate the effect of fire on critical life events to investigate mechanisms that determine floristic patterns.

1.4.2 Thesis structure

The various components of this thesis will be presented with reference to a diagrammatic model (Figure 1.2). The model portrays the critical life events influenced by fire, that will be addressed in this study, and their role in driving floristic patterns. It is based on the critical "events", "hurdles" and "processes" in a plant's life cycle, as expressed in previous work, such as Harper (1977); Keith (1996); Midgley and Bond (2001) and Whelan *et al*. (2002). The model deliberately depicts life events rather than life cycle stages, such as the seed, seedling and adult phases, to focus the investigation on fire impacts on dynamic life cycle processes. This study examines whether the influence of fire on any or all of these life events limits population growth, and therefore investigates central processes that drive savanna function.

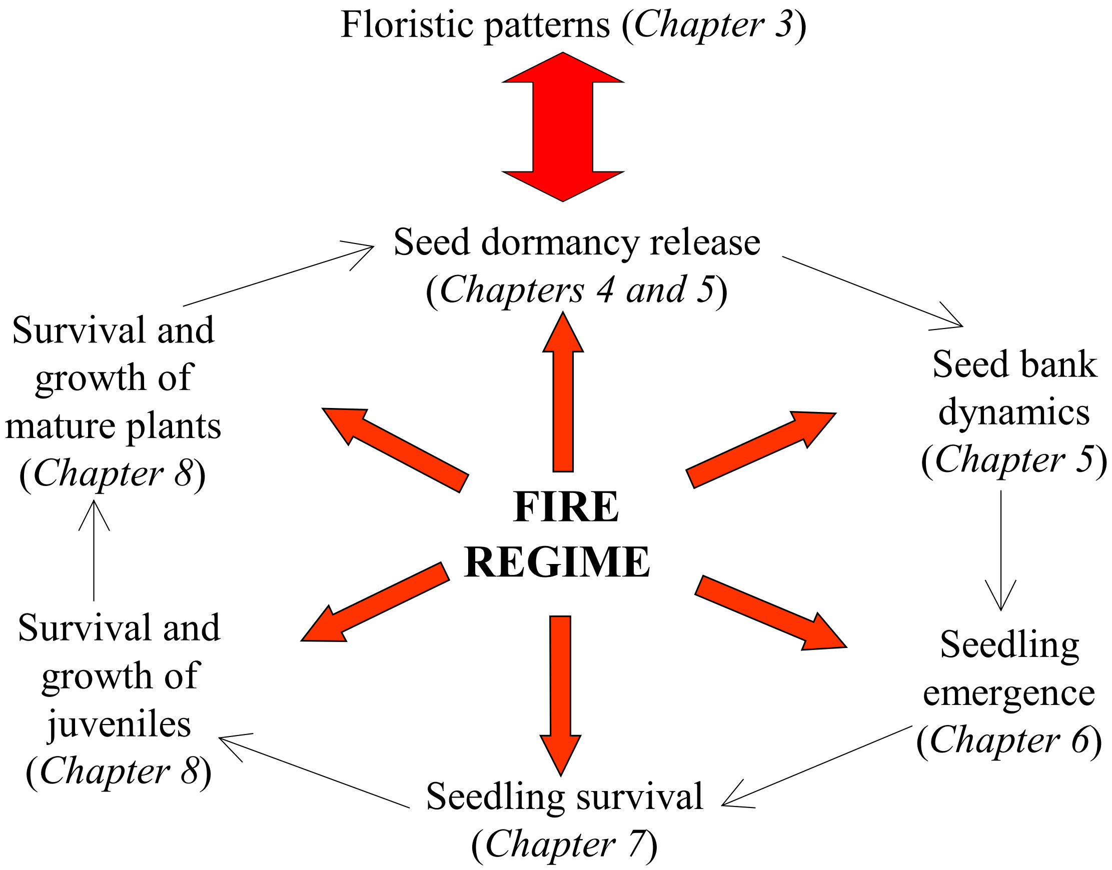


Figure 1.2. Diagrammatic model of the influence of fire regime on critical life events and floristic patterns in tropical savannas, and the chapters of the thesis in which they are investigated.

Chapter 2 describes the study site, climate and the design of a manipulative fire regime experiment. Chapter 3 examines the dynamic patterns in species composition and abundance in response to variation in fire regime. The assessment of floristic patterns is based on changes detected over five years using annual plot surveys. Multivariate analyses are used to detect community-level changes, and univariate analyses to examine fire effects on the abundance of species groups and common species. Fuel load dynamics and fire intensities are also examined.

Chapters 4 to 8 examine the effect of fire regime on critical life events to investigate the way in which fire affects floristic patterns (Figure 1.2). The effect of fire on seed production is only directly assessed for the dominant tree, *Corymbia clarksoniana*, and seed dispersal is not specifically examined, however the outcome of these important events are examined in the study of soil seed bank dynamics.

Chapter 4 examines the effect of fire on seed dormancy release of ten legumes (both native and exotic) in a laboratory experiment that investigates the effects of exposure to heat shock, smoke and nitrate on seed germination. These factors are related to the passage of fire and have been shown to break seed dormancy in species of fire-prone communities (Bell 1999). The temperatures during the passage of early and late dry season fires are documented and the link between temperature elevation and depth of seed germination in the topsoil is examined and interpreted with reference to the results of the laboratory experiment.

Chapter 5 broadens the investigation of seed dormancy to examine a wide range of species while investigating the effect of fire on seasonal and annual fluctuations in the germinable soil seed bank. The dynamics in soil seed bank are related to fruiting phenology and the species composition is also compared with that of the standing vegetation documented in Chapter 3.

Chapter 6 assesses patterns of seedling emergence. It examines whether germination is an annual wet season event or primarily a response to fire. An assessment is made of the influence of fire season on seedling emergence, and the experimental removal of herbaceous biomass is used to test the importance of ground cover removal during fire on seedling emergence. A further experiment examines the safe site requirements for the germination of the dominant tree, *Corymbia clarksoniana*. The species composition of the seedling surveys is compared with that of the standing vegetation and germinable soil seed bank detected in Chapters 3 and 5, to help determine processes involved with seedling emergence.

Chapter 7 examines the influence of fire regime on seedling survival. It compares the survival of seedlings that germinated from recently burnt savanna, unburnt savanna with the herbaceous layer removed or undisturbed savanna. The fire tolerance of seedlings of common perennial species is documented. The survival of seedlings of the dominant tree *C. clarksoniana* is assessed three years after a mass germination event.

Chapter 8 documents the sprouting ability of all species and assesses the influence of fire on the survival and growth of juvenile and mature trees, and the survival of common herbs. This chapter also examines the effect of disturbance type (burning and cutting) and season of disturbance on stem reproduction in a root suckering subshrub, *Breynia oblongifolia*.

Chapter 9 ties together information on the effect of fire on critical life events to interpret floristic patterns. The implications of the results are discussed in terms of current concepts of the role of fire in tropical savanna function and the management of tropical eucalypt savannas in north-eastern Australia.

Chapter 2. Study sites, climate and design of the Cape Cleveland fire regime experiment.

Eucalypt savanna of the Townsville region.

2.1 Study sites and climate

This thesis examines the impact of fire regime in tropical eucalypt savannas in the vicinity of Townsville, north-eastern Australia (19° 15’S, 146° 46’E; Figure 1.1). The primary field site of this study is located at Cape Cleveland, Bowling Green Bay National Park, approximately 25 km east of Townsville (19° 16’ 30”S, 147° 02’ 30”E; Figure 2.1). Seedling emergence and post-fire vegetative regeneration data were collected at additional sites in the Townsville region. These were: Castle Hill, a Townsville City Council reserve (19° 15’S, 146° 48’E); Many Peaks Range, within Townsville Town Common Conservation Park (19° 11’ 30”S, 146° 45’ 30”E) and Mt Elliot, within Bowling Green Bay National Park (19° 27’S, 146° 57’E; Figure 2.1). All sites have been protected from stock grazing for at least 20 years and are based on soils derived from a granitic parent material, with the exception of Many Peaks Range, which is primarily based on a metamorphosed acid volcanic parent material (Paine and Smith 1972). The soils at each site are free draining and loamy, and are not seasonally water logged.

Townsville experiences summer wet seasons, with 78% of the 1143 mm mean annual rain falling between December and March (Figure 2.2). The highest mean daily maximum temperature per month, recorded between 1940 and 2001 by the Australian Bureau of Meteorology at the Townsville airport, approximately 4 km west of Castle Hill, was 31.3°C in both December and January. The lowest mean daily minimum temperature per month was 13.6°C, recorded in July.

The annual rainfall in Townsville was higher than average during 1997, 1998 and 2000, and below average for 1999 and 2001 (Table 2.1a). Rainfall records for Cape Cleveland during the study period were recorded by the Australian Bureau of Meteorology at a location approximately 10 km south of the study site (Table 2.1b).

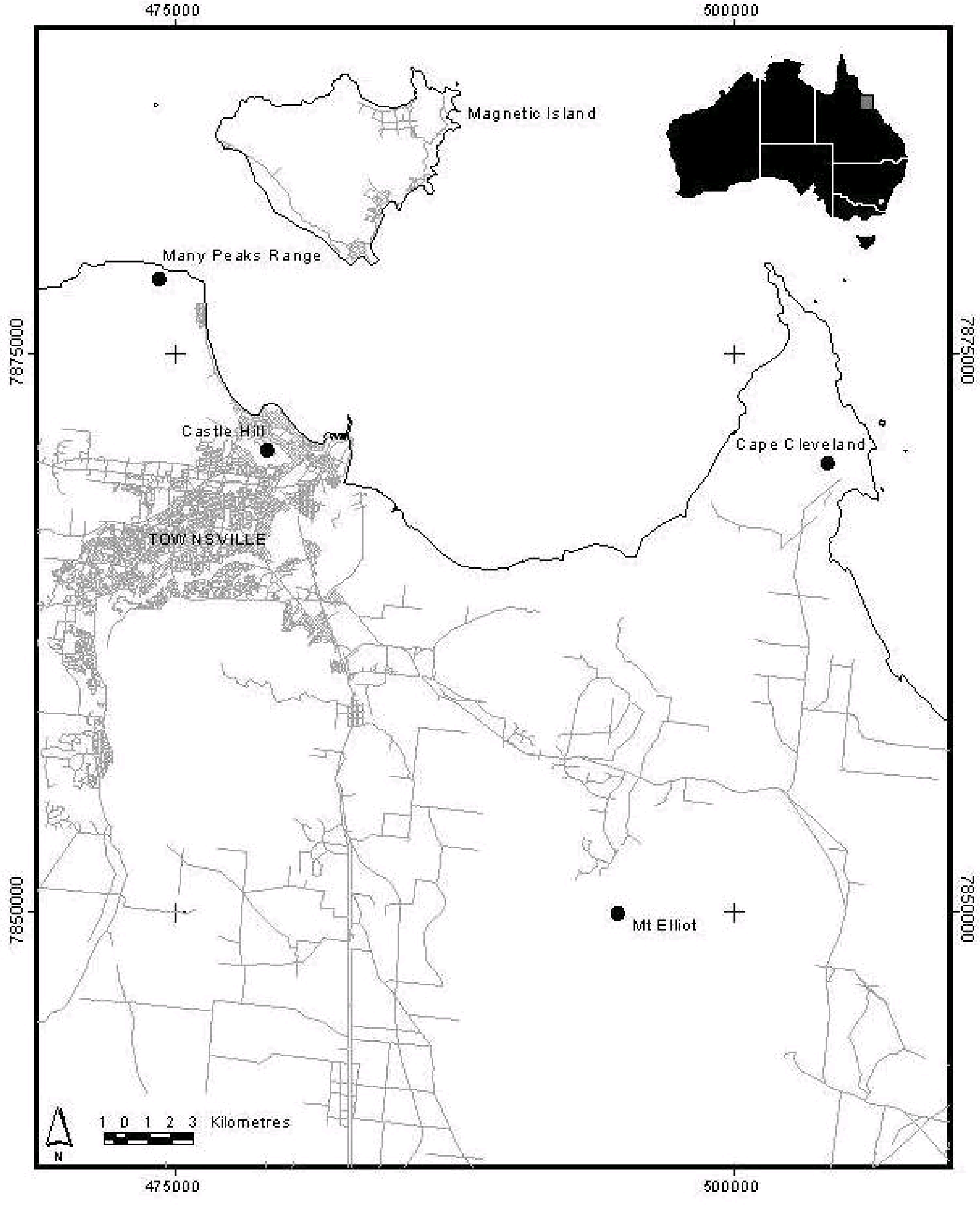


Figure 2.1. Map of study sites in the vicinity of Townsville, north-eastern Australia: Many Peaks Range, Castle Hill, Mt Elliot and Cape Cleveland. Townsville road network and Australian map grids indicated.

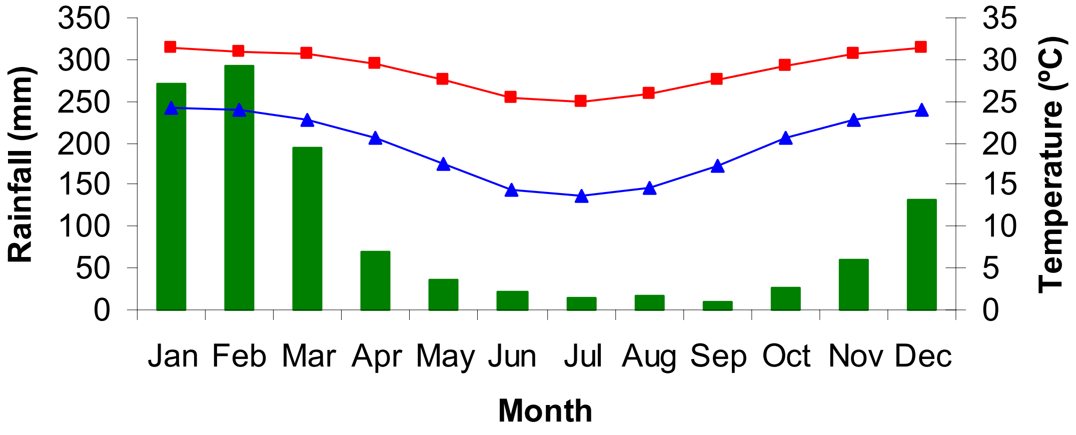


Figure 2.2. Mean monthly rainfall, and mean daily minimum (▲) and maximum temperatures (■) per month, recorded by the Australian Bureau of Meteorology at the Townsville airport between 1940 and 2001.

Table 2.1. Monthly rainfall between 1997 and 2001 recorded by the Australian Bureau of Meteorology at (a) the Townsville airport and (b) Cape Cleveland, 10 km from the primary study site.

Year	Annual total	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
(a)													
1997	1496.8	121.6	400.2	453.8	9.0	49.2	9.0	6.2	19.0	16.6	8.4	3.2	400.6
1998	1992.2	973.8	159.8	72.4	52.0	92.0	9.0	8.6	258.2	31.2	108.0	104.8	122.4
1999	1076.4	149.8	317.4	138.4	100.0	9.8	0.4	14.4	6.2	0.2	2.2	186.0	151.6
2000	2399.8	157.4	845.4	176.6	546.2	32.0	31.4	0.4	0.2	0.4	45.4	345.2	219.2
2001	467.2	47.2	236.0	58.4	10.0	0.0	9.4	8.0	0.0	1.2	25.8	71.2	0.0
(b)													
1997	1478.7	132.6	393.2	279.3	2.2	67.6	9.3	10.0	14.0	9.6	43.2	3.0	440.4
1998	1837.1	544.9	303.8	55.0	96.6	89.8	16.6	26.4	52.6	44.4	200.4	140.8	242.0
1999	1111.0	160.6	238.6	102.8	111.0	14.4	0.0	8.0	31.2	4.6	1.6	233.4	204.8
2000	2716.6	79.4	937.6	184.4	442.0	132.6	35.2	0.0	1.2	0.0	46.8	437.2	418.4
2001	441.5	77.2	176.2	64.7	26.2	0.0	22.2	17.0	0.0	2.8	39.4	9.4	6.4

2.2 Design and implementation of the Cape Cleveland manipulative fire experiment

In 1997, a manipulative fire experiment was established within a 10 ha section of eucalypt savanna on level ground, at approximately 5 m altitude at Cape Cleveland (Figure 2.1). The site contains eucalypt savanna typical of the Townsville region and is dominated by the trees *Corymbia clarksoniana*, *C. tessellaris* and *Eucalyptus platyphylla*, approximately 15 to 20 m in height and which form a 20 to 30% canopy cover (Figure 2.3). The ground stratum is dominated by the perennial grasses *Heteropogon triticeus*, *H. contortus* and *Themeda triandra*. There is also an abundance of twining forbs, particularly *Galactia tenuiflora*, *Glycine tomentella* and *Pycnospora lutescens*. Taxonomy for the thesis follows the Queensland Herbarium (Henderson 1997).

Figure 2.3. Eucalypt savanna at the Cape Cleveland fire regime experimental site.

The Cape Cleveland site was grazed by a low density of free ranging cattle from the early 1900's to the 1970's (C. Adams *pers. com.* 1997). Queensland Parks and Wildlife Service records indicate the eucalypt savanna of Cape Cleveland has a history of regular fires, with intervals ranging from one to five years and typically occurring between May to December. The trial site was burnt prior to this study by unplanned fires in December 1990 and December 1994.

Three experimental fire regimes were implemented across the Cape Cleveland site, between 1997 and 2001:

1. Control: savanna burnt mid dry season (July) 1997 only.
2. Early burnt: savanna burnt July 1997 and early dry season (May) 1999.
3. Late burnt: savanna burnt July 1997 and late dry season (Oct) 1999.

The benefit of this experimental design is that it examines fire regimes of mixed intervals, intensity and season, typical of the Townsville region. One of the criticisms of previous savanna fire trials has been the repeated implementation of fixed fire regime treatments (e.g. successive annual early dry season fires), which were not true representations of contemporary fire regimes (Russell-Smith *et al.* in press).

The entire 10 ha study site was deliberately burnt in the mid dry season of 1997, after the establishment of permanent survey plots (Chapter 3). The fire was ignited at 1 pm, 15th July. The air temperature at ignition was 25° C, relative humidity was 54% and a north-easterly wind was fluctuating around 8 km hr $^{-1}$. Ignition began in the south-west corner of the block and drip torches were used to guide the fire around the site perimeter in both clock-wise and anti-clockwise directions along slashed fire lines. This initial mid dry season fire was undertaken across the entire 10 ha area to provide valuable pre-fire floristic data for all plots, including those that remained unburnt for the remainder of the study (Chapter 3). While it is acknowledged that burning the whole site as one unit in 1997 fire does not adequately replicate the mid dry season fire, the unit of comparison for the experiment is the fire regime encompassing the five years of study and no analyses were undertaken on responses to the 1997 fire in isolation.

Following the July 1997 fire, the site was split into nine parallel blocks of approximately 1 ha in area (80 m width by 130 m length); by slashing 4 m wide fire lines between the blocks (Figure 2.4). A 20 m wide buffer zone was established along the roadside boundary, perpendicular to the main blocks, and was burnt annually during the dry season from 1997 to 2000, to create a fire break. Each fire treatment was imposed on three of the nine, 1 ha blocks. The blocks were allocated to treatments using a randomised block design. One replicate of each treatment was randomly allocated a position in each of blocks 1 - 3, 4 - 6 and 7 - 9 (Figure 2.4). Blocking was undertaken rather than a full randomisation to account for a floristic gradient across the study site detected in initial field inspections, prior to establishing plots in 1997. That is, a few common species, most notably *Eucalyptus platyphylla* and *Heteropogon contortus*, occurred in greatest abundance in blocks 7 - 9. Surface soil samples indicated no corresponding gradient in the topsoil.

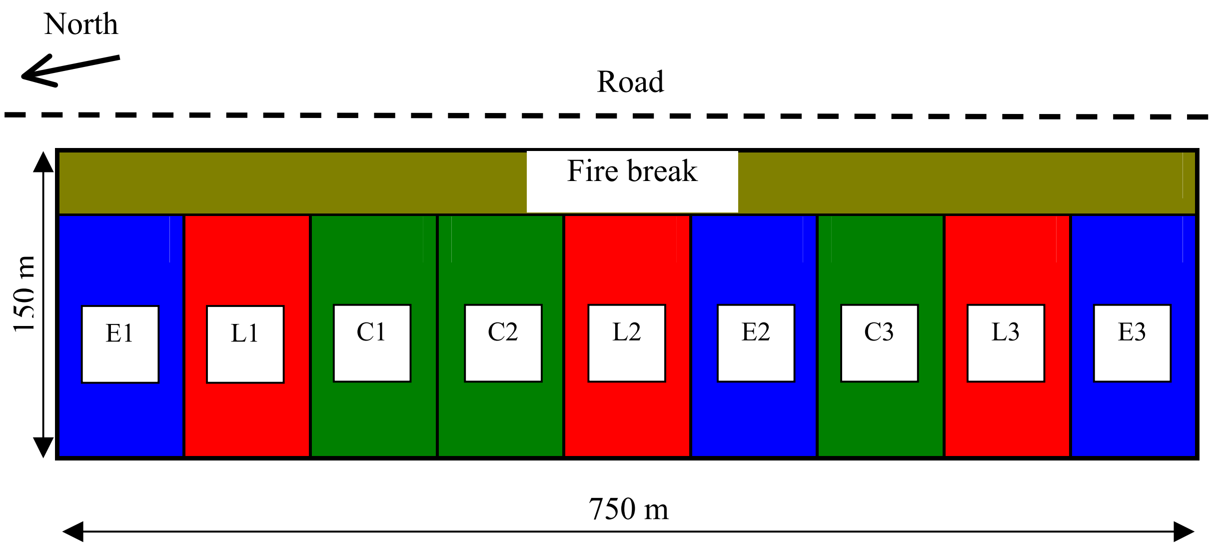
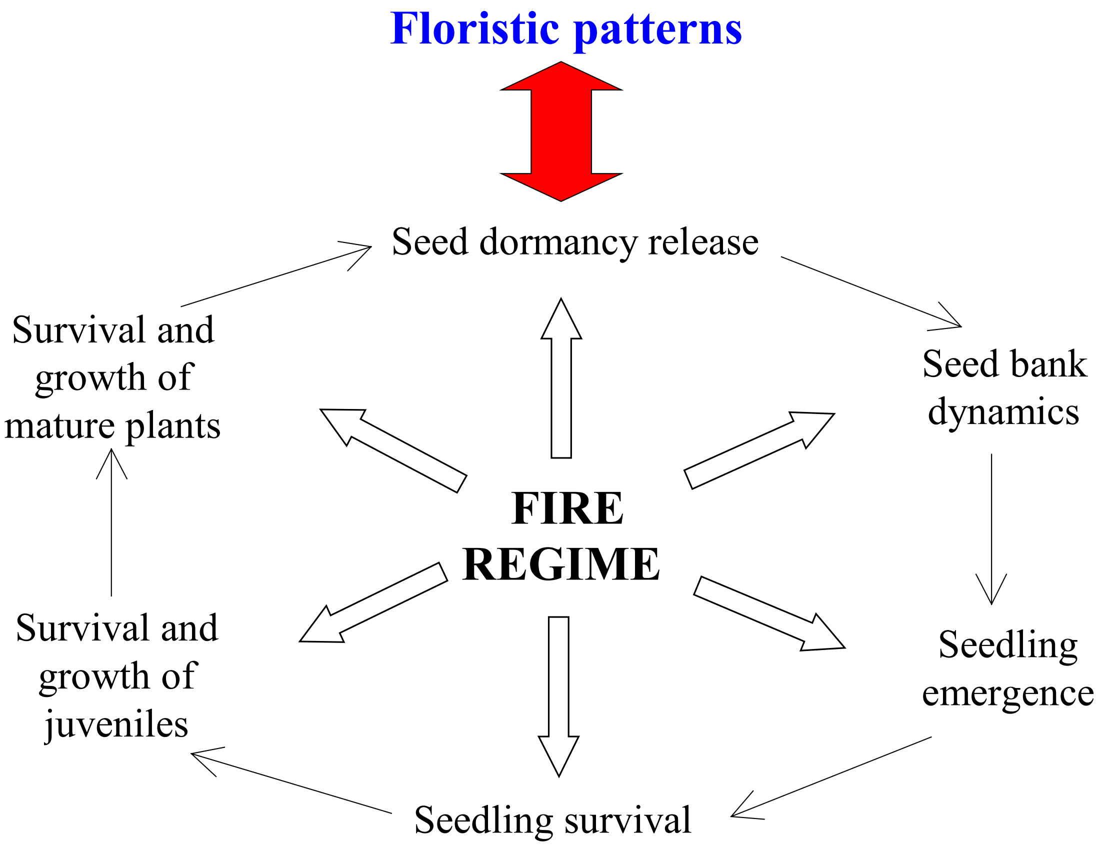


Figure 2.4. Schematic diagram of the layout of experimental fire regimes at the Cape Cleveland study site. Control (🟩); Early burnt (🟦); Late burnt (🟥). C1, Control block 1; E2, Early burnt block 2; L3, Late burnt block 3, etc.; a 20 m wide fire break was burnt annually from 1997 to 2000 (🟫).

The three 1 ha blocks assigned to the early burnt treatment (Figure 2.4) were burnt on the 24th May 1999, with ignition commencing at 10.30 am. At the time of ignition, the air temperature was 27.5°C, relative humidity was 70% and a north-easterly wind remained < 5 km hr $^{-1}$. The three 1 ha blocks assigned to the late burnt treatment (Figure 2.4) were burnt on the 13th October 1999, with ignition commencing at 8.10 am. At the time of ignition, the air temperature was 28ºC, relative humidity was 53% and a north-easterly wind typically ranged from 5 to 10 km hr $^{-1}$. The implementation technique used for the early and late dry season fires was the same as that described for the July 1997 fire. Ignition began in the south-west corner of the relevant block and the fire was guided around the perimeter of the block in both clock-wise and anti-clockwise directions using drip-torches.

Surveys of standing plants and seedlings were undertaken across the Cape Cleveland study site between 1997 and 2001. The specific methodologies for assessing floristic patterns and the effect of fire on critical life events at Cape Cleveland and additional sites, at Castle Hill, Many Peaks Range and Mt Elliot (Figure 2.1), are described in Chapters 3 to 7.

Chapter 3. The effect of fire regime on floristic patterns in a tropical savanna of north-eastern Australia.



3.1 Introduction

Australian tropical savannas display stability of floristic composition in response to a range of fire regimes (Bowman *et al*. 1988; Williams *et al*. in press). However, fire regime can affect floristic patterns, primarily through changes in species abundance rather than significant species replacement (Bowman *et al*. 1988; Fensham 1990; Lonsdale and Braithwaite 1991; Russell-Smith *et al*. in press).

Contrasting responses to fire frequency have been detected in savanna species. For instance, the annual grass *Sorghum stipoideum*, and the sprouting shrub *Grevillea goodii* increase in density with annual burning, while the perennial grass *Alloteropsis semialata* and the obligate seeder shrub *Acacia holosericea* show a preference for longer fire intervals (Russell-Smith *et al*. in press; Williams *et al*. in press). The density of some savanna trees, especially non-eucalypts, also increase with fire intervals of three or more years (Sandercoe 1988; Pressland *et al*. 1989; Fensham 1990; Bowman and Panton 1995; Williams *et al*. 1999*b*). Eucalypts vary in their response to fire protection, with increased tree density documented in several species, including *Eucalyptus tetrodonta*, whereas the density of *E. miniata* remains stable, even after 21 years of fire exclusion (Fensham 1990; Bowman and Panton 1995; Russell-Smith *et al*. in press).

The timing and intensity of fire can affect floristic patterns in Australian tropical savannas. The mortality of woody species is directly related to fire intensity (Williams *et al*. 1999*b*). Late dry season fires can promote some grasses, such as *Heteropogon contortus*, while earlier dry season fires may promote others, including *Themeda triandra* (Shaw 1957; Walker *et al*. 1989; Orr *et al*. 1991). Wet season fires can reduce the abundance of both annual and perennial grasses, while promoting some annual forbs (Williams and Lane 1999). The abundance of many woody and herbaceous species is also correlated with climatic, edaphic and topographic variables (Fensham 1990; Williams *et al*. 2002*a*).

Much of the research into fire effects on floristic patterns in Australian tropical savannas has centred on the monsoonal regions of the Northern Territory and, to a lesser extent, Cape York Peninsula (e.g. Bowman *et al*. 1988; Fensham 1990; Crowley and Garnett 1998; Williams and Lane 1999; Williams *et al*. 1999*b*; Crowley and Garnett 2000). Data are also more prevalent for dominant woody and grass species, with less information on the influence of fire on forbs and other sub-dominant species.

This chapter examines the influence of fire regime on floristic patterns in a tropical savanna of north-eastern Australia, south of Cape York Peninsula. Questions that are addressed are:

1. What is the rate of fuel load accumulation after fire?
2. Does fire intensity vary with fire season?
3. Does fire regime influence species composition and abundance?
4. Does fire regime influence species richness?
5. Are these patterns similar to those observed in other regions of northern Australia?

3.2 Methods

3.2.1 Study site

The influence of fire regimes on the floristic patterns, fuel loads and fire intensity in eucalypt savanna in north-eastern Australia was assessed at the Cape Cleveland experimental site, 25 km east of Townsville (Figure 2.1), using the fire regimes described in Chapter 2 (Figure 2.4). Rainfall data for Cape Cleveland over the period of study are provided in Table 2.1.

3.2.2 Sampling methods

3.2.2a Fuel load sampling

Fuel dynamics were assessed from 1997 to 2001 (Table 3.1). Ground layer fine fuels, including herbaceous material, leaf litter and twigs < 6 mm in diameter, were sampled to a height of 2 m. Fuel load samples were collected from randomly located 0.5 m^2 quadrats. Fifteen samples were collected prior to the July 1997 fire, and 15 samples in June 1998, from across the entire 10 ha study site. In May 1999, prior to the early dry season fires, three samples were collected from each of the three relevant 1 ha blocks. Likewise, three samples were taken from each of the three late burnt 1 ha blocks, prior to the late fires in October 1999. In June 2000 and August 2001, three fuel load samples were taken from each of the nine 1 ha blocks. To provide additional samples from recently burnt savanna, four samples were collected from the annually burnt roadside fire break block in September 1998 and three in May 1999. All fuel load samples were oven dried at 65ºC for at least 48 hours prior to weighing.

Table 3.1. Summary of fuel samples from eucalypt savanna at Cape Cleveland.

Date of collection	Number of samples ($0.5m^2$)	Fire regime	Years since fire
July 1997	15	Combined	3
June 1998	15	Combined	1
September 1998	4	Annual fire (roadside fire break)	1
May 1999	9	Early burnt	2
May 1999	3	Annual fire (roadside fire break)	1
October 1999	9	Late burnt	2
June 2000	9	Control	3
June 2000	9	Early burnt	1
June 2000	9	Late burnt	1
August 2001	9	Control	4
August 2001	9	Early burnt	2
August 2001	9	Late burnt	2

3.2.2b Fire intensity sampling

The entire 10 ha study site was burnt in a single fire implemented in the mid dry season of 1997 (Chapter 2) and the rate of spread was determined at ten separate locations across the site. At each location, two metal markers, spaced between 2 m and 7 m apart, were dropped in front of, and perpendicular to, the fire front. The time taken for the fire front to move between markers was recorded. The exact distance between the markers was measured after the fire and the rate of spread calculated by dividing the distance between the markers by the time taken for the fire to move between them. The mean from the ten measurements was used as the rate of spread in the calculation of fire intensity for the 1997 fire.

The rate of spread estimates of the early and late dry season 1999 fires differed from that of the 1997 fire. The time taken for the fire front to move between two or three pairs of trees was measured from the fire line. This is a less precise, although still effective, measure of fire spread than that of the July 1997 fire, but was necessary as all personnel were involved in implementing the 1999 fires. While the ground layer was completely combusted during the October 1999 fires, there were unconsumed grass stalks after the May 1999 fires, up to 0.75 m in height. Three 0.5 m^2 samples of the remaining fuel were collected and used to subtract from the original fuel load to provide a figure of fuel actually consumed in the fire. The post-fire fuel load after the July 1997 fire was not quantified, and therefore is a slightly high estimate of fire intensity.

Fire intensity was calculated using the standard equation (Byram's fire line intensity): Fire intensity = heat yield of burnt fuel (constant of 20 000 kJ kg^{-1}) X fuel consumed in fire (g m^{-2}) X rate of fire spread (m sec^{-1}) (Byram 1959; Gill and Knight 1991).

3.2.2c Floristic sampling

Species composition and abundance data were sampled at Cape Cleveland to determine the effect of fire on floristic patterns. Studies of fire regimes in tropical savannas of the Northern Territory have detected only subtle and sometimes variable species responses (e.g. Bowman *et al.* 1998). This lead Lonsdale and Braithwaite (1991) to recommend the use of repeated surveys of permanent plots to document species change over time, rather than once-off comparative studies of plots with different recent fire histories. Repeated surveys have been successful in detecting significant floristic patterns in response to fire regimes in savannas of the Northern Territory (Hoare *et al.* 1980; Russell-Smith *et al.* in press; Williams *et al.* in press).

Changes in species abundance were determined using annual surveys of permanently marked plots at the Cape Cleveland study site. A pilot study was used to determine an appropriate plot size, through an assessment of the relationship between species richness and plot area. A species-area curve was produced using 20 separate plots, each with nested sub-plots increasing in size from 1 m^2 to 400 m^2 (Figure 3.1). The point where the species- area curve begins to plateau, in this case at 100 m^2, is considered the minimal area required for effective samples, although the value of "minimal area" has been debated (Barbour *et al.* 1987). Plots of 100 m^2 have successfully detected floristic patterns in previous studies in Australian tropical savannas (Bowman *et al.* 1988; Fensham 1990). Four spatially separate plots were used to sample the variation across each 1 ha block at Cape Cleveland. Therefore, four 100 m^2 plots were used to sample each of the nine, 1 ha blocks, providing a total of 36 plots. This sampling effort is considered effective for assessing the herbaceous layer and hence community composition, although it is acknowledged that larger plots may be more useful for documenting changes in tree densities.

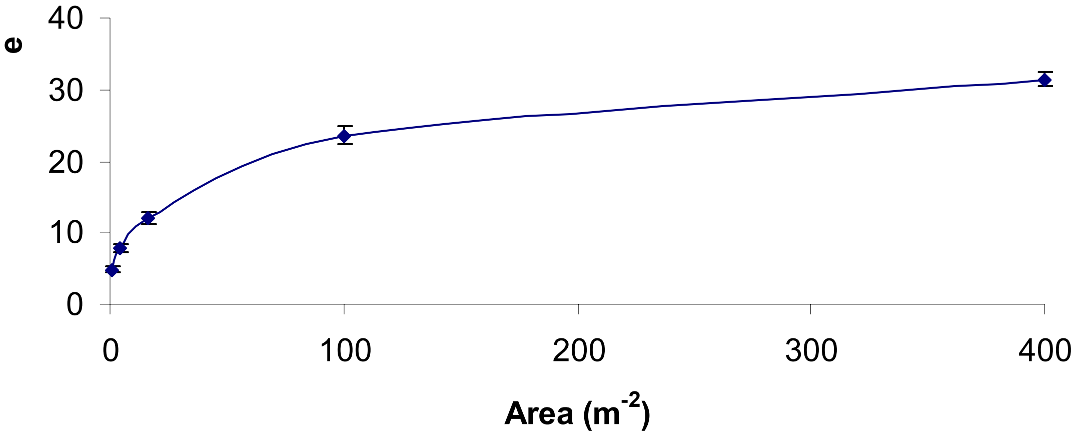


Figure 3.1. Species-area curve of the mean number (± 1 standard error) of species per unit area within 20 plots in eucalypt savanna, unburnt for three years, at Cape Cleveland prior to the establishment of the study.

The four 100 m^2 plots were located within each 1 ha block through the use of random X and Y coordinates, with the stipulation that all plots were at least 10 m from the block edge and that plots were separated by at least 2 m. The first restriction ensured fires developed some speed, and therefore intensity, before passing into a plot.

A stratified random sampling technique was used to sample species abundance in each plot, involving the use of 20 throws of a 1 m^2 quadrat into the plot from 20 points of equal spacing around the plot perimeter. The presence of all species within (or growing across for twining forbs) each quadrat was recorded. This provided an abundance out of 20 for all species per plot, in each of the five annual surveys. Additional species within the plot that were not recorded within the 20 quadrats were also documented to record species richness at the 100 m^2 scale. This was considered the most appropriate estimation of species abundance, although frequency does not distinguish abundance within each quadrat. A pilot trial of percentage cover estimates indicated large variation between re-assessments of quadrats, making this sampling unrepeatable. The difficulty in this method arose from the difficulty in estimating the comparative cover of different growth forms, particularly tufted grasses, woody species and the twining forbs. Point cover estimates did not detect the many sub-dominant species. Density counts were not possible for many herbaceous and multi-stemmed subshrub species, as individual plants could not be distinguished. Density measures are effective for many woody species, and counts of the dominant trees were undertaken during the annual surveys to document survival and growth, which are presented in Chapter 8. However a single measure of species abundance was required to assess floristic patterns at a community level, and therefore density was not appropriate.

All of the 36 plots were surveyed annually for five years (1997 to 2001), in the late wet to early dry seasons (March to May), to ensure detection of annual species. Thus the five annual surveys provided a total of 180 survey records.

3.2.3 Statistical analyses

3.2.3a Fuel load analyses

Analyses of variance (ANOVA) were performed separately on the 2000 and 2001 fuel loads, to assess the significance of variations between the three fire treatments (unburnt control, and burnt early and late dry season 1999). A third ANOVA assessed the significance of differences in fuel load between times since last fire categories, with samples grouped to the nearest year. All univariate analyses in this thesis were computed using the *Statistica* program (StatSoft 1999). The ANOVA assumption of homogeneity of variances was assessed using Cochran's test (Underwood 1997). Log (x) transformations were required to resolve variance heterogeneity in the analysis of the 2000 fuel loads.

3.2.3b Fire intensity analyses

A *t*-test was used to examine differences between the May and October 1999 fires. No statistical comparisons were made using the July 1997 fire data, due to a lack of replication. A Cochran's test indicated homogeneity of variances of raw data, hence no transformations were required.

3.2.3c Multivariate analyses of floristic dynamics

The aim of the multivariate analyses was to determine community level dynamics in floristic composition and abundance. This was done by comparing the species composition and abundance data for the 180 surveys of the 36 plots, as well as comparisons of the fire treatments in a subset of years. The term "survey(s)" is used here to refer to the floristic composition and abundance data collected during one or more annual inspections of the 36 permanent plots at Cape Cleveland.

First, to detect the influence of fire regime on floristic composition, a cluster analysis was performed on the 180 surveys, based on species composition data (i.e. species presence or absence), using the PATN program (Belbin 1995). An agglomerative hierarchical method of clustering was performed using the Kulczynski distance measure and group average linkage agglomerate technique (unweighted pair group arithmetic averaging, UPGMA; Belbin 1995). The Kulczynski distance measure calculates similarity scores for plots, based on comparisons of species presence or absence in each survey. This distance measure is effective in determining survey similarities for ecological data (Faith *et al*. 1987). The UPGMA technique groups surveys based on the similarities scores for the centre of each developing cluster, and is especially useful for grouping surveys with compositions intermediate between two clusters (McArdle 2001). The resulting clusters were presented in a dendrogram.

An additional cluster analysis was performed using species abundance scores documented in the 180 surveys. This analysis incorporates fluctuations in species abundance with the compositional data to assess the influence of fire on both species composition and abundance. The cluster analysis was undertaken using the same technique described above, with the Kulczynski distance measure and the group average linkage agglomerate technique, based on species abundance rather than presence or absence data, and was computed using the PATN program (Belbin 1995).

Secondly, a Principle Components Analysis (PCA) was performed on the species composition and abundance data using the CANOCO program (ter Braak and Smilauer 1998). PCA, which is an ordination technique, displays the inter-relationships between all surveys, without forcing them into groups (ter Braak and Wiertz 1994). PCA is a linear response model, which is appropriate when the variation between surveys is narrow, such as this study of repeated annual surveys of permanent plots (ter Braak and Prentice 1988). Other ordination methods, such as semistrong hybrid multidimensional scaling, were assessed and produced similar scatterplots.

A PCA was undertaken to look at community composition and abundance relationships for all 180 surveys (1997-2001), and the results are presented in a scatter plot. To assist in the interpretation of the PCA of the entire 180 surveys, an additional scatter plot was produced using the mean PCA coordinates for each fire regime, for each of the five years.

Thirdly, a partial Redundancy Analysis (RDA) was used to assess the correlation between species composition and fire variables, using the CANOCO program (ter Braak and Smilauer 1998). A RDA is based on PCA and performs a multiple regression of environmental variables and species abundance data (McArdle 2001). A “partial” RDA uses additional environmental variables as covariates, to help decipher the unique effect of the environmental variables of interest. For example, Morrison *et al*. (1995) used time since last fire as a covariate to focus an analysis onto the effect of inter-fire interval of species abundance. A partial RDA is especially useful for examining permanent plot data, because it allows the removal of background effects, such as intrinsic plot differences and fluctuations over time that are consistent to all treatments (ter Braak and Smilauer 1998).

A partial RDA was performed for the entire data set (1997 to 2001 surveys) to correlate species composition with elements of the fire regime. Knowledge of the fire history of the area prior to 1997 (i.e. fires in December 1990 and 1994) allowed allocation of fire variables for the initial 1997 plot surveys. The fire variables correlated with species composition were: (i) time since last fire (years); (ii) fire interval prior to last fire (years); and (iii) season of last fire. Fire season alternatives used were early dry (May), mid dry (July), late dry (October) and early wet season (December). The fire seasons were represented as nominal variables. That is, each of the four fire season options were represented by a separate row in the spread sheet being analysed and surveys were allocated a zero or one to indicate the relevant fire season (ter Braak and Smilauer 1998).

Three covariates were used to remove background differences between the 180 surveys that were not attributable to fire variables. The 36 plots were identified as covariables. This allowed the removal of background differences between plots that were irrespective of the fire treatments. As a randomised block design was used in the survey design (Chapter 2; Figure 2.4), blocking was used as a covariate to remove differences between the three groups of blocks across the trial plot (i.e. C, E and L block 1; C, E and L block 2; C, E and L block 3; Figure 2.4). The third covariate used was the year of survey (1997 to 2001), which allowed the removal of annual fluctuations not attributable to fire treatments.

A partial RDA of the 1999 and 2000 surveys assessed the effect of fire season on species composition and abundance in the year following fire. An additional fire variable, fire intensity (using logged data due to large variances), was available for this analysis because the intensity of the most recent fire was known for both 1999 and 2000 recordings. Fire intensity data was not available for analysis of the full 1997 to 2001 data set, because the intensity of the fire prior to the initial 1997 recordings (i.e. the 1994 fire) was unknown.

The analyses of both the 1997 to 2001 surveys and the 1999 and 2000 subset, followed ter Braak and Smilauer's (1998) recommendations for before and after, control and impact (BACI) studies. Monte Carlo permutations (199 permutations for each analysis) were used to assess the significance of the correlation between species variation and environmental variables. This is a test of significance obtained by repeated shuffling of samples (ter Braak and Smilauer 1998). The annual surveys were permutated as a time-series of the 36 plots.

Initially all fire variables were analysed as a group, with the plot, block and year of survey as covariates. This determined the variance in species abundance explained by the fire variables. A forward selection analysis was then undertaken on the individual fire variables, which is analogous to a *post-hoc* test (ter Braak and Smilauer 1998). The importance of each individual fire variable was ranked and the species variation explained separately by each fire variable was denoted as “Lambda-1”. Lambda-1 is the eigenvalue of the ordination when only that individual variable is used with the covariables. Secondly, a model is produced to determine the best combination of fire variables for explaining species variation. The variable with the largest Lambda-1 is used as the basis, with separate variables subsequently tested to see which combination of two variables provides the best explanation of species variance. The significance to the model of the additional variable is tested using a Monte Carlo permutation test. “Lambda-A” describes the additional species variance explained by the fire variable, given those already in the model. This continues until no further correlation with the species dataset can be provided by extra fire variables.

To quantify the relative effect of the three covariates and their interactions, separate analyses were run using plot and then years, with the remaining two covariates plus the fire variables designated as “covariables”, as described by ter Braak and Smilauer (1998, pp. 263 - 266). The floristic variation accounted for by specific variables and interactions is denoted as “% variation explained”. This is the sum of canonical eigenvalues for each respective analysis, and is analogous to the sums of squares in ANOVA (ter Braak and Smilauer 1998). The significance of specific variables was assessed using a Monte Carlo test with 199 permutations. As blocking was a fundamental element in the analyses, it could not be analysed separately as an independent variable. The assessment of species variance between blocks was calculated by deducting the sum of all unconstrained eigenvalues from the total variance of 1.0. The unexplained variance represents the variance that remains after fitting all variables, including blocks, and was calculated as the sum of all unconstrained eigenvalues minus the sum of all canonical eigenvalues (ter Braak and Smilauer 1998).

3.2.3d Univariate analyses of species richness and abundance

The aim of the univariate analyses was to examine the response to fire regime of individual species and growth form groups. Univariate analyses assessed the effects of fire regime, rather than survey clusters or axes determined from mulitvariate analyses. This is a more direct assessment of fire regime and Lonsdale and Braithwaite (1991) argued that univariate analyses of groups determined from DCA analyses were not sensitive to the variable and subtle species dynamics in tropical savannas.

Species were grouped according to growth form to aid the interpretation of fire response, and their abundance scores were summed to provide the abundance of each growth form. The determination of growth form groups is presented in Figure 3.2. All species were first separated into woody and herbaceous species, due to the importance of these functionally distinct groups (Walker 1985). The woody species were divided into trees and shrubs, and subshrubs, based on height at maturity (the latter group being less than 2 m; Harden 1990). The trees and shrubs were then separated into woodland and rainforest species, because these two groups may respond differently to fire regimes. The distinction between these groups is subjective, with species more commonly found in savanna than rainforest allocated to the “woodland trees and shrubs” group. The selection of species within the “rainforest” group was conservative and restricted to those primarily found within rainforest patches, rather than ecotonal species.

Herbaceous species were first split into monocotyledons and dicotyledons (i.e. forbs as defined by Harden 1990). The grasses were assessed separately from all other monocotyledons due to the significance of grasses in savanna function (Higgins *et al*. 2000). All monocotyledons other than grasses were broadly labelled as “non-grass monocots”.

Herbaceous dicotyledons were separated into perennial and ephemeral forbs. The latter typically complete their life cycle within a year, although a few individuals of these species may survive into a second year. The perennial forbs were divided on the basis of growth form into twining and upright forbs.

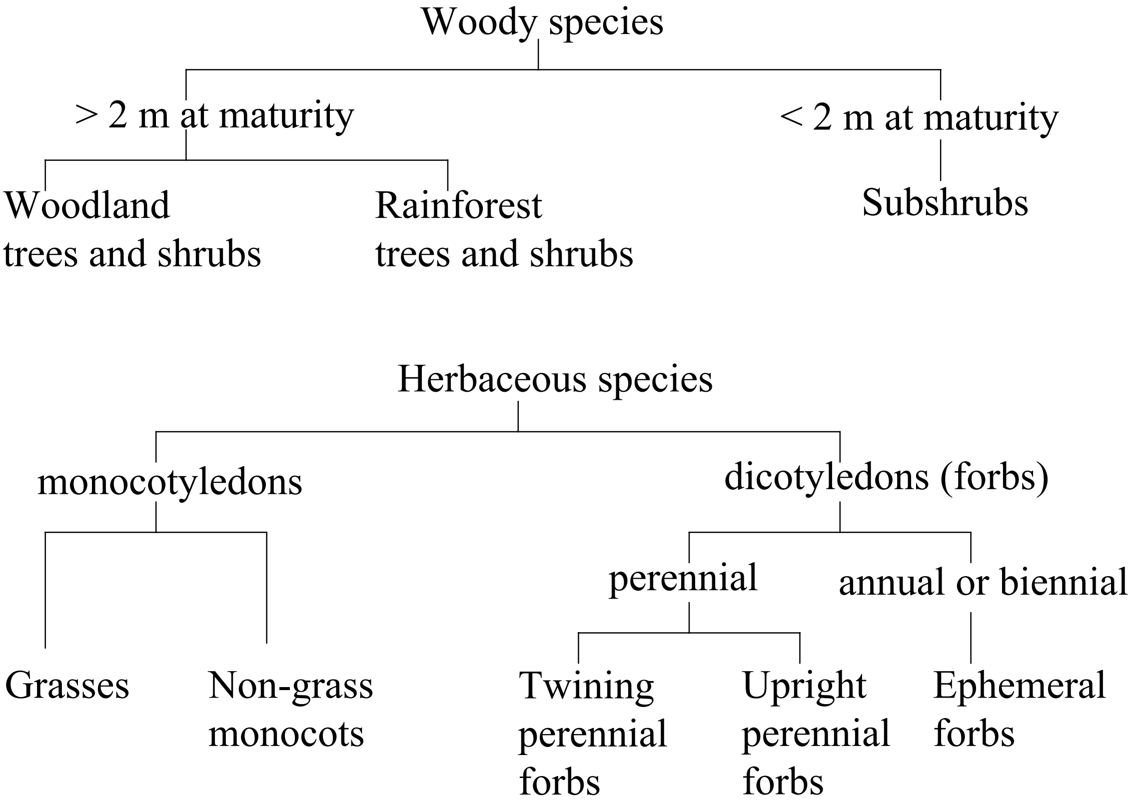


Figure 3.2. Diagrammatic key to the distinction of growth form groups used throughout this thesis.

Species were also classified as “natives” and “exotics” as identified by Henderson (1997) and univariate analyses assessed whether exotic species were advantaged over natives by particular fire regimes. The effect of fire on species richness was examined at 1 m^2 and 100 m^2 scales.

The most common individual species were examined for evidence of fire response. For efficiency, analyses of individual species were only performed on those with at least 1% of the total abundance out of the 180 surveys (i.e. species present within 1% of all quadrats). This limited the analyses to 24 out of the total 118 species detected in the surveys.

To provide an assessment of the overall effect of fire regimes (control, early and late burnt) from 1997 to 2001, on species richness and the abundance of species groups and common species, an analysis of covariance (ANCOVA) was performed on the 2000 survey data using the 1997 data as a covariate (Zar 1999). This allowed the assessment of changes over the course of the five year fire experiment, by analysing the differences at the end of the trial (2001) once adjusted for differences present prior to the trial (1997). Separate analyses were not undertaken on the unique effects of the 1997 fire, due to a lack of unburnt comparisons.

The effect of the 1999 fire season experiment on species richness and the abundance of species groups and common species, was analysed using two complimentary univariate analyses. First, an ANCOVA was performed on the 2000 survey data using the 1999 data as a covariate, to assess the change before and immediately after the fire treatments (control, early and late burnt). In addition, a repeated measures ANOVA of the three fire treatments in the 1999, 2000 and 2001 data sets was performed, thus assessing the change in species with fire treatment before fire through to the second year after fire. The critical factor in repeated measures ANOVA of before and after impact assessments (BACIs) is the interaction between year and treatment (Green 1993).

In each of these analyses, the four plots in each of the three replicate 1 ha blocks were considered nested within the fire treatments (control, early or late burnt). The nested plots were treated as random factors, while fire treatments (and year in the repeated measures ANOVA) as fixed factors. Where the variation between treatment replicates of separate blocks was low ($P > 0.25$), the block replicates were pooled to increase the power of the tests (Underwood 1997).

ANOVA assumptions of homogeneity of variances between treatments were checked using Cochran’s test (Underwood 1997) and where significant differences were detected, analyses were performed on $\log(x + 1)$ transformed data. Where data transformation did not fix significant heterogeneity of variances, a non-parametric test was used. However, no non-parametric test is available that simultaneously assesses both the change over time and the differences between the fire treatments. Therefore separate Kruskal-Wallis ANOVA by ranks tests were performed to check for significant fire treatment differences in each of 1999, 2000 and 2001 surveys. This enabled an assessment of pre-existing differences as well as differences in the first and second years post-fire. No nesting option is available in this analysis, and therefore all plots were treated as independent replicates. Where a significant difference was found, a Mann-Whitney *U*-test was used as a *post-hoc* test, with a Bonferoni adjustment of the significance level for multiple comparisons (Sokal and Rohlf 1995).

The large number of separate analyses from the same species abundance data sets increased the probability (alpha) of incorrectly rejecting the null hypothesis (Type I error; ter Braak and Wiertz 1994). To account for this, a conservative probability level ($P < 0.01$) was set for the species abundance analyses. While this increases the probability of incorrectly rejecting a significant result, it is less likely to result in an inappropriate claim of significant fire effects, enabling greater confidence when ascribing a fire response.

3.3 Results

3.3.1 Fuel load dynamics

Fuel accumulated rapidly after fire, with just over half of the maximum fuel load recorded one year post-fire and stabilising at the maximum weight of approximately 10 tonnes ha^{-1} after two years (Figure 3.3). There was no significant difference between fuel loads two, three and four years after fire, which were all significantly greater than the fuel load one year post-fire ($F_{3,76} = 14.323$; $P < 0.001$). There were significantly more fuel in the unburnt control blocks than both the early and late burnt blocks in 2000, the first year after the 1999 fire season treatments ($F_{2,24} = 13.269$; $P < 0.001$; Figure 3.4). No significant differences were detected across the treatments by 2000, the second year post-fire ($F_{2,24} = 0.222$;
$P > 0.05$; Figure 3.4).

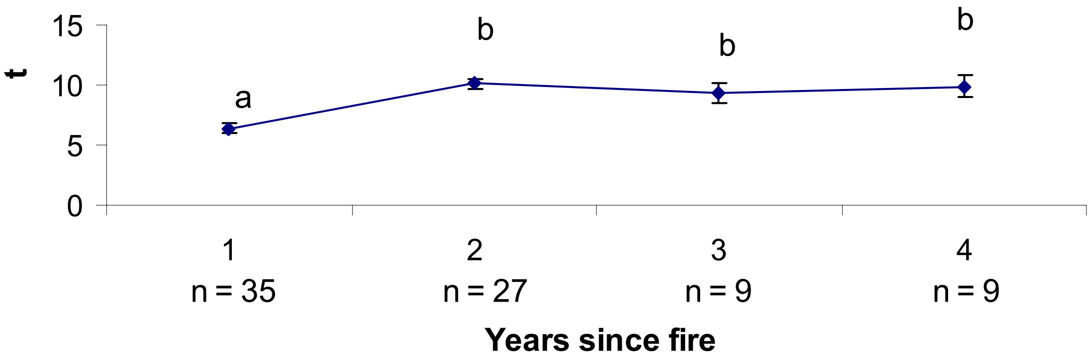


Figure 3.3. Mean (± 1 standard error) fuel accumulation with years since fire in eucalypt savanna at Cape Cleveland. Means with the same superscript are not significantly different at $P < 0.05$; n = the number of 0.05 m^2 samples.

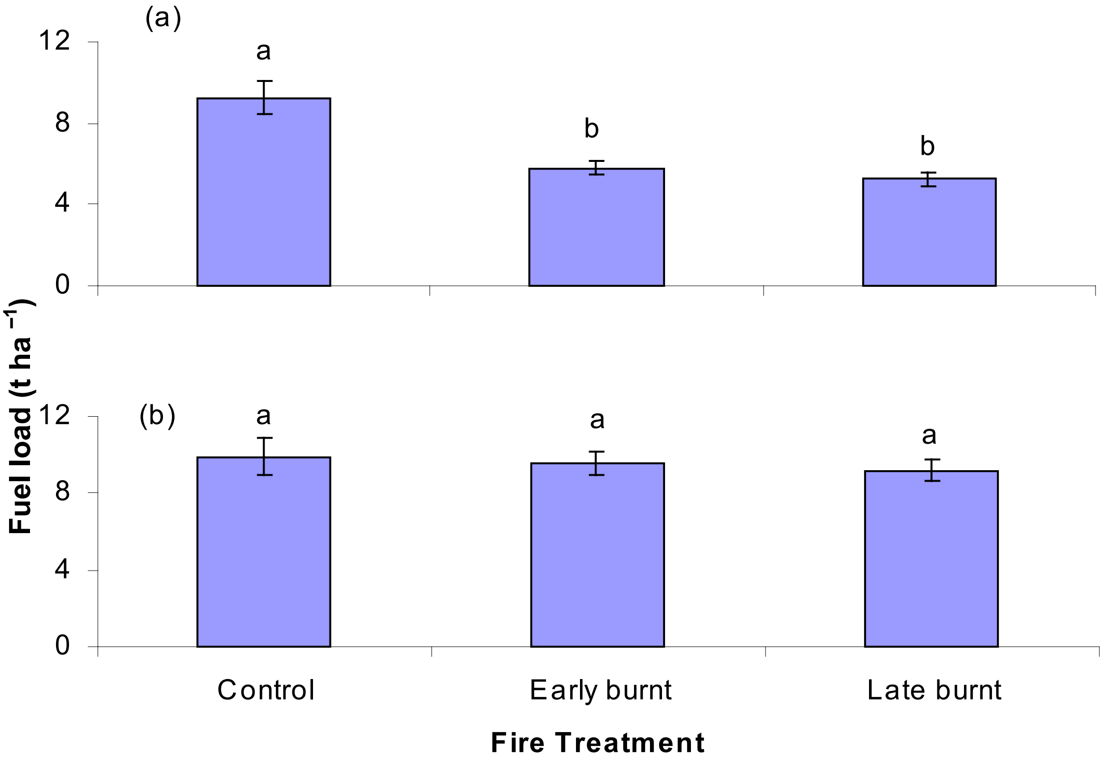


Figure 3.4. Mean (± 1 standard error) fuel load in unburnt, early dry season burnt and late dry season burnt eucalypt savanna at Cape Cleveland in (a) 2000 and (b) 2001. Means with the same superscript are not significantly different at $P < 0.05$. Time since fire in 2000: Control 3 years, Early burnt and Late burnt 1 year; Time since fire in 2001: Control 4 years, Early burnt and Late burnt 2 years.

3.3.2 Fire intensity

Fire intensity was significantly higher during the late dry season 1999 fires than those during the early dry season ($t_5 = 3.980$; $P < 0.02$; Figure 3.5). The intensity recorded during the 1997 fire was lower than the means for both early and late dry season fires, although it fell within the range of intensities documented during the three early dry season fires.

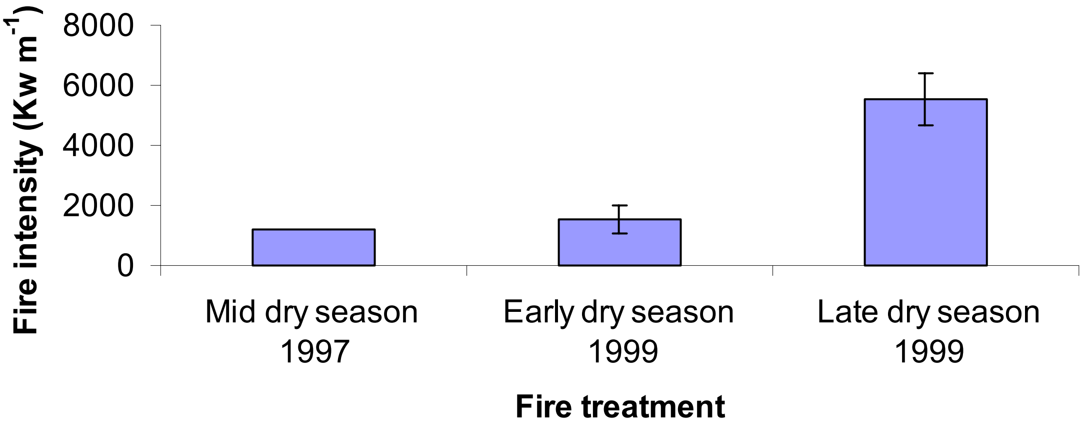


Figure 3.5. Intensity of the mid dry season (1997), early dry season (1999) and late dry season (1999) fires in eucalypt savanna at Cape Cleveland. A single value is provided for the mid dry season fire. Values for early and late dry season 1999 fires are means (± 1 standard error).

3.3.3 Multivariate analyses of species composition and abundance

3.3.3a Cluster Analysis

The cluster analysis of species composition data first isolated all surveys of each plot within control block 3 (C3A-D) and late burnt block 3 (L3A-D), all five surveys of plot L2B, four of the five annual surveys of plots E3B and C2B and the 1997 survey of plot E3A (Figure 3.6; see Figure 2.4 for block layout). This clustering reflects a floristic variation across the study site and justifies the use a randomised block design rather than full randomisation of fire treatments (Chapter 2).

The second pattern that can be seen in the cluster analysis is the widespread clumping of annual surveys of the same plot, which occurred in all three fire regimes. All five annual surveys were grouped together for 16 (44%) of the 36 plots, 26 (72%) had at least four of the five surveys grouped together and 33 (92%) of the plots had at least three of the surveys clustered together. The fact that all annual surveys of each plot were not grouped together indicates some dynamics in species composition over the study, however there was no consistency in which of the surveys were separated, suggesting fire regime effects were variable, and interacted with dynamics over time and plot variation.

Incorporating species abundance with composition data in the cluster analysis affected the grouping of surveys (Figure 3.7). Three of the four plots from late burnt block 3 (L3A, L3B and L3D) were separated from all other surveys (Figure 2.4). Fire appeared to have had little effect on this primary distinction between plots, as all five annual surveys were clustered together for each of L3A, L3B and L3D. The most distinctive feature of these three plots is that they all contain a lot of *Heteropogon contortus* but little of *H. triticeus*, which is the dominant grass of other plots. Other plots with high *H. contortus* abundance also contained a moderate to high abundance of *H. triticeus*.

Clustering of annual surveys of plots remained widespread with the inclusion of abundance data in the analysis. A total of 14 (39%) of the 36 plots, with representatives from each of the three fire regimes, had all five annual surveys clustered together (Figure 3.7). Twenty three plots (64%) had at least four, and 33 plots (92%) had at least three of the five annual surveys clumped together. This suggests species differences were usually greater between plots than annual surveys of a specific plot. However, the fact that the annual surveys of several plots were separated indicates some fluctuations in species composition and abundance occurred during the study, which may be attributable to fire regime.

3.3.3b Principle Components Analysis

The PCA scatter plot of the entire 180 surveys displays symbols representing surveys of the control plots clustered within the centre of the scatter plot, while those of the late and early burnt plots radiate out to the periphery (Figure 3.8). All surveys for a particular treatment were not grouped together.

Figure 3.6. Cluster analysis dendrogram from the 180 surveys in eucalypt savanna at Cape Cleveland, based on species **composition data** only. Survey codes: first digit identifies the fire treatment C, Control; E, Early burnt; L, Late burnt. The second digit identifies the 1 ha block number, 1 – 3 (see Figure 2.4 for block layout). The third digit identifies the four plots within each 1 ha block, A – D. The year of survey is also indicated.

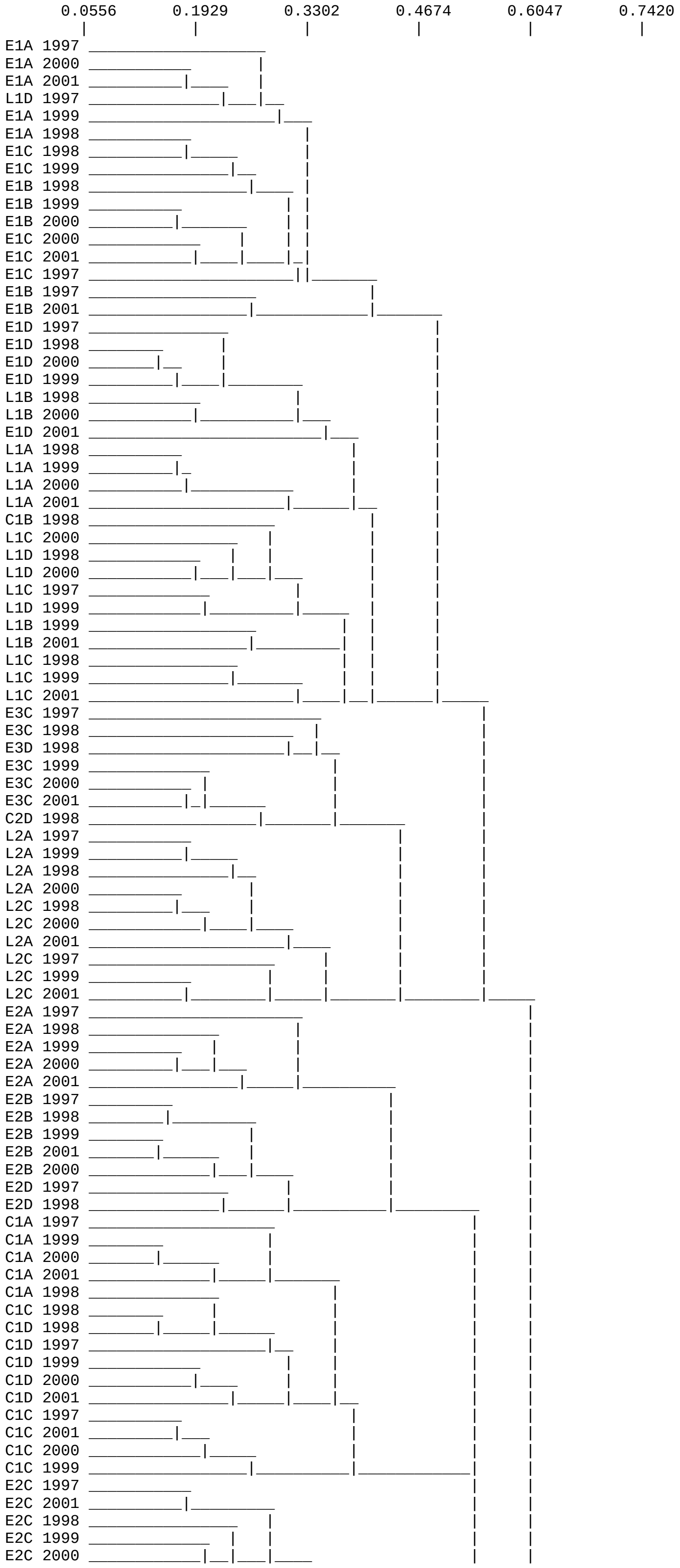


Figure 3.6. (cont.)

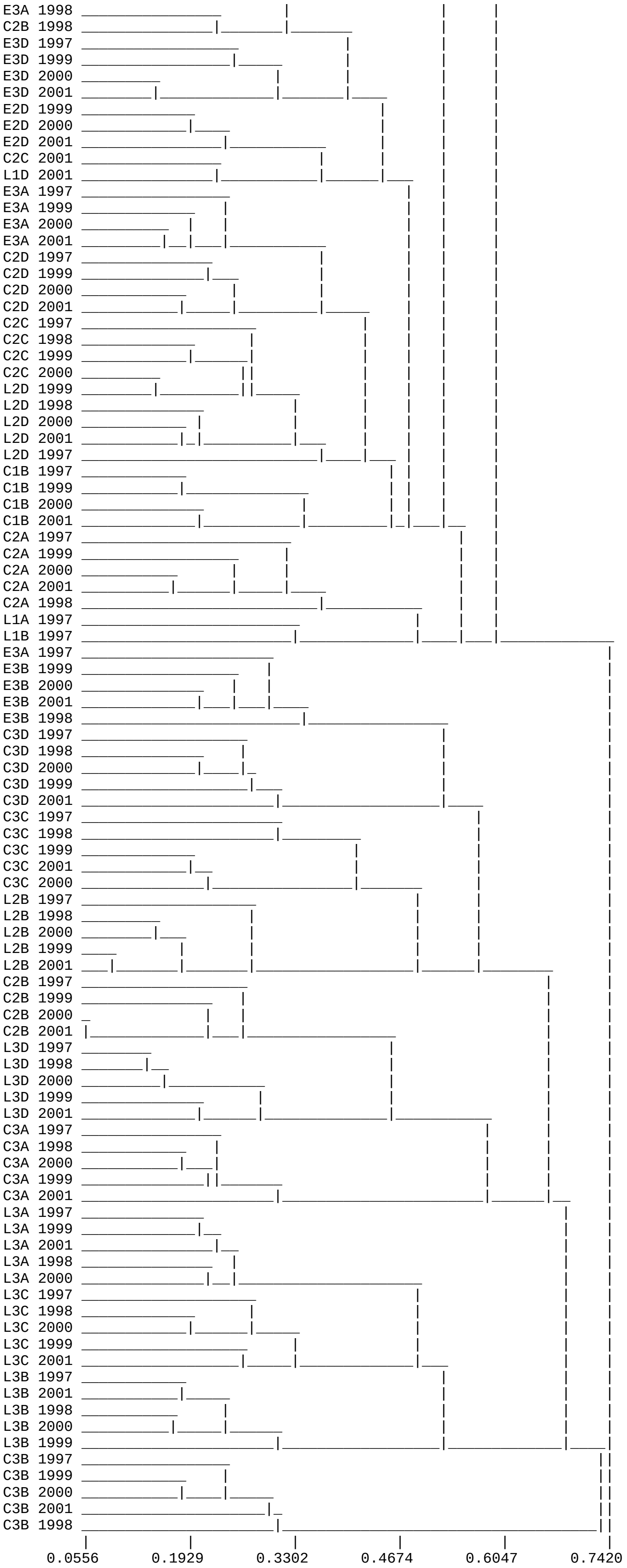


Figure 3.7. Cluster analysis dendrogram from the 180 surveys in eucalypt savanna at Cape Cleveland, based on species **composition and abundance data**. Survey codes: first digit identifies the fire treatment C, Control; E, Early burnt; L, Late burnt. Second digit identifies the 1 ha block number, 1 – 3 (see Figure 2.4 for block layout). Third digit identifies the four plots within each block, A – D. The year of survey is also indicated.

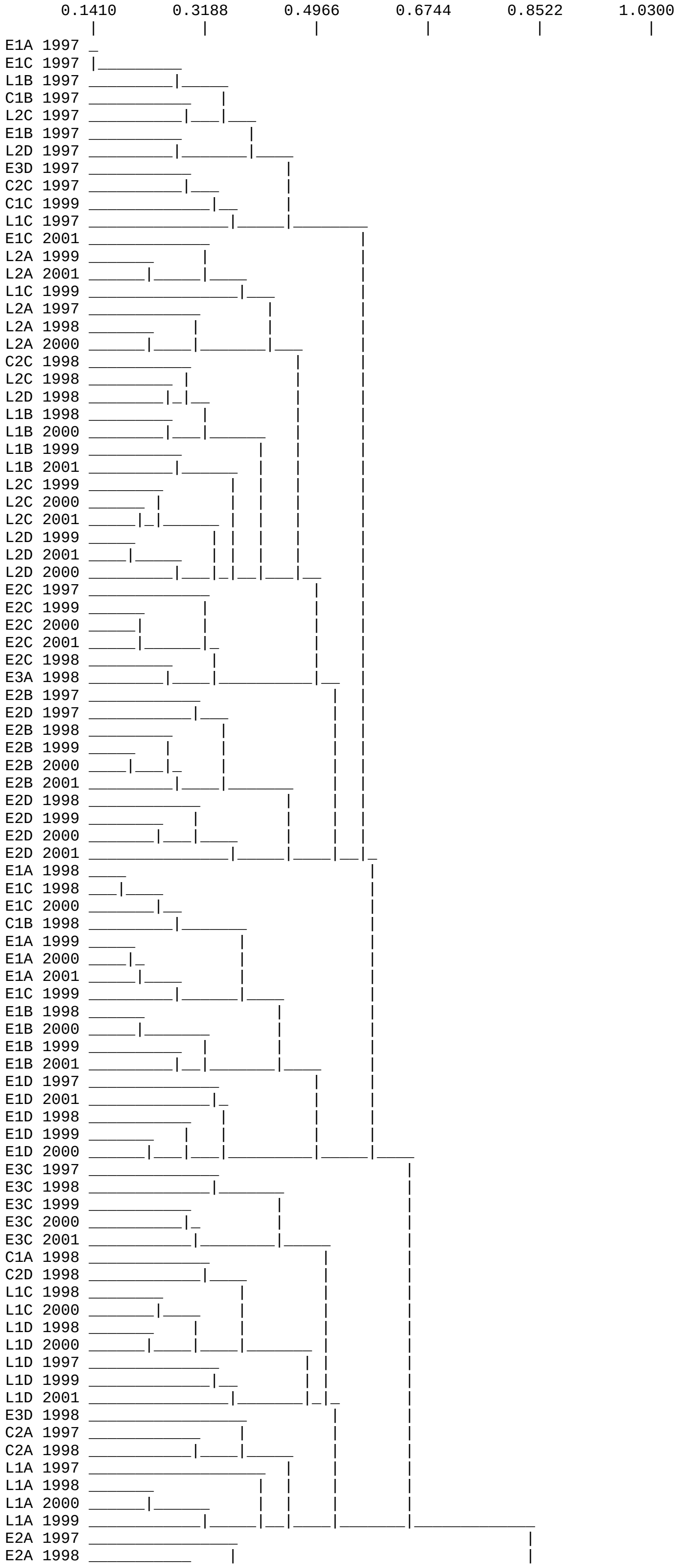
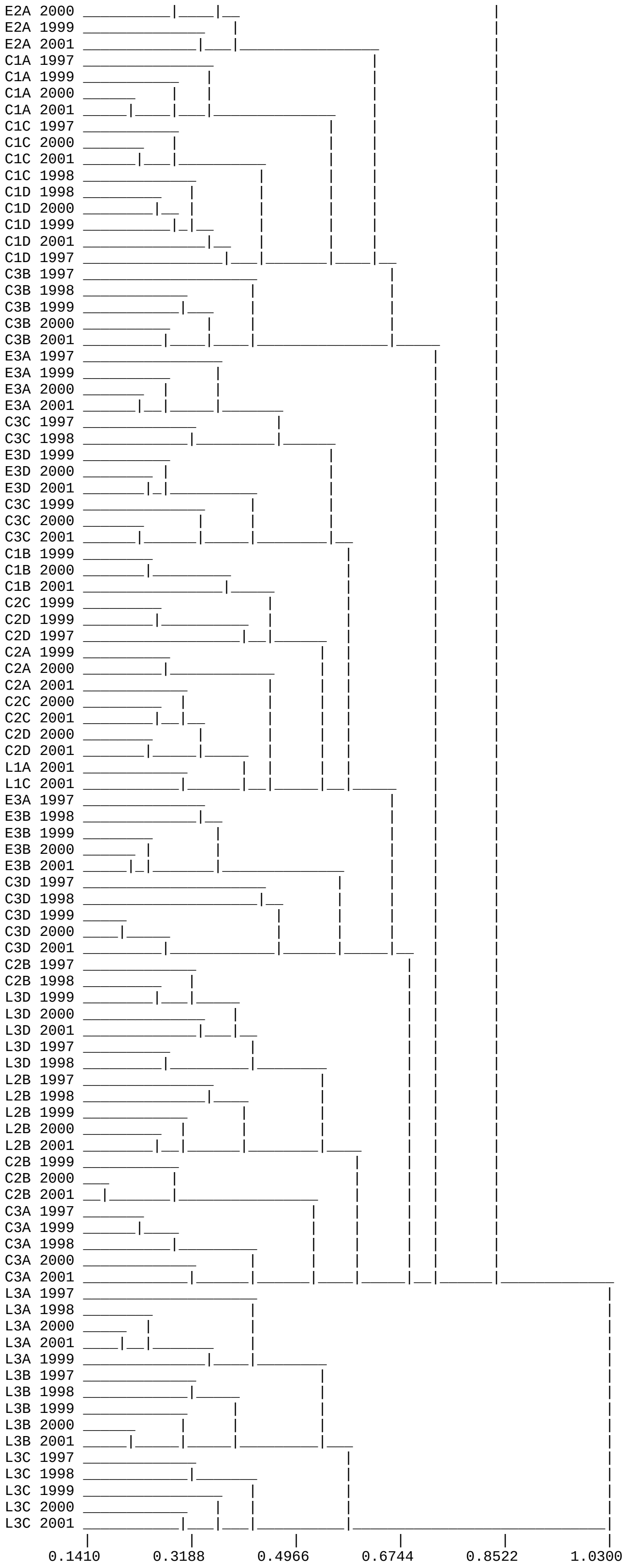


Figure 3.7. (cont.)



A simplified scatter plot of the PCA for the entire 180 surveys is presented in Figure 3.9. The trends in floristic response to fire treatments over the five years can be seen from the shift in symbols between years. Each symbol represents the mean PCA coordinate for an annual survey of the 12 plots (i.e. the four plots in each of the three 1 ha blocks) in each of the three fire regimes. There is consistency in the shift in symbols from 1997 to 1999 for the three fire regimes, when all plots received identical treatment. However, the shift in symbols from 1999 to 2000 differs between treatments following the 1999 fires, indicating different floristic patterns. The symbol representing the control plots in 2000 is more negative on axis 1 and positive on axis 2 than the 1999 symbol. The 2000 symbols for the early and late burnt plots are more positive on axis 1, so that the shift between the 1999 and 2000 is towards the right of the scatter plot. In 2001, the symbols representing the early and late burnt plots shift in a similar direction to that of the control plots.

These scatter plots document a similar trend in floristic patterns while all plots received the same treatment, prior to the 1999 fires (which were implemented after the 1999 surveys). The floristic patterns differ between fire regime in the first year after the 1999 fires (i.e. the 2000 surveys), but return to a similar pattern in 2001. The scatter plots also suggest that the floristic composition and abundance in 2001 differed to that of 1997, so that even in control plots, four years after fire, the species composition and abundance differed to that of the start of the study.

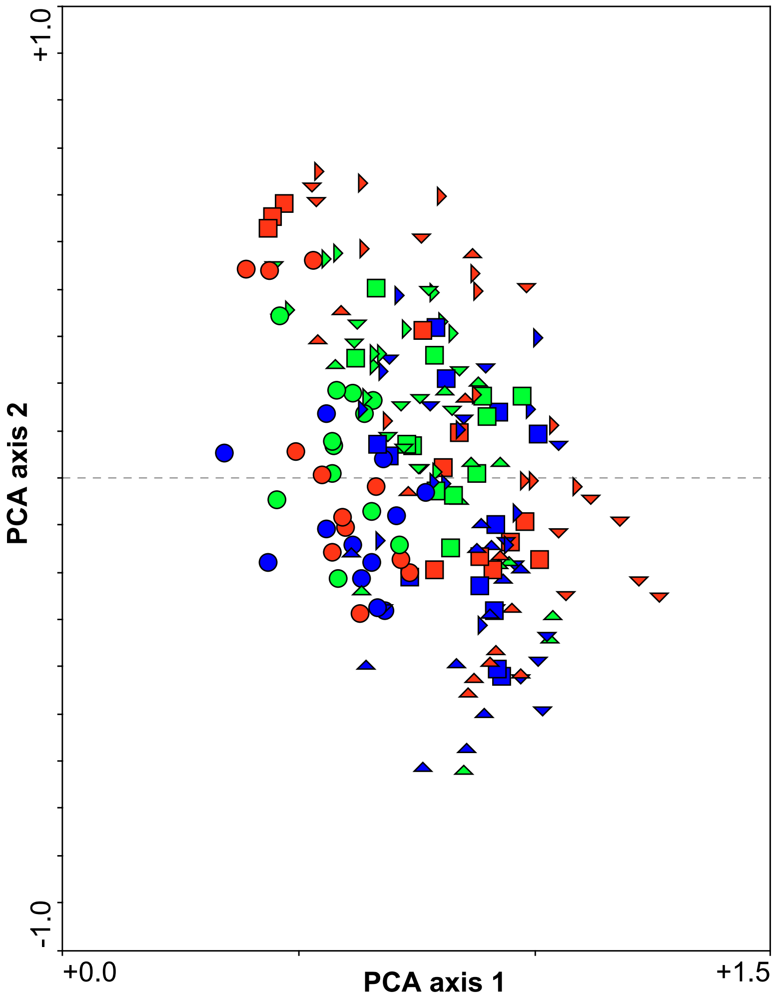


Figure 3.8. PCA scatter plot of the 180 surveys in eucalypt savanna at Cape Cleveland, from 1997 to 2001, showing the change in species composition and abundance over five years and after various fires. Symbols represent the coordinates of surveys of the same groups: Control 1997 (●); Control 1998 (▲); Control 1999 (■); Control 2000 (▼); Control 2001 (▶); Early burnt 1997 (●); Early burnt 1998 (▲); Early burnt 1999 (■); Early burnt 2000 (▼);Early burnt 2001 (▶); Late burnt 1997 (●); Late burnt 1998 (▲); Late burnt 1999 (■); Late burnt 2000 (▼); Late burnt 2001 (▶).

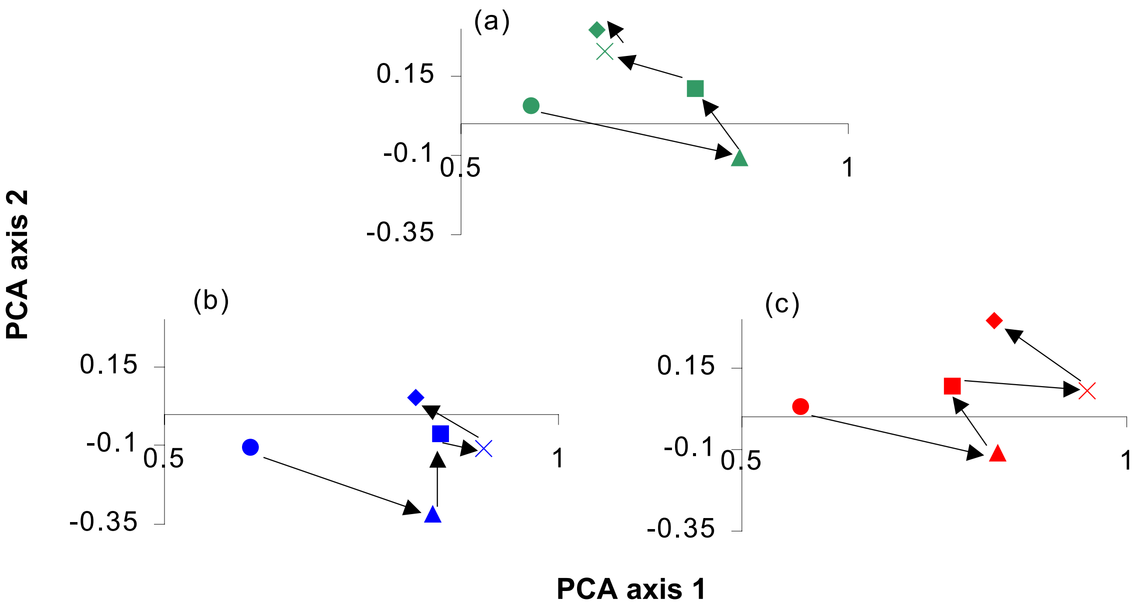


Figure 3.9. Simplified PCA scatter plot showing the pattern of floristic change from 1997 to 2001. Each point represents the mean PCA coordinates for annual surveys of the 12 (a) Control, (b) Early burnt and (c) Late burnt plots. 1997 survey (●); 1998 survey (▲); 1999 survey (■); 2000 survey (x); 2001 survey (◆). Arrows indicate the direction of change between annual surveys.

3.3.3c Partial Redundancy Analysis

A significant correlation was detected between fire variables and floristic variation over the five year study (Table 3.2). The combined fire variables explained only 2.1% of the species variation across the 180 surveys after the removal of background effects of covariables, however the correlation with species variance and fire was statistically significant due to the consistency of the relationship. Species differences between plots, fluctuations over years irrespective of fire treatment, and blocking accounted for 42.0%, 3.5% and 10.5% of the variance respectively. The high correlation between plots and species variance indicates that many of the species differences between plots at the start of the study remained unaffected by fire. Interactions between fire, year and plots accounted for 15.1% of species variation. A total of 26.8% of the species variance could not be accounted for by these variables.

Table 3.2. Partial RDA of floristic variation across the 180 surveys at Cape Cleveland, between 1997 and 2001, attributable to fire variables, fluctuations between years, plots, interactions and blocking. Fire variables are time since last fire, interval before last fire and fire seasons. [1]The floristic variation accounted for by specific variables and interactions is denoted as "% variation explained". This is the sum of canonical eigenvalues for each respective analysis, and is analogous to the sums of squares in ANOVA. [2]The significance of correlations between species variation and tested variables was assessed using a Monte Carlo test with 199 permutations.

Variable	d.f.	% variation explained[1]	*F* statistic	*P* value[2]
Fire variables	5	2.1	5.387	0.005
Year	4	3.5	9.115	0.005
Plot	35	42.0	6.540	0.005
Fire x Year x Plot		15.1		
Blocks		10.5		
Unexplained variation		26.8		

The results of the forward selection of fire variables, which is analogous to a *post-hoc* test in ANOVA, is displayed in Table 3.3. The interval before last fire was the fire variable with the best correlation with floristic variance, although time since last fire and several fire seasons also accounted for 1% of the variation. The combination of fire variables that best accounted for species variation was interval before last fire and early dry season fire. Although the latter was not ranked as the second most important individual variable (Lambda-1), it provides explanatory power additional to that of interval before last fire, so that together they produced the best correlation with floristic variation. This indicates that both fire interval and season are important for explaining floristic variation. Note that fire intensity values were not available for the fire prior to 1997, and therefore fire intensity was not used this analysis.

Table 3.3. Forward selection results of the partial RDA of floristic variance across the 180 surveys at Cape Cleveland, between 1997 and 2001, with individual fire variables. [1] The species variation explained separately by each fire variable, after allowance for covariables, is denoted as "Lambda-1." The individual fire variables are ranked by their importance in explaining floristic variation. [2] A "Lambda-A" score is produced for each variable, describing the additional species variance a variable explains, given the variables already correlated with species variance. [3] The significance of the correlation with species variance, once the new variable is added, was assessed using Monte Carlo tests with 199 permutations.

Variable	Lambda1[1]	Lambda A[2]	*F* statistic	*P* value[3]
Interval before last fire	0.01	0.01	7.08	0.005
Time since last fire	0.01			
Mid dry season fire	0.01			
Early dry season fire	0.01	0.01	3.57	0.005
Late dry season fire	0.01			
Early wet season fire	0.00			

The partial RDA of the full 180 surveys is portrayed in a biplot, which presents the correlation between fire variables and species variance (Figure 3.10). To help interpretation, the symbols representing surveys are grouped into fire regime (control, early burnt and late burnt), before and after the implementation of the 1999 fire season treatments. The angle between variables depends on their correlation, with a small angle indicating a strong correlation. The early, mid and late dry season fire variables were evenly spaced around the biplot, while the wet season fire was of such limited correlation it was ignored by the RDA. The mid dry season fire was strongly correlated with increasing time since last fire and fire intervals, because the longest unburnt plots, those of the control treatment surveyed in 2000 and 2001, were last burnt in the mid dry season fire of 1997.

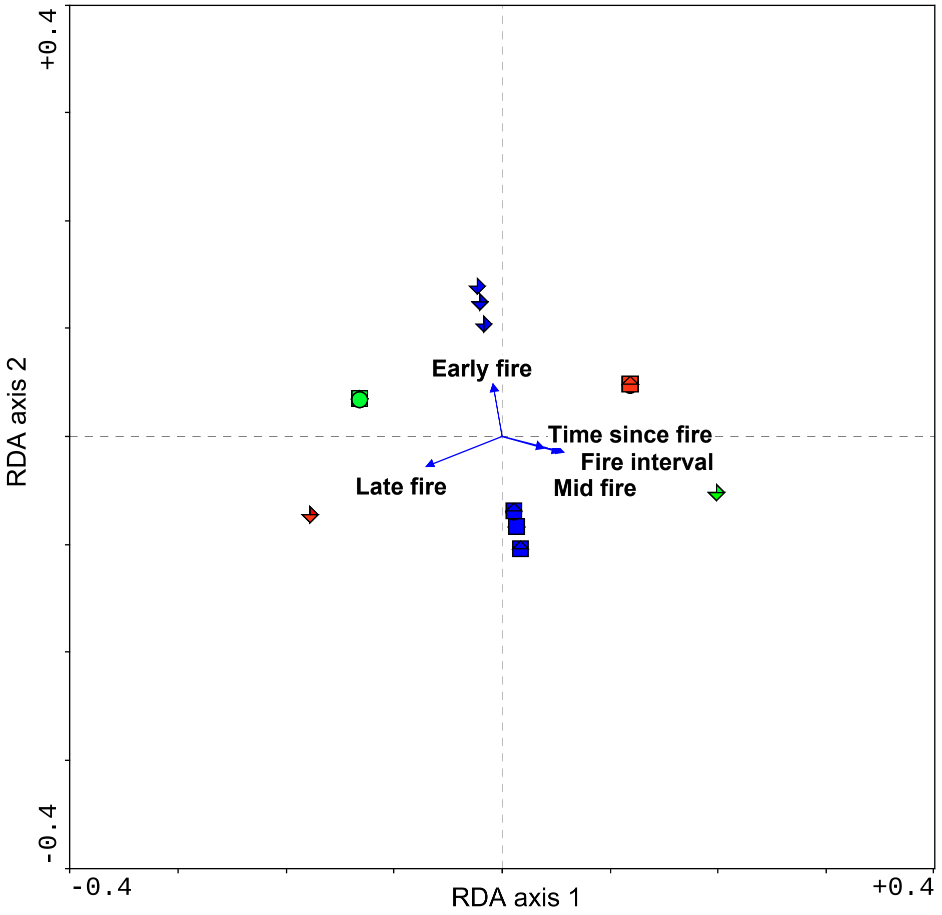


Figure 3.10. Biplot from the partial RDA of the entire 180 surveys in eucalypt savanna at Cape Cleveland from 1997 to 2001, showing the correlation between species composition and abundance and fire variables. Arrow length indicates the strength of the correlation between fire variable and species composition and abundance. Small angles between arrows indicate a strong correlation between fire variables. Symbols represent the coordinates of annual surveys of the three fire regimes: Control 1997 (●); Control 1998 (▲); Control 1999 (■); Control 2000 (▼); Control 2001 (▶); Early burnt 1997 (●); Early burnt 1998 (▲); Early burnt 1999 (■); Early burnt 2000 (▼); Early burnt 2001 (▶); Late burnt 1997 (●); Late burnt 1998 (▲); Late burnt 1999 (■); Late burnt 2000 (▼); Late burnt 2001 (▶).

The partial RDA of the 1999 and 2000 surveys indicated that fire variables together accounted for 4.6% of the species variation before and after the 1999 fires (Table 3.4). The species variance in 1999 and 2000 explained by the fire variables was higher than that for the entire five year study. This was not simply because fire intensity data was unavailable for the full 1997 to 2001 analysis, as a re-analysis of the 1999 and 2000 data set without fire intensity indicated the remaining fire variables still accounted for a higher percentage of the species variation (3.8%).

Plots and blocking accounted for 56.7% and 15.6% of the species variation respectively and interactions between fire, plot and year 11.7% (Table 3.4). As only two years were analysed, year fluctuations provided negligible explanation after adjustment for covariables of fire and plots, due to collinearity, especially with time since last fire. The higher correlation between floristic variation and fire variables, plots and blocking resulted in a lower proportion of unexplained floristic variation (11.4%) in the 1999 and 2000 analysis, than that of the full five years.

Table 3.4. Partial RDA of floristic variation across surveys undertaken in both 1999 and 2000, attributable to fire variables, fluctuations between years, plots, interactions and blocking. Fire variables were time since last fire, interval before last fire, fire intensity and various fire seasons. [1]The floristic variation accounted for by specific variables and interactions is denoted as "% variation explained". This is the sum of canonical eigenvalues for each respective analysis, and is analogous to the sums of squares in ANOVA. [2]The significance of specific variables was assessed using Monte Carlo test with 199 permutations.

Variable	d.f.	% variation explained[1]	*F* statistic	*P* value[2]
Fire variables	5	4.6	4.271	0.005
Year	2	0.0		
Plot	35	56.7	4.832	0.005
Fire x Year x Plot		11.7		
Blocks		15.6		
Unexplained variation		11.4		

Forward selection of fire variables indicated that fire intensity had the single greatest explanatory power, accounting for 3% of the species variation (Table 3.5). Fire intensity, plus mid and early dry season fire produced the best combination of fire variables to explain floristic variation. This, as well as the high individual explanatory values of time since last fire and interval before last fire, indicate that fire intensity, interval and season each had an important influence on floristic variation in 1999 to 2000.

Table 3.5. Forward selection results of the partial RDA of floristic variance across the 1999 and 2000 surveys, with individual fire variables. [1] The species variation explained separately by each fire variable, after allowance for covariables, is denoted as "Lambda-1." The individual fire variables are ranked by their importance in explaining floristic variation. [2] A "Lambda-A" score is produced for each variable, describing the additional species variance a variable explains, given the variables already correlated with species variance. [3] The significance of the correlation with species variance, once the new variable is added, was assessed using Monte Carlo tests with 199 permutations.

Variable	Lambda1[1]	Lambda A[2]	F-ratio	P value[3]
Fire intensity	0.03	0.03	7.03	0.005
Mid dry season fire	0.03	0.01	3.80	0.005
Time since last fire	0.03			
Interval before last fire	0.03			
Late dry season fire	0.03			
Early dry season fire	0.01	0.01	1.31	0.160

The biplot of the 1999 and 2000 partial RDA displays floristic change immediately after the 1999 fire season trial (Figure 3.11). The change in coordinates between 1999 and 2000 for surveys in both the early and late burnt plots is in the opposite direction to that in the unburnt controls. The biplot grouped together surveys of all four plots in each of the early and late burnt blocks, for both 1999 and 2000, while the surveys of all 12 unburnt control plots were positioned in the same point in 1999 and 2000. The reason for this is that separate fire intensity figures for 1999 were available for each early and late burnt block, whereas all fire variables, including the intensity of the previous fire (July 1997), were identical for all unburnt control plots. Hence the unburnt control surveys were each correlated with the same set of fire variables, resulting in an average correlation with floristic variation for the annual surveys of the 12 control plots.

The biplot of the 1999 and 2000 data set positioned the variable “late dry season fire” close to fire intensity, indicating the strong relationship between increasing fire intensity and late dry season fires (Figure 3.11). The mid dry season fire, fire interval and time since last fire were also closely associated. The length of the arrows represent the strength of the correlation between the fire variables and floristic variance. The early dry season fire variable is shorter than the other arrows, indicating less individual power for explaining species variance than the late dry season fires.

3.3.3d Univariate analyses of species richness and abundance

Twining perennial forbs were the most species rich growth form group, containing 22 species, or 18% of the community (Table 3.6). Upright perennial forbs were the least diverse group, with 8 species. Twining perennial forbs and grasses were the most abundant groups, providing 29 and 28% of the total abundance respectively, while rainforest trees and shrubs produced the least abundance, they were represented by 18 species.

There were no significant differences in species richness at the 100 m^2 scale in either the 2000 or 2001 surveys (Table 3.7). There was however, significantly higher species richness at the 1 m^2 scale in 2000, after late dry season fires compared to early dry season or unburnt control plots, and in early burnt compared with control plots in 2000. There were no species richness differences at the 1 m^2 scale by 2001.
An increase in the abundance of several common species and growth form groups, especially grasses, twining perennial forbs and ephemeral forbs, occurred immediately after fire but were reduced by 2001 (Table 3.7). A summary of the results presented in Table 3.7 are provided below.

The abundance of both native and exotic species fluctuated over the five years, and was higher in 2001 than 1997. The mean percentage increase of combined exotic species (668%, s.e. 98) was significantly greater than that of natives (130%, s.e. = 4; U_{70} =

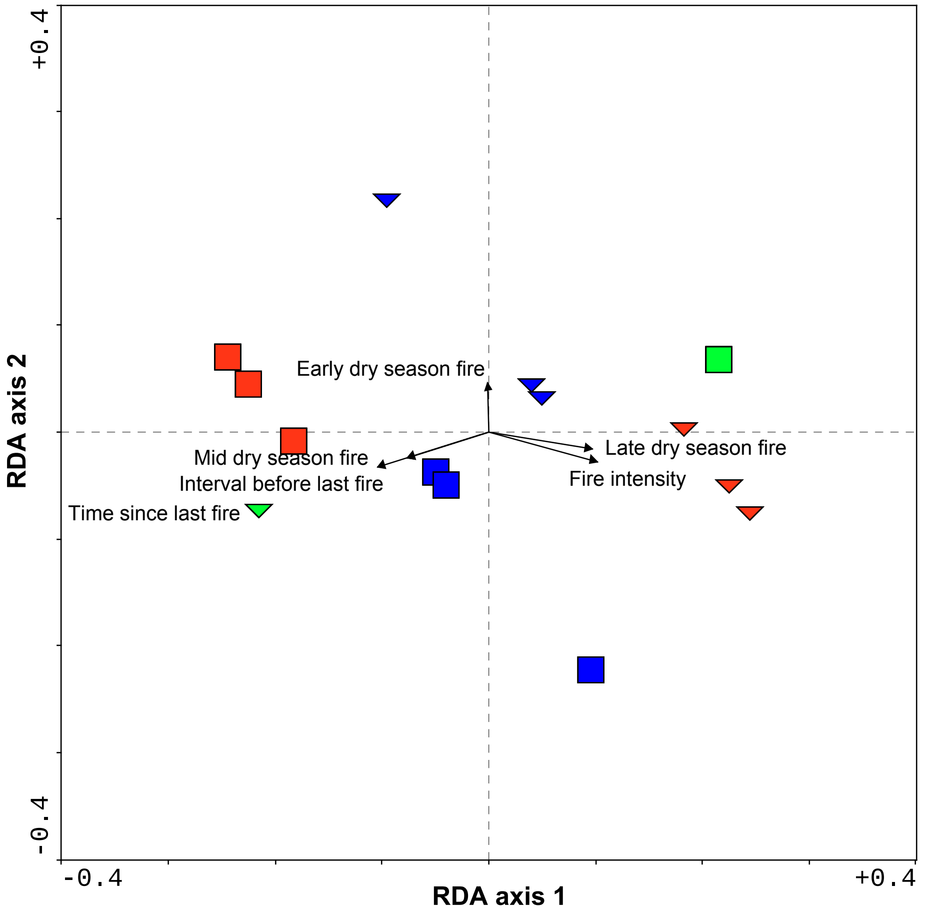


Figure 3.11. Biplot from the partial RDA of surveys in eucalypt savanna at Cape Cleveland in 1999 and 2000, showing the correlation between species composition and abundance and fire variables. Arrow length indicates the strength of the correlation between fire variable and species composition and abundance. Small angles between arrows indicate a strong correlation between fire variables. Symbols represent the coordinates of annual surveys of fire treatments: Control 1999 (🟩); Control 2000 (▼); Early burnt 1999 (🟦); Early burnt 2000 (▼); Late burnt 1999 (🟥); Late burnt 2000 (▼).

Table 3.6. Species number and abundance of growth form groups in the five annual surveys in eucalypt savanna at Cape Cleveland. [1]Total abundance was calculated as the sum abundance of all species of a growth form group.

Growth form	Number of species	% of total species	Total abundance[1]	% of total abundance
Woodland trees and shrubs	15	13	1671	7
Rainforest trees and shrubs	18	15	610	3
Subshrubs	13	11	1537	6
Upright perennial forbs	8	7	1173	5
Twining perennial forbs	22	18	7146	29
Ephemeral forbs	13	11	1648	7
Grasses	16	14	6872	28
Non-grass monocots	13	11	3564	15
Combined species	118	100	24226	100

142.000; $P < 0.001$). There was no significant fire effect on the abundance of the native species as a whole. Late dry season fires increased the abundance of combined exotic species to a significantly greater extent than early dry season burnt or unburnt plots, in 2000. This difference had disappeared by 2001.

Woodland trees and shrubs as a group did not differ in abundance between fire treatments. Neither were any significant differences detected in the common trees, *Corymbia clarksoniana* and *Planchonia careya*. Likewise, no significant effect could be detected for rainforest trees and shrubs, as a group, and the common rainforest tree, *Canarium australianum*.

Subshrubs, as a group, did not differ in abundance between fire treatments. However, the late dry season fires of 1999 significantly enhanced the abundance of the common subshrub, *Breynia oblongifolia*, over unburnt controls. This difference was not apparent in 2001. There was more of the exotic subshrub, *Triumfetta rhomboidea*, in both unburnt control and late dry season burnt plots, than in early dry season burnt plots in 2000.

Upright perennial forbs, as well as the common species *Hybanthus stellarioides* and *Rostellularia adscendens*, showed no significant fire effects. There was, however, a significant fluctuation between the years 1999 and 2001 in the upright perennial forb group that was not related to fire treatment.

Twining perennial forbs responded to fire treatment, with significantly greater abundance in the late dry season burnt plots compared to unburnt control plots in 2000. Treatment effects disappeared by 2001. The abundance of the dominant twiner, *Galactia tenuifolia*, was significantly enhanced by burning. This was the only species to show a significantly greater enhancement after early rather than late dry season burning. The exotic twining perennial forb *Passiflora foetida* was significantly more abundant after late dry season fires than early dry season fires or unburnt controls, in both 2000 and 2001. This fire effect was confirmed by a significant fire by year interaction, between 1999 and 2001.

The common twining perennial forbs, *Flemingia parvifolia*, *Jasminum didymum* and the exotic *Macroptilium atropurpureum* showed no significant response to fire regime. *Glycine tomentella* and *Pycnospora lutescens* showed significant fluctuations between 1999 and 2001 that were not related to fire regime.

Ephemeral forbs, as a group, showed a strong response to fire. Their highest abundance occurred in 2000, following fire, with greater abundance after both early and late dry season fires compared to unburnt controls. Few ephemeral forbs were present in the 2001 survey and consequently there were no treatment differences in that year. There was significantly greater abundance of the ephemeral forb *Indigofera hirsuta* in early and late burnt plots than unburnt controls in 2000. There was no significant fire effect detected for *Tephrosia juncea*.

The grasses, as a group, were significantly more abundant in late dry season burnt plots than unburnt controls in 2000, however this difference was not evident by 2001. No significant fire effects could be detected for the common perennial grasses *Digitaria breviglumis*, *Heteropogon contortus* and *Themeda triandra*. In 2001, the dominant grass *H. triticeus*, was significantly more abundant in early and late dry season burnt plots than control plots, which had remained unburnt for four years by that time.

There were no significant fire effects detected for the non-grass monocots, or the common monocots *Commelina* spp., *Curculigo ensifolia*, *Eustrephus latifolius* and *Scleria mackaviensis*.

Table 3.7. Mean (standard error) of species richness, abundance of species groups and the 21 most common species, and statistical results, for fire regime in eucalypt savanna at Cape Cleveland. Note that for repeated measures ANOVAs, the "Fire x Year" interaction is the term of primary interest, indicating the significance of interactions between treatment and years; a significant "Fire" term indicates treatment plots differed before treatment applied; a significant "Year" term indicates significant fluctuations over the years in all treatments.

Depend-ent factors Common species listed under relevant growth form groups	**Annual abundance means for each treatment (n = 12)** C = control, burnt July 1997 only; E = burnt July 1997 and early dry season 1999; L = burnt July 1997 and late dry season 1999. Significantly different treatments for the separate 2000 and 2001 ANCOVA at $P < 0.01$ are indicated by different superscripts.					**Statistical results** See section 3.2.3d for methodology. $F_{2,6}$ indicates F value, denominator d.f., numerator d.f.; F or H values without an asterisk (*) are not significantly different at $P > 0.01$; *$P < 0.01$; **$P < 0.001$. The term "*log*" indicates log (x + 1) transformation was used to rectify heterogeneity of variances; "*pooled*" indicates block P value > 0.25 and replicates pooled; "*block,*" significant bock effect at P <0.01; and "*K-W*" indicates the non-parametric Kruskal-Wallis ANOVA by ranks test used instead of parametric ANOVA, where variance heterogeneity unresolved.		
Species richness	1997	1998	1999	2000	2001	1999-2001 Repeated measures ANOVA of fire treatments (C, E, L)	2000 ANCOVA of fire treatments (C, E, L) using 1999 data as a covariate	2001 ANCOVA of fire treatments (C, E, L) using 1999 data as a covariate
Species richness per plot (100m^2)	C 29.25 (1.05)	36.92 (1.10)	36.08 (1.07)	35.92 (0.93)^{a}	37.17 (0.98)^{z}	*Fire* $F_{2,6} = 0.015$	$F_{2,6} = 1.104$	$F_{2,6} = 0.545$
	E 31.00 (1.72)	34.75 (1.41)	35.33 (1.50)	37.25 (1.90)^{a}	35.83 (1.85)^{z}	*Year* $F_{2,12} = 3.730$		
	L 30.08 (1.27)	35.17 (1.27)	34.75 (1.27)	39.75 (1.49)^{a}	35.50 (4.95)^{z}	*Fire x Year* $F_{4,12} = 2.287$		
Species richness per quadrat (1m^2)	C 4.68 (0.09)	7.75 (0.16)	6.92 (0.12)	6.27 (0.11)^{a}	6.54 (0.12)^{z}	*K-W* of 1999 $H_2 = 6.55$	*K-W* of 2000 $H_2 = 160.97$**	*K-W* of 2001 $H_2 = 24.33$**
	E 4.44 (0.10)	7.33 (0.14)	7.20 (0.13)	7.94 (0.15)^{b}	6.59 (0.12)^{z}			
	L 4.60 (0.09)	7.76 (0.14)	6.78 (0.13)	9.22 (0.18)^{c}	7.25 (0.13)^{y}			

Table 3.7 (cont.)

Species		1997	1998	1999	2000	2001	1999-2001 ANOVA	2000 ANCOVA	2001 ANCOVA
Native species	C	84.08 (2.74)	141.42 (8.35)	112.08 (6.45)	99.42 (6.62) ^{a}	103.67 (6.23) ^{z}	*Fire* $F_{2,6} = 0.383$	$F_{2,6} = 5.820$	$F_{2,6} = 0.143$
	E	80.75 (4.46)	135.33 (5.87)	117.58 (6.22)	133.83 (8.73) ^{a}	107.42 (5.25) ^{z}	*Year* $F_{2,12} = 9.435$*		
	L	85.33 (4.17)	138.83 (7.02)	109.92 (9.42)	147.83 (12.44) ^{a}	111.25 (7.52) ^{z}	*Fire x Year* $F_{4,12} = 5.868$*		
Exotic species	C	9.50 (2.17)	11.83 (1.56)	26.25 (2.61)	25.83 (2.23) ^{a}	27.25 (2.68) ^{z}	*log* *Fire* $F_{2,6} = 1.032$	*log, pooled* $F_{2,6} = 25.341$**	*log, pooled* $F_{2,6} = 4.335$
	E	6.92 (1.96)	10.42 (2.25)	26.08 (3.15)	22.83 (2.60) ^{a}	24.08 (2.39) ^{z}	*Year* $F_{2,12} = 1.810$		
	L	6.75 (2.34)	15.58 (4.53)	26.17 (3.88)	37.08 (4.52) ^{b}	33.58 (3.01) ^{z}	*Fire x Year* $F_{4,12} = 3.612$		
Woodland trees and shrubs	C	12.08 (1.37)	9.08 (1.32)	11.58 (1.52)	10.33 (1.27) ^{a}	8.50 (2.06) ^{z}	*Fire* $F_{2,6} = 0.529$	*pooled* $F_{2,6} = 4.776$	$F_{2,6} = 0.360$
	E	10.08 (1.77)	9.42 (1.811)	9.083 (1.71)	7.42 (1.38) ^{a}	5.667 (1.60) ^{z}	*Year* $F_{2,12} = 4.147$		
	L	10.33 (1.86)	9.92 (1.56)	8.33 (1.38)	10.25 (1.83) ^{a}	7.67 (1.01) ^{z}	*Fire x Year* $F_{4,12} = 0.867$		
Corymbia clarksoniana	C	2.92 (0.96)	3.25 (1.07)	2.67 (0.86)	2.33 (0.83) ^{a}	2.83 (1.02) ^{z}	*Fire* $F_{2,6} = 0.263$	*block* $F_{2,6} = 1.292$	$F_{2,6} = 0.824$
	E	3.67 (0.69)	3.50 (0.71)	4.25 (0.86)	3.50 (0.87) ^{a}	2.25 (0.64) ^{z}	*Year* $F_{2,12} = 3.135$		
	L	2.17 (0.65)	2.75 (0.52)	2.00 (0.54)	2.42 (0.65) ^{a}	2.08 (0.43) ^{z}	*Fire x Year* $F_{4,12} = 5.270$		
Planchonia careya	C	2.58 (0.87)	2.00 (0.49)	1.75 (0.65)	1.83 (0.70) ^{a}	1.50 (0.71) ^{z}	*pooled* *Fire* $F_{2,6} = 0.161$	*pooled* $F_{2,6} = 2.162$	$F_{2,6} = 0.155$
	E	2.92 (0.98)	2.42 (0.94)	1.67 (0.63)	1.75 (0.70) ^{a}	1.50 (0.73) ^{z}	*Year* $F_{2,12} = 1.808$		
	L	2.92 (0.78)	2.67 (0.64)	1.67 (0.47)	2.67 (0.58) ^{a}	1.92 (0.67) ^{z}	*Fire x Year* *F 4,12* = 0.726		

Table 3.7 (cont.)

Species		1997	1998	1999	2000	2001	1999-2001 ANOVA	2000 ANCOVA	2001 ANCOVA
Rainforest trees and shrubs	C	3.50 (1.10)	3.42 (0.81)	4.20 (0.73)	4.08 (0.91)^{a}	3.00 (0.75)^{z}	*log, pooled* *Fire* $F_{2,6} = 2.856$	*log, pooled* $F_{2,6} = 2.976$	*pooled* $F_{2,6} = 2.115$
	E	2.00 (0.94)	1.83 (0.73)	1.83 (0.80)	2.25 (0.91)^{a}	1.75 (5.24)^{z}	*Year* $F_{2,12} = 2.127$		
	L	4.08 (1.42)	4.67 (1.25)	4.08 (1.31)	5.50 (1.26)^{a}	4.67 (1.38)^{z}	*Fire x Year* $F_{4,12} = 2.462$		
Canarium australianum	C	2.83 (1.01)	2.75 (0.65)	3.25 (0.58)	3.08 (0.78)^{a}	2.33 (0.62)^{z}	*log, pooled* *Fire* $F_{2,6} = 1.986$	*pooled* $F_{2,6} = 5.285$	*log, pooled* $F_{2,6} = 1.651$
	E	1.92 (0.88)	1.58 (0.60)	1.75 (0.74)	2.00 (0.87)^{a}	1.42 (0.48)^{z}	*Year* $F_{2,12} = 2.171$		
	L	2.42 (1.03)	3.67 (1.11)	2.92 (1.10)	4.17 (0.93)^{a}	3.42 (1.08)^{z}	*Fire x Year* $F_{4,12} = 2.954$		
Subshrubs	C	6.75 (1.01)	9.33 (1.96)	8.17 (1.64)	7.92 (1.64)^{a}	7.92 (1.45)^{z}	*pooled* *Fire* $F_{2,6} = 3.284$	*pooled* $F_{2,6} = 1.177$	*pooled* $F_{2,6} = 3.833$
	E	5.17 (1.15)	6.67 (1.41)	7.33 (1.79)	7.92 (1.60)^{a}	7.92 (1.67)^{z}	*Year* $F_{2,12} = 1.402$		
	L	6.50 (1.71)	10.0 (1.11)	10.33 (0.95)	13.17 (1.59)^{a}	13.0 (1.40)^{z}	*Fire x Year* $F_{4,12} = 1.062$		
Breynia oblongifolia	C	3.58 (0.97)	4.50 (1.18)	1.67 (0.43)	1.00 (0.33)^{a}	1.17 (0.35)^{z}	*log, pooled* *Fire* $F_{2,6} = 2.429$	*log, pooled* $F_{2,6} = 5.660$*	*pooled* $F_{2,6} = 3.744$
	E	2.42 (0.84)	2.50 (0.87)	1.25 (0.49)	3.42 (1.05)^{ab}	3.08 (1.14)^{z}	*Year* $F_{2,12} = 2.868$		
	L	4.58 (1.16)	5.25 (1.11)	2.58 (0.89)	4.25 (0.97)^{b}	3.00 (0.67)^{z}	*Fire x Year* $F_{4,12} = 3.031$		

Table 3.7 (cont.)

Species		1997	1998	1999	2000	2001	1999-2001 ANOVA	2000 ANCOVA	2001 ANCOVA
Triumfetta rhomboidea	C	0.92 (0.34)	2.08 (0.53)	3.58 (0.92)	4.33 (1.15)^{a}	4.58 (0.89)^{z}	*log, pooled* *Fire* $F_{2,6}$ = 4.761	*log, pooled* $F_{2,6}$ = 9.243*	*pooled* $F_{2,6}$ = 5.294
	E	0.58 (0.29)	1.58 (0.96)	3.42 (1.23)	1.42 (0.80)^{b}	1.67 (0.75)^{z}	*Year* $F_{2,12}$ = 0.729		
	L	0.67 (0.19)	2.08 (0.73)	5.08 (1.32)	4.58 (0.74)^{a}	5.50 (0.97)^{z}	*Fire x Year* $F_{4,12}$ = 3.577		
Upright perennial forbs	C	2.92 (0.92)	9.42 (1.75)	6.17 (1.39)	6.25 (6.25)^{a}	5.08 (0.93)^{z}	*Fire* $F_{2,6}$ = 0.190	*pooled* $F_{2,6}$ = 1.153	*log* $F_{2,6}$ = 0.083
	E	3.25 (0.62)	8.17 (1.87)	8.19 (1.52)	10.08 (1.71)^{a}	4.75 (1.01)^{z}	*Year* $F_{2,12}$ = 2.939*		
	L	3.67 (1.26)	8.17 (2.32)	6.67 (2.52)	9.42 (2.51)^{a}	5.42 (1.66)^{z}	*Fire x Year* $F_{4,12}$ = 1.318		
Hybanthus stellarioides	C	0.67 (0.36)	2.33 (1.05)	1.50 (0.79)	1.67 (0.79)^{a}	1.33 (0.54)^{z}	*K-W* of 1997 $H_{2,6}$ = 1.741	$F_{2,6}$ = 0.764	*K-W* of 2001 $H_{2,6}$ = 0.612
	E	0.33 (0.19)	0.58 (0.36)	0.92 (0.65)	1.42 (0.84)^{a}	2.0 (0.62)^{z}			
	L	1.67 (0.74)	3.58 (1.31)	2.92 (1.38)	4.42 (1.78)^{a}	2.58 (1.22)^{z}			
Rostellularia adscendens	C	0.58 (0.29)	1.50 (0.45)	0.92 (0.38)	1.08 (0.31)^{a}	1.17 (0.42)^{z}	*Fire* $F_{2,6}$ = 0.924	$F^{2,6}$ = 2.038	*pooled* $F_{2,6}$ = 0.260
	E	1.25 (0.25)	1.925 (0.57)	1.83 (0.47)	3.00 (0.66)^{a}	1.42 (0.42)^{z}	*Year* $F_{2,12}$ = 0.621		
	L	0.92 (0.42)	0.75 (0.43)	1.33 (0.48)	1.25 (0.51)^{a}	1.67 (0.69)^{z}	*Fire x Year* $F_{4,12}$ = 1.183		
Twining perennial forbs	C	24.17 (2.63)	36.67 (3.32)	46.25 (3.82)	36.50 (3.00)^{a}	43.08 (2.90)^{z}	*Fire* $F_{2,6}$ = 0.780	*pooled* $F_{2,6}$ = 9.734**	$F_{2,6}$ = 0.785
	E	26.17 (2.66)	37.42 (3.07)	52.42 (3.17)	48.83 (3.53)^{b}	47.92 (3.22)^{z}	*Year* $F_{2,12}$ = 4.420*		
	L	21.25 (2.06)	34.67 (3.18)	41.92 (2.37)	49.08 (3.40)^{b}	49.17 (2.94)^{z}	*Fire x Year* $F_{4,12}$ = 3.680		

Table 3.7 (cont.)

Species		1997	1998	1999	2000	2001	1999-2001 ANOVA	2000 ANCOVA	2001 ANCOVA
Flemingia parviflora	C	1.33 (0.38)	2.33 (0.50)	1.17 (0.32)	1.50 (0.36) ^{a}	1.75 (0.51) ^{z}	*log* *Fire* $F_{2,6} = 0.263$ *Year* $F_{2,12} = 2.608$ *Fire x Year* $F_{4,12} = 1.230$	*log, pooled* $F_{2,6} = 1.514$	*log, pooled* $F_{2,6} = 0.144$
	E	1.92 (0.61)	2.17 (0.51)	1.00 (0.37)	2.75 (0.68) ^{a}	2.67 (0.89) ^{z}			
	L	2.42 (0.75)	2.83 (0.53)	1.58 (0.43)	2.75 (0.64) ^{a}	2.67 (0.90) ^{z}			
Galactia tenuiflora	C	6.58 (1.69)	9.25 (1.86)	7.83 (1.70)	4.58 (1.23) ^{a}	5.50 (1.20) ^{z}	*K-W* of 1999 $H_{2,6} = 5.262$	*K-W* of 2000 $H_{2,6} = 12.922*$	*K-W* of 2001 $H_{2,6} = 7.651$
	E	11.25 (1.75)	14.17 (1.69)	12.83 (1.63)	14.50 (1.85) ^{b}	11.17 (1.42) ^{z}			
	L	7.58 (1.72)	10.83 (1.70)	8.58 (1.50)	9.00 (1.58) ^{c}	9.58 (1.55) ^{z}			
Glycine tomentella	C	1.00 (0.39)	3.67 (0.89)	6.58 (1.27)	0.58 (0.26) ^{a}	0.67 (0.28) ^{z}	*log* *Fire* $F_{2,6} = 0.862$ *Year* $F_{2,12} = 39.664**$ *Fire x Year* $F_{4,12} = 3.524$	*log* $F_{2,6} = 5.000$	$F_{2,6} = 0.379$
	E	2.17 (0.64)	4.75 (0.84)	8.50 (1.86)	5.00 (1.36) ^{a}	2.50 (0.99) ^{z}			
	L	1.92 (0.66)	3.75 (0.91)	5.42 (1.25)	3.50 (1.07) ^{a}	2.00 (0.56) ^{z}			
Jasminum didymum	C	4.33 (0.86)	3.08 (0.67)	3.33 (0.83)	3.25 (0.80) ^{a}	3.50 (0.89) ^{z}	*Fire* $F_{2,6} = 0.924$ *Year* $F_{2,12} = 0.621$ *Fire x Year* $F_{4,12} = 1.183$	$F_{2,6} = 2.038$	*pooled* $F_{2,6} = 0.260$
	E	0.17 (0.11)	0.17 (0.17)	0.50 (0.19)	0.33 (0.14) ^{a}	0.08 (0.08) ^{z}			
	L	0.75 (0.30)	1.25 (0.59)	1.42 (0.53)	1.17 (0.37) ^{a}	1.08 (0.43) ^{z}			
Macroptilium atropurpureum	C	1.00 (0.62)	1.08 (0.57)	6.92 (2.30)	9.08 (2.15) ^{a}	8.00 (1.81) ^{z}	*Fire* $F_{2,6} = 0.156$ *Year* $F_{2,12} = 0.011$ *Fire x Year* $F_{4,12} = 1.055$	$F_{2,6} = 4.440$	$F_{2,6} = 0.690$
	E	0.83 (0.53)	0.75 (0.46)	6.50 (2.08)	6.25 (2.15) ^{a}	5.00 (1.78) ^{z}			
	L	0.83 (0.46)	2.42 (1.20)	7.42 (2.48)	5.50 (1.80) ^{a}	8.25 (2.13) ^{z}			

Table 3.7 (cont.)

Species		1997	1998	1999	2000	2001	1999-2001 ANOVA	2000 ANCOVA	2001 ANCOVA
Passiflora foetida	C	5.33 (1.57)	6.08 (1.19)	10.58 (1.29)	8.58 (0.75) ^{a}	10.25 (0.83) ^{z}	*pooled* *Fire* $F_{2,6} = 8.683*$	$F_{2,6} = 26.016*$	*log, pooled* $F_{2,6} = 8.428*$
	E	3.92 (1.55)	4.67 (0.86)	8.83 (1.22)	9.75 (0.87) ^{a}	12.75 (1.01) ^{z}	*Year* $F_{2,12} = 16.969**$		
	L	3.08 (1.77)	4.92 (0.96)	8.33 (1.06)	16.42 (0.87) ^{b}	16.50 (0.84) ^{y}	*Fire x Year* $F_{4,12} = 11.442**$		
Pycnospora lutescens	C	2.00 (0.91)	4.83 (1.66)	4.92 (1.32)	3.83 (1.04) ^{a}	3.67 (1.19) ^{z}	*Fire* $F_{2,6} = 0.225$	*pooled* $F_{2,6} = 0.235$	$F_{2,6} = 0.115$
	E	2.83 (0.80)	5.58 (0.96)	7.00 (1.69)	5.67 (1.32) ^{a}	5.42 (1.52) ^{z}	*Year* $F_{2,12} = 9.263*$		
	L	2.25 (0.72)	3.67 (1.42)	5.58 (1.89)	4.50 (1.17) ^{a}	5.00 (1.50) ^{z}	*Fire x Year* $F_{4,12} = 0.522$		
Ephemeral forbs	C	1.42 (0.51)	19.75 (3.83)	2.75 (0.98)	1.33 (0.98) ^{a}	1.33 (0.50) ^{z}	*log* *Fire* $F_{2,6} = 4.044$	*log* $F_{2,6} = 41.117**$	*Log* $F_{2,6} = 1.715$
	E	1.50 (0.36)	25.25 (2.84)	5.75 (1.52)	17.25 (3.74) ^{b}	3.17 (0.78) ^{z}	*Year* $F_{2,12} = 3.028$		
	L	1.59 (0.79)	23.58 (2.99)	4.25 (1.12)	27.17 (4.67) ^{b}	1.25 (0.52) ^{z}	*Fire x Year* $F_{4,12} = 19.952**$		
Indigofera hirsuta	C	0.33 (0.22)	9.67 (1.83)	0.00 (0.00)	0.17 (0.11) ^{a}	0.08 (0.08) ^{z}	*K-W* of 1999 $H_{2,6} = 8.620$	*K-W* of 2000 $H_{2,6} = 25.308**$	*K-W* of 2001 $H_{2,6} = 6.049$
	E	0.83 (0.27)	13.92 (1.08)	0.83 (0.32)	7.25 (1.39) ^{b}	0.50 (0.15) ^{z}			
	L	0.17 (0.11)	11.33 (1.48)	0.08 (0.08)	12.50 (2.17) ^{b}	0.17 (0.11) ^{z}			
Tephrosia juncea	C	0.25 (0.13)	7.00 (2.32)	0.92 (0.47)	0.17 (0.11) ^{a}	0.08 (0.00) ^{z}	*K-W* of 1999 $H_{2,6} = 0.579$	*K-W* of 2000 $H_{2,6} = 7.414$	*K-W* of 2001 $H_{2,6} = 2.178$
	E	0.33 (0.22)	7.08 (2.14)	1.17 (0.47)	3.67 (1.35) ^{a}	0.33 (0.26) ^{z}			
	L	0.25 (0.18)	5.92 (1.73)	1.17 (0.42)	4.17 (1.31) ^{a}	0.08 (0.08) ^{z}			

Table 3.7 (cont.)

Species		1997	1998	1999	2000	2001	1999-2001 ANOVA	2000 ANCOVA	2001 ANCOVA
Grasses	C	35.33 (1.61)	38.67 (2.23)	44.17 (2.18)	37.5 (1.86)^{a}	38.17 (2.13)^{z}	*Fire* $F_{2,6} = 0.186$	*pooled* $F_{2,6} = 8.55$*	*pooled* $F_{2,6} = 2.790$
	E	30.75 (1.99)	34.75 (2.37)	40.0 (2.5)	40.08 (2.42)^{ab}	40.17 (2.02)^{z}	*Year* $F_{2,12} = 0.161$		
	L	33.33 (1.59)	33.83 (1.66)	38.92 (2.56)	43.92 (2.7)^{b}	43.08 (2.04)^{z}	*Fire x Year* $F_{4,12} = 5.568$*		
Digitaria breviglumis	C	4.33 (0.84)	5.08 (0.92)	7.58 (1.38)	8.42 (1.05)^{a}	9.00 (1.29)^{z}	*pooled* *Fire* $F_{2,6} = 4.469$	*pooled* $F_{2,6} = 0.592$	*pooled* $F_{2,6} = 1.847$
	E	2.25 (0.39)	1.58 (0.43)	3.83 (0.66)	5.08 (1.07)^{a}	5.08 (1.04)^{z}	*Year* $F_{2,12} = 2.153$		
	L	4.25 (1.09)	4.00 (0.55)	7.08 (0.79)	7.00 (0.82)^{a}	7.67 (1.05)^{z}	*Fire x Year* $F_{4,12} = 0.3171$		
Heteropogon contortus	C	10.25 (1.62)	10.25 (1.62)	8.33 (1.41)	8.33 (1.29)^{a}	10.33 (1.46)^{z}	*Fire* $F_{2,6} = 1.910$	$F_{2,6} = 2.355$	$F_{2,6} = 0.704$
	E	5.92 (1.31)	5.58 (1.49)	5.00 (0.95)	5.58 (1.25)^{a}	7.25 (1.27)^{z}	*Year* $F_{2,12} = 1.874$		
	L	10.58 (1.88)	9.42 (2.40)	6.92 (1.57)	10.83 (1.95)^{a}	12.75 (1.58)^{z}	*Fire x Year* $F_{4,12} = 0.684$		
Heteropogon triticeus	C	16.58 (1.25)	18.16 (0.90)	18.50 (0.79)	13.83 (1.30)^{a}	9.75 (0.90)^{z}	*K-W* of 1999 $H_{2,6} = 2.905$	*K-W* of 2000 $H_{2,6} = 7.988$	*pooled* $F_{2,6} = 17.028$**
	E	17.42 (1.48)	19.00 (1.00)	19.25 (0.66)	18.83 (0.99)^{b}	17.92 (1.04)^{y}			
	L	14.58 (2.50)	15.25 (2.30)	15.33 (2.28)	15.00 (2.36)^{ab}	12.50 (2.11)^{z}			
Themeda triandra	C	2.17 (0.64)	2.29 (1.09)	4.92 (1.20)	3.00 (1.09)^{a}	3.08 (1.31)^{z}	*log* *Fire* $F_{2,6} = 0.163$	*pooled* $F_{2,6} = 5.208$	*log* $F_{2,6} = 1.196$
	E	3.33 (1.24)	4.08 (1.49)	5.25 (1.47)	5.25 (1.33)^{b}	4.92 (1.45)^{z}	*Year* $F_{2,12} = 3.219$		
	L	2.75 (1.07)	3.08 (1.09)	4.75 (1.49)	5.00 (1.53)^{b}	3.58 (1.18)^{z}	*Fire x Year* $F_{4,12} = 2.779$		

Table 3.7 (cont.)

Species		1997	1998	1999	2000	2001	1999-2001 ANOVA	2000 ANCOVA	2001 ANCOVA
Non-grass monocots	C	7.42 (1.5)	26.92 (2.17)	14.83 (1.81)	21.33 (2.59) ^{a}	23.83 (1.53) ^{z}	*Fire* $F_{2,6} = 0.216$	*log, pooled* $F_{2,6} = 0.110$	*log* $F_{2,6} = 0.848$
	E	8.75 (1.81)	22.25 (2.75)	18.92 (1.25)	22.83 (1.97) ^{a}	20.17 (1.9) ^{z}	*Year* $F_{2,12} = 3.802$		
	L	11.5 (1.47)	29.58 (2.28)	21.58 (2.3)	26.42 (3.69) ^{a}	20.67 (2.37) ^{z}	*Fire x Year* $F_{4,12} = 1.489$		
Commelina spp.	C	2.08 (0.53)	10.50 (1.38)	7.08 (1.31)	7.16 (1.26) ^{a}	7.75 (1.09) ^{z}	*Fire* $F_{2,6} = 0.260$	$F_{2,6} = 0.088$	$F_{2,6} = 0.110$
	E	3.17(0.87)	7.17 (1.66)	9.17 (1.05)	9.08 (1.39) ^{a}	7.58 (0.87) ^{z}	*Year* $F_{2,12} = 1.042$		
	L	4.25 (0.74)	12.25 (0.97)	11.25 (1.69)	8.83 (1.81) ^{a}	7.00 (1.09) ^{z}	*Fire x Year* $F_{4,12} = 0.759$		
Curculigo ensifolia	C	1.83 (0.58)	5.58 (1.27)	1.17 (1.27)	2.83 (0.77) ^{a}	3.33 (0.97) ^{z}	*log* *Fire* $F_{2,6} = 0.391$	*log* $F_{2,6} = 0.507$	*log* $F_{2,6} = 0.204$
	E	2.58 (1.00)	6.33 (1.34)	6.33 (1.34)	3.83 (1.15) ^{a}	2.92 (1.14) ^{z}	*Year* $F_{2,12} = 4.186$		
	L	3.00 (1.01)	7.08 (1.38)	7.08 (1.38)	6.33 (1.47) ^{a}	4.67 (1.42) ^{z}	*Fire x Year* $F_{4,12} = 1.972$		
Eustrephus latifolius	C	2.42 (0.89)	1.83 (0.66)	2.33 (0.68)	2.17 (0.68) ^{a}	2.25 (0.73) ^{z}	*pooled* *Fire* $F_{2,6} = 0.640$	*pooled* $F_{2,6} = 1.963$	*pooled* $F_{2,6} = 0.507$
	E	1.67 (0.81)	1.50 (0.79)	1.67 (0.72)	2.75 (0.99) ^{a}	1.83 (0.69) ^{z}	*Year* $F_{2,12} = 3.726$		
	L	3.42 (1.10)	2.50 (0.73)	3.75 (1.05)	3.58 (0.99) ^{a}	2.42 (0.79) ^{z}	*Fire x Year* $F_{4,12} = 2.927$		
Scleria mackaviensis	C	0.75 (0.39)	7.58 (1.06)	2.75 (0.85)	7.42 (0.85) ^{a}	9.17 (0.78) ^{z}	*pooled* *Fire* $F_{2,6} = 1.397$	$F_{2,6} = 2.685$	*pooled* $F_{2,6} = 3.733$
	E	0.92 (0.34)	5.92 (1.10)	3.83 (0.90)	4.92 (0.84) ^{a}	5.83 (1.15) ^{z}	*Year* $F_{2,12} = 27.056^{**}$		
	L	0.58 (0.23)	6.33 (1.08)	2.75 (0.64)	7.08 (1.01) ^{a}	6.17 (0.98) ^{z}	*Fire x Year* $F_{4,12} = 3.60$		

3.4 Discussion

3.4.1 Fuel load dynamics

Fine-fuel in eucalypt savanna at Cape Cleveland accumulated rapidly after fire, reaching approximately half the maximum biomass over the first wet season, and stabilising after two years, at approximately ten tonnes per hectare (Figure 3.3). Fuel loads of around six tonnes per hectare, recorded one year after fire, are similar, or slightly higher than those documented in annually burnt savannas in the Northern Territory (Williams *et al*. 1999*b*; Russell-Smith *et al*. in press). While this study only sampled fuel to four years post-fire, 10 tonnes per hectare is probably the maximum for this savanna, as it is the maximum fuel load recorded in eucalypt savannas of the Northern Territory that have remained unburnt for 21 years (Russell-Smith *et al*. in press), and in "long unburnt" savanna on Magnetic Island, off the coast from Townsville (Sandercoe 1989).

3.4.2 Fire intensity

After two years without fire, burning during the late dry season produced significantly higher fire intensities than in the early dry season (Figure 3.5). The late dry season fires were also of greater intensity than the single mid dry season fire implemented after a three year interval. The fire intensities recorded at Cape Cleveland are within the range recorded in other Australian tropical savanna studies (Williams *et al*. 1999*b*; Russell-Smith *et al*. in press). However annual late dry season fires in eucalypt savanna at Kapalga research station, in the Northern Territory, were greater than those recorded after a two year interval at Cape Cleveland (Williams *et al*. 1999*b*). A late dry season fire after a seven year interval was considerably more intense again (Williams *et al*. 1999*b*).

Given that maximum fine fuel biomass is reached after two years in savanna at Cape Cleveland, the season of burning will have a greater influence on fire intensity than the number of years since last fire, once two years has elapsed. This has implications for hazard reduction maintenance in north-eastern Australia.

3.4.3 Multivariate analyses of species composition and abundance

The cluster analyses, of species composition alone and composition plus abundance data, clustered together many of the annual surveys of the same plots, with clusters primarily reflecting differences in the 36 plots (Figures 3.6 and 3.7). However, the fact that there was separation of annual surveys for some plots indicates some floristic changes occurred during the course of the study, and increased species variation was detected once species abundance was included in the analysis. Thus the cluster analyses suggest that much of the pre-existing species variation between plots was not dramatically altered by the fire treatments, however some floristic changes were apparent. This indicates fire has an influence on floristic patterns but that a strong degree of stability in composition is displayed in response to dry season fires over five years and fire protection for four years.

The fact that the PCA scatter plot did not position together all surveys of any fire treatments confirms the cluster analyses result that pre-existing plot differences were not overturned by fire regimes (Figure 3.8). However, the PCA scatter plot documents distinct floristic patterns which fluctuate both annually and in response to fire regimes (Figures 3.8 and 3.9). They indicate floristic response to the mid dry season 1997 fire was consistent across plots, and differed only after the implementation of different fire season treatments in 1999. It is noteworthy that the scatter plots show that species composition and abundance did not return to that of the initial 1997 surveys. This may in part be a response to a general increase in the abundance of exotic and to some degree native species over the duration of the study, which was consistent across all treatments (Table 3.7).

The partial RDA demonstrated fire variables were significantly correlated with floristic variation, although after the removal of background effects of intrinsic plot variation, annual fluctuations consistent to all treatments, and differences between blocks, fire variables accounted for only a small percentage of species variance (Tables 3.2 and 3.4). All aspects of the fire regime proved important, with fire interval, intensity and season each affecting species dynamics (Tables 3.3 and 3.5).

The factor with the greatest correlation with floristic variance between the surveys was the intrinsic differences between the 36 plots (Tables 3.2 and 3.4). That is, pre-existing plot differences, and subtle changes within each plot that were irrespective of fire, accounted for species variation between surveys to a greater extent than the fire treatments. The large interaction between fire, plot and year suggests that considerable floristic changes did occur after fire that were dependent on existing species composition within plots, and annual conditions such as rainfall. This may have resulted from increases in the abundance of existing species in response to fire. The partial RDA results confirm a strong degree of stability in species composition and abundance in response to several dry season fires and fire protection for four years, but also provides evidence that fire was responsible for floristic patterns, particularly by interacting with or enhancing existing plot variation.

The importance of intrinsic plot variation re-enforces the value of repeat surveys of permanently marked plots and BACI designs in understanding fire dynamics in tropical savannas (Lonsdale and Braithwaite 1991). It is apparent that the use of one-off surveys in this savanna to distinguish short-term fire history effects, such as differences in season of the most recent fires, would inadvertently mix the effect of recent fire with pre-existing plot differences. Species variation between plots may be due to a complex interaction between edaphic, climatic and topographic factors (Fensham 1990) as well as biotic factors, including short distances of seed dispersal (Whelan 1985) and the persistence of established plants (Bond and Midgley 2001).

3.4.4 Univariate analyses of species richness and abundance

Late dry season fires increased species richness at the 1 m^2 scale in the year following fire, but as there was no corresponding effect at the 100 m^2 scale, this probably reflects an increase in the density, rather than number of species in the savanna (Whelan 1995). The documented species richness of 30 to 40 species 100 m^{-2} is similar to that of eucalypt savanna in the Northern Territory (Fensham 1990). However, Fensham (1990) was able to detect significantly lower species richness at the 100 m^2 scale in plots unburnt for ten years, compared with regularly and irregularly burnt savanna. Assessment of longer fire intervals than examined in this study may detect a similar decline in species richness in the absence of fire in savannas of north-eastern Australia.

A significant response to dry season fires was not detected in several of the growth form groups and common species, over the five year experiment (Table 3.7). This was apparent for trees and shrubs, upright perennial forbs, and non-grass monocots, and reflects the floristic stability documented in the multivariate analyses. However, burning did enhance several other common species and growth form groups in the year immediately following fire (Table 3.7). This was apparent for the subshrub *Breynia oblongifolia*, combined twining perennial forbs, the common twiners *Galactia tenuiflora* and *Passiflora foetida*, combined ephemeral forbs, *Indigofera hirsuta*, and grasses as a group. Late dry season fire typically produced the greatest change in abundance, although for *Galactia tenuiflora*, the highest abundance was produced under early dry season burning. The increase in species abundance in the first year after fire corresponds with the period of lowest fuel load, suggesting a competitive inhibition by dense ground cover. While most fire effects were undetectable by the second year after fire, *Passiflora foetida* maintained a higher abundance in recently burnt plots and the dominant grass, *Heteropogon triticeus*, significantly declined with the absence of fire for four years.

3.4.5 Study Constraints

As with all research, these results must be considered within the study limitations. This experiment was restricted to replicate blocks of 1 ha. While this provided a manageable size for the limited resources available for implementing the study, there may be problems with these relatively small experimental units. For example, it has been argued that 1 ha blocks may not provide the full potential fire intensity, nor the patchiness, produced by a larger landscape fire (Russell-Smith *et al.* in press). While the lack of patchiness in burnt and unburnt ground is certain, fire intensity may not have been significantly reduced, as recent research indicates fire fronts of 120 m or greater (as present in this trial of 130 m long blocks) reach their maximum potential rate of spread, and hence potential intensity, almost immediately (Cheney *et al.* 2001).

Small fire block sizes may also lead to concentrated herbivory in recently burnt ground (Whelan 1995). While no cattle were within the trial area during the study, native herbivores, specifically Agile wallabies (*Macropus agilis*), were present throughout the five years. However, the intensity of herbivory after the July 1997 fire was probably minimised by the 10 ha extent of the fire. In August 1999, a wildfire burnt the surrounding savanna, hence greatly increasing the area of recently burnt ground soon after the first 1999 fires and prior to any seedling emergence in the early burnt blocks (Chapter 6).

The restriction of the experiment to a single 10 ha section of savanna may limit extrapolation of results. However, comparisons with other Australian tropical savanna studies allow some evaluation of the broader applicability of results. Data on regeneration after fire from additional sites around Townsville are also provided in Chapters 6 and 8 to examine the consistency of fire response across the Townsville region.

Only a few combinations of fire frequency, intensity and season were assessed in this experiment, and differing results may occur with other regimes. However, the assessment of fire intervals from two to four years, with burning undertaken at differing times throughout the dry season, is relevant to the current fire regimes experienced in tropical savannas of north-eastern Australia (Crowley 1995; Queensland Parks and Wildlife Service unpublished fire history records for Townsville).

The short time span of this study (five years) may also limit the ability to establish fire effects. However, the fire response of herbaceous species, detected over 21 years in eucalypt savanna at Munmarlary, Northern Territory, were generally evident within the initial five years (Russell-Smith *et al*. in press).

3.5 Conclusion

Fine fuel loads in eucalypt savanna at Cape Cleveland reach an equilibrium of approximately ten tonnes per hectare in the second year after fire. While data are only available for four years post-fire, evidence from other sites in tropical eucalypt savanna suggest fuel loads can remain in equilibrium at ten tonnes per hectare for several decades in the absence of fire. This indicates that by the second year after fire, fire season, rather than time since fire, governs fire intensity, with highest intensity during late dry season burns.

It is apparent that the eucalypt savanna of Cape Cleveland has a high degree of floristic stability in the response to one or two dry season fires over a period of five years and fire protection for four years. Intrinsic plot differences were of greater importance in explaining floristic variation than recent fire history. However, floristic patterns were influenced by fire regime, and the interaction between fire, plot and year increased existing plot variation. The effects of fire regime were most evident in the herbaceous layer, particularly in promoting ephemeral and twining perennial forbs and grasses. The only trends identified in the abundance of woody species was the short-term promotion of the subshrub *Breynia oblongifolia* by late dry season fire.

Both the interval between fires and the fire events themselves affected floristic composition and abundance. An initial flush of abundance of combined twining perennial forbs, the common twiners *Galactia tenuiflora* and *Passiflora foetida*, combined ephemeral forbs, the common ephemeral *Indigofera hirsuta*, and grasses as a group, occurred in the year following fire. With the except of *Galactia tenuiflora*, the flush of abundance was especially apparent after late dry season fires. Many herbaceous species may store carbon reserves, enhance seed production and recruit seedlings in the immediate post-fire period. The decline in the dominant grass *Heteropogon triticeus* with fire intervals of four years reduces competition faced by co-existing species, although the maintenance of high fuel loads at four years post-fire indicates the decline in biomass of *H. triticeus* is replaced by the increase in biomass of other species.

The failure to detect effects of fire on trees and shrubs may have been due to the use of frequency rather than density counts (although see Chapter 8). Changes in the overall abundance of woody species in Australian tropical savannas are less common than dynamics of size classes, although significant differences in the overall density of non-eucalypt trees and shrubs, and *Eucalyptus tetrodonta* and *E. porrecta* have been detected between frequently burnt and long unburnt savanna (Bowman and Panton 1995; Russell-Smith *et al.* in press; Williams *et al.* in press).

The lack of short-term fire effects detected for rainforest trees and shrubs is consistent with the results of other studies in Australian tropical savanna (Bowman *et al.* 1988;

Fensham 1990; Bowman 1993; Bowman and Panton 1995; Russell-Smith *et al.* in press; Williams *et al.* in press). The assessment of fire effects on different life events, such as seedling emergence and survival, and growth rates of juvenile trees, is needed to shed further light onto the influence of fire regime on this group.

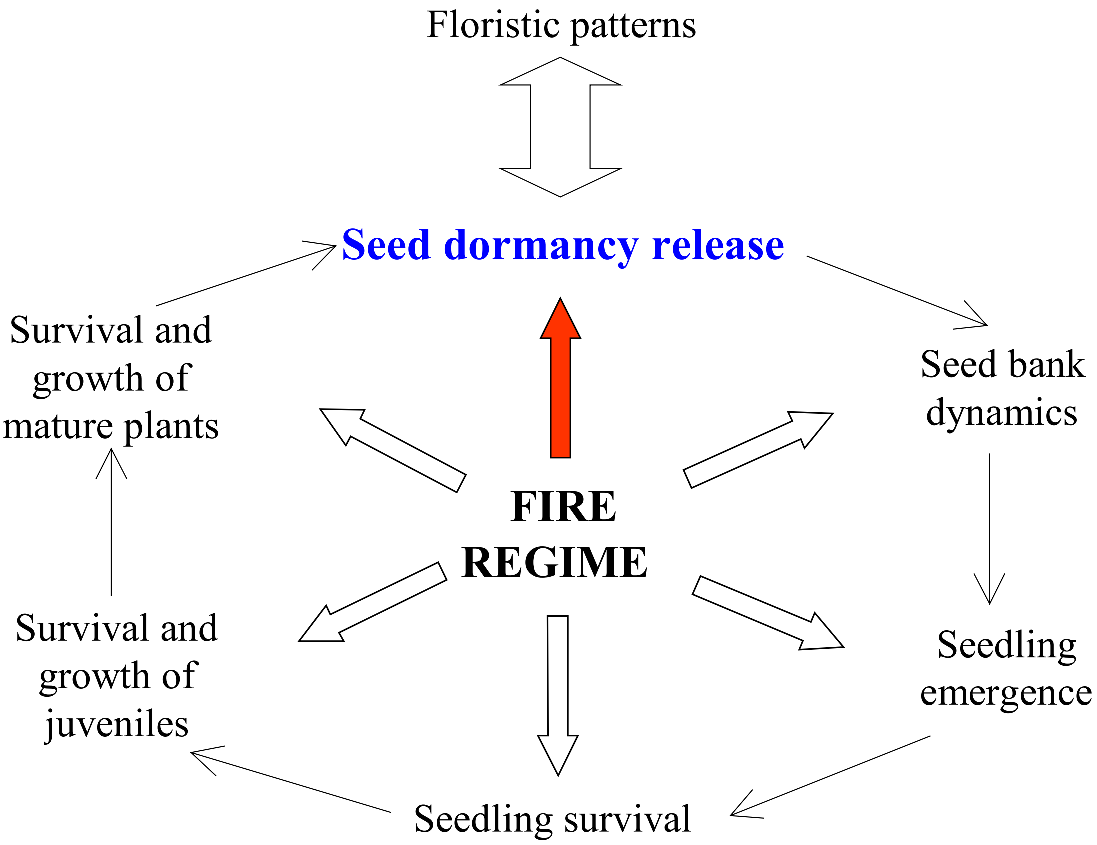
A variety of responses to fire regime have been documented for herbaceous species in Australian tropical savannas (e.g. Bowman *et al.* 1988; Fensham 1990; Williams and Lane 1999). However, the significant effect of fire on both species richness and the abundance of herbaceous species contrasts with the findings of Williams *et al.* (in press) who did not detect clear fire effects on grasses and forbs during a five year experiment in eucalypt savanna at the Kapalga research station in the Northern Territory. Neither the abundance of herbs nor species richness responded to fire regime at Kapalga, but responded instead to fluctuations in wet season rainfall and the cover of annual *Sorghum* species. The cause of these differences between Kapalga and Cape Cleveland may in part lie in the high proportion of dry season dormant forbs and the dominance of annual grasses at Kapalga, which show strong germination and growth responses to the intense wet and dry seasons of the Northern Territory (Brennan 1996; Williams *et al.* in press).

Frequent fires over two decades have been shown to promote the dominance of a few annual grasses in eucalypt savanna of the Northern Territory (Russell-Smith *et al.* in press). An increased abundance of perennial grasses has also been documented in recently or frequently burnt tropical savanna (e.g. Shaw 1957; Norman 1963; Sandercoe 1989; Walker *et al.* 1989; Orr *et al.* 1991; Trollope 1996). While much attention has been given to *Heteropogon contortus*, less research has examined the larger *H. triticeus*. It has been found at greatest abundance in frequently or most recently burnt plots (Sandercoe 1989; Fensham 1990). However, *H. triticeus* has also increased simultaneously in annually burnt and unburnt savanna of the Northern Territory (Russell-Smith *et al.* in press), and has been documented at reduced abundance in recently burnt plots on Cape York Peninsula (Crowley and Garnett 1998). Differences in response may result from edaphic, climatic and biotic factors, including competitive interactions, and the examination of life events is crucial to resolving the reasons of these differences.

Forbs have been found to respond variously to fire regime (Bowman *et al*. 1988; Fensham 1990). Some forbs, such as the leguminous *Crotalaria* spp. are more abundant in frequently burnt savanna, while the ephemeral *Polygala orbicularis* has shown contrasting responses to fire frequency (Bowman *et al*. 1988; Fensham 1990). Fire-enhanced short-term pulses of forb abundance have also been documented in sandstone heathy communities of the Northern Territory and north-western Queensland (Russell-Smith *et al*. 2002; Williams *et al*. 2002*b*).

Fire regime therefore was found to influence floristic patterns by affecting the abundance of herbaceous species. However, details of the fire-related mechanisms that determine floristic patterns are required to better understand the effects of fire regimes. The remainder of this thesis systematically examines the effect of fire on critical life events on a range of coexisting savanna species, to provide an insight into the processes that allow fire to influence floristic patterns.

Chapter 4. The effect of regime fire on seed dormancy release in Australian tropical savanna species.



4.1 Introduction

Seed dormancy is a critical mechanism that can increase the chances of seedling establishment by delaying germination until the presence of appropriate climatic and micro-site conditions, and spreading the germination of a seed bank across several rainfall events (Harper 1977; Bell 1999). Some Australian tropical savanna species possess no apparent innate dormancy, being capable of germination immediately after seed fall. Examples of these include *Eucalyptus miniata* and *Alloteropsis semialata* (Setterfield 1997; Crowley and Garnett 2001). The seeds of many grasses possess an after-ripening requirement in the seed embryo that lapses during the dry season, linking germination with the onset of the wet season (Bell 1999). This has been detected in both annual and perennial grasses, including *Chrysopogon fallax*, *Heteropogon contortus*, *Sorghum* spp. and *Themeda triandra* (Mott 1978; Andrew and Mott 1983; Mott and Andrew 1985; McIvor and Howden 2000).

There has been limited research into fire-related dormancy mechanisms in Australian tropical savanna species. Fire-related chemicals that have been found to break seed dormancy include nitrates, the availability of which can increase in the soil with the first rain following fire (Thanos and Rundel 1995; Bell *et al.* 1999), as well as compounds present in smoke (Dixon *et al.* 1995; Keith 1997) and charcoal (Bell *et al.* 1987). Smoke has been demonstrated to break seed dormancy of the tropical savanna grasses *Heteropogon contortus* and *Themeda triandra*, and the fire sensitive tree *Callitris intratropica* (Baxter *et al.* 1994; Campbell *et al.* 1996; Roche *et al.* 1997).

The brief exposure of seeds to elevated temperatures is known as “heat shock” (Bell *et al.* 1993). Heat shock typically breaks a physical barrier in the seed coat that inhibits moisture uptake by the seed (Bell 1999). This can result from either the cracking of the cuticular layer or opening of a strophiolar plug in the seed coat (Figure 4.1; Bell *et al.* 1993). Heat shock may also influence physiological processes within the embryo (Bell and Williams 1998). High soil surface temperatures experienced in the late dry season (30ºC to 60ºC) can increase seed germination of some tropical savanna grasses (Mott 1978). Exposure to elevated temperatures between 40ºC to 120ºC break innate seed

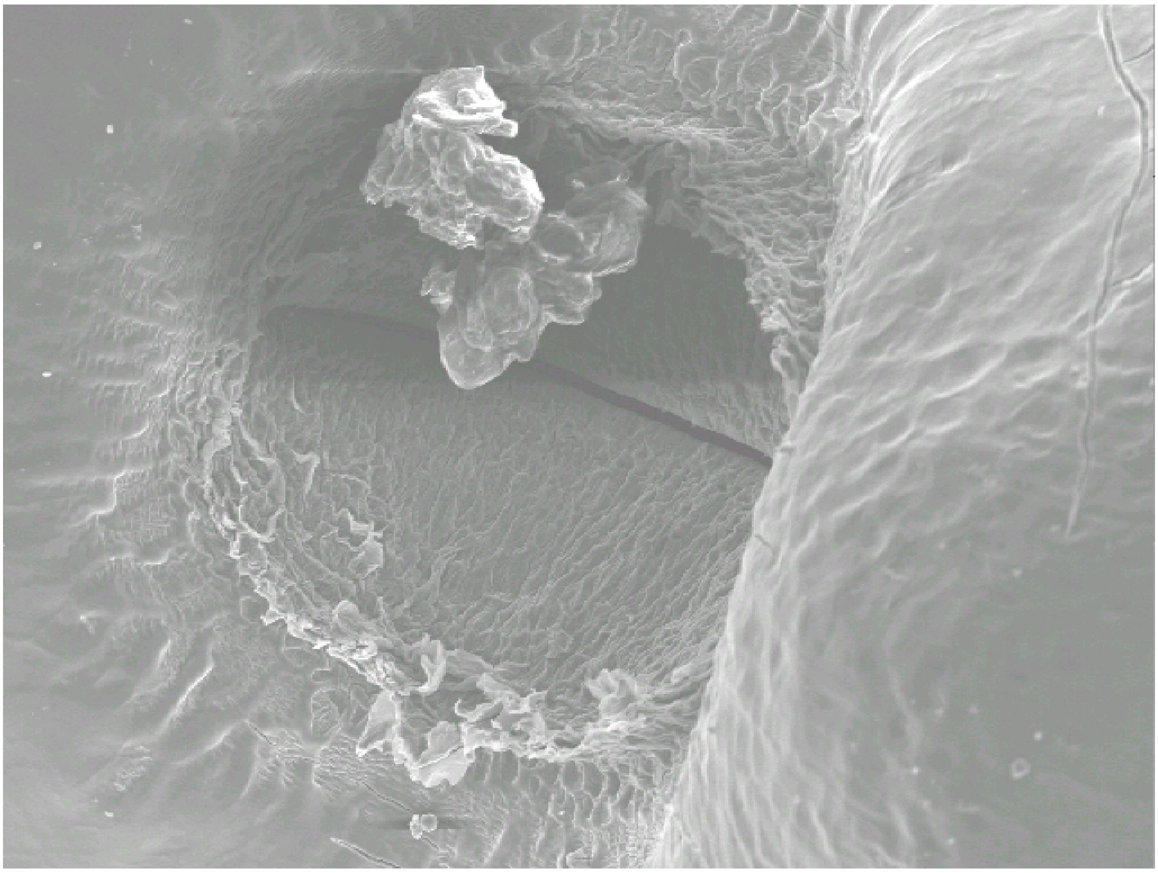


Figure 4.1. Scanning electron microscope image of the strophiolar plug, magnified 350 times, of an untreated *Crotalaria montana* seed. The strophiolar plug inhibits water uptake and is broken by exposure to heat shock. *C. montana* is a leguminous ephemeral forb, native to Townsville eucalypt savannas. Image produced by Adam Felton, James Cook University.

Dormancy in many species of south-eastern and south-western Australia, although exposure to 120ºC beyond one minute duration can kill seeds (Shea *et al*. 1979; Auld and O'Connell 1991). Arid zone shrubs *Acacia aneura* and *Senna nemophila*, which extend into tropical savannas, show increased germination after brief exposure to temperatures between 40ºC and 70ºC (Hodgkinson and Oxley 1990).

A direct relationship has been shown between heat penetration into the topsoil during the passage of fire and the depth of germination of temperate species (Bradstock and Auld 1995; Auld and Tozer 1999). Heat penetration into the topsoil varies between fires, with soil characteristics and the quantity of fine ground fuel consumed during fire

(Bradstock and Auld 1995; Whelan 1995). During fires that consume sufficient fine fuel, seeds in the top few centimetres of soil can be exposed to temperatures that break seed dormancy in legumes of southern Australia (Floyd 1976; Bradstock and Auld 1995; Smith *et al*. 2000).

This chapter examines the role of fire in breaking innate seed dormancy in species of Townsville eucalypt savannas. To date, research into the effects of fire on seed germination in Australian tropical savannas has focused primarily of dominant grasses (e.g. Andrew and Mott 1983; Mott and Andrew 1985; Campbell *et al*. 1996; McIvor and Howden 2000). Ten legume species were selected for investigation in this study, because legumes as group account for 20% of the species diversity at Cape Cleveland, representing both twining perennial forbs and ephemeral forbs, and several of the test species increased in abundance after fire, which suggests fire-driven release from seed dormancy (Chapter 3). Questions to be addressed in this chapter include:

1. Is the percentage germination of legumes in Australian tropical savannas increased by exposure to heat shock?
2. Is the percentage germination of legumes increased by exposure to chemicals related to the passage of fire, specifically nitrate and compounds found in smoke?
3. Is the percentage germination of legumes enhanced by exposure to heat shock and chemicals?
4. If heat shock does increase germination, do those temperatures occur in the topsoil during the passage of early and late dry season fires?
5. Does the depth of seed germination, of species with seed dormancy released by heat shock, increase with greater heat penetration into the topsoil?

4.2 Methods

4.2.1 General methods

4.2.1a Laboratory experiment

The ten species examined in the laboratory experiment are listed in Table 4.1. Seeds were collected between March and June 1999, from a wide variety of plants along the roadside fire break block and adjacent areas at Cape Cleveland (Figure 2.4). Seeds were not collected from within the nine, 1 ha blocks, so that seed bank and seedling

emergence processes remained unaffected. Seeds were stored in paper bags in the dark at room temperature, for several months prior to the germination experiment.
An initial pilot study was used to assess an appropriate incubation temperature for the laboratory experiment. Three species were examined in this pilot trial: *Chamaecrista mimosoides*, *Crotalaria lanceolata* and *C. pallida*. Three replicates of 30 seeds were exposed to 80ºC for five minutes before placement onto filter paper in petri dishes and storage in germination cabinets in total darkness. This temperature and exposure time were used because they have been shown to enhance germination of a range Australian legumes (e.g. Shea *et al*. 1979; Auld and O'Connell 1991). Constant incubation temperatures assessed were 17.5ºC, 25ºC, 30ºC and 40ºC. The germination cabinet set at 40ºC was found to be defective and therefore germination from this treatment is not reported. Despite the use of fungicide, fungal attack of seeds occurred and may have reduced the percentage of seed germination.

No significant differences could be detected between percentage germination across the three incubation temperatures, using a one-factor ANOVA, for *Chamaecrista mimosoides* ($F_{2,6} = 0.341$, $P > 0.05$); *Crotalaria lanceolata* ($F_{2,6} = 1.113$, $P > 0.05$) or *Crotalaria pallida* ($F_{2,6} = 3.23$, $P > 0.05$). The overall percentage germination of two of the species was low and the mean percentage germination of *Chamaecrista mimosoides* and *Crotalaria pallida* was highest at 25ºC, while 30ºC produced the highest percentage germination of *C. lanceolata* (Figure 4.2). This suggested an incubation temperature between 25ºC and 30ºC would be suitable for use in the laboratory experiment and is consistent with the results of Andrew and Mott's (1983) study that demonstrated incubation temperatures between 25ºC and 35ºC were most appropriate for germination of Northern Territory grasses.

The laboratory experiment was undertaken on ten herbaceous legume species between September and December 1999. Three replicates of 30 seeds were used for each treatment, and seed weights were determined for each species by weighing three replicates of thirty seeds. Up to 11 different treatments were used to examine seed dormancy (Table 4.1). A subset of treatments were implemented for several species where seed availability was limited. The five minute duration for most oven treatments was used because it is a realistic residence time for the peak elevated temperatures in the topsoil during the passage of fire (Bradstock and Auld 1995; Smith *et al*. 2000).

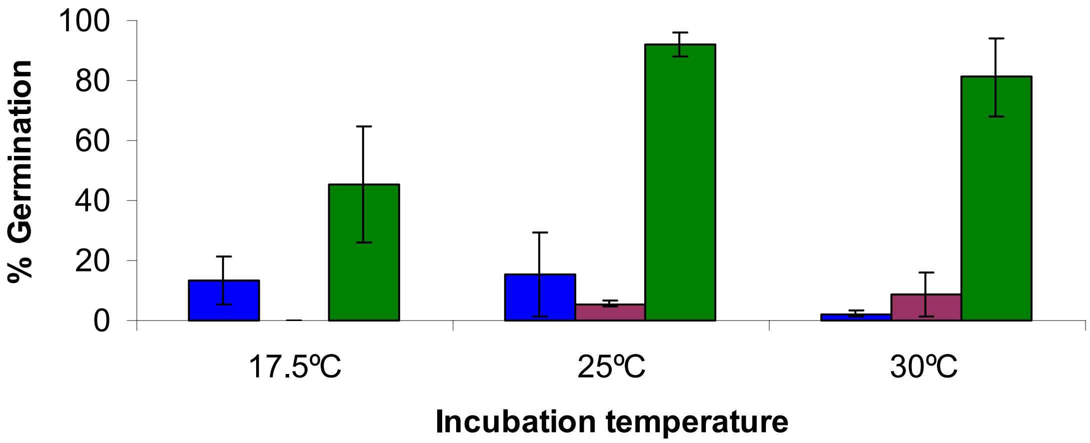


Figure 4.2. Mean (± 1 standard error) percentage seed germination at different incubation temperatures during the pilot trial for *Chamaecrista mimosoides* (🟦); *Crotalaria lanceolata* (🟪); and *Crotalaria pallida* (🟩). Seeds were exposed to 80°C for 5 minutes prior to placement in incubation cabinets.

The 45 minute duration at 85ºC was used as an assessment of the treatment used in the soil seed bank study, which required extended duration of heating to allow heat penetration into soil samples (Chapter 5). Ovens were pre-heated to the appropriate temperatures, which were monitored with a thermometer. The three replicates for each treatment were exposed to the oven temperatures separately, with oven temperatures altered between treatments to allow appropriate replication (Morrison and Morris 2000).

The smoke treatment followed the method described in Dixon *et al.* (1995). Smoke was produced in a 20 L metal drum filled with smouldering grass and litter collected from the Cape Cleveland site. The smoke was pumped through a 3 m length of flexible metal tubing which allowed the cooling of smoke prior to entry into a plastic tent, in which seeds were placed (Figure 4.3). Smoke was pumped into the tent for 90 min before seeds were removed for incubation in the laboratory. The smoke treatment, and that of the nitrate treatment described below, were applied simultaneously to all pertinent replicates, although it is acknowledged that three separate applications would have produced a more appropriate replication of these treatments (Morrison and Morris 2000).

Figure 4.3. Apparatus used to produce smoke at ambient temperature. Smoke was produced within the drum and pumped through the metal pipe into the tent, in which seeds were exposed to the smoke.

An assessment was also made of multiple cues by examining the interactions between exposure to chemicals and heat shock. In these two treatments, seeds were exposed to 80ºC for five minutes prior to exposure to smoke, or watering with nitrate solution.

After exposure to heat shock and smoke treatments, all seeds were placed onto filter paper in petri dishes, sprayed with a 2g L $^{-1}$ solution of fungicide (Thiram ®) and watered with 5 mL of distilled water. Replicates subjected to the nitrate treatment were watered with 5 mL of a 1g L $^{-1}$ solution of potassium nitrate, rather than distilled water, which has been found to promote germination of Western Australian species (Bell *et al*. 1999). All petri dishes were placed randomly within a controlled temperature room set at 27.5ºC with a 12 h diurnal light regime. The diurnal light regime was used because the low germination of *Chamaecrista mimisoides* and *Crotalaria lanceolata* in the pilot trial may have been partially due to incubation in total darkness. A 12 h diurnal light regime has been shown to significantly enhance germination of many eucalypt woodland species in south-eastern Australia (Clarke *et al*. 2000). Germination was defined by radicle emergence, and germinants were removed. Petri dishes were sprayed with distilled water as required, and periodically with fungicide.

Germination was assessed daily for 12 weeks. At the end of this period, all ungerminated seeds in the control treatment were assessed for viability using a tetrazolium test (Moore 1985). A slit was made in seeds which were subsequently soaked in a 1% tetrazolium solution in the dark for 48 h. Seeds were then dissected under a microscope and assessed for the pink colouration that indicates a viable embryo. The number of viable seeds detected in the tetrazolium test were added to the number of germinants to give a total number of viable seeds for each replicate of the control treatment and the means were used as the percentage viability for each species. A tetrazolium test was also performed on *Crotalaria pallida* seeds exposed to 120ºC, to assess whether the absence of germination after exposure to this temperature was due to seed mortality.

4.2.1b Temperature elevation in the topsoil during the passage of fire

Temperature elevation in the topsoil during the passage of early and late dry season fires was documented as a comparison with the temperatures found to break seed dormancy in the laboratory experiment. Topsoil temperatures were measured at ten locations in each of the three replicate 1 ha blocks burnt during the early and late dry season fires of 1999 (Chapter 2). To allow ease of re-location, each point was randomly located adjacent to one of the four corners of the four 100 m^2 plots described in Chapter 3. To assess the micro-site variation in temperatures between grass tussocks and gaps, five of the ten points were located at the base of a grass tussock. The remaining five per block were located in a gap with at least 30 cm to the nearest grass tussock.

Topsoil temperatures during the passage of fire were measured using Thermax ® temperature strips. These strips contain segments that turn black when a designated temperature is reached. The strips recorded temperatures ranging from 37ºC to 182ºC, providing increments of 3ºC to 5ºC. Strips were placed at four depths at each of the temperature measurement points (surface, 3 mm, 10 mm and 30 mm). To ensure as little disturbance to the topsoil as possible, a small hole with a vertical wall was dug at each point. A knife was used to slit gaps at 10 mm and 30 mm in the wall, parallel to the soil surface. The temperature strips were pushed into gaps and the hole re-filled (Figure 4.4). The temperature at 3 mm was documented directly above the 10 mm and 30 mm measurements, by scraping away approximately 3 mm of topsoil which was then replaced over the top of the temperature strips. The soil surface measurement was made by placing strips on the soil surface, adjacent to the strips at 3 mm, and replacing leaf litter over the top.

Figure 4.4. Placement of a temperature measurement strip at the 30 mm depth.

Table 4.1. Species and treatments examined in the laboratory experiment of fire-related seed dormancy mechanisms. "✓" indicates species exposed to specific treatments: Control, no pre-treatment; S, exposure to ambient temperature smoke for 90 minutes; N, initially watered with 5 ml 1g L $^{-1}$ potassium nitrate solution; 40ºC 5 min, exposure in oven at 40ºC for five minutes; 80ºC W 5 min, exposure to 80ºC water for five minutes; *, exotic species.

Species	Control	S	N	40ºC 5 min	60ºC 5 min	80ºC 5 min	80ºC W 5 min	85ºC 45 min	100ºC 5 min	120ºC 5 min	S + 80ºC 5 min	N + 80ºC 5 min
*Chamaecrista absus**	✓	✓		✓	✓	✓			✓			
Chamaecrista mimoisoides	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Crotalaria calycina	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
*Crotalaria lanceolata**	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Crotalaria montana	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
*Crotalaria pallida**	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Galactia tenuiflora	✓	✓		✓	✓	✓			✓	✓		
Glycine tomentella	✓	✓		✓	✓	✓						
Indigofera hirsuta	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Tephrosia juncea	✓	✓		✓	✓	✓		✓	✓	✓		

4.2.1c Depth of seed germination

The depth of seed germination was assessed in relation to the temperatures recorded during the passage of fires, for two of the species examined in the laboratory experiment. *Galactia tenuiflora* and *Indigofera hirsuta* were examined because they produced sufficient germination in the vicinity of temperature measurement points. The depth of germination was measured by digging around recently germinated seedlings, in early December 1999. The depth of germination was measured to the junction between radicle and hypocotyl (Bradstock and Auld 1995). The two locations with the highest, and two with the lowest, temperatures in each of the early and late dry season fires (i.e. a total of four points in each) were assessed to cover the range of temperatures experienced during the fires. All seedlings within a 1 m radius of these points were assessed. There was almost no germination of these species in the unburnt control blocks, precluding the assessment of seed germination depth in undisturbed savanna. Therefore seedlings over a 30 m stretch of the 4 m wide unburnt but slashed fire line between blocks C1 and C2 (Figure 2.4) were measured as a comparison to germination depth in the early and late burnt blocks, although it is acknowledged that the removal of the grass layer is likely to have elevated the temperatures of the topsoil to some degree (Auld and Bradstock 1996).

4.2.2 Statistical analyses

4.2.2a Laboratory experiment

The number of germinants for each treatment was converted to percentage germination of viable seeds. This was calculated for each replicate by dividing the number of germinants by the mean number of viable seeds and multiplying by 100. A one-factor ANOVA was used to assess the effects of differences among all treatments, excluding those combining exposure to smoke (or nitrate) plus 80ºC. The latter were analysed with the control, and separate smoke (or nitrate) and 80ºC treatments, in a two-factor ANOVA, which assessed the factors smoke (or nitrate) and exposure to 80ºC. Scheffe's *post-hoc* test was used to determine significant differences between treatments of the one-factor ANOVA (Underwood 1997). Cochran's test was used to assess homogeneity of variance. *Glycine tomentella* germination data required arcsine transformation. Variance heterogeneity for the two-factor ANOVA for *Crotalaria montana* could not be resolved by transformations. Therefore separate non-parametric Kruskal-Wallis

ANOVA by ranks were performed for the individual factors nitrate and 80º C (Zar 1999).

The proportion of non-dormant seed, approximated by the percentage germination of seeds in control treatments, of the three exotic species (identified in Table 4.1) was contrasted with that of the seven native species. A Mann-Whitney *U*-test was used to test the significance of this comparison, as the homogeneity of variance assumptions of a *t*-test (Zar 1999) were not met, even after data transformations.

4.2.2b Temperature elevation in the topsoil during the passage of fire

Temperature elevation in the topsoil was compared between early and late dry season fires. A multivariate analysis of variance (MANOVA) was initially attempted, however the assumption of homogeneity of variances could not be met, even after data transformations. Therefore, the comparison in temperatures between early and late dry season fires were assessed using separate non-parametric Mann-Whitney *U*-tests at each of the four soil depths (surface, 3 mm, 10 mm and 30 mm). The Bonferroni method of adjustment of alpha was made to compensate for the multiple comparisons by the *U*-tests (Sokal and Rohlf 1995). Mann-Whitney *U*-tests, with a Bonferroni adjustment for multiple comparisons, were also used to compare the elevated temperatures recorded at the base of grass tussocks with that in gaps, separately for the early and late burnt sites.

A non-parametric Spearman rank correlation was used to determine the relationship between temperature and soil depth, for both early and late dry season fires. Where elevated temperatures were not detected (e.g. at 30 mm depths), the ambient temperature recorded on the day of each fire (Chapter 2) was used in the analysis.

4.2.2c Depth of seed germination

The relationship between the depth of seed germination of *Galactia tenuiflora* and *Indigofera hirsuta* and temperatures recorded in the topsoil was examined using a Spearman rank correlation. Ambient temperatures were used where elevated temperatures were not detected, including along the slashed fire break, although it is acknowledged that this may underestimate the temperature at the soil surface, which may have been elevated as a result of the removal of the grass layer. Differences in the depth of germination between the slashed track, early and late burnt sites were compared using a one-factor ANOVA for both species. Seedling density around the temperature measurement points in the early and late dry season burnt sites was compared using a *t*-test for both species. As seedling assessment along the slashed fire break was not restricted to a precise area, seedling density could not be calculated and therefore the germination along the slashed track was not included in this analysis.

4.3 Results

4.3.1 Laboratory experiment

The mean weights for groups of 30 seeds of each species ranged from 0.433 g to 0.018 g and mean percentage viability ranged from 82 to 100% (Table 4.2).

Table 4.2. Mean (standard error) seed weight, percentage viability and size ranking of each species examined in the laboratory experiment.

Species	Size ranking, heaviest (1) to lightest (10)	Mean (s.e.) weight (g) per 30 seeds (n = 3)	Mean (s.e.) Viability (%)
Chamaecrista absus	1	0.433 (0.008)	95.56 (1.11)
Chamaecrista mimosoides	10	0.018 (0.005)	93.33 (1.93)
Crotalaria calycina	6	0.111 (0.002)	97.78 (2.22)
Crotalaria lanceolata	7	0.079 (0.002)	98.89 (1.11)
Crotalaria montana	9	0.051 (0.001)	90.00 (3.33)
Crotalaria pallida	3	0.159 (0.005)	95.56 (2.94)
Galactia tenuiflora	2	0.298 (0.021)	100.00 (0.00)
Glycine tomentella	4	0.118 (0.003)	94.45 (2.22)
Indigofera hirsuta	8	0.070 (0.003)	82.22 (9.88)
Tephrosia juncea	5	0.116 (0.002)	92.22 (2.94)

The mean percentage germination of viable seed varied between species, ranging from 98% in *Crotalaria montana* to 20% for *Galactia tenuiflora* (Figure 4.5). Exposure to

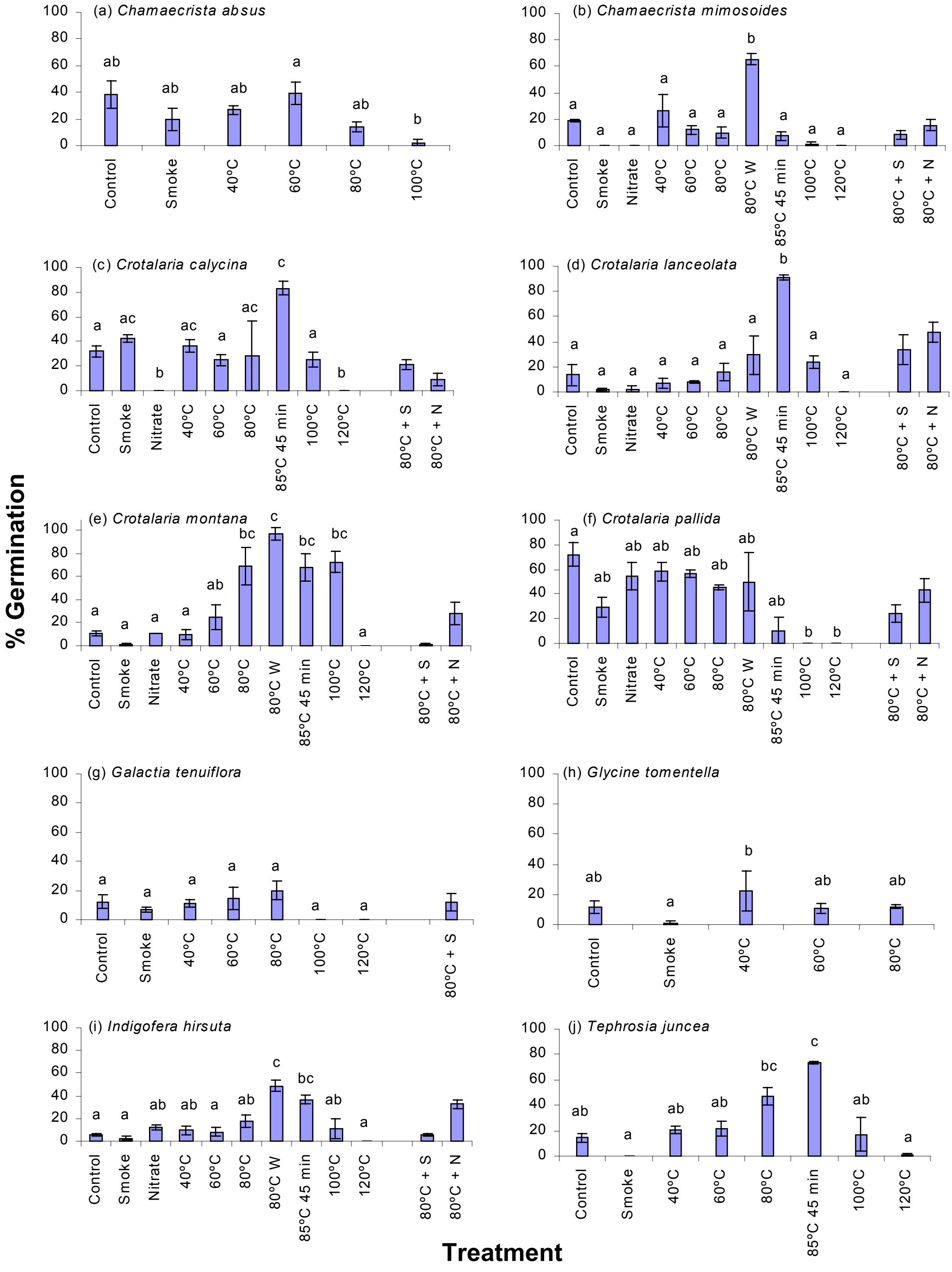


Figure 4.5. Mean (± 1 standard error) percentage germination of viable seed after exposure to various levels of heat shock, as well as smoke and nitrate. Columns in each graph with the same superscript are not significantly different at $P > 0.05$. Germination results from the two-factor ANOVA 80ºC + smoke (or nitrate) are provided without superscripts. All temperature exposures are for 5 minutes, except the 45 minute duration of 85°C 45 min; 80°C W, exposure to 80°C water for 5 minutes.

Table 4.3. Statistical results of one- and two-factor ANOVAs for the laboratory experiment of seed germination. Due to variation in seed supply, two-factor ANOVA were not performed for all species. Non-parametric Kruskal-Wallis ANOVA by ranks was used in place of the two-factor ANOVA for assessing the effect of heat and nitrate for *Crotalaria montana*. $F_{5,12}$ indicates F value, denominator d.f., numerator d.f.; F or H values without an asterisk (*) are not significantly different at $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Species	One-factor ANOVA	Two-factor ANOVA Heat x Smoke			Two-factor ANOVA Heat x Nitrate		
	Treatment	Heat	Smoke	Heat x Smoke	Heat	Nitrate	Heat x Nitrate
Chamaecrista absus	$F_{5,12} = 4.512$*						
Chamaecrista mimosoides	$F_{9,20} = 19.151$***	$F_{1,8} = 0.182$	$F_{1,8} = 11.636$**	$F_{1,8} = 8.909$*	$F_{1,8} = 956$	$F_{1,8} = 4.481$	$F_{1,8} = 16.333$**
Crotalaria calycina	$F_{8,18} = 62.370$***	$F_{1,8} = 5.188$	$F_{1,8} = 0.1059$	$F_{1,8} = 2.647$	$F_{1,8} = 2.223$	$F_{1,8} = 31.711$***	$F_{1,8} = 3.943$
Crotalaria lanceolata	$F_{9,20} = 13.806$***	$F_{1,8} = 4.433$	$F_{1,8} = 0.177$	$F_{1,8} = 3.330$	$F_{1,8} = 12.082$**	$F_{1,8} = 2.219$	$F_{1,8} = 9.890$*
Crotalaria montana	$F_{9,20} = 19.883$***	$F_{1,8} = 12.149$**	$F_{1,8} = 73.644$***	F = 12.149**	$H_{1,8} = 6.203$*	$H_{1,8} = 6.203$*	
Crotalaria pallida	$F_{9,20} = 6.824$***	$F_{1,8} = 4.796$	$F_{1,8} = 19.901$**	$F_{1,8} = 2.375$	$F_{1,8} = 4.840$	$F_{1,8} = 1.284$	$F_{1,8} = 0.751$
Galactia tenuiflora	$F_{6,14} = 2.757$	$F_{1,8} = 1.734$	$F_{1,8} = 1.735$	$F_{1,8} = 0.048$			
Glycine tomentella	$F_{4,10} = 4.432$*						
Indigofera hirsuta	$F_{9,20} = 13.087$***	$F_{1,8} = 6.368$*	$F_{1,8} = 6.368$*	$F_{1,8} = 2.579$	$F_{1,8} = 19.862$**	$F_{1,8} = 8.828$*	$F_{1,8} = 1.241$
Tephrosia juncea	$F_{7,16} = 16.744$***						

elevated temperatures between 80ºC and 100ºC significantly increased the germination of six of the ten species (Figure 4.5; Table 4.3). The treatments which produced the most germination were exposure to 80ºC water for five minutes and 85ºC dry heat for 45 minutes. The four species with no enhancement of germination by heat shock were the four largest seeded species (Tables 4.2 and 4.3).

The percentage germination of viable seeds in the control treatments, (i.e. non-dormant seeds), averaged 23% across the ten species and ranged from 72% in *Crotalaria pallida* to 5% in *Indigofera hirsuta*. The three exotic species, as a group, had a significantly higher percentage of non-dormant seeds (mean = 41, s.e. = 10; $U = 43.00$; $P < 0.02$) compared to the seven native species (mean = 15, s.e. = 2).

Seeds of seven out of the eight species exposed to 120ºC did not germinate (Figure 4.5). The only species to germinate after exposure to 120ºC was *Tephrosia juncea*, with just 1% germination. A tetrazolium test of the *Crotalaria pallida* seeds exposed to 120ºC found none were viable, indicating exposure to 120ºC for 5 minutes was lethal.

Exposure to smoke or nitrate in isolation did not significantly enhance germination. In fact several species showed no germination after these treatments and significant inhibition by smoke was demonstrated for *Chamaechrista mimosoides*, *Crotalaria montana*, *C. pallida* and *Indigofera hirsuta* (Figure 4.5). Exposure to nitrate significantly inhibited the germination of *Crotalaria calycina*. However, significant enhancement of germination resulted from the combination of nitrate and exposure to 80ºC for *Crotalaria lanceolata* and *Indigofera hirsuta* (Figure 4.5).

The results for individual species are summarised as follows: *Chamaecrista absus* displayed significantly greater germination in the control and after exposure for five minutes at 60ºC than exposure to 100ºC (Figure 4.5a; Table 4.3).

Chamaecrista mimosoides showed significantly higher germination after exposure to water at 80ºC for five minutes than in all other treatments (Figure 4.5b; Table 4.3). The two-factor ANOVA indicated significant inhibition of germination with smoke exposure, but significant interactions between smoke and heat shock and between nitrate and heat shock.

Exposure of *Crotalaria calycina* seed to 85ºC for 45 minutes significantly enhanced germination over all other treatments except smoke, 40ºC and 80ºC (Figure 4.5c; Table 4.3). Exposure to the nitrate solution and 120ºC produced significantly lower germination than all other treatments. There were no significant interactions between heat shock and smoke.

Crotalaria lanceolata showed enhanced germination after exposure to 85ºC for 45 minutes, which was significantly greater than under all other treatments (Figure 4.5d; Table 4.3). There was a significant interaction between nitrate and heat shock, with exposure to both treatments resulting in greater germination than the additive effect of each in isolation. The combination of smoke and heat shock also produced germination greater than each in isolation, however large variation between replicates inhibited the detection of a significant interaction.

Percentage germination of *Crotalaria montana* was significantly enhanced by exposure to 80ºC and 100ºC for five minutes, 80ºC water for five minutes, and 85ºC for 45 minutes compared to the control treatment and exposure to smoke, nitrate solution, 40ºC and 120ºC for five minutes (Figure 4.5e; Table 4.3). Exposure to 80ºC water also enhanced germination over 60ºC for five minutes. In the two-factor ANOVA indicated that exposure to smoke and nitrate significantly inhibited germination.

Crotalaria pallida showed significantly enhanced germination in the control treatments compared with exposure to 100ºC and 120ºC for five minutes (Figure 4.5f; Table 4.3). There were no significant interactions between exposure to smoke and heat shock, or nitrate solution and heat shock. However, the two-factor ANOVA of the combined smoke with heat shock treatment, indicated an overall significant inhibition of germination after exposure to smoke.

Galactia tenuiflora showed no significant differences between treatments (Figure 4.5g), while exposure to 40ºC for five minutes significantly increased the percentage seed germination of *Glycine tomentella* compared with the smoke treatment (Figure 4.5h; Table 4.3).

A significantly higher percentage of *Indigofera hirsuta* seed germinated after exposure to 80ºC water for five minutes compared to all other treatments, with the exception of 85ºC for 45 minutes (Figure 4.5i; Table 4.3). The latter produced significantly greater germination than the control and exposure to smoke, 60ºC and 120ºC for five minutes. In the two-factor ANOVA, 80ºC produced greater germination than the control, while the smoke treatment significantly inhibited germination. However, exposure to nitrate plus 80ºC significantly increased percentage germination.

Tephrosia juncea germinated in significant numbers after exposure to 85ºC for 45 minutes compared to all other treatments, except 80ºC for five minutes (Figure 4.5j; Table 4.3). The latter produced significantly greater germination than exposure to smoke and 120ºC for five minutes.

4.3.2 Temperature elevation in the topsoil during the passage of fire

There were no statistical differences between temperatures recorded at the base of grass clumps and in gaps of at least 30 cm, for any soil depth during either early or late dry season fires (Table 4.4). A significant negative correlation was detected between soil temperature and soil depth for both early and late dry season fires, indicating the decline in temperature with soil depth (Figure 4.6). Temperatures were significantly higher at all depths during late compared to early dry season fires (Table 4.5) and are displayed using the mode and upper and lower temperatures (Figure 4.6). Modal values are presented rather than means due to the use of incremental temperature records, and as the upper temperature records were capped at 182ºC, precluding the calculation of a true mean. While temperatures at the surface during the early fires ranged from at least 182ºC to 49º C, all surface measurements during the late fires were at least 182º C as were most recordings at 3 mm (Figure 4.6). The modes for both early and late dry season fires indicate that there was usually no elevation of temperature at 30 mm, although temperatures did reach 65ºC in during the late fire.

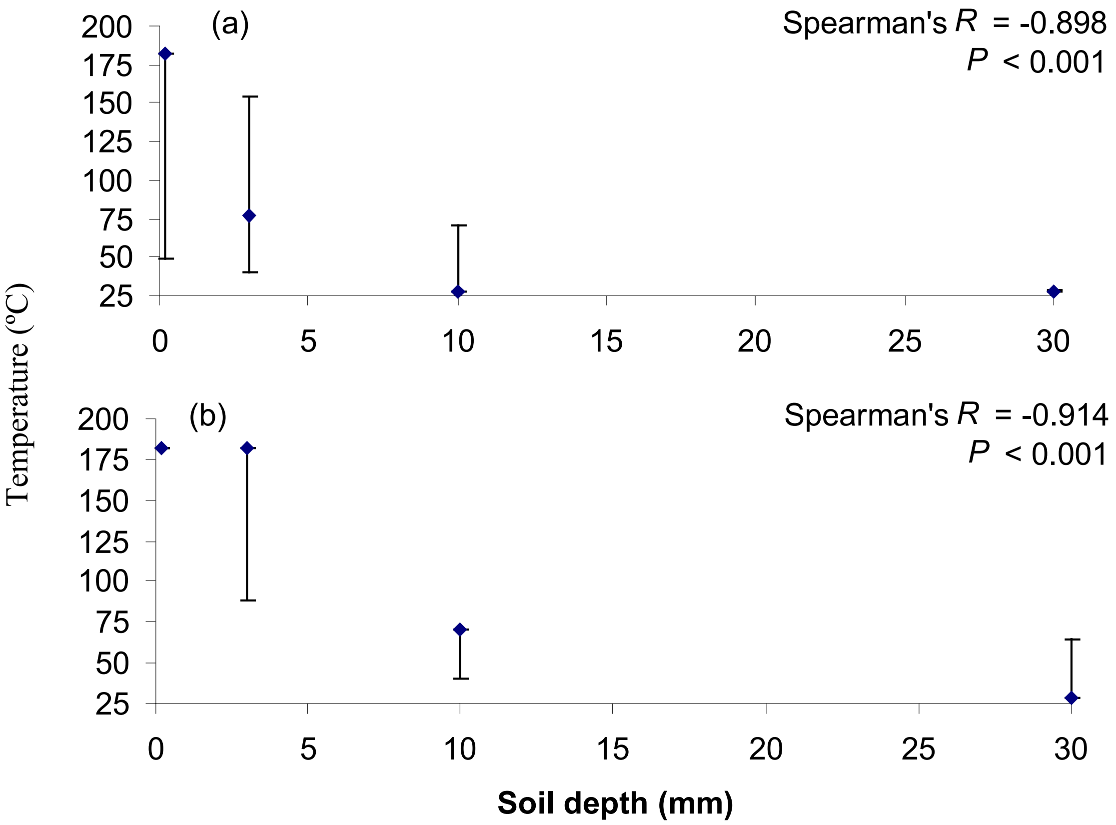


Figure 4.6. Modal temperatures recorded at four depths in the topsoil during (a) early and (b) late dry season fires in eucalypt savanna at Cape Cleveland during 1999 (n = 30 measurements). Error bars represent upper and lower temperatures recorded, maximum ≥ 182°C, minimum 37°C. Results of the Spearman rank correlation of temperature with soil depth are provided.

Table 4.4. Modal temperature and statistical results of non-parametric Mann-Whitney *U*-tests of soil temperatures at the base of grass tussocks compared with tussock gaps, during early and late dry season fires in eucalypt savanna at Cape Cleveland. Significance level after Bonferroni adjustment for multiple comparisons is $P < 0.013$.

Depth	Modal Temperature (ºC) Gap	Tussock base	*U* statistic	*P* value
Early dry season fires				
Surface	182	182	106.000	> 0.787
3 mm	54	77	83.000	> 0.221
10 mm	27.5	27.5	112.500	1.000
30 mm	27.5	27.5	105.000	> 0.756
Late dry season fires				
Surface	182	182	112.500	1.000
3 mm	182	182	103.000	> 0.694
10 mm	71	71	112.000	> 0.983
30 mm	30	30	83.000	> 0.221

Table 4.5. Statistical results of non-parametric Mann-Whitney *U*-tests comparing soil temperatures during early and late dry season fires in eucalypt savanna at Cape Cleveland. Significance level after Bonferroni adjustment for multiple comparisons is $P < 0.013$.

Depth	*U* Statistic	*P* value
Surface	0.000	**< 0.001**
3 mm	15.000	**< 0.001**
10 mm	65.000	**< 0.001**
30 mm	17.000	**< 0.001**

4.3.3 Depth of germination

The depth of seed germination of both *Galactia tenuiflora* and *Indigofera hirsuta* was significantly correlated with temperatures recorded in the topsoil (Table 4.6). Both *G. tenuiflora* and *I. hirsuta* germinated to greater depth after late dry season fires compared to early fires and along the slashed fire break (Figure 4.7). The mean and deepest germination depths were lower after late dry season fires, suggesting both greater depth of dormancy release, and greater depth of seed mortality. *Indigofera hirsuta* germinated to a depth of 32 mm after late dry season fires, which recorded elevated temperatures to 65ºC at 30 mm; and to a depth of 17 mm after early fires, where temperatures of 40ºC at 10 mm and 37ºC at 30 mm were recorded.

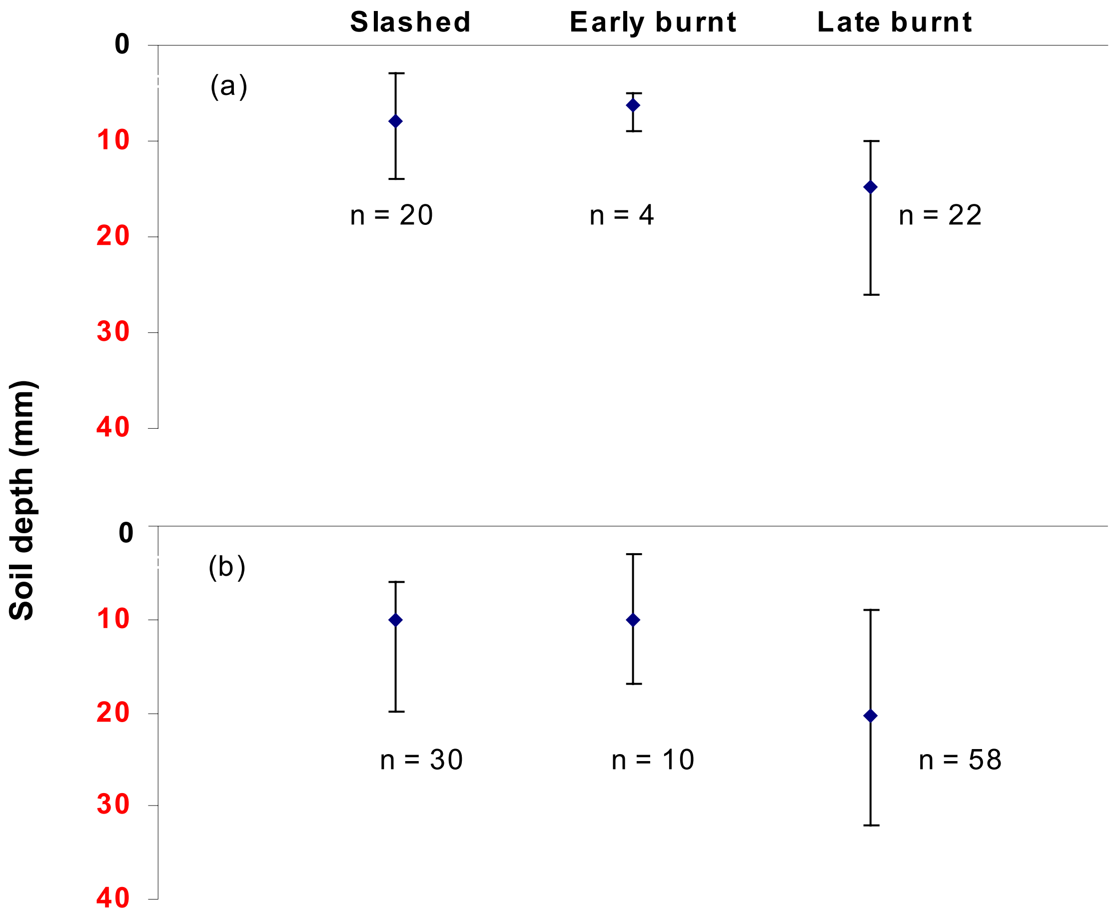


Figure 4.7. Depth of seed germination in eucalypt savanna that has been slashed, or burnt early or late in the dry season for (a) *Galactia tenuiflora* and (b) *Indigofera hirsuta*. Dots represent mean depth of germination. Error bars display the upper and lower germination depths recorded.

Table 4.6. Results of the Spearman rank correlation analysis of seed germination depth with temperatures recorded at four separate soil depths.

Soil depth	*R* statistic	*P* value
Galactia tenuiflora (n = 46 seedlings)		
Surface	0.590	**< 0.001**
3 mm	0.719	**< 0.001**
10 mm	0.647	**< 0.001**
30 mm	0.505	**< 0.001**
Indigofera hirsuta (n = 98 seedlings)		
Surface	0.675	**< 0.001**
3 mm	0.747	**< 0.001**
10 mm	0.675	**< 0.001**
30 mm	0.332	**< 0.001**

The broader range in germination depth after late rather than early dry season fires resulted in greater seedling densities of both species (Figure 4.8). Density differences were statistically significant for *I. hirsuta* ($t_6 = 5.041$; $P < 0.002$) but not for *G. tenuiflora* ($t_6 = 2.141$; $P > 0.05$).

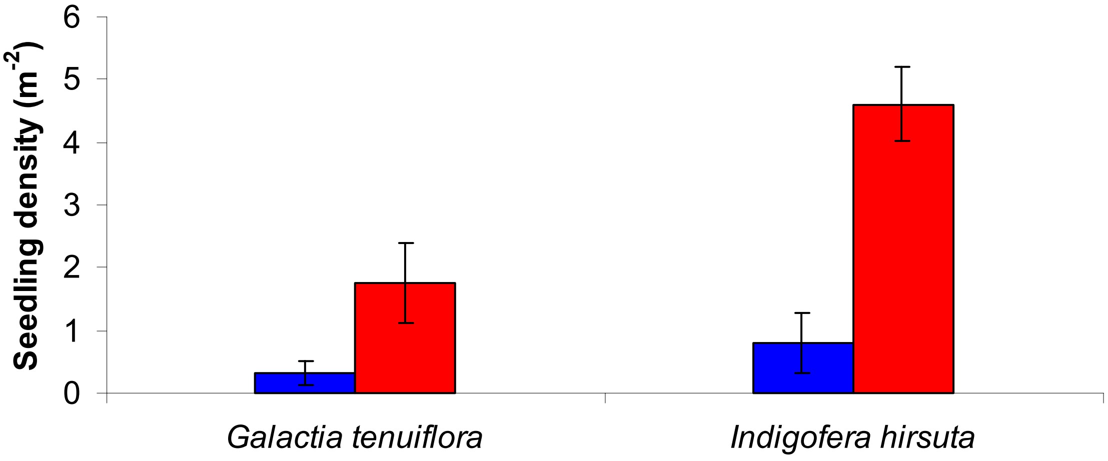


Figure 4.8. Mean seedling density (± 1 standard error) of *Galactia tenuiflora* and *Indigofera hirsuta* at four temperature measurement points in Early (🟦) and Late (🟥) dry season burnt eucalypt savanna at Cape Cleveland.

4.4 Discussion

4.4.1 Laboratory experiment

The influence of fire-related factors in breaking seed dormancy was evident for six of the ten species examined (Figure 4.5; Table 4.3). Significantly greater germination occurred after exposure to temperatures between 80ºC to 100ºC which is consistent with the germination requirements of many legumes of southern Australia (Floyd 1976; Shea *et al*. 1979; Auld and O'Connell 1991; Bell *et al*. 1993; Jhurree *et al*. 1998).

The 80ºC water treatment produced significantly more germination than the five minute exposure to 80ºC air temperature for seeds of *Chamaecrista mimosoides* and *Indigofera hirsuta* (Figure 4.5; Table 4.3). Moisture is available in the topsoil, although the quantity varies with season, soil structure and organic content, and Martin and Cushwa (1966) and Martin *et al*. (1975) considered heating seeds in hot water may more accurately depict conditions in the soil seed bank during fire than oven heating. The 85ºC air temperature for 45 minutes produced significantly greater germination than 80ºC air temperature for five minutes in *Crotalaria lanceolata*. This may have been due to the extra 5ºC and/or the longer duration of heating.

Exposures to temperatures as low as 40ºC can significantly enhance germination of some legumes in south-eastern Australia (Auld and O'Connell 1991). It is possible that temperatures of 40ºC or 60ºC may have increased the percentage seed germination of some species in this study, had the seeds been heated in the oven for longer than five minutes or placed in water or soil at those temperatures.

The four largest seeded species displayed no significant increase in germination with exposure to elevated temperatures, but were tolerant of exposure to at least 80º C (Figure 4.5; Table 4.3). This suggests an ability to tolerate the passage of fire, but provides no evidence of fire-promoted germination. Exposure to 120º C for five minutes was lethal to most seeds in this experiment, which is consistent with reports from other studies (e.g. Auld and O'Connell 1991). The second and third largest seeded species, *Galactia tenuiflora* and *Crotalaria pallida*, showed the lowest tolerance to heat shock, with apparent mortality at 100ºC. This contrasts with African acacias, where larger seeded species possess a greater tolerance of heat shock than those with smaller seeds (Midgley and Bond 2001), although no correlation between seed size and thermal tolerance is apparent for legumes of south-western Australia (Bell and Williams 1998).

The two native species that did not respond significantly to heat shock, *Galactia tenuiflora* and *Glycine tomentella*, were the only perennial species examined, and each is capable of sprouting after fire (Chapter 8). Sprouting species may be able to maintain population density with less seedling recruitment than needed by annual or ephemeral species, and therefore the requirements to break seed dormancy may differ with life history and fire response (Bell 2001). However the germination of *Galactia tenuiflora* and *Glycine tomentella* was low (< 25%) in all treatments, including the control, and may have been due to sub-optimal incubation conditions, an after-ripening requirement not satisfied by the few months of storage, and/or the absence of a heat shock or chemical treatment that would have produced greater germination. Therefore further examination of the dormancy requirements of these species is required.

While germination in the laboratory without pre-treatment does not necessarily indicate the absence of seed dormancy (Whelan 1995), the germination in control treatments does suggest fire-related stimuli are not obligatory. The mean percentage of "non-dormant" seeds (i.e. those lacking an innate dormancy related to fire cues) for the seven native species in this study (15%) is similar to averages reported for legumes of south-eastern (11 to 15%) and south-western (11 to 18%) Australia (Shea *et al*. 1979; Auld and O'Connell 1991; Morrison *et al*. 1992; Bell *et al*. 1993; Clarke *et al*. 2000). However, the exotic species of this study had a significantly higher mean percentage of non-dormant seeds (41%) compared with the natives. This suggests some exotic legumes possess a greater capacity for recruitment in the absence of fire than native legumes in savannas of north-eastern Australia. Indeed several exotic pasture legumes used in the region, including *Macroptilium atropurpureum* and *Stylosanthes humilis*, do not require fire for seed germination (McIvor *et al*. 1993).

Neither smoke nor nitrate in isolation significantly promoted seed germination (Figure 4.5; Table 4.3). In fact smoke significantly inhibited the germination of *Chamaecrista mimosoides*, *Crotalaria montana*, *Crotalaria pallida* and *Indigofera hirsuta*. This may have resulted from the use of the 90 minute exposure to smoke, which increases seed germination in some species (e.g. Dixon *et al*. 1995; Keith 1997), however Roche *et al*. (1997) demonstrated that a duration of more than 60 minutes can inhibit seed germination of other species. Exposure to nitrate inhibited *Crotalaria calycina* and *C. montana* germination, which suggests the concentration of nitrate used was toxic to these species, even though it has been shown to increase germination of Western Australian plants (Bell *et al*. 1999).

Significant enhancement of germination was produced by the combination of heat shock followed by nitrate application for *Crotalaria lanceolata* and *Indigofera hirsuta* (Figure 4.5; Table 4.3). This suggests multiple components of fire operate to promote germination. The synergistic effect of smoke and heat shock has been recently reported for several shrubs of fire prone regions in south-eastern Australia (Keith 1997; Gilmour *et al*. 2000; Kenny 2000; Morris 2000). Nitrate has been demonstrated to interact with light regime to increase the germination of several Western Australian species (Bell *et al*. 1999), but I am not aware of previous reports of the additive effect of nitrate and heat shock. The greatest change in soil nitrate levels can occur with the first rains after fire (Bell 1999). The enhanced response to nitrate and heat shock may therefore be particularly useful in timing recruitment with the first rain following fire, thus allowing seedlings of these ephemeral species to take advantage of the full wet season to grow and produce seeds. Multiple fire cues are also beneficial for ensuring increased germination after fire when elevation of temperature in the topsoil is inadequate to break seed dormancy (Kenny 2000).

4.4.2 Temperature elevation in the topsoil during the passage of fire

Early and late dry season fires elevated topsoil temperature, which declined rapidly with increasing soil depth (Figure 4.6). No differences in temperature were detected between tussock gaps and the base of grass tussocks, suggesting uniformity in heating at the scale of tens of centimetres (Table 4.4). Temperature elevation reached at least 30 mm depth during late dry season fires, but did not penetrate as deep during earlier fires. Temperatures that were demonstrated to significantly increase seed germination (i.e. 80ºC to 100ºC) were documented at the surface and 3 mm depth during early dry season fires. During late dry season fires, all surface temperatures were lethal to seeds, while temperatures between 80ºC to 100ºC were only recorded at a depth of 3 mm. The increased temperature penetration into the topsoil recorded during these fires is consistent with temperatures recorded during fires in other eucalypt communities (Shea *et al*. 1979; Bradstock and Auld 1995; Bebawi and Campbell 2000; Smith *et al*. 2000). These data highlight the insulating capacity of soil that protects seeds from lethal temperatures during fires, while exposing a narrow band of seed bank to temperatures capable of breaking dormancy. Bradstock and Auld (1995) demonstrated the importance of fine fuel consumption for influencing soil temperatures during fires. In this study the greatest temperature elevation was recorded during the late dry season fires which completely consumed fine fuels, whereas some fuel remained after early fires (Chapter 3). The seasonal variation is also consistent with the findings of Grant *et al*. (1997), who documented higher temperature penetration into the topsoil during autumn (i.e. late dry season) fires than spring (i.e. early dry season) fires in southern Western Australia.

4.4.3 Depth of seed germination

The depth of seed germination in both *Galactia tenuiflora* and *Indigofera hirsuta* was positively related to the temperature elevation in the topsoil during fires and was documented at greater depths after late dry season fires (Figure 4.7; Table 4.6). Mean germination depths of *G. tenuiflora* and *I. hirsuta* are consistent with those recorded for the New South Wales legume, *Acacia suaveolens*, although the latter is able to germinate from greater depths (Bradstock and Auld 1995). Germination of *G. tenuiflora* and *I. hirsuta* was closer to the soil surface along the unburnt slashed track and after early rather than late dry season fires. This suggests greater seed mortality occurred in the upper topsoil during late dry season fires, and is consistent with results from the laboratory experiment that indicated temperatures of at least 100ºC are lethal to *G. tenuiflora* and of at least 120ºC are lethal to *I. hirsuta* seeds.

Larger seeded species may benefit more than smaller seeded species from increased temperature penetration into the topsoil, because their greater starch reserves may allow survival of germinants from further depths in the topsoil (Midgley and Bond 2001). However in this instance, the smaller seeded *I. hirsuta* germinated from greater depths, even though the larger seeded *G. tenuiflora* displayed a greater percentage of non-dormant seeds in the laboratory experiment.

The depth of seed germination of *G. tenuiflora* was correlated with temperature penetration even though no significant heat shock cue was demonstrated in the laboratory experiment. *Indigofera hirsuta* germinated from a depth of 32 mm, where the highest temperature recorded was 65ºC during the late fires; and from 17 mm after early fires, where maximum temperatures at 10 mm were 40ºC. The field germination therefore suggests seed dormancy of *G. tenuiflora* is broken by heat shock and that germination of *I. hirsuta* may be promoted by lower temperatures than indicated in the laboratory experiment. This re-affirms the suggestion that exposure of seeds to 40ºC and 60ºC using hot water, heated soil, or an extended duration in heated air, may have produced significantly enhanced germination below 80ºC in the laboratory experiment.

There was a greater density of *I. hirsuta* seedlings recorded within the 1 m radius of temperature measurement points after late rather than early dry season fires (Figure 4.8). This reflects the greater range in depth of germination after late fires and therefore greater proportion of the soil seed bank from which germination was triggered.

4.5 Conclusion

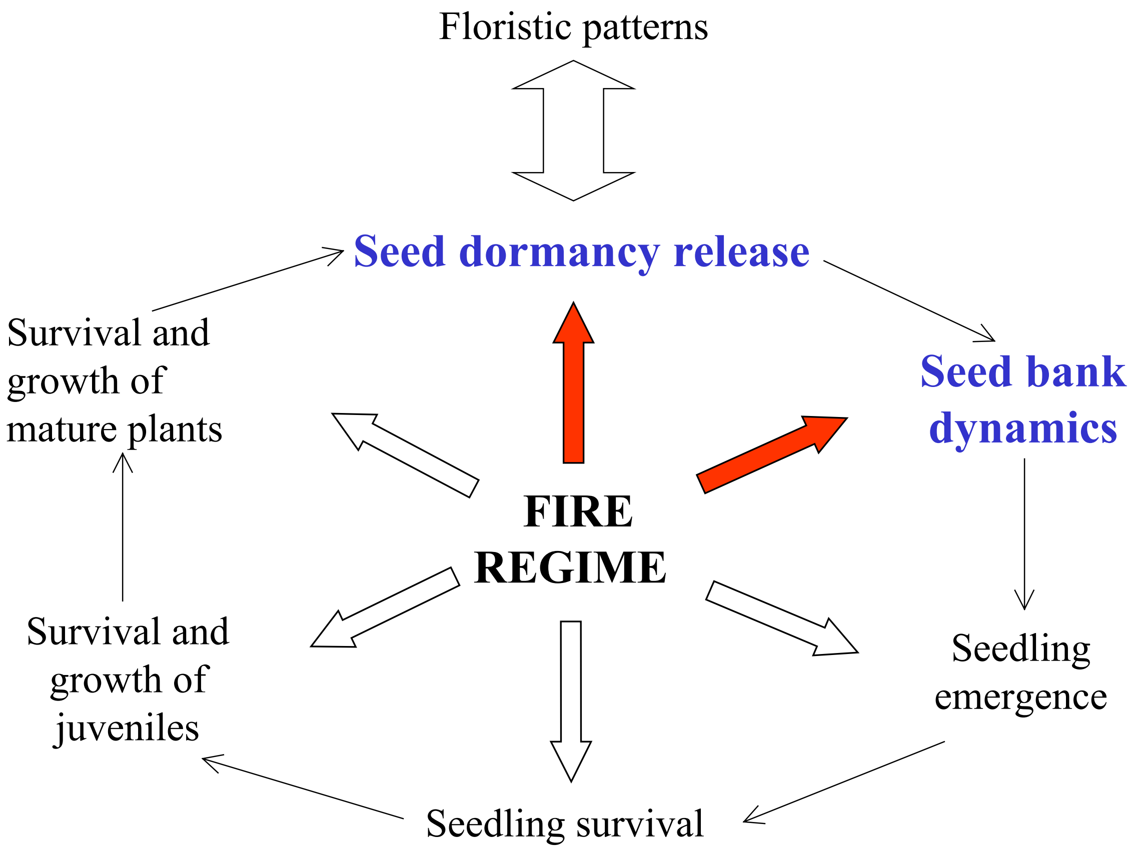
In summary, the ten legume species responded variously to the exposure to heat shock and chemicals related to the passage of fire. While several species displayed no significant increase in germination with exposure to fire-related cues, heat shock, by itself and in combination with nitrate, was found to break the seed dormancy of several species. The presence of seeds of all species with no apparent innate dormancy suggests germination can occur in the absence of fire, and for a higher percentage of seeds of exotic species than natives. Variation in seed dormancy requirements may be important for maintaining species coexistence (Grubb 1977).

Temperatures that break seed dormancy did occur in the topsoil during the passage of both early and late dry season fires. Greater penetration of elevated temperatures occurred during late dry season fires, however this included temperatures lethal to seeds. The depth of germination of two native legumes confirmed that temperatures experienced during fires are capable of triggering germination in the topsoil. The data also suggest temperatures as low as 40ºC may increase germination of these species. A greater range in germination depth, resulting in higher seedling densities, was recorded after late dry season fires, suggesting more abundant seedling emergence may occur after late rather than early dry season fires.

The results in this chapter suggest that the post-fire pulse in species abundance documented in Chapter 3 may in part be due to the release of some seeds from a state of dormancy by the temperature elevation and enhanced nitrate concentrations in the topsoil as a result of fire. The pulse of species abundance documented in Chapter 3 was especially evident after late dry season fires, and this chapter presents evidence that late fires release seed from dormancy to a greater depth in the topsoil, and hence a greater volume of the soil seed bank.

This chapter has examined only a small selection of savanna species and further information is needed on the effect of fire on seed dormancy for a wider range of species. Chapter 5 broadens the investigation of the effect of fire-related cues on seed dormancy, to include more species. It also identifies species that store seed in the soil, and provides details on the distribution of the seed bank in the topsoil, seasonal fluctuations in the seed bank, and the influence of fire on the soil seed bank dynamics.

Chapter 5. The effect of fire regime on soil seed bank dynamics in a tropical savanna of north-eastern Australia.



5.1 Introduction

Seed banks bridge the gap between seed production and seed germination. They provide a mechanism for population persistence through harsh seasons and supply propagules for re-establishment after disturbance (Lunt 1997; Auld *et al*. 2000).

Canopy seed storage (bradyspory) is uncommon in northern Australia, with seed of savanna species primarily stored within the soil (McIvor 1987; Andrew and Mott 1983; Williams *et al*. 1999a). Several annual grasses in Australian tropical savannas produce soil seed banks of high density. For example, initial input into the soil seed bank by *Sorghum intrans* can average 2150 seeds m^{-2} (Andrew 1986). Seed bank densities of perennial grasses can be considerably lower, for instance up to 150 seeds m^{-2} for *Themeda triandra* and less than 100 seeds m^{-2} for *Heteropogon contortus* (Shaw 1957; Mott *et al*. 1985; McIvor 1987).

Many Australian tropical savanna species do not produce seed banks that persist longer than a few weeks, with seeds either germinating or succumbing to predation or disease soon after seed fall. Examples of this syndrome include several tropical eucalypts and the perennial grasses *Alloteropsis semialata* and *Dichanthium fecundum* (Mott and Andrew 1985; Setterfield 1997*a*; Crowley and Garnett 2001).

Many dominant grasses of tropical savannas, including annual *Sorghum* spp. and *Themeda triandra*, produce a transient seed bank, with seed stored through the dry season and exhausted during the wet season, requiring replenishment for the following year (Andrew and Mott 1983; McIvor 1987). For many of these grasses, storage through the dry season is made possible by an after-ripening seed dormancy mechanism (McIvor and Howden 2000). Persistent seed banks contain seeds that remain viable for more than one year and can be important mechanisms for population survival, especially for short-lived or non-sprouter species (Thompson and Grime 1979; Bond and van Wilgen 1996). Innate and secondary, enforced, seed dormancy mechanisms are fundamental for allowing seed bank persistence (Bell 1999; Auld *et al*. 2000). Examples of species with persistent seed banks in tropical Australian savannas include the native forb *Epaltes australis* and the exotic pasture legume, *Stylosanthes hamata* (McIvor 1987).

In many fire-prone communities, seedlings primarily recruit from the local seed bank rather than seed dispersed from outside the immediate area, and therefore seed bank density, distribution and response to fire-related cues are important factors influencing post-fire seedling emergence (Whelan 1986; Auld *et al*. 2000). Soil seed banks are dynamic, fluctuating in composition and abundance in response to seed input, seed mortality, release of seeds from dormancy and seed germination (Thompson and Grime 1979). All of these processes can be influenced by fire, which can enhance or restrict seed production, affect seed dispersal agents, cause seed mortality, and break seed dormancy to allow germination (Keith 1996; Whelan *et al*. 2002).

As fire can influence seed bank processes, variations in fire regime may be expected to have a considerable effect on seed bank dynamics. Fire interval may be particularly important for species with seed input restricted to the early phase of fire intervals, such as ephemerals with fire-triggered germination, and plants with fire-promoted flowering and fruiting (Keith 1996). Seed banks of these species receive a pulse of post-fire seed input, but may gradually decline between fires (Bond and van Wilgen 1996). Seed banks of some perennial species, or ephemerals with continuous recruitment, may build up during the years following fire, so that long fire intervals promote dense seed banks (Keith 1996). However, fire frequency may have less influence on seed banks of perennial species that rely heavily on annual input, due to high annual seed losses irrespective of fire (Bond and van Wilgen 1996).

Fire intensity can affect seed bank dynamics through its influence on plant mortality and subsequent seed input, as well as direct affects on seed mortality and release from seed dormancy (Whelan 1995). Fire season can influence seed bank dynamics by interacting with reproductive phenology, and fires that are synchronised with seasonal peaks in seed bank density will influence the survival and germination of a greater number of seeds. Post-fire climatic conditions also influence seed germination, and therefore seed bank dynamics (Whelan 1995).

The scale and patchiness of fire can influence seed bank dynamics, with a patchy fire producing a fine-scale spatial mosaic in seed mortality and germination. Williams and Lane (1999) considered the re-establishment of *Sorghum brachypodum* after initial declines in density following wet season burning, may have been due to small-scale seed dispersal from adjacent unburnt areas.

Research into the effect of fire regime on seed production and seed bank dynamics in Australian tropical savannas has focused on a few dominant species. Setterfield (1997) demonstrated that the seed production of *Eucalyptus miniata* and *E. tetrodonta* can be reduced by both early and late dry season fires. Most research on seed banks has concentrated on grasses, many of which produce seed banks lasting from several weeks to one year (Andrew and Mott 1983; Andrew 1986; McIvor 1987; Crowley and Garnett 2001).

Harper (1977) produced a valuable model for interpreting seed bank dynamics, in which he described soil seed banks as containing both dormant and "active" components, the latter requiring only soil moisture and favourable temperatures to promote germination (Figure 5.1). The dormant component of the seed bank may contain seeds with an innate dormancy, which in some seeds can be broken by fire-related factors (Bell 1999; Chapter 4). The dormant seed bank may also contain seeds lacking innate dormancy, but inhibited from germination by a secondary, enforced dormancy. Auld *et al*. (2000) found evidence that seeds of some shrubs in temperate woodlands may have remained viable within the soil seed bank for two years as the result of a secondary dormancy mechanism, possibly enforced by the absence of light.

Experimental treatment of soil seed banks (e.g. exposing to heat shock and smoke) can indirectly assess the effect of fire on seed dormancy, and therefore the balance between dormant and active seed banks (e.g. Enright *et al*. 1997; Read *et al*. 2000). While the untreated germinable soil seed bank may include seeds that have been released from dormancy through the process of soil collection and incubation in shadehouse conditions (Whelan 1995), it provides a useful approximation of seeds that do not require a fire stimulus prior to germination. Comparisons of untreated germinable soil seed banks before and after fire, and in burnt and adjacent unburnt savanna, can provide a direct assessment of the influence of fire on the active fraction of soil seed banks.

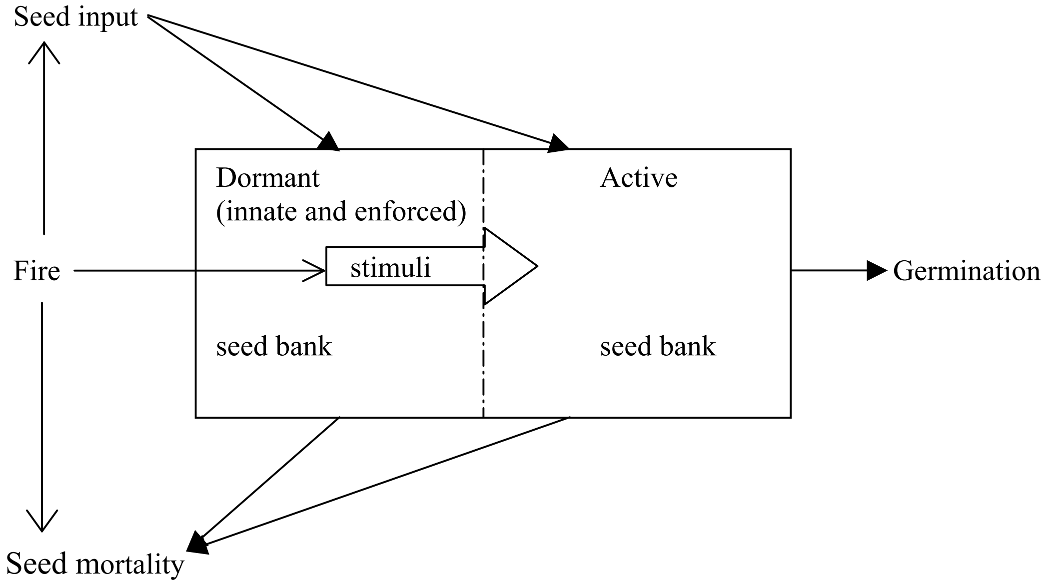


Figure 5.1. Model of the influence of fire on soil seed bank dynamics, based on Harper (1977) and Whelan (1995), depicting the impact of fire on seed input, seed mortality and as a stimulus for releasing seed reserves from a state of innate and enforced dormancy. Note that the germinable soil seed bank (i.e. the portion of seed bank detected using a seedling emergence technique) of untreated soil may be a close approximation to the "Active" component of the seed bank, however the process of soil collection and incubation in the shadehouse may release seed from a state of innate or enforced dormancy.

Chapter 3 documented dynamics in the composition and abundance of the standing vegetation in response to fire in a tropical savanna of north-eastern Australia. This chapter examines seasonal and annual seed bank fluctuations, and the influence of fire regime on soil seed bank dynamics. It investigates the effect of fire on the transfer of seed from the dormant to the active fraction of the seed bank, both indirectly, by experimental exposure to heat shock and smoke; and directly, through comparisons of untreated soil before and after fire, and in adjacent burnt and unburnt savanna. This chapter also contrasts the soil seed bank composition with the standing vegetation, and examines the influence of fire regime on seed production of the dominant tree, *Corymbia clarksoniana*. Specific questions addressed are:

1. How is the seed bank distributed within the topsoil?

2. Does the soil seed bank contain seeds which can be released from dormancy through exposure to fire-related factors (i.e. heat shock and smoke)?
3. Does fire increase the density of the active seed bank?
4. What annual and seasonal fluctuations occur in the soil seed bank and does fire affect these patterns?
5. How does the species composition of the germinable soil seed bank compare with the standing vegetation?
6. What is the phenology of seed production of plants at Cape Cleveland and how does this relate to seasonal dynamics in the soil seed bank?
7. What is the effect of fire season on seed production in *C. clarksoniana*, a species that produces a very short-lived seed bank?

5.2 Methods

5.2.1 Sampling methods

5.2.1a Soil seed bank sampling

Pre- and post- mid dry season fire 1997

Soil seed bank of eucalypt savanna at the Cape Cleveland study site (Figures 2.1 and 2.4) was sampled regularly between July 1997 and October 2000. The initial sampling in July 1997 was undertaken to investigate the effects of the mid dry season fire of that year on soil seed bank dynamics, and to examine the distribution of seeds in the topsoil. It was also useful as a pilot study to refine sampling methodology for the remainder of the seed bank study.

Soil samples were collected from eight points across each of the 1 ha blocks, several days prior to the July 1997 fire. The sampling method involved walking through each 1 ha block and stopping approximately every 20 paces. A random direction was then used to locate a point for soil sampling. At each point, duplicate 125 cm^3 sub-samples were collected from three separate depths: the upper 3 mm; 3 to 20 mm; and 20 to 40 mm. The collection depths were made as accurate as possible by marking depths on the spade used for soil collection. The upper 3 mm was collected by scraping together the loose surface soil to the required depth. The lower two depths were collected by digging, to the appropriate depth, a spadeful of soil with a surface area of 459 cm^2. This provided a bulk sample at each point of approximately 780 cm^3 for the 3 to 20 mm depth, and 918 cm^3 for 20 to 40 mm depth. Each spadeful of soil was mixed and the duplicate sub-samples of 125 cm^3 were collected. At the end of the pre-fire collection, three sets of duplicate samples had been collected from each of the three soil depths (18 pre-fire soil samples; Figure 5.2). Each of these samples contained 3000 cm^3 of soil, collected from 24 points (the result of pooling eight sub-samples from each of three 1 ha blocks).

To assess the effect of fire on the seed bank, soil was collected in an identical fashion a few days after the July 1997 fire (one week after the pre-fire soil collection). The sampling methodology differed only in the collection of a single set of samples, rather than duplicates, thereby providing three replicates of each of the three soil depths (nine post-fire samples, each containing 3000 cm^3 of soil; Figure 5.2).

Seed bank composition and abundance were assessed using a seedling emergence technique, which therefore examined the germinable soil seed bank. The post-fire samples, plus three replicates of each soil depth from the pre-fire collection, were placed without treatment into a shadehouse covered with 50% shadecloth. The samples were watered daily from overhead sprinklers, which provided approximately 21 mm of water per day. The remaining three replicates of soil samples collected prior to the fire were put into aluminium trays and placed in an oven at 85ºC for 45 minutes prior to placing in the shadehouse. This pre-treatment was used to assess the effect of heat shock on seed dormancy of species present in the soil seed bank. It also allowed detection of a wider range of species from the germinable soil seed bank. The 85ºC temperature occurs in the topsoil during the passage of fire and has been shown to release seed from a dormancy (Auld and O'Connell 1991; Chapter 4). The 45 minute duration is longer than that experienced in the topsoil during the passage of fire (e.g. Bradstock and Auld 1995), but thermometer readings of the soil whilst in the oven indicated this duration was required to allow temperatures of approximately 80ºC to penetrate into the soil mass. Soil was mixed after 20 minutes in the oven to aid heat penetration through the soil and spread the heating effect through the seed bank. Exposure to 85ºC for 45 minutes has been demonstrated to break the dormancy of several local species (Chapter 4). Similar soil heating treatments have been shown to promote seed germination from soil seed banks in tropical Australia (Hopkins and Graham 1984; Skull 1992; Williams 2000).

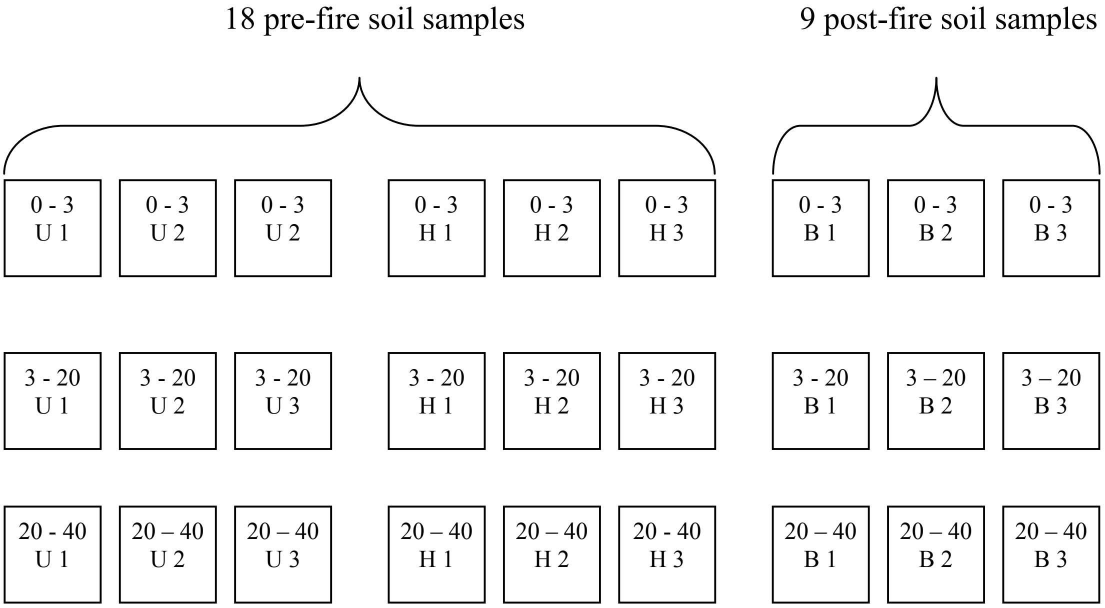


Figure 5.2. Schematic diagram of the sampling design used in the July 1997 germinable soil seed bank study in eucalypt savanna at Cape Cleveland. Each box represents a soil seed bank sample of 3000 cm^3 collected from 24 points. 0 – 3, surface samples from a depth of 0 to 3 mm; 3 – 20 samples from 3 to 20 mm depth; 20 – 40, samples from 20 to 40 mm depth; U, soil collected prior to fire and remained untreated; H, soil collected prior to fire and heated in an oven at 85º C for 45 minutes; B, soil collected after fire, but otherwise untreated. Numbers 1, 2 and 3 represent the replicate number, each replicate contains 24 sub-samples collected from three 1 ha blocks.

Soil samples were assessed regularly for seedlings, which were removed once large enough to be identified. Additional trays of sand were placed adjacent to the soil trays to detect the presence of weed seeds in the shadehouse. Assessment of soil samples continued for six months.

Soil seed bank sampling from October 1997 to October 2000

Soil seed bank at the Cape Cleveland experimental site was sampled over three years, from October 1997 to October 2000, to investigate seasonal and annual fluctuations, and the influence of fire regime on seed bank dynamics. Soil was collected in four seasons in each of 1998, 1999 and 2000: mid wet season, i.e. February; early dry season, i.e. May; mid dry season, i.e. July; and late dry season, i.e. October.

Soil collection was similar to that described for the pre- and post- 1997 fire (section *5.2.1a*), but involved more sub-samples, which were not separated into soil depth categories (Figure 5.3). Soil samples were collected to a depth of 5 cm, as seed density usually declines below this depth (Roberts 1981). Samples were collected from 20 points across each of the nine, 1 ha blocks in the initial October 1997 and February 1998 collections, but from 32 points per block thereafter to ensure adequate sampling of site variation. The points were spaced approximately five paces apart, while walking in a zig-zag pattern across each 1 ha block. At each point a random direction was selected and a spadeful of soil dug to 5 cm, providing a volume of 2295 cm^3. The soil was mixed and then two duplicate 125 cm^3 sub-samples were collected. The duplicate samples were kept in separate bags, each containing the pooled 32 sub-samples collected across each 1 ha block. This provided soil collections of 4000 cm^3 (2500 cm^3 in October 1997 and February 1998) sub-sampled from a total of 73440 cm^3 (45900cm^3 in October 1997 and February 1998) of soil from each 1 ha block. Samples from each block were regarded as replicates.

The soil samples were treated identically to those collected in July 1997 (section *5.2.1a*). One of the duplicate samples from each 1 ha block remained untreated and was placed in the shadehouse and watered daily. The other duplicate sample was placed in an oven at 85ºC for 45 minutes prior to placement in the shadehouse. Seedlings were recorded regularly and removed once large enough to be identified. Each collection was kept in the shadehouse for six months.

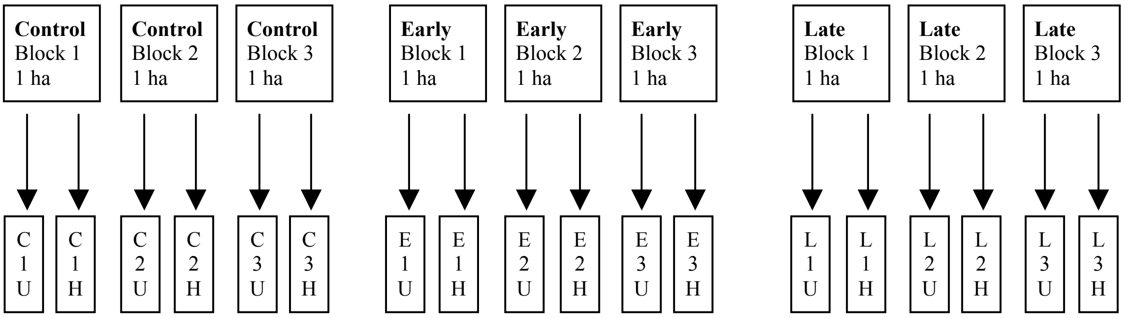


Figure 5. 3. Schematic diagram of the sampling design used in the soil seed bank study of eucalypt savanna at Cape Cleveland between October 1997 and October 2000. A complete set of soil seed bank samples was collected in the mid wet season, i.e. February; early dry season, i.e. May; mid dry season. i.e. July; and late dry season, i.e. October; in each year. The top row of boxes represents the 1 ha blocks at Cape Cleveland. The lower row of boxes represents individual soil samples taken at each collection date. Each soil sample contained 4000 cm^3 of soil, combined from 32, 125 cm^3 sub-samples (October 1997 and February 1998 collections contained only 2500 cm^3 of soil from 20 sub-samples). Each sub-sample of 125 cm^3 was collected from a soil mass of 73440 cm^3, dug to a depth of 5 cm. C, control, burnt in July 1997 only; E, early burnt, burnt in July 1997 and May 1999; L, late burnt, burnt July 1997 and October 1999; numbers 1 to 3 represent replicates; U, untreated soil; H, soil heated in oven at 85ºC for 45 minutes. Soil collections in May, July and October 2000 included an additional 4000 cm^3 sample of soil per block (each from 32, 125 cm^3 sub-samples), which was exposed to smoke at ambient temperature for 30 minutes.

In May, July and October 2000, three samples (rather than duplicates) were collected from each of the 32 points across each block, to allow a third soil treatment. In addition to the untreated control and oven heated treatment, the third sample from each of the nine, 1 ha blocks was exposed to smoke at ambient temperature (Figure 5.4). The method of smoke treatment was similar to that described in Chapter 4, except replicate collections from each of the control, early and late fire treatments were exposed to smoke separately, as recommended by Morrison and Morris (2000). Soil samples were exposed to the smoking treatment for 60 minutes rather than 90 minutes, as the longer duration may inhibit germination of some species (Roche *et al.* 1997; Chapter 4).

Figure 5.4. Image of smoke application to soil seed bank samples collected from eucalypt savanna at Cape Cleveland in May, July and October 2000. Replicate samples for fire regimes were treated separately. Each sample was spread into two trays to allow adequate exposure to smoke at ambient temperature for 30 minutes.

5.2.1b Phenology of seed production

The timing of seed production for eucalypt savanna species at Cape Cleveland was documented through monthly records of mature seed pods, capsules or fruit, between 1997 and 2001. The purpose of these data was to link the phenology of seed production with seasonal fluctuations detected in the germinable soil seed bank. No attempt was made to quantify seed production, nor assess the effects of fire regime, other than for the dominant tree *Corymbia clarksoniana*, described below.

5.2.1c Fire effects on Corymbia clarksoniana *seed production*

Seeds of the dominant tree, *Corymbia clarksoniana*, were only detected in October 1998 and October 2000 soil seed bank samples, and at very low densities. This suggested *C. clarksoniana* produces a very short-lived soil seed bank. Therefore the effect of fire season on seed supply of this dominant species could not be adequately assessed using the seed bank data, and direct surveys of capsule density were made.

Capsules of *C. clarksoniana* were observed to fall when mature, in October and November each year, which is consistent with other tropical eucalypts (Burrows and Burrows 1992; Setterfield 1997). Seed is shed both prior to and immediately following capsule fall. The density of fallen *C. clarksoniana* capsules was counted in December 2000, after the majority of capsules had fallen, to estimate seed production in the year following fire season treatments. Capsules were counted within 50, $1m^2$ quadrats in each of the nine, 1 ha blocks during the annual seedling survey (Chapter 6). The quadrat was thrown in a random direction at points spaced five paces apart whilst walking up and back across each 1 ha block. The number of seeds in each of 30 capsules of *C. clarksoniana*, collected prior to opening, were counted to allow an estimate of seed density from the capsule density data.

5.2.2 Statistical analyses

5.2.2a Overview of analyses

To evaluate seed bank distribution in the topsoil; seasonal and annual fluctuations; the effect of fire and fire-related cues (i.e. heat shock and smoke) on the germinable soil seed bank; and the effect of fire regime on seed production of the dominant eucalypt; data were analysed in six sections:

1. Pre- and post-mid dry season fire (July 1997 soil seed bank collections).
2. Seasonal and annual fluctuations with time since fire (soil seed bank samples collected from Control blocks only, between February 1998 to October 2000).
3. Pre- and post-early and late dry season fires (soil seed bank samples collected between May 1999 and February 2000).
4. Soil seed banks during the dry season following fire season treatments (soil seed bank samples collected between May and October 2000).
5. A comparison of species composition between soil seed bank and the standing vegetation described in Chapter 3.
6. The effect of fire season on the seed production of *C. clarksoniana*.

The phenological records of seed production were qualitative in nature, and therefore no statistical analyses were undertaken on these data, but they were used for interpretation of the seasonal variation in the soil seed banks.

5.2.2b Seed bank dynamics pre- and post-mid dry season 1997 fire

The soil seed bank before and after the mid dry season 1997 fire was analysed in a two-factor ANOVA to examine the effect of soil treatment with three levels (untreated, heated and burnt) and soil depth with three levels (surface 3 mm; 3 to 20 mm and 21 to 40 mm), with a Scheffe's *post-hoc* test to examine where differences between treatments lay (Underwood 1997). To allow consistency across soil depths, seedling numbers per sample were converted to density (m^{-2}). The surface 3 mm data required no conversion, as the 24, 125 cm^3 samples per replicate equates to 1 m^2 of soil surface (24 samples * 125 cm^3 / 0.3 cm depth = 10000 cm^2 = 1 m^2). Counts from the 3 to 20 mm samples were multiplied by 5.667, and those from the 20 to 40 mm samples were multiplied by 6.667 to give seedling density (m^{-2}). In all soil seed bank analyses, seedling density was interpreted as the germinable soil seed bank density.

Homogeneity of variances was tested using Cochran's test (Underwood 1997). Where variance heterogeneity problems violating ANOVA assumptions could not be resolved with data transformation, a Kruskal-Wallis ANOVA by rank was performed separately for the two factors, soil treatment and soil depth (Zar 1999). Where the Kruskal-Wallis ANOVA detected significant differences, Mann-Whitney U-tests were used to detect differences within treatments, with a Bonferroni adjustment of significance values for multiple comparisons (Sokal and Rohlf 1995).

Analyses were performed on species richness (per sample), total soil seed bank, native and exotic species, the growth form groups described in Chapter 3, and the most abundant individual species detected in the soil seed banks. Analyses of individual species were only performed on those comprising at least 5% of the total seed density. This was done because species with lower abundance had large variations within treatments. Due to the large overall number of analyses undertaken on the soil seed bank data, the significance value was set at $P < 0.01$, to reduce the possibility of inappropriately assigning a significant conclusion (type 1 error; Zar 1999) and therefore providing confidence in all differences that are identified as significant.

5.2.2c Seasonal and annual fluctuations with time since fire

Seasonal and annual fluctuations in the soil seed bank were assessed over the first three years after fire using the replicate samples collected from the three control blocks (Figure 2.4). The effect of soil heating, plus annual and seasonal fluctuations were analysed for species richness per sample, the total seed bank, native and exotic groups, growth form groups and the most abundant species. Species comprising at least 5% of the total seed density recorded for this set of analyses were assessed.

Soil seed bank data from the control blocks were converted to seed density (m^{-2}) to provide consistency between the February 1998 soil collection of 2500 cm^3 and the subsequent data from soil samples of 4000 cm^3. The data were analysed in a repeated measures ANOVA, with soil treatment as the main factor, with two levels (untreated and heated). Two repeated measures factors were assessed: year with three levels (1998, 1999 and 2000), and season with four levels (wet season, early, mid and late dry seasons). Repeated measures ANOVA was used because the same 1 ha blocks (which were the unit of comparison) were repeatedly sampled in all four seasons of each year.

ANOVA assumptions of homogeneity were assessed using Cochran's test (Underwood 1997). Where significant variance heterogeneity could not be resolved with data transformations for one or two seasons, the repeated measures ANOVA was performed with the remaining levels of the factor "season". Where heterogeneity of variances was significant in more than two seasons, non-parametric analyses were performed separately on the soil treatment, year and seasonal effects. A Mann-Whitney *U*-test was used for analysis of the soil treatment, and Friedman ANOVA by ranks, which is appropriate for repeated measures analyses, was performed on the seasonal effects (Zar 1999). Where the Friedman ANOVA detected a significant difference, a Wilcoxon's matched pair analysis was undertaken as a *post-hoc* test, with a Bonferroni adjustment of significance level for multiple comparisons, to determine where differences lay (Sokal and Rohlf 1995). For the exotic species and grasses groups, significant heterogeneity of variance in the 1998 data could not be resolved by transformations, therefore the year fluctuations were analysed from 1998 to 2000 using a Friedman's ANOVA by ranks, while the soil treatment and seasonal fluctuations were analysed in a two-factor ANOVA for 1999 and 2000 data only.

5.2.2d Seed bank dynamics immediately before and after the 1999 fire season treatments

An examination was made of the soil seed bank before and after the implementation of fire season treatments in 1999 (described in Chapter 2). Data from untreated and heated soils for control, early burnt and late burnt blocks between May 1999 and February 2000 were assessed.

A three-factor ANOVA was used to examine differences between fire treatments, with three levels (unburnt, early and late dry season burnt); soil treatment, with two levels (untreated and heated); and season of soil collection, which was a repeated measures factor, with four levels (early, mid and late dry season 1999 and wet season 2000). Cochran's test was used to assess homogeneity of variances and all problems were resolved by either log (x +1) data transformation and/or excluding one of the four levels of the factor "season" from the analysis.

An assessment was also made of the effect of the 1999 fires on the "active" component of the seed bank (see Figure 5.1), through comparisons of the untreated soil samples from control and burnt blocks. An independent *t*-test was performed on the control and early burnt untreated soil seed bank collected in July 1999 (the first collection after the early dry season fire). An independent *t*-test was also performed on the control and late burnt untreated soil seed bank collected in October 1999 (the first collection after the late dry season fire).

Separate analyses were performed for species richness per sample, total seed bank density, native and exotic species, growth form groups and common species with at least 5% of total seed bank abundance. Variance heterogeneity was checked using a Cochran's test (Underwood 1997). Significant variance heterogeneity could not be resolved by data transformation for *Glycine tomentella* and *Indigofera hirsuta* in the

July 1999 collections, and therefore non-parametric Mann-Whitney *U*-tests were performed.

5.2.2e Seed bank dynamics following fire season treatments

The soil seed bank was assessed for fire effects during the dry season following the 1999 fires (i.e. soil samples collected between May and October 2000) and the effects of exposure to heat shock and smoke. The data were analysed using a three-factor ANOVA with the factor soil treatment possessing three levels (untreated, heated and smoked soil); fire season with three levels (unburnt, and burnt in the early or late dry season of 1999); and season of soil collection as a repeated measures factor, with three levels (early, mid and late dry season). Where significant differences for one of the seasons could not be resolved by data transformation, the three-factor ANOVA was undertaken using the remaining two seasons.

5.2.2f Comparison of seed bank composition with the standing vegetation

To examine the relationship between soil seed bank and the standing vegetation, a Principle Components Analysis (PCA) was performed using the CANOCO program (ter Braak and Smilauer 1998) on a data set containing the species composition in the 180 floristic surveys, recorded between 1997 and 2001 (Chapter 3) and the 288 soil seed bank samples collected from July 1997 to October 2000. The PCA was based on species presence or absence data, as methods of estimating abundance differed between the floristic surveys and the soil seed bank samples.

5.2.2g Fire effects on Corymbia clarksoniana *seed production*

The effect of fire season on seed production of the dominant tree, *Corymbia clarksoniana*, in the year following fire, was based on the density of capsules on the ground, converted to seed density (m^{-2}) using the mean number of seeds per capsule estimated from 30 capsules. An initial assessment of statistical differences employed a one-factor ANOVA with three levels (unburnt, early and late dry season burnt), with blocks nested within fire treatments. However, Cochran's tests indicated heterogeneity of variances could not be resolved with data transformations. Therefore a non-parametric Kruskal-Wallis ANOVA by ranks was used to assess the statistical significance of differences between fire treatments. This test does not allow for nesting of block replicates, so the 50 replicates from each 1 ha block were pooled to provide 150 replicates for each fire treatment. A Mann-Whitney *U*-test was used as a *post-hoc* comparison, with a Bonferroni adjustment of significance level for multiple comparisons (Sokal and Rohlf 1995).

5.3 Results

5.3.1 Seed bank dynamics pre- and post-mid dry season 1997 fire

A total of 26 species were detected in the germinable soil seed bank (henceforth referred to as "seed bank") collected in July 1997, and no significant differences in species richness were detected between soil depths or with soil treatment (Figure 5.5a; Table 5.1). Total seed bank density was greatest below 3 mm depth and more seeds germinated from soil collected after the fire than in untreated soil collected prior to the fire (Figure 5.5b; Table 5.1).

The results of soil treatment and differences between soil depths for species groups and individual species are displayed in Tables 5.1 and 5.2. More seedlings of upright forbs germinated from burnt soil than heated soil collected prior to the fire. The density of seedling emergence of the dominant grass, *Heteropogon triticeus*, was significantly higher in burnt soil compared with untreated and heated soil collected prior to the fire. Soil heating increased the germination of ephemeral forbs as a group and the common ephemeral *Indigofera hirsuta*, compared to untreated and burnt soil, but inhibited the germination of grasses as a group and the common grass, *Digitaria breviglumis*.

The seed banks of native species and ephemeral forbs were significantly denser below 3 mm, while that of upright perennial forbs and grasses were significantly more abundant at a depth of 3 to 20 mm than the surface 3 mm and 20 to 40 mm. The seed bank of the common ephemeral forb, *Indigofera hirsuta* was more abundant at 20 to 40 mm than in the surface 3 mm. A significant interaction between soil treatment and soil depth was detected for native species as a group.

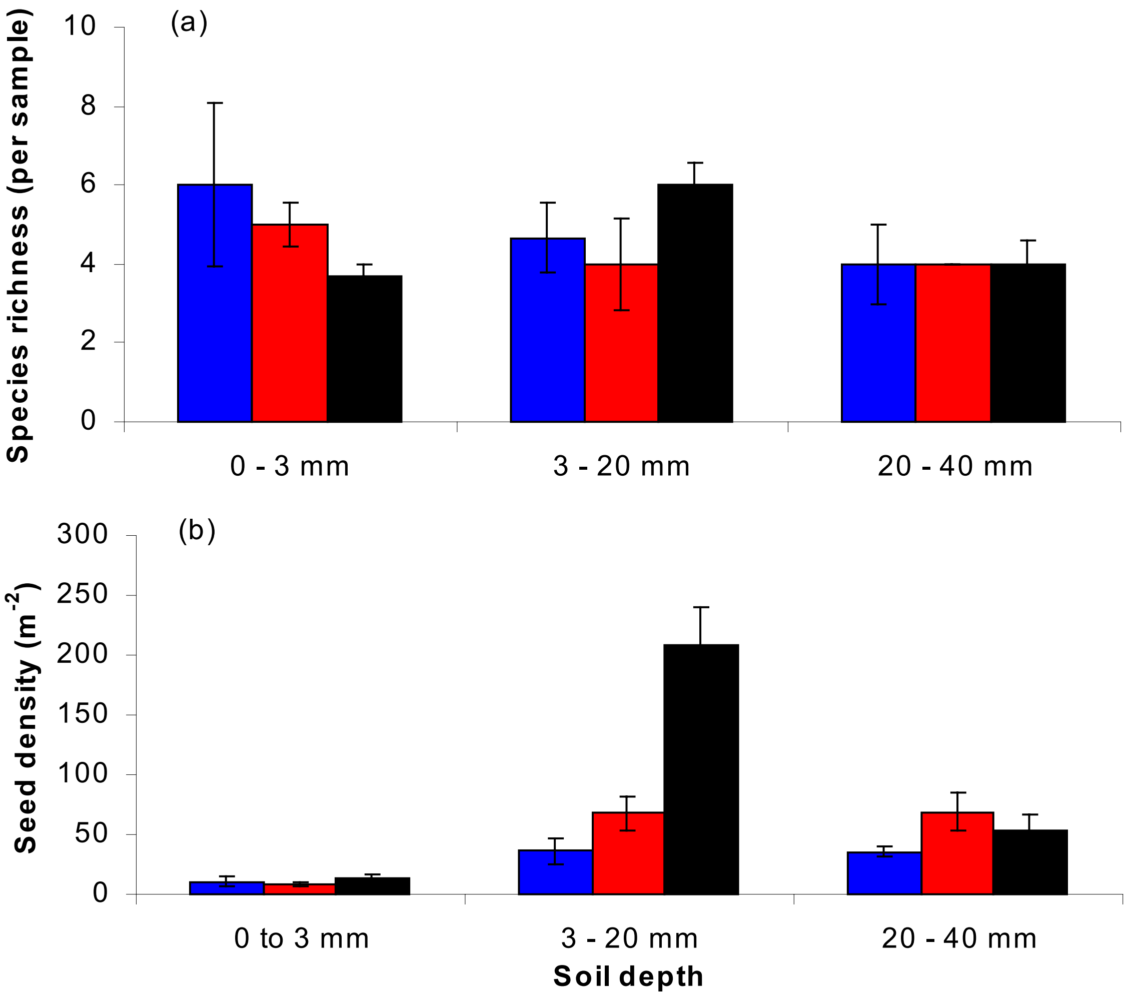


Figure 5.5. Mean (! 1 standard error) (a) species richness per sample and (b) total seed density of germinable soil seed bank, collected in eucalypt savanna at Cape Cleveland, before and after the 1997 mid dry season fire. Soil samples were collected prior to fire and remained untreated (🟦); collected prior to fire and heated in an oven at 85ºC for 45 minutes (🟥); or collected after fire, but otherwise untreated (■). Sample area varies between soil depths. 0 – 3, surface samples from a depth of 0 to 3 mm, with a surface area of 1 m^{-2}; 3 – 20 samples from 3 to 20 mm depth, with a surface area of 0.18 m^{-2}; 20 – 40, samples from 20 to 40 mm depth, with a surface area of 0.15 m^{-2}.

Table 5.1. ANOVA results of soil treatment and depth of germinable soil seed bank collected before and after fire in July 1997 at Cape Cleveland. *Log*, log (x + 1) transformation was used to rectify heterogeneity of variances; *Kruskal-Wallis*, the non-parametric Kruskal-Wallis ANOVA by ranks used due to unresolvable variance heterogeneity. $F_{2,18}$, F value, denominator d.f., numerator d.f.; F or H values without an asterisk (*) are not significantly different at $P > 0.01$; $*P < 0.01$; $**P < 0.001$. Scheffe's *post-hoc* test results of the significant differences within soil treatments and soil depths are provided. U, soil collected prior to fire and untreated; H, soil collected prior to fire and heated in oven at 85° C for 45 minutes; B, soil collected after fire but other wise untreated. 3 mm, 0 to 3 mm soil depth; 20mm, 3 to 20 mm soil depth; 40mm, 20 to 40 mm soil depth.

Dependent factors	Soil treatment	Soil depth	Soil treatment x Soil depth
Species richness	$F_{2,18} = 0.247$	$F_{2,18} = 0.831$	$F_{4,18} = 1.143$
Combined species (n = 26) *logged*	$F_{2,18} = 9.436*$ B > U	$F_{2,18} = 52.872**$ 20mm and 40mm > 3mm	$F_{4,18} = 3.450$
Native species (n = 20) *logged*	$F_{2,18} = 11.304**$ B > U	$F_{2,18} = 65.072**$ 20mm and 40mm > 3mm	$F_{4,18} = 4.578*$
Exotic species (n = 6) *logged*	$F_{2,18} = 0.511$	$F_{2,18} = 1.452$	$F_{4,18} = 0.530$
Subshrubs (n = 2) *logged*	F = 2.491	$F_{2,18} = 0.831$	$F_{4,18} = 0.740$
Upright perennial forbs (n = 5)	$F_{2,18} = 6.119*$ B > H	F = 12.124** 20mm > 3mm and 40mm	$F_{4,18} = 2.882$
Twining perennial forbs (n = 7) *logged*	$F_{2,18} = 5.867$	$F_{2,18} = 3.999$	$F_{4,18} = 0.662$
Ephemeral forbs (n= 5) *logged*	$F_{2,18} = 27.898**$ H > U and B	$F_{2,18} = 12.811**$ 20mm and 40mm > 3mm	$F_{4,18} = 2.810$
Indigofera hirsuta logged	$F_{2,18} = 29.871**$ H > U and B	$F_{2,18} = 12.628**$ 40mm > 3mm	$F_{4,18} = 2.614$
Grasses (n = 4) *logged*	$F_{2,18} = 37.396**$ U and B > H	$F_{2,18} = 7.539*$ 20mm >3mm and 40mm	$F_{4,18} = 2.355$
Digitaria breviglumis Kruskal-Wallis	$H_{2,18} = 9.928*$ U > H	$H_{2,18} = 3.099$	
Heteropogon triticeus logged	$F_{2,18} = 29.495**$ B > U and H	$F_{2,18} = 3.981$	$F_{4,18} = 1.681$
Non-grass monocots (n = 3)	$F_{2,18} = 2.991$	$F_{2,18} = 1.504$	$F_{4,18} = 0.908$

Table 5.2. Mean (standard error) germinable soil seed bank density of native and exotic species, growth form groups and common species, collected at three soil depths before and after the July 1997 fire at Cape Cleveland. Untreated, soil collected prior to fire and untreated; Heated, soil collected prior to fire and heated in oven at 85º C for 45 minutes; Burnt, soil collected after fire but other wise untreated. 0 - 3mm, 0 to 3 mm soil depth; 3 - 20 mm, 3 to 20 mm soil depth; 20 - 40 mm, 20 to 40 mm soil depth.

	Untreated 0 - 3mm	Untreated 3 - 20 mm	Untreated 20 - 40 mm	Heated 0 - 3mm	Heated 3 - 20 mm	Heated 20 - 40 mm	Burnt 0 - 3mm	Burnt 3 - 20 mm	Burnt 20 - 40mm
Native species (n = 20)	9.67 (4.26)	30.22 (6.81)	35.56 (4.44)	7.33 (0.88)	64.23 (10.52)	64.23 (10.52)	13.33 (2.19)	200.23 (33.10)	48.89 (12.37)
Exotic species (n = 6)	0.67 (0.33)	5.67 (5.67)	4.44 (4.44)	1.67 (0.88)	3.78 (3.78)	8.89 (2.22)	0.67 (0.33)	7.56 (5.00)	4.44 (2.22)
Subshrubs (n = 2)	0.33 (0.33)	0.00 (0.00)	2.22 (2.22)	0.67 (0.33)	3.78 (3.78)	6.67 (3.85)	0.67 (0.33)	0.00 (0.00)	0.00 (0.00)
Upright perennial forbs (n = 5)	1.67 (0.88)	9.44 (3.78)	0.00 (0.00)	1.67 (1.67)	3.78 (1.89)	0.00 (0.00)	0.67 (0.67)	20.78 (6.81)	6.67 (0.00)
Twining perennial forbs (n= 7)	0.33 (0.33)	3.78 (1.89)	6.67 (3.85)	1.33 (0.33)	9.45 (5.00)	13.33 (0.00)	0.33 (0.33)	0.00 (0.00)	2.22 (2.22)
Ephemeral forbs (n = 5)	0.33 (0.33)	1.89 (1.89)	13.33 (6.67)	4.33 (0.33)	43.45 (9.45)	48.89 (13.52)	0.00 (0.00)	3.78 (1.89)	2.22 (2.22)
Indigofera hirsuta	0.33 (0.33)	1.89 (1.89)	13.33 (6.67)	3.67 (0.33)	41.56 (7.56)	46.67 (13.88)	0.00 (0.00)	1.89 (1.89)	2.22 (2.22)
Grasses (n = 4)	5.67 (2.19)	17.00 (5.67)	15.56 (4.44)	1.00 (0.58)	7.56 (7.56)	0.00 (0.00)	11.00 (2.65)	171.90 (32.94)	37.78 (17.78)
Digitaria breviglumis	2.67 (1.33)	5.67 (0.00)	13.33 (3.85)	1.00 (0.58)	0.00 (0.00)	0.00 (0.00)	1.33 (1.33)	37.78 (13.22)	6.67 (3.85)
Heteropogon triticeus	1.67 (1.20)	1.89 (1.89)	2.22 (2.22)	0.00 (0.00)	7.56 (7.56)	0.00 (0.00)	9.67 (1.86)	132.23 (19.99)	26.67 (13.88)
Non-grass monocots (n = 3)	2.00 (1.53)	3.78 (1.89)	2.22 (2.22)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	1.33 (0.33)	11.33 (6.54)	4.44 (4.44)

5.3.2 Seasonal and annual fluctuations in soil seed bank with time since fire

Seasonal and annual fluctuations were detected in the seed bank in the first three years following the mid dry season fire of 1997, and soil heating increased the germination of several species and species groups. Species richness of the germinants from the seed bank was significantly increased by soil heating and was significantly higher in 1999 and 2000 than 1998 (Figure 5.6a; Table 5.3). Species richness was also higher in the mid and late dry season compared to the wet season, and in the late dry season than in the early dry season. Soil heating increased overall seedling numbers, and total seed bank was higher in 1999 and 2000 than 1998 (Figure 5.6b; Table 5.3). Total seed bank density was also higher in the mid and late dry season compared to the wet season, and in the late dry season than in the early dry season.

The annual and seasonal fluctuations in seed bank, and the effect of soil heating on seed germination, for individual species and species groups are presented in Tables 5.3 and 5.4a-c. The germination of subshrubs as a group, the common subshrubs, *Triumfetta rhomboidea*, the common twiner, *Pycnospora lutescens*, ephemeral forbs as a group and the common ephemeral forb, *Indigofera hirsuta* was increased by soil heating. Soil heating did not significantly inhibit the germination of any species or species groups.

Seed banks of native and exotic species, grasses and non-grass monocots were denser in 1999 and 2000 than 1998, and the seed bank of ephemeral forbs was more abundant in 2000 than 1998.

The seed bank of native species was greater in the mid and late dry seasons compared to the wet season, and in the late dry season than in the early dry season. Seed banks of exotic species and grasses were more abundant in the late dry season than the wet season. Seed bank density of *T. rhomboidea* was greater in the mid and late dry seasons than the wet season, and in the late dry season than in the early and mid dry seasons. Seed banks of twining perennial forbs and the dominant grass, *Heteropogon triticeus*, were greater in the mid dry season than the wet season. The non-grass monocot seed bank was greater in the late dry season than the wet and early dry seasons.

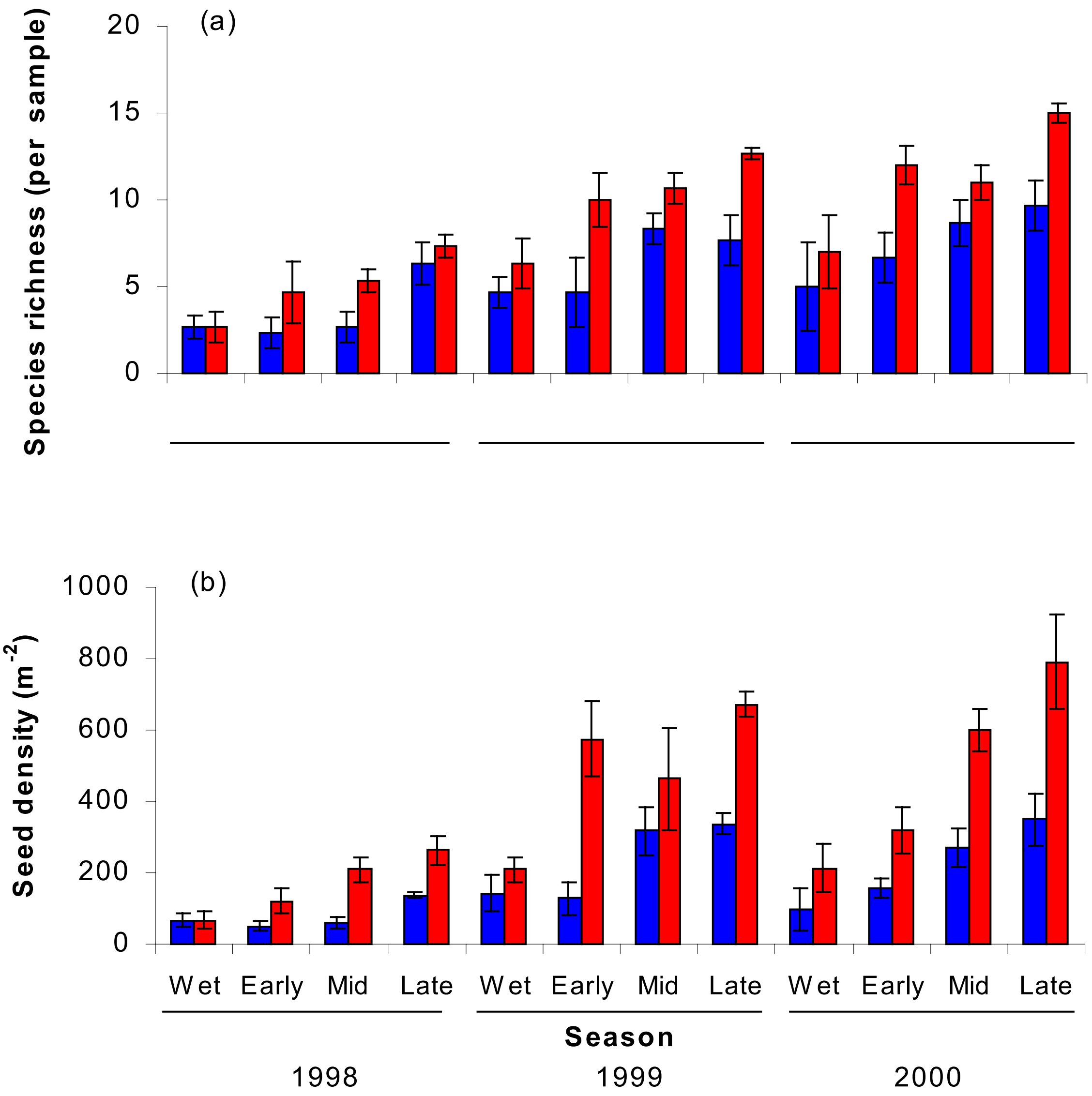


Figure 5.6. Mean (! 1 standard error) (a) species richness per sample and (b) total seed density of germinable soil seed bank, collected in eucalypt savanna at Cape Cleveland, between February 1998 and October 2000, in sites last burnt in July 1997. Soil samples remained untreated (🟦); or were heated in an oven at 85ºC for 45 minutes (🟥). Sample area equals 0.05 m^{-2} in February 1998 and 0.08 m^{-2} for all other samples. Soil samples collected in four seasons of each year: Wet, mid wet season, i.e. February; Early, early dry season, i.e. May; Mid, mid dry season, i.e. July; Late, late dry season, i.e. October.

Table 5.3. Statistical significance of differences between soil treatment, annual and seasonal fluctuations in germinable soil seed bank collected between February 1998 and October 2000 in eucalypt savanna last burnt in July 1997, at Cape Cleveland. *Log*, log (x + 1) transformation was used to rectify heterogeneity of variances; *non-parametric*, the non-parametric Mann-Whitney *U*-test was used for soil treatment and Friedman's ANOVA by ranks were used for annual and seasonal fluctuations where variance heterogeneity could not be resolved by data transformation. $F_{2,8}$ indicates *F* value, denominator d.f., numerator d.f.; *F*, *U* or ❹^{2} values without an asterisk (*) are not significantly different at $P > 0.01$; *$P < 0.01$; **$P < 0.001$. Results from a Scheffe's *post hoc* test, Wilcoxon matched pair test for Friedman ANOVA, of significant differences between soil treatments and soil depths are provided. U, untreated soil; H, soil heated in oven at 85°C for 45 minutes; 98, 1998; 99, 1999; 00, 2000; W, wet season; E, early dry season; M, mid dry season; L, late dry season.

	Soil Treatment	Year	Season	Soil Treatment x Year	Soil Treatment x Season	Year x Season	Soil Treatment x Year x Season
Species richness	$F_{1,4}$ = 34.152* H > U	$F_{2,8}$ = 22.640** 99 & 00 > 98	$F_{3,12}$ = 10.649* L & M > W, L > E	$F_{2,8}$ = 1.246	$F_{3,12}$ = 1.166	$F_{6,24}$ = 0.733	$F_{6,24}$ = 0.365
All species (n = 64)	$F_{1,4}$ = 34.994* H > U	$F_{2,8}$ = 47.237** 99 & 00 > 98	$F_{3,12}$ = 27.192** M & L > W, L > E	$F_{2,8}$ = 6.291	$F_{3,12}$ = 4.291	$F_{6,24}$ = 2.681	$F_{6,24}$ = 1.754
Native species (n = 49)	$F_{1,4}$ = 19.168	$F_{2,8}$ = 56.554** 99 & 00 > 98	$F_{3,12}$ = 22.445** M & L > W, L > E	$F_{2,8}$ = 7.806	$F_{3,12}$ = 1.956	$F_{6,24}$ = 1.383	$F_{6,24}$ = 1.307
Exotic species (n = 15) *Treatment X Season 99 & 00, log*; *Friedman for year*	$F_{1,4}$ = 4.586	❹$^{2}_{2,24}$ = 16.909** 99 & 00 > 98	$F_{3,12}$ = 6.094* L > W		$F_{3,12}$ = 1.151		
Subshrubs (n = 9) *Non-parametric*	U_{1} = 4.753** H > U	❹$^{2}_{2,24}$ = 4.388	❹$^{2}_{3,18}$ = 5.832				
Triumfetta rhomboidea non-parametric	U_{1} = 215.000** H > U	❹$^{2}_{2,24}$ = 5.143	❹$^{2}_{3,18}$ = 10.703				

Table 5.3. (cont.)

	Soil Treatment	Year	Season	Soil Treatment x Year	Soil Treatment x Season	Year x Season	Soil Treatment x Year x Season
Upright perennial forbs (n = 9) *Non-parametric*	$U_1 = 540.000$	❹$^2_{2,24} = 7.243$	❹$^2_{3,18} = 9.226$				
Twining perennial forbs (n = 16) *log*	$F_{1,4} = 5.008$	$F_{2,8} = 8.313$ $P < 0.011$	$F_{3,12} = 6.131$* M > W	$F_{2,8} = 0.030$	$F_{3,12} = 0.886$	$F_{6,24} = 1.019$	$F_{6,24} = 3.391$
Pycnospora lutescens non-parametric	$U_1 = 213.000$** H > U	❹$^2_{2,24} = 3.031$	❹$^2_{3,18} = 4.991$				
Ephemeral forbs (n= 12) *non-parametric*	$U_1 = 62.500$** H > U	❹$^2_{2,24} = 16.929$** 00 > 98	❹$^2_{3,18} = 4.587$				
Indigofera hirsuta non-parametric	$U_1 = 1.500$** H > U	❹$^2_{2,24} = 4.392$	❹$^2_{3,18} = 6.971$				
Grasses (n = 10) *Treatment x Season 99 & 00*; *Friedman for Year*	$F_{1,4} = 6.188$	❹$^2_{2,24} = 14.439$** 99 & 00 > 98	$F_{3,12} = 9.864$** L > W		$F_{3,12} = 1.675$		
Digitaria breviglumis Non-parametric	$U_1 = 522.500$	❹$^2_{2,24} = 13.703$** 00 > 98	❹$^2_{3,18} = 8.396$				
Heteropogon triticeus non-parametric	$U_1 = 421.500$* U > H	❹$^2_{2,24} = 12.286$* 99 > 98	❹$^2_{3,18} = 14.978$* E, M & L > W				
Non-grass monocots (n = 6) *non-parametric*	$U_1 = 643.500$	❹$^2_{2,24} = 16.353$** 99 & 00 > 98	❹$^2_{3,18} = 30.986$** L > W & E				

Table 5.4a. Mean (standard error) untreated and heated germinable soil seed bank density (m^{-2}) of natives and exotic species, growth form groups and common species, collected in the wet season, early, mid and late dry seasons of **1998** at Cape Cleveland, in savanna last burnt in July 1997. Columns are identified by the season of soil collection: Mid wet, mid wet season, i.e. February; Early, early dry season i.e. May; Mid, mid dry season, i.e. July; Late, late dry season, i.e. October.

	Untreated soil				Heated soil			
	Mid wet	Early	Mid	Late	Mid wet	Early	Mid	Late
Native species (n= 49)	66.67 (17.64)	41.67 (11.02)	45.83 (23.20)	129.17 (11.02)	46.67 (13.33)	104.17 (33.33)	175.00 (33.07)	245.83 (41.04)
Exotic species (n = 15)	0.00 (0.00)	8.33 (4.17)	12.50 (7.22)	8.33 (4.17)	20.00 (11.55)	16.67 (11.02)	33.33 (4.17)	16.67 (4.17)
Woodland trees and shrubs (n =1)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	4.17 (4.17)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Subshrubs (n = 9)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	8.33 (8.33)	20.00 (11.55)	8.33 (8.33)	33.33 (4.17)	4.17 (4.17)
Triumfetta rhomboidea	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	20.00 (11.55)	4.17 (4.17)	33.33 (41.17)	4.17 (4.17)
Upright perennial forbs (n = 9)	33.33 (6.67)	0.00 (0.00)	4.17 (4.17)	12.50 (7.22)	13.33 (13.33)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Twining perennial forbs (n = 16)	13.33 (6.67)	8.33 (4.17)	12.50 (7.22)	4.17 (4.17)	6.67 (6.67)	66.67 (33.33)	87.5 (57.28)	116.67 (57.89)
Pycnospora lutescens	13.33 (6.67)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	6.67 (6.67)	16.67 (11.02)	75.00 (57.28)	87.50 (47.32)
Ephemeral forbs (n = 12)	0.00 (0.00)	4.17 (4.17)	4.17 (4.17)	4.17 (4.17)	26.67 (6.67)	41.67 (4.17)	62.50 (14.43)	125.00 (52.04)
Indigofera hirsuta	0.00 (0.00)	4.17 (4.17)	4.17 (4.17)	0.00 (0.00)	20.00 (0.00)	33.33 (4.17)	62.50 (14.43)	87.50 (33.07)
Grasses (n = 10)	13.33 (6.67)	37.50 (7.22)	25.00 (19.09)	87.50 (26.02)	0.00 (0.00)	4.17 (4.17)	12.50 (7.22)	12.50 (7.22)
Digitaria breviglumis	13.33 (6.67)	12.50 (7.22)	4.17 (4.17)	4.17 (4.17)	0.00 (0.00)	0.00 (0.00)	4.17 (4.17)	8.33 (4.17)
Heteropogon triticeus	0.00 (0.00)	25.00 (12.50)	16.67 (16.67)	33.33 (15.02)	0.00 (0.00)	4.17 (4.17)	0.00 (0.00)	0.00 (0.00)
Non-grass monocots (n = 6)	6.67 (6.67)	0.00 (0.00)	12.50 (12.50)	16.67 (16.67)	0.00 (0.00)	0.00 (0.00)	12.50 (7.22)	4.17 (4.17)

Table 5.4b. Mean (standard error) of untreated and heated germinable soil seed bank density (m^{-2}) of natives and exotic species, growth form groups and common species, collected in the wet season, early, mid and late dry seasons of **1999** at Cape Cleveland, in savanna last burnt in July 1997. Columns are identified by the season of soil collection: Mid wet, mid wet season, i.e. February; Early, early dry season i.e. May; Mid, mid dry season, i.e. July; Late, late dry season, i.e. October.

	Untreated soil				Heated soil			
	Mid wet	Early	Mid	Late	Mid	Early	Mid	Late
Native species (n = 49)	66.67 (29.17)	75.00 (40.18)	279.17 (48.05)	295.83 (41.04)	187.50 (33.07)	470.83 (86.10)	391.67 (141.85)	537.50 (19.09)
Exotic species (n = 15)	75.00 (62.92)	54.17 (11.02)	37.50 (19.09)	41.67 (29.17)	20.83 (15.02)	104.17 (34.11)	70.83 (29.17)	133.33 (25.34)
Woodland trees and shrubs (n =1)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Subshrubs (n = 9)	8.33 (8.33)	12.50 (12.50)	4.17 (4.17)	4.17 (4.17)	16.67 (4.17)	108.33 (18.16)	54.17 (35.60)	91.67 (39.75)
Triumfetta rhomboidea	0.00 (0.00)	0.00 (0.00)	4.17 (4.17)	4.17 (4.17)	4.17 (4.17)	79.17 (33.33)	54.17 (35.60)	91.67 (39.75)
Upright perennial forbs (n = 9)	12.50 (0.00)	0.00 (0.00)	25.00 (14.43)	8.33 (4.17)	0.00 (0.00)	4.17 (4.17)	12.50 (7.22)	16.67 (4.17)
Twining perennial forbs (n = 16)	12.50 (12.50)	37.50 (14.43)	62.50 (28.87)	79.17 (33.33)	95.83 (53.20)	250.00 (111.10)	137.52 (101.04)	170.83 (43.50)
Pycnospora lutescens	0.00 (0.00)	4.17 (4.17)	12.50 (7.22)	8.33 (8.33)	50.00 (33.07)	187.50 (94.65)	95.83 (83.65)	58.33 (23.20)
Ephemeral forbs (n = 12)	66.67 (54.17)	33.33 (18.16)	16.67 (16.67)	4.17 (4.17)	87.50 (21.65)	187.50 (38.19)	183.33 (72.29)	95.83 (25.34)
Indigofera hirsuta	0.00 (0.00)	4.17 (4.17)	0.00 (0.00)	0.00 (0.00)	62.50 (19.09)	141.67 (39.75)	120.083 (46.93)	62.50 (14.43)
Grasses (n = 10)	33.33 (18.16)	41.67 (30.05)	191.67 (67.06)	175.00 (26.02)	8.33 (8.33)	20.83 (20.83)	41.67 (15.02)	195.83 (41.67)
Digitaria breviglumis	29.17 (15.02)	25.00 (25.00)	45.83 (39.75)	25.00 (19.09)	8.33 (8.33)	4.17 (4.17)	20.83 (11.02)	25.00 (7.22)
Heteropogon triticeus	4.17 (4.17)	16.67 (16.67)	120.83 (43.50)	150.00 (25.00)	0.00 (0.00)	12.50 (15.50)	16.67 (4.17)	170.83 (48.05)
Non-grass monocots (n = 6)	8.33 (4.17)	4.17 (4.17)	16.67 (16.67)	66.67 (4.17)	0.00 (0.00)	4.17 (4.17)	33.33 (4.17)	100.000 (12.50)

Table 5.4c. Mean (standard error) of untreated and heated germinable soil seed bank density (m^{-2}) of natives and exotic species, growth form groups and common species, collected in the wet season, early, mid and late dry seasons of **2000** at Cape Cleveland, in savanna last burnt in July 1997. Columns are identified by the season of soil collection: Mid wet, mid wet season, i.e. February; Early, early dry season i.e. May; Mid, mid dry season, i.e. July; Late, late dry season, i.e. October.

	Untreated soil				Heated soil			
	Mid wet	Early	Mid	Late	Mid	Early	Mid	Late
Native species (n = 49)	75.00 (50.00)	141.67 (18.16)	229.17 (48.05)	295.83 (77.17)	179.17 (58.33)	258.33 (84.27)	416.67 (54.17)	525.00 (73.24)
Exotic species (n = 15)	20.83 (11.02)	16.67 (11.02)	41.67 (16.67)	54.17 (30.05)	33.33 (11.02)	58.33 (20.83)	183.33 (11.02)	266.67 (65.48)
Woodland trees and shrubs (n =1)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Subshrubs (n = 9)	4.17 (4.17)	4.17 (4.17)	0.00 (0.00)	20.83 (15.02)	8.33 (4.17)	33.33 (22.05)	137.50 (19.09)	241.67 (46.96)
Triumfetta rhomboidea	4.17 (4.17)	0.00 (0.00)	0.00 (0.00)	20.83 (15.02)	8.33 (4.17)	29.17 (18.16)	137.50 (19.09)	220.83 (44.10)
Upright perennial forbs (n = 9)	4.17 (4.17)	29.17 (18.16)	33.33 (20.83)	45.83 (29.17)	8.33 (4.17)	12.50 (7.22)	16.67 (11.02)	50.00 (21.65)
Twining perennial forbs (n = 16)	20.83 (4.17)	29.17 (8.33)	41.67 (15.02)	20.83 (4.17)	87.50 (50.52)	83.33 (34.11)	225.00 (59.07)	129.17 (58.33)
Pycnospora lutescens	0.00 (0.00)	8.33 (4.17)	4.17 (4.17)	0.00 (0.00)	33.33 (15.02)	37.50 (26.02)	158.33 (63.05)	41.67 (23.30)
Ephemeral forbs (n = 12)	8.33 (8.33)	8.33 (4.17)	12.50 (0.00)	20.83 (8.33)	91.67 (15.02)	75.00 (25.00)	133.33 (32.54)	154.17 (49.12)
Indigofera hirsuta	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	79.17 (11.02)	37.50 (14.43)	108.33 (29.17)	95.83 (32.54)
Grasses (n = 10)	45.83 (33.33)	83.33 (25.34)	125.00 (21.65)	141.67 (23.20)	12.50 (12.50)	87.50 (45.07)	62.50 (43.90)	70.83 (8.33)
Digitaria breviglumis	20.83 (8.33)	20.83 (8.33)	50.00 (25.00)	104.17 (22.05)	12.50 (12.50)	25.00 (19.09)	54.17 (48.05)	62.50 (0.00)
Heteropogon triticeus	16.67 (16.67)	45.83 (23.20)	54.17 (25.34)	25.00 (14.43)	0.00 (0.00)	37.50 (19.09)	4.17 (4.17)	4.17 (4.17)
Non- grass monocots (n = 6)	12.50 (12.50)	4.17 (4.17)	58.33 (11.02)	100.00 (12.50)	4.17 (4.17)	25.00 (19.09)	25.00 (0.00)	145.83 (43.50)

5.3.3 Seed bank dynamics immediately before and after the 1999 fire season treatments

The seed bank of 39 species was detected between May 1999 and February 2000. Soil heating significantly increased the species richness of seedlings from the seed bank (Figure 5.7a; Table 5.5). Species richness was highest in seed banks collected in the mid and late dry seasons compared to the wet season, and in the late dry season compared to the early dry season. Total density of seedlings germinating from the seed bank was significantly increased by soil heating (Figure 5.7b; Table 5.5). There was a significantly higher total seed bank density detected in the early, mid and late dry seasons compared to the wet season, and in the late dry season compared to the early dry season. A significant interaction between soil treatment and season of collection was also demonstrated.

The annual and seasonal fluctuations, and the effect of soil heating, for individual species and species groups are presented in Tables 5.5 and 5.6. The germination of native species, twining perennial forbs, the common twiner *P. lutescens*, ephemeral forbs, and the common ephemeral *I. hirsuta*, was significantly increased by soil heating. Significant interactions between fire and season of soil collection were detected for natives as a group and for the common grass *Digitaria breviglumis*, indicating seed bank density increased following early and late dry season fires (Table 5.5).

The seed bank density of native species was higher in the mid and late dry seasons than the wet season, and in the late rather than early dry season. The seed bank of upright perennial forbs was more abundant in the late dry season rather than the wet season, and that of twining perennial forbs was greater in the early and late dry seasons than the wet season. Seed bank density of grasses and non-grass monocots was higher in the mid and late dry seasons than in the wet season, and in the late rather than mid dry season. The seed bank of the common grass *D. breviglumis* was more abundant in the late dry season than the wet and early dry seasons, while that of *H. triticeus* was greater in the late rather than mid dry season, in the mid dry season compared with the early dry season. A significant interaction was detected between soil treatment and season of collection for the seed banks of native species, upright perennial forbs, grasses and *I. hirsuta*.

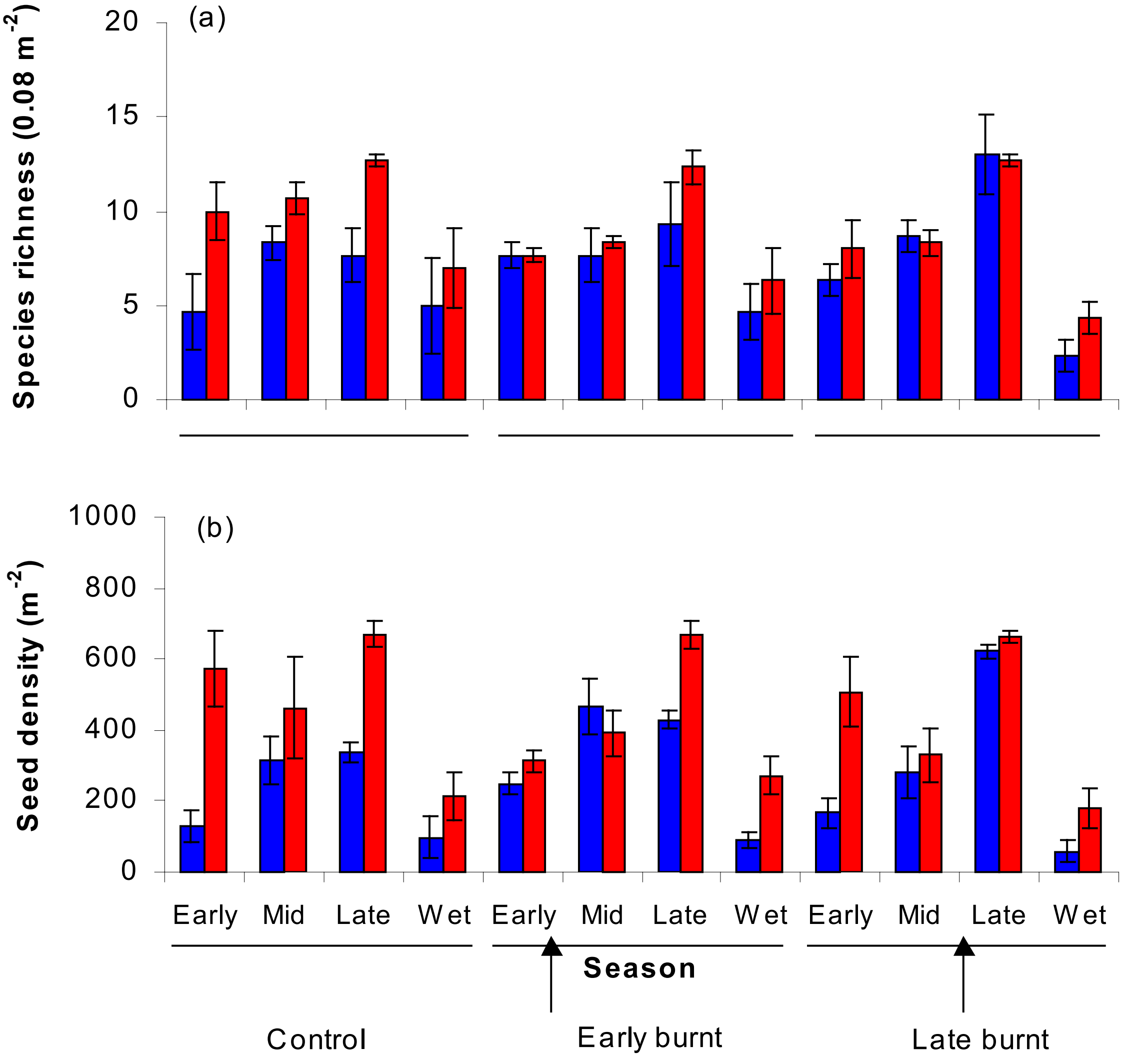


Figure 5.7. Mean (! 1 standard error) (a) species richness and (b) total seed density of germinable soil seed bank, collected in eucalypt savanna at Cape Cleveland, between May 1999 and February 2000. Soil samples remained untreated (🟦); or were heated in an oven at 85ºC for 45 minutes (🟥). Arrows indicate timing of early and late dry season fires in relation to soil sample collections. Early, early dry season, i.e. May 1999; Mid, mid dry season, i.e. July1999; Late, late dry season, i.e. October 1999; Wet, mid wet season, i.e. February 2000. Control, sites last burnt in July 1997; Early burnt, sites burnt July 1997 and May 1999; Late burnt, sites burnt July 1997 and October 1999.

Table 5.5. ANOVA of the statistical significance of differences between fire treatment, soil treatment and season of soil seed bank collection, before and after the 1999 fire season treatments in eucalypt savanna at Cape Cleveland. *log* indicates log (x + 1) transformation was used to rectify heterogeneity of variances; $F_{2,12}$ indicates F value, denominator d.f., numerator d.f.; F values without an asterisk (*) are not significantly different at $P > 0.01$; *$P < 0.01$; **$P < 0.001$.; *Early & Late*, indicate the subset of seasons of collection used in analysis where data transformation did not resolve variance heterogeneity for other seasons. Results presented from a Scheffe's *post-hoc* test for soil treatment, fire and season of collection differences. U, untreated soil; H, soil heated in oven at 85°C for 45 minutes; W, wet season; E, early dry season; M, mid dry season; L, late dry season.

Species group	Fire	Soil Treatment	Season	Fire x Soil Treatment	Fire x season	Soil Treatment x Season	Fire x Soil Treatment x Season
Species richness	$F_{2,12} = 0.107$	$F_{1,12} = 11.814$** H > U	$F_{3,36} = 22.381$** M & L > W, L > E	$F_{2,12} = 2.553$	$F_{6,36} = 1.602$	$F_{3,36} = 0.439$	$F_{6,36} = 0.628$
All species (n = 39)	$F_{2,12} = 0.036$	$F_{1,12} = 24.340$** H > U	$F_{3,36} = 53.822$** E, M & L > W; L > E	$F_{2,12} = 2.028$	$F_{6,36} = 2.332$	$F_{3,36} = 4.928$*	$F_{6,36} = 2.436$
Native species (n = 31)	$F_{2,12} = 0.569$	$F_{1,12} = 21.539$** H > U	$F_{3,36} = 64.940$** E, M & L > W; L > E & M	$F_{2,12} = 0.897$	$F_{6,36} = 4.083$*	$F_{3,36} = 7.236$**	$F_{6,36} = 2.048$
Exotic species (n = 8)	$F_{2,12} = 5.730$	$F_{1,12} = 1.600$	$F_{3,36} = 2.197$	$F_{2,12} = 4.202$	$F_{6,36} = 1.167$	$F_{3,36} = 0.753$	$F_{6,36} = 1.480$
Subshrubs (n = 5) *Early, Mid & Late*	$F_{2,12} = 5.122$	$F_{1,12} = 6.814$	$F_{2,24} = 3.485$	$F_{2,12} = 6.817$	$F_{4,24} = 0.357$	$F_{2,24} = 0.126$	$F_{4,24} = 1.345$
Upright perennial forbs *(n = 6) Mid, Late & Wet*	$F_{2,12} = 3.214$	$F_{1,12} = 0.624$	$F_{2,24} = 12.538$* L > W	$F_{2,12} = 0.225$	$F_{4,24} = 2.809$	$F_{2,24} = 6.585$*	$F_{6,36} = 0.710$
Twining perennial forbs (n = 10) *log*	$F_{2,12} = 1.283$	$F_{1,12} = 11.019$* H > U	$F_{3,36} = 9.823$** E & L > W	$F_{2,12} = 0.322$	$F_{6,36} = 1.100$	$F_{3,36} = 0.879$	$F_{4,24} = 1.539$
Glycine tomentella	$F_{2,12} = 0.232$	$F_{1,12} = 3.889$	$F_{3,36} = 0.627$	$F_{2,12} = 0.022$	$F_{6,36} = 1.205$	$F_{3,36} = 0.795$	$F_{6,36} = 0.556$

Table 5.5 (cont.)

Species group	Fire	Soil Treatment	Season	Fire x Soil Treatment	Fire x season	Soil Treatment x Season	Fire x Soil Treatment x Season
Pycnospora lutescens *Log;Early, Late*	$F_{2,12} = 2.858$	$F_{1,12} = 44.555$** H > U	$F_{1,12} = 1.561$	$F_{2,12} = 0.682$	$F_{2,12} = 1.162$	$F_{1,12} = 1.763$	$F_{2,12} = 0.981$
Ephemeral forbs (n = 9) *Mid, Late & Wet*	$F_{2,12} = 3.263$	$F_{1,12} = 64.001$** H > U	$F_{2,24} = 1.583$	$F_{2,12} = 2.559$	$F_{4,24}= 0.726$	$F\ 2_{,24} = 1.819$	$F_{4,24} = 0.913$
Indigofera hirsuta *Log; Early, Mid & Late*	$F_{2,12} = 1.441$	$F_{1,12} = 93.866$** H > U	$F_{2,24} = 0.112$	$F_{2,12} = 0.408$	$F_{4,24} = 1.840$ $P < 0.154$	$F_{2,24} = 5.559$*	$F_{4,24} = 3.761$
Grasses (n = 6)	$F_{2,12} = 2.054$	$F_{1,12} = 6.091$	$F_{3,36} = 52.607$** M & L > W, L > M	$F_{2,12} = 1.714$	$F_{6,36} = 2.822$	$F_{3,36} = 4.457$*	$F_{6,36} = 1.739$
Digitaria breviglumis	$F_{2,12} = 1.687$	$F_{1,12} = 4.529$	$F_{3,36} = 13.395$** L > W & E	$F_{2,12} = 1.534$	$F_{6,36} = 5.652$**	$F_{3,36} = 2.658$	$F_{6,36} = 1.428$
Heteropogon triticeus *Early, Mid & Late*	$F_{2,12} = 1.820$	$F_{1,12} = 4.934$	$F_{2,24} = 32.653$** M & L > E, L > M	$F_{2,12} = 0.908$	$F_{4,24} = 0.560$	$F_{2,24} = 2.472$	$F_{4,24} = 1.339$
Non-grass monocots *(n = 3), Mid,Late & Wet*	$F_{2,12} = 0.418$	$F_{1,12} = 0.268$	$F_{2,24} = 47.042$** M & L > W, L > M	$F_{2,12} = 2.527$	$F_{4,24} = 1.654$	$F_{2,24} = 0.217$	$F_{4,24} = 2.073$

Table 5.6a. Mean (standard error) germinable soil seed bank density (m^{-2}) of untreated and heated soil samples collected between May 1999 and February 2000 at Cape Cleveland, from the **control** treatment (i.e. savanna that remained unburnt since July 1997). Columns are identified by the season of soil collection: Early, early dry season i.e. May; Mid, mid dry season, i.e. July; Late, late dry season, i.e. October.

	Untreated soil				Heated soil			
	Early	Mid	Late	Wet	Early	Mid	Late	Wet
Native species (n = 31)	75.00 (40.18)	279.17 (48.05)	295.83 (41.04)	75.00 (50.00)	470.83 (86.10)	391.67 (141.85)	537.50 (19.09)	179.17 (58.33)
Exotic species (n = 8)	54.17 (11.02)	37.50 (19.09)	41.07 (29.17)	20.83 (11.02)	104.17 (34.11)	70.83 (29.17)	133.33 (25.34)	33.33 (11.02)
Subshrubs (n = 5)	12.50 (12.50)	4.17 (4.17)	4.17 (4.17)	4.17 (4.17)	108.33 (18.16)	54.17 (35.60)	91.67 (39.75)	8.33 (4.17)
Upright perennial forbs (n = 6)	0.00 (0.00)	25.00 (14.43)	8.33 (4.17)	4.17 (4.17)	4.17 (4.17)	12.50 (7.22)	16.67 (4.17)	8.33 (4.17)
Twining perennial forbs (n = 10)	37.50 (14.43)	62.50 (28.87)	79.17 (33.33)	20.83 (4.17)	250.00 (111.10)	137.50 (101.04)	170.83 (43.50)	87.50 (50.52)
Glycine tomentella	0.00 (0.00)	20.83 (20.83)	25.00 (19.09)	8.33 (4.17)	29.17 (18.16)	16.67 (8.33)	29.17 (15.02)	33.33 (22.05)
Pycnospora lutescens	4.17 (4.17)	12.50 (7.22)	8.33 (8.33)	0.00 (0.00)	187.50 (94.65)	95.83 (93.65)	58.33 (23.20)	33.33 (15.02)
Ephemeral forbs (n = 9)	33.33 (18.16)	16.67 (16.67)	4.17 (4.17)	8.33 (8.33)	187.50 (38.19)	183.33 (72.29)	95.83 (25.34)	91.67 (15.02)
Indigofera hirsuta	4.17 (4.17)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	141.67 (39.75)	120.83 (46.96)	62.50 (14.43)	79.17 (11.02)
Grasses (n =6)	41.67 (30.05)	191.67 (67.06)	175.00 (26.02)	45.83 (33.33)	20.83 (20.83)	41.67 (15.02)	195.83 (41.67)	12.50 (12.50)
Digitaria breviglumis	25.00 (25.00)	45.83 (39.75)	25.00 (19.09)	20.83 (8.33)	4.17 (4.17)	20.83 (11.02)	25.00 (7.22)	12.50 (12.50)
Heteropogon triticeus	16.67 (8.33)	120.83 (43.50)	150.00 (25.00)	16.67 (16.67)	12.50 (12.50)	16.67 (4.17)	170.83 (48.05)	0.00 (0.00)
Non-grass monocots (n = 3)	4.17 (4.17)	16.67 (16.67)	66.67 (4.17)	12.50 (12.50)	4.17 (4.17)	33.33 (4.17)	100.50 (12.50)	4.17 (4.17)

Table 5.6b. Mean (standard error) germinable soil seed bank density (m^{-2}) of untreated and heated soil samples collected between May 1999 and February 2000 at Cape Cleveland, from **early burnt** savanna (May 1999), after the early dry season soil seed bank collection. Columns are identified by the season of soil collection: Early, early dry season i.e. May; Mid, mid dry season, i.e. July; Late, late dry season, i.e. October.

	Untreated soil				Heated soil			
	Early	Mid	Late	Wet	Early	Mid	Late	Wet
Native species (n = 31)	191.67 (36.32)	445.83 (67.06)	400.00 (61.66)	75.00 (28.87)	308.33 (27.33)	358.33 (49.12)	612.50 (57.28)	250.00 (52.04)
Exotic species (n = 8)	58.33 (11.02)	20.83 (15.02)	29.17 (23.20)	16.67 (11.02)	4.17 (4.17)	33.33 (16.67)	54.17 (35.60)	20.83 (11.02)
Subshrubs (n = 5)	25.00 (25.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	8.33 (8.33)	16.67 (11.02)	8.33 (4.17)
Upright perennial forbs (n = 6)	41.67 (15.02)	45.83 (18.16)	50.00 (19.09)	20.83 (20.83)	0.00 (0.00)	0.00 (0.00)	75.00 (31.46)	4.17 (4.17)
Twining perennial forbs (n = 10)	62.50 (7.22)	8.33 (4.17)	45.83 (18.16)	12.50 (7.22)	83.33 (29.17)	70.83 (22.05)	100.00 (33.07)	50.00 (19.09)
Glycine tomentella	29.17 (8.33)	0.00 (0.00)	4.17 (4.17)	4.17 (4.17)	29.17 (8.33)	8.33 (8.33)	25.00 (12.50)	25.00 (12.50)
Pycnospora lutescens	0.00 (0.00)	0.00 (0.00)	4.17 (4.17)	0.00 (0.00)	16.67 (11.02)	20.83 (20.83)	33.33 (15.02)	4.17 (4.17)
Ephemeral forbs (n = 9)	37.50 (19.09)	33.33 (20.83)	25.00 (14.43)	16.67 (11.02)	191.67 (18.16)	195.85 (34.16)	175.00 (38.19)	191.67 (18.16)
Indigofera hirsuta	4.17 (4.17)	4.17 (4.17)	8.33 (4.17)	0.00 (0.00)	150.00 (26.02)	179.17 (23.20)	141.67 (35.60)	170.83 (32.54)
Grasses (n = 6)	79.17 (34.11)	341.67 (29.17)	262.50 (83.23)	29.17 (4.17)	33.33 (20.83)	83.33 (32.54)	237.50 (90.14)	16.67 (11.02)
Digitaria breviglumis	58.33 (23.20)	112.50 (12.50)	41.67 (16.67)	20.83 (4.17)	4.17 (4.17)	12.50 (7.22)	66.67 (42.29)	4.17 (4.17)
Heteropogon triticeus	12.50 (12.50)	200.00 (40.18)	212.50 (64.15)	8.33 (8.33)	29.17 (16.67)	54.17 (29.17)	170.83 (48.05)	0.00 (0.00)
Non-grass monocots (n = 3)	4.17 (4.17)	37.50 (19.09)	45.83 (8.33)	12.50 (7.22)	4.17 (4.17)	33.33 (8.33)	62.50 (26.02)	0.00 (0.00)

Table 5.6c. Mean (standard error) germinable soil seed bank density (m^{-2}) of untreated and heated soil samples collected between May 1999 and February 2000 at Cape Cleveland, from **late burnt** savanna (October 1999), prior to the late dry season soil seed bank collection. Columns are identified by the season of soil collection: Early, early dry season i.e. May; Mid, mid dry season, i.e. July; Late, late dry season, i.e. October.

	Untreated soil				Heated soil			
	Early	Mid	Late	Wet	Early	Mid	Late	Wet
Native species (n = 31)	141.67 (23.20)	245.83 (60.52)	575.00 (12.50)	16.67 (11.02)	475.00 (109.21)	291.67 (67.06)	650.00 (26.02)	158.33 (46.96)
Exotic species (n = 8)	25.00 (19.09)	33.33 (15.02)	45.83 (11.02)	41.67 (29.17)	33.33 (27.32)	37.50 (7.22)	12.50 (7.27)	20.83 (11.02)
Subshrubs (n = 5)	29.17 (4.17)	0.00 (0.00)	25.00 (12.00)	0.00 (0.00)	33.33 (27.32)	8.33 (8.33)	12.50 (7.22)	4.17 (4.17)
Upright perennial forbs (n = 6)	12.50 (7.22)	50.00 (19.09)	50.00 (7.22)	8.33 (4.17)	0.00 (0.00)	4.17 (4.17)	83.33 (29.17)	4.17 (4.17)
Twining perennial forbs (n = 10)	66.67 (23.20)	66.67 (15.02)	108.33 (37.03)	33.33 (33.33)	125.00 (19.09)	70.83 (25.34)	120.83 (15.02)	45.83 (27.32)
Glycine tomentella	16.67 (8.33)	20.83 (11.02)	20.83 (15.02)	4.17 (4.17)	29.17 (15.02)	29.17 (11.02)	20.83 (8.33)	20.83 (11.02)
Pycnospora lutescens	0.00 (0.00)	12.50 (12.50)	37.50 (26.02)	0.00 (0.00)	50.00 (7.22)	20.83 (20.83)	50.00 (26.02)	12.50 (7.22)
Ephemeral forbs (n = 9)	4.17 (4.17)	16.67 (11.02)	50.00 (19.09)	8.33 (4.17)	341.67 (101.38)	116.67 (18.16)	79.17 (16.67)	120.83 (41.67)
Indigofera hirsuta	4.17 (4.17)	8.33 (4.17)	33.33 (16.67)	0.00 (0.00)	295.83 (102.40)	104.17 (25.34)	75.00 (19.09)	112.50 (37.50)
Grasses (n = 6)	54.17 (16.67)	95.83 (29.17)	287.50 (59.07)	4.17 (4.17)	8.33 (8.33)	108.33 (18.16)	312.50 (28.87)	0.00 (0.00)
Digitaria breviglumis	8.33 (8.33)	25.00 (12.50)	112.50 (28.87)	0.00 (0.00)	0.00 (0.00)	25.00 (12.50)	112.50 (14.43)	0.00 (0.00)
Heteropogon triticeus	41.67 (4.17)	62.50 (19.09)	175.00 (45.07)	4.17 (4.17)	4.17 (4.17)	66.67 (18.16)	179.17 (45.83)	0.00 (0.00)
Non-grass monocots (n = 3)	0.00 (0.00)	50.00 (26.02)	100.00 (12.50)	4.17 (4.17)	0.00 (0.00)	20.83 (15.02)	54.17 (8.33)	4.17 (4.17)

Table 5.7. Results of an independent *t*-test of untreated germinable soil seed bank after early dry season fire (control vs early burnt, July 1999 soil collection) and late dry season fire (control vs late burnt, October 1999 soil collection) at Cape Cleveland. *U*, Mann-Whitney *U*-test used for *Indigofera hirsuta* and *Glycine tomentella* July 1999 collected soil seed bank, due to variance heterogeneity. n.s., not significant at *P* > 0.01.

Species and groups (n = number of species in mid/late)	Mid dry season (d.f. = 4)		Late dry season (d.f. = 4)	
	t value	P value	t value	P value
Species richness	0.392	n.s.	2.101	n.s.
All species n = 23/20	1.449	n.s.	8.308	**< 0.001**
Native species n = 18/17	2.020	n.s.	6.508	**< 0.003**
Exotic species n = 5/3	0.686	n.s.	0.134	n.s.
Subshrubs n = 1/3	1.000	n.s.	1.581	n.s.
Upright perennial forbs n = 4/3	0.898	n.s.	5.00	**< 0.007**
Twining perennial forbs d.f. = 6/6	1.857	n.s.	0.585	n.s.
Glycine tomentella	*U* = 3.000	n.s.	0.171	n.s.
Pycnospora lutescens	1.732	n.s.	1.067	n.s.
Ephemeral forbs n = 5/4	0.625	n.s.	1.868	n.s.
Indigofera hirsuta	*U* = 3.000	n.s.	0.179	n.s.
Grasses n = 5/2	2.051	n.s.	1.743	n.s.
Digitaria breviglumis	1.600	n.s.	2.528	n.s.
Heteropogon triticeus	1.337	n.s.	0.171	n.s.
Non-grass monocots n = 2/2	0.822	n.s.	2.530	n.s.

Analyses of the untreated seed bank immediately following the early dry season fire indicated that neither total seed density nor species richness significantly differed between the unburnt control and early dry season burnt blocks (Table 5.7). However, the late dry season fire significantly increased the total untreated seed bank and that of native species and upright perennial forbs (Table 5.7), indicating that the late dry season fire released seed from dormancy. A considerable increase in germination from the untreated seed bank samples collected following the late dry season fire was detected for ephemeral forbs and *Indigofera hirsuta* (Tables 5.6a - c), however low germinable seed banks in the second of three late burnt blocks reduced the chance of detecting a significant effect.

5.3.4 Seed bank dynamics following fire season treatments

A total of 53 species was detected in the seed bank during the dry season in the year following the 1999 fires. Species richness was not influenced by fire history (Figure 5.8a; Table 5.8). However species richness was significantly increased after soil heating compared to untreated soil, and was significantly higher in the late dry season compared to the early dry season.

No significant variation with fire treatment was detected for total seed bank density (Figure 5.8b; Table 5.8). However, soil heating increased the total number of seedlings that geminated from the seed bank, which was significantly higher in the late rather than early dry season. There was a significant interaction between soil treatment and the season of seed bank collection.

Seed bank densities in the dry season of 2000, and the statistical significance of differences between treatments, of individual species and species groups are displayed in Tables 5.8 and 5.9. The seed bank of *I. hirsuta* was denser in blocks burnt in the early dry season fires of 1999 than blocks that remained unburnt. Conversely, the seed bank density of subshrubs was significantly reduced by both early and late dry season fires of 1999, while that of non-grasss monocots was lower in blocks burnt in late dry season fires compared with the control blocks that remained unburnt in 1999.

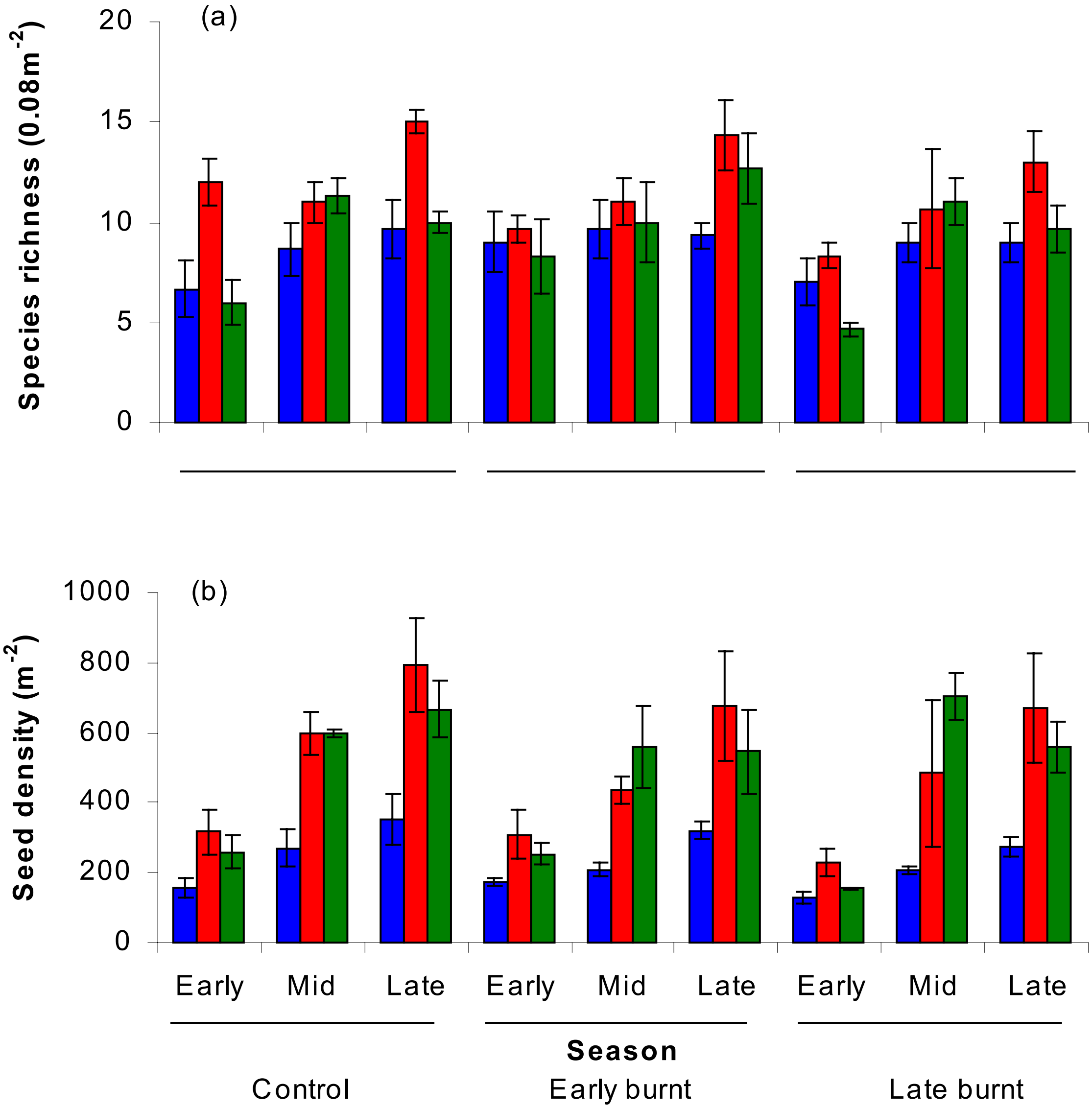


Figure 5.8. Mean (± 1 standard error) (a) species richness and (b) total seed density of germinable soil seed bank, collected in eucalypt savanna at Cape Cleveland, between May and October 2000. Soil samples remained untreated (🟦); or were heated in an oven at 85ºC for 45 minutes (🟥); or exposed to smoke at ambient temperature for 60 minutes (🟩). Early, soil collected in the early dry season, i.e. May; Mid, soil collected in the mid dry season, i.e. July; Late, soil collected in the late dry season, i.e. October. Control, sites last burnt in July 1997; Early burnt, sites burnt July 1997 and May 1999; Late burnt, sites burnt July 1997 and October 1999.

Table 5.8. ANOVA results of fire treatment, soil treatment, and seasonal of collection in germinable soil seed bank collected in the year following fire, between May and October 2000, at Cape Cleveland. *Log*, log (x + 1) transformation was used to rectify heterogeneity of variances; $F_{2,12}$ indicates F value, denominator d.f., numerator d.f.; F values without an asterisk (*) are not significantly different at $P > 0.01$; *$P < 0.01$; **$P < 0.001$.; *Early & Late*, indicate seasons of collection used in analysis where data transformation did not resolve variance heterogeneity for other seasons. *non-parametric*, the non-parametric Kruskal-Wallis ANOVA by ranks used for fire history and soil treatment, and Friedman ANOVA by ranks for seasonal fluctuations, where variance heterogeneity could not be resolved by data. Results from a Scheffe's post hoc test (Mann-Whitney *U*-test for Kruskal-Wallis ANOVA and Wilcoxon matched pair test for Friedman ANOVA) of significant differences between soil treatments and soil depths are provided. U, untreated soil; H, soil heated in oven at 85°C for 45 minutes; S, exposure to smoke at ambient temperature for 30 minutes; W, wet season; E, early dry season; M, mid dry season; L, late dry season.

Species Group	Fire	Soil Treatment	Season	Fire x Soil Treatment	Fire x season	Soil Treatment x Season	Fire x Soil Treatment x Season
Species richness	$F_{2,18}$ = 1.452	$F_{2,18}$ = 8.267* H > U	$F_{2,36}$ =20.171** L > E	$F_{4,18}$ = 0.514	$F_{4,36}$ = 0.786	$F_{4,36}$ = 3.250	$F_{8,36}$ = 0.765
All species (n = 53) *Early & Late*	$F_{2,18}$ = 1.458	$F_{2,18}$ = 213.734** H > U	$F_{1,18}$ = 95.182** L > E	$F_{4,18}$ = 0.082	$F_{2,18}$ = 0.643	$F_{2,18}$ = 6.021**	$F_{4,18}$ = 0.098
Native species (n = 40) *Early & Late*	$F_{2,18}$ = 0.546	$F_{2,18}$ = 10.255** H & S > U	$F_{1,18}$ = 86.145** L > E	$F_{4,18}$ = 0.091	$F_{2,18}$ = 0.018	$F_{2,18}$ = 4.873	$F_{4,18}$ = 0.374
Exotic species (n = 13) *log*	$F_{2,18}$ = 3.224	$F_{2,18}$ = 7.922* H > U	$F_{2,36}$ = 13.215** M & L > E	$F_{4,18}$ = 1.234	$F_{4,36}$ = 9.083**	$F_{4,36}$ = 4.082*	$F_{8,36}$ = 1.986
Subshrubs (n = 5) *Early & Late*	$F_{2,18}$ = 28.357** U > E & L	$F_{2,18}$ = 61.928** H > U & S	$F_{1,18}$ = 3.539	$F_{4,18}$ = 27.179**	$F_{2,18}$ = 8.539*	$F_{2,18}$ = 3.657	$F_{4,18}$ = 7.377**
Triumfetta rhomboidea *Non-parametric*	$H_{2,18}$ = 2.498	$H_{2,18}$ = 41.822** H > U & S	❹$^{2}_{2,36}$ = 21.500** L > E				

Table 5.8 (cont.)

Species group	Fire	Soil Treatment	Season	Fire x Soil Treatment	Fire x season	Soil Treatment x Season	Fire x Soil Treatment x Season
Uprightperennial forbs (n = 6)	$F_{2,18} = 0.866$	$F_{2,18} = 9.085$* S > U & H	$F_{2,36} = 6.302$* L > E	$F_{4,18} = 0.338$	$F_{4,36} = 0.721$	$F_{4,36} = 1.266$	$F_{8,36} = 0.337$
Spermacoce brachystema	$F_{2,18} = 2.496$	$F_{2,18} = 3.751$	$F_{2,36} = 2.800$	$F_{4,18} = 0.751$	$F_{4,36} = 1.798$	$F_{4,36} = 0.494$	$F_{8,36} = 1.531$
Twining perennial forbs (n = 12), *log*	$F_{2,18} = 2.305$	$F_{2,18} = 15.887$** H > U & S	$F_{2,36} = 2.760$	$F_{4,18} = 2.374$	$F_{4,36} = 0.451$	$F_{4,36} = 0.453$	$F_{8,36} = 0.318$
Pycnospora lutescens *Early & Late*	$F_{2,18} = 0.390$	$F_{2,18} = 9.197$* H > U & S	$F_{1,18} = 0.000$	$F_{4,18} = 0.396$	$F_{2,18} = 0.733$	$F_{2,18} = 0.419$	$F_{8,36} = 0.262$
Ephemeral forbs (n = 12) *log*	$F_{2,18} = 3.512$	$F_{2,18} = 31.243$** H > U & S	$F_{2,36} = 5.912$* L > E	$F_{4,18} = 0.489$	$F_{4,36} = 0.950$	$F_{4,36} = 0.060$	$F_{8,36} = 0.480$
Indigofera hirsuta *Log; Mid & Late*	$F_{2,18} = 7.161$* E > U	$F_{2,18} = 55.135$** H > U & S	$F_{2,36} = 0.619$	$F_{4,18} = 0.632$	$F_{2,18} = 5.484$	$F_{4,36} = 0.136$	$F_{8,36} = 1.879$
Grasses (n = 10) *Early & Late*	$F_{2,18} = 0.143$	$F_{2,18} = 16.749$** S > U & H	$F_{2,36} = 36.856$** L > E	$F_{4,18} = 0.460$	$F_{2,18} = 3.304$	$F_{4,36} = 5.312$	$F_{8,36} = 0.771$
Digitaria breviglumis *Non-parametirc*	$H_{2,18} = 1.057$	$H_{2,18} = 36.878$** S > U & H	❹$^{2}{}_{2,36} = 6.433$				
Heteropogon contortus *Non-parametric*	$H_{2,18} = 4.175$	$H_{2,18} = 8.622$	❹$^{2}{}_{2,36} = 6.433$				
Heteropogon triticeus	$F_{2,18} = 1.939$	$F_{2,18} = 15.506$** S > U & H	$F_{2,36} = 6.321$* M > L	$F_{4,18} = 1.277$	$F_{4,36} = 0.724$	$F_{4,36} = 4.605$*	$F_{8,36} = 0.948$
Non-grass monocots (n = 6)	$F_{2,18} = 13.167$** U > L	$F_{2,18} = 0.205$	$F_{2,36} = 31.443$** L > E & M	$F_{4,18} = 0.518$	$F_{4,36} = 5.573$**	$F_{4,36} = 0.617$	$F_{8,36} = 0.890$
Commelina spp Mid & Late	F = 4.657 $P < 0.023$	F = 3.909 $P < 0.039$	$F_{2,36} = 6.293$	$F_{4,18} = 0.548$	$F_{2,18} = 0.832$	$F_{2,18} = 1.353$	$F_{4,18} = 0.353$

The germination of native species was significantly increased by both heating and smoking treatments. The germination of subshrubs, the common subshrub, *Triumfetta rhomboidea*, twining perennial forbs, the common twiner, *Pycnospora lutescens*, ephemeral forbs and the common ephemeral *I. hirsuta*, was significantly increased by heating compared to untreated soil and exposure to smoke. Exposure to smoke significantly increased the germination of upright perennial forbs, grasses and the common grasses, *Digitaria breviglumis* and *H. triticeus*, compared with heated and untreated soil. A significant interaction between fire and soil treatment was demonstrated for subshrubs, with the highest seed bank density detected in heated samples collected from control blocks, which remained unburnt since 1997.

The seed bank density of natives, *T. rhomboidea*, upright perennial forbs, ephemeral forbs, grasses was significantly greater during the late rather than early dry season. The seed bank of exotic species was significantly greater in the mid and late, rather than early dry season. The seed bank of *H. triticeus* was larger in the mid rather than late dry season and that of the non-grass monocots was greater during the late dry season rather than both early and mid dry seasons.

A significant interaction between fire and season of soil collection was demonstrated for exotic species, subshrubs and non-grass monocots. Exotic species and *H. triticeus* displayed a significant interaction between soil treatment and season of collection, with exotic seed bank density was highest in late dry season samples that were heated, while *H. triticeus* seed bank density was highest in mid dry season samples that were smoked. Significant interactions were also detected between the combinations of all three factors in the subshrub seed bank.

Table 5.9a. Mean (standard error) germinable soil seed bank density (m^{-2}) collected from **control** treatment (i.e. savanna last burnt in July 1997), at Cape Cleveland between May and October 2000. The first letter of column headings denotes soil treatment: U, untreated; H, heated; S, smoked. The second letter indicates season of collection E, early dry season i.e. May; M, mid dry, i.e. July; L, late dry season, i.e. October.

Species group	U & E	U & M	U & L	H & E	H & M	H & L	S & E	S & M	S & L
All species (n = 53)	158.33 (27.33)	270.83 (54.17)	350.00 (73.24)	316.67 (65.09)	600.00 (61.66)	791.67 (133.92)	258.33 (48.05)	595.83 (11.02)	666.67 (79.17)
Native species (n = 40)	141.67 (18.16)	225.00 (47.32)	295.83 (77.17)	258.33 (84.27)	416.67 (54.17)	529.17 (72.65)	220.83 (42.29)	558.83 (4.17)	616.67 (85.49)
Exotic species (n = 13)	16.67 (11.02)	41.67 (16.67)	54.17 (30.05)	58.33 (20.83)	183.33 (11.02)	262.50 (64.15)	37.50 (7.22)	37.50 (14.43)	50.00 (7.22)
Woodland trees & shrubs (n = 2)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Subshrubs (n = 5)	4.17 (4.17)	0.00 (0.00)	20.83 (15.02)	33.33 (22.05)	137.50 (19.09)	241.67 (46.96)	0.00 (0.00)	8.33 (8.33)	12.50 (12.50)
Triumfetta rhomboidea	0.00 (0.00)	0.00 (0.00)	20.83 (15.02)	29.17 (18.16)	137.50 (19.09)	220.83 (44.10)	0.00 (0.00)	4.17 (4.17)	8.33 (8.33)
Upright perennial forbs (n = 6)	29.17 (18.16)	33.33 (20.83)	45.83 (29.17)	12.50 (7.22)	16.67 (11.02)	50.00 (21.65)	37.50 (19.09)	41.67 (8.33)	100.00 (14.43)
Spermacoce brachystema	29.17 (18.16)	1250 (12.50)	33.33 (22.05)	4.17 (4.17)	8.33 (4.17)	37.50 (21.65)	33.33 (18.16)	20.83 (4.17)	75.00 (7.22)
Twining perennial forbs (n = 12)	29.17 (8.33)	37.50 (12.50)	141.67 (23.20)	83.33 (34.11)	225.00 (59.07)	129.17 (58.33)	16.67 (11.02)	37.50 (12.50)	33.33 (27.32)
Pycnospora lutescens	8.33 (4.17)	4.17 (4.17)	0.00 (0.00)	37.50 (26.02)	158.33 (63.05)	41.67 (23.20)	0.00 (0.00)	8.33 (8.33)	8.33 (8.33)
Ephemeral forbs (n = 12)	8.33 (4.17)	12.50 (0.00)	20.83 (8.33)	75.00 (25.00)	133.33 (32.54)	154.17 (49.12)	16.67 (4.17)	20.83 (15.02)	29.17 (15.02)
Indigofera hirsuta	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	37.50 (14.43)	108.33 (29.17)	95.83 (32.54)	0.00 (0.00)	8.33 (8.33)	0.00 (0.00)
Grasses (n = 10)	83.33 (25.34)	125.00 (21.65)	141.67 (23.20)	87.50 (45.07)	62.50 (43.90)	70.83 (8.33)	187.50 (28.87)	441.67 (18.16)	358.33 (41.04)
Digitaria breviglumis	20.83 (8.33)	50.00 (25.00)	104.17 (22.05)	25.00 (19.09)	54.17 (48.05)	62.50 (0.00)	104.17 (11.02)	237.50 (50.52)	270.83 (20.83)
Heteropogon contortus	12.50 (7.22)	12.50 (12.50)	4.17 (4.17)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	54.17 (48.05)	25.00 (25.00)
Heteropogon triticeus	45.83 (23.20)	54.17 (25.34)	25.00 (14.43)	37.50 (19.09)	4.17 (4.17)	4.17 (4.17)	62.50 (14.43)	141.67 (8.33)	54.17 (18.16)
Non-grass monocots (n = 6)	4.17 (4.17)	58.33 (11.02)	100.00 (12.50)	25.00 (19.09)	25.00 (0.00)	145.83 (43.50)	0.00 (0.00)	45.83 (4.17)	133.33 (22.05)
Commelina spp.	4.17 (4.17)	41.67 (4.17)	66.67 (25.34)	0.00 (0.00)	12.50 (7.22)	37.50 (19.09)	0.00 (0.00)	33.33 (11.02)	95.83 (36.32)

Table 5.9b. Mean (standard error) germinable soil seed bank density (m^{-2}) collected from **early burnt** savanna (last burnt in May 1999), at Cape Cleveland between May and October 2000. The first letter of column headings denotes soil treatment: U, untreated; H, heated; S, smoked. The second letter indicates season of collection E, early dry season i.e. May; M, mid dry, i.e. July; L, late dry season, i.e. October.

Species (group)	U & E	U & M	U & L	H & E	H & M	H & L	S & E	S & M	S & L
All species (n = 53)	170.83	208.33	320.83	308.33	437.50	675.00	254.17	558.33	545.83
	(11.02)	(18.16)	(25.34)	(69.35)	(38.19)	(157.29)	(32.54)	(116.89)	(119.10)
Native species (n = 40)	137.50	175.00	300.00	195.83	420.83	587.50	212.50	520.83	520.83
	(19.09)	(21.65)	(26.02)	(36.32)	(32.54)	(131.70)	(43.90)	(129.37)	(115.55)
Exotic species (n = 13)	33.33	33.33	20.83	112.50	16.67	87.50	41.67	37.50	25.00
	(15.02)	(4.17)	(4.17)	(50.52)	(11.02)	(26.02)	(23.20)	(12.50)	(7.22)
Woodland trees & shrubs (n = 2)	0.00	0.00	0.00	0.00	0.00	8.33	0.00	0.00	8.33
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(4.17)	(0.00)	(0.00)	(4.17)
Subshrubs (n = 5)	4.17	0.00	8.33	20.83	8.33	45.83	0.00	4.17	4.17
	(4.17)	(0.00)	(8.33)	(11.02)	(4.17)	(22.05)	(0.00)	(4.17)	(4.17)
Triumfetta rhomboidea	0.00	0.00	4.17	20.83	33.33	33.33	0.00	4.17	4.17
	(0.00)	(0.00)	(4.17)	(4.17)	(11.02)	(11.02)	(0.00)	(4.17)	(4.17)
Upright perennial forbs (n = 6)	25.00	29.17	58.33	8.33	8.33	20.83	20.83	75.00	79.17
	(7.22)	(15.02)	(36.32)	(8.33)	(4.17)	(15.02)	(4.17)	(43.30)	(4.17)
Spermacoce brachystema	8.33	12.50	54.17	0.00	4.17	0.00	12.50	33.33	4.17
	(4.17)	(7.22)	(32.54)	(0.00)	(4.17)	(0.00)	(7.22)	(18.16)	(4.17)
Twining perennial forbs (n = 12)	54.17	66.67	16.67	83.33	125.00	162.50	37.50	41.67	29.17
	(15.02)	(30.05)	(4.17)	(15.02)	(54.49)	(64.15)	(31.46)	(30.05)	(8.33)
Pycnospora lutescens	12.50	16.57	8.33	45.83	37.50	58.33	4.17	8.33	12.50
	(12.50)	(11.02)	(4.17)	(15.02)	(25.00)	(18.16)	(4.17)	(4.17)	(0.00)
Ephemeral forbs (n = 12)	33.33	20.83	33.33	108.33	212.50	254.17	20.83	29.17	75.00
	(22.05)	(8.33)	(15.02)	(29.17)	(38.19)	(43.50)	(8.33)	(4.17)	(19.09)
Indigofera hirsuta	4.17	8.33	20.83	20.83	187.50	183.33	0.00	4.17	54.17
	(4.17)	(8.33)	(4.17)	(11.02)	(38.19)	(41.04)	(0.00)	(4.17)	(29.17)
Grasses (n = 10)	50.00	54.17	112.50	83.33	58.33	154.17	170.83	387.50	279.17
	(19.09)	(15.02)	(33.07)	(29.17)	(41.04)	(79.49)	(48.05)	(156.12)	(71.20)
Digitaria breviglumis	20.83	25.00	50.00	54.17	16.67	58.33	83.33	141.67	187.50
	(4.17)	(7.22)	(12.50)	(25.34)	(11.02)	(23.20)	(35.60)	(46.40)	(43.30)
Heteropogon contortus	8.33	8.33	25.00	0.00	4.17	45.83	20.83	154.17	25.00
	(8.33)	(4.17)	(19.09)	(0.00)	(4.17)	(39.75)	(15.02)	(72.29)	(14.43)
Heteropogon triticeus	16.67	16.67	29.17	4.17	33.33	33.33	54.17	91.67	33.33
	(11.02)	(11.02)	(8.33)	(4.17)	(22.05)	(18.16)	(25.34)	(39.75)	(11.02)
Non-grass monocots (n = 6)	4.17	37.50	83.33	4.17	25.00	37.50	4.17	20.83	70.83
	(4.17)	(19.09)	(40.05)	(4.17)	(7.22)	(26.02)	(4.17)	(8.33)	(39.75)
Commelina spp.	4.17	33.33	66.67	0.00	20.83	8.33	4.17	20.83	45.83
	(4.17)	(20.83)	(32.54)	(0.00)	(8.33)	(4.17)	(4.17)	(8.33)	(34.11)

Table 5.9c. Mean (standard error) germinable soil seed bank density (m^{-2}) collected from **late burnt** savanna (last burnt in October 1999), at Cape Cleveland between May and October 2000. The first letter of column headings denotes soil treatment: U, untreated; H, heated; S, smoked. The second letter indicates season of collection E, early dry season i.e. May; M, mid dry, i.e. July; L, late dry season, i.e. October.

Species (group)	U & E	U & M	U & L	H & E	H & M	H & L	S & E	S & M	S & L
All species	129.17	208.17	275.00	229.17	483.33	670.83	154.17	704.17	558.33
(n = 53)	(15.02)	(11.02)	(28.87)	(37.03)	(207.46)	(155.51)	(4.17)	(65.09)	(72.65)
Native species	125.00	158.33	254.17	200.00	412.50	525.00	150.00	616.67	537.50
(n = 40)	(19.09)	(30.05)	(22.05)	(37.50)	(188.75)	(131.30)	(7.22)	(51.20)	(76.03)
Exotic species	4.17	45.83	20.83	29.17	70.83	145.83	4.17	87.50	20.83
(n = 13)	(4.17)	(20.83)	(8.33)	(11.02)	(29.17)	(35.60)	(4.17)	(19.09)	(4.17)
Woodland trees &	0.00	0.00	0.00	0.00	0.00	4.17	0.00	0.00	0.00
shrubs (n = 2)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(4.17)	(0.00)	(0.00)	(0.00)
Subshrubs	4.17	4.17	0.00	20.83	8.33	50.00	4.17	0.00	8.33
(n = 5)	(4.17)	(4.17)	(0.00)	(8.33)	(4.17)	(7.22)	(4.17)	(0.00)	(4.17)
Triumfetta	0.00	0.00	0.00	20.83	8.33	50.00	0.00	0.00	4.17
rhomboidea	(0.00)	(0.00)	(0.00)	(8.33)	(4.17)	(7.22)	(0.00)	(0.00)	(4.17)
Upright perennial	20.83	25.00	20.83	12.50	25.00	20.83	12.50	62.50	66.67
forbs	(15.02)	(12.50)	(4.17)	(7.22)	(12.50)	(15.02)	(7.22)	(19.09)	(36.32)
(n = 6)									
Spermacoce	20.83	4.17	4.17	4.17	12.50	4.17	12.50	29.17	33.33
brachystema	(15.02)	(4.17)	(4.17)	(4.17)	(12.50)	(4.17)	(7.22)	(16.67)	(33.33)
Twining perennial	4.17	20.83	8.33	70.83	145.83	112.50	20.83	45.83	16.67
forbs	(4.17)	(15.02)	(8.33)	(25.34)	(77.17)	(47.32)	(11.02)	(15.02)	(4.17)
(n = 12)									
Pycnospora	4.17	4.17	0.00	37.50	70.83	29.17	20.83	0.00	12.50
lutescens	(4.17)	(4.17)	(0.00)	(21.65)	(39.75)	(18.16)	(11.02)	(0.00)	(7.22)
Ephemeral forbs	29.17	58.33	37.50	83.33	233.33	320.83	12.50	66.67	33.33
(n = 12)	(15.02)	(18.16)	(7.22)	(39.75)	(109.29)	(121.26)	(7.22)	(15.02)	(20.83)
Indigofera hirsuta	8.3	12.50	4.17	33.33	170.83	191.67	0.00	8.33	8.33
	(4.17)	(7.22)	(4.17)	(18.16)	(90.24)	(66.67)	(0.00)	(4.17)	(8.33)
Grasses	62.50	79.17	175.00	41.67	50.00	158.33	104.17	520.83	391.67
(n = 10)	(12.50)	(15.02)	(28.87)	(23.20)	(26.02)	(39.75)	(4.17)	(27.32)	(105.16)
Digitaria	12.50	25.00	87.50	12.50	20.83	87.50	70.83	350.00	245.83
breviglumis	(0.00)	(7.22)	(19.09)	(0.00)	(11.02)	(19.09)	(11.02)	(68.84)	(37.03)
Heteropogon	0.00	0.00	45.83	0.00	8.33	20.83	0.00	83.33	91.67
contortus	(0.00)	(0.00)	(34.11)	(0.00)	(8.33)	(11.02)	(0.00)	(22.05)	(68.21)
Heteropogon	37.50	41.67	25.00	12.50	8.33	8.33	25.00	83.33	37.50
triticeus	(7.22)	(15.02)	(7.22)	(12.50)	(8.33)	(8.33)	(7.22)	(30.05)	(14.43)
Non-grass	8.33	16.67	29.12	0.00	20.83	8.33	0.00	8.33	41.67
monocots	(4.17)	(11.02)	(15.02)	(0.00)	(11.02)	(4.17)	(0.00)	(8.33)	(18.67)
(n = 6)									
Commelina spp.	8.33	16.67	16.67	0.00	4.17	8.33	0.00	8.33	41.67
	(4.17)	(11.02)	(11.02)	(0.00)	(4.17)	(4.17)	(0.00)	(8.33)	(18.16)

5.3.5 Phenology of seed production

The phenology of seed production was documented for 86 species at Cape Cleveland (Table 5.10). Mature seed was produced, with seed subsequently dispersed, by woodland trees and shrubs generally between the mid dry season to the wet season; rainforest trees and shrubs, subshrubs and ephemeral forbs throughout the dry season; and upright and twining perennial forbs, grasses and non-grass monocots throughout the year. The month with the lowest number of species with mature seed was January, with only 20 species, and was highest in May, when 52 species were recorded with mature seeds. Seed production continued through the dry season, with 59% of the species having begun seed production by the start of May, and 92% by the start of October. This indicates seed accumulated through the dry season, so that the greatest quantity of seed had been produced by the late dry season, as documented in the soil seed bank study.

5.3.6 Comparison of seed bank composition with the standing vegetation

A total of 64 species were detected in the 288 soil seed bank samples, collected during the wet season, early, mid and late dry seasons between July 1997 and October 2000 (Appendix 1). Fifty nine species (50% of total) detected in the 180 floristic surveys between 1997 an 2001 (Chapter 3) were detected in the seed bank. An additional five species were present in the seed bank, but not recorded during the floristic surveys, although all five were observed in the standing vegetation at the Cape Cleveland site, adjacent to survey plots. Therefore no additional species were detected in the soil seed bank that were not present in the standing vegetation, while only half of the species in the standing vegetation were detected in the seed bank.

The seed bank was dominated by herbaceous species, which represented 83% of the species number, and 94% of the total seed bank abundance recorded in the 288 samples. No rainforest species, only two woodland trees and shrubs, and nine subshrubs were detected in the germinable seed bank (Appendix 1). By comparison, in the floristic surveys, herbaceous species represented 61% of total species number and 84% of the abundance in the floristic surveys (Chapter 3), indicating a greater proportional representation of herbaceous species in the seed bank than standing vegetation.

Table 5.10. Phenology of seed production of eucalypt savanna plants at Cape Cleveland. Shading indicates months in which mature seed was present on plants. Records collected between 1997 to 2001. J, January; F, February etc.; * exotic species.

Species	J	F	M	A	M	J	J	A	S	O	N	D
Woodland trees and shrubs												
Acacia crassicarpa										🟩	🟩	
Alphitonia excelsa						🟩			🟩	🟩	🟩	
Cochlospermum gillivraei									🟩	🟩	🟩	
Corymbia clarksoniana									🟩	🟩	🟩	🟩
C. tessellaris	🟩											🟩
Eucalyptus platyphylla											🟩	🟩
Ficus opposita												🟩
Flueggea virosa		🟩	🟩	🟩								
*Lantana camara**				🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	
Larsenaikia ochreata	🟩				🟩		🟩	🟩	🟩	🟩	🟩	
Vitex trifolia							🟩					
Rainforest trees and shrubs												
Canarium australianum		🟩										
Diospyros geminata									🟩			
Garuga floribunda					🟩							
Mallotus philippensis											🟩	
Sterculia quadrifida											🟩	🟩
Tabernaemontana orientalis	🟩											
Subshrubs												
Abelmoschus moschatus			🟩	🟩	🟩							
Anisomeles malabarica				🟩	🟩							
Breynia oblongifolia	🟩	🟩	🟩	🟩	🟩				🟩	🟩	🟩	🟩
Cajanus confertiflorus										🟩	🟩	🟩
Grewia retusifolia			🟩	🟩	🟩	🟩	🟩					
Hibiscus meraukensis	🟩	🟩	🟩		🟩							
*Sida acuta**				🟩	🟩	🟩						
Sida cordifolia					🟩	🟩	🟩					
Sida subspicata						🟩						
*Triumfetta rhomboidea**						🟩	🟩	🟩	🟩	🟩	🟩	
Waltheria indica							🟩	🟩	🟩	🟩		
Upright perennial forbs												
*Chamaesyce hirta**						🟩						
Hybanthus enneaspermus					🟩	🟩						
Hybanthus stellarioides					🟩	🟩						
Phyllanthus virgatus		🟩	🟩	🟩	🟩					🟩	🟩	🟩
Rostellularia adscendens		🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	
Spermacoce brachystema				🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	
Vernonia cinerea	🟩				🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
Twining perennial forbs												
Cassthya filiformis			🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩		
Desmodium gangeticum			🟩	🟩	🟩			🟩	🟩	🟩	🟩	
Evolvulus alsinoides			🟩	🟩	🟩	🟩						
Galactia tenuiflora	🟩	🟩	🟩	🟩	🟩					🟩	🟩	🟩
Glycine tomentella	🟩			🟩	🟩	🟩						🟩
Jasminum didymum							🟩					
*Macroptilium atropurpureum**					🟩	🟩	🟩	🟩	🟩	🟩	🟩	

Table 5.10 (cont.)

Species	J	F	M	A	M	J	J	A	S	O	N	D
Twining perennial forbs (cont.)												
*Merremia quinquefolia**						🟩	🟩					
*Passiflora foetida**	🟩	🟩	🟩	🟩	🟩	🟩			🟩	🟩	🟩	🟩
Pycnospora lutescens	🟩	🟩	🟩	🟩	🟩							🟩
Stephania japonica			🟩									
*Tridax procumbens**									🟩	🟩	🟩	🟩
Uraria lagopodioides	🟩	🟩	🟩	🟩	🟩	🟩						
Vigna radiata				🟩	🟩							
Ephemeral forbs												
*Chamaecrista absus**		🟩	🟩	🟩	🟩							🟩
C. mimosioides			🟩	🟩	🟩							🟩
Crotalaria brevis			🟩	🟩	🟩	🟩				🟩	🟩	🟩
C. calycina	🟩	🟩	🟩	🟩	🟩							🟩
*C. goreensis**					🟩	🟩	🟩	🟩				
*C. laburnifolia**				🟩								
C. lanceolata			🟩	🟩	🟩	🟩	🟩	🟩	🟩			
C. montana			🟩	🟩	🟩	🟩						🟩
*C. pallida**			🟩	🟩	🟩	🟩	🟩					
*Emilia sonchifolia**			🟩	🟩	🟩		🟩					🟩
*Hyptis suaveolens**					🟩	🟩	🟩					
Indigofera hirsuta				🟩	🟩	🟩	🟩	🟩				
Polygala linariifolia					🟩							
*Stylosanthes humilis**								🟩	🟩	🟩		
Tephrosia juncea			🟩	🟩	🟩	🟩						
Grasses												
Alloteropsis semialata	🟩	🟩		🟩	🟩							🟩
Aristida queenslandica				🟩	🟩	🟩						
Bothriochloa bladhii					🟩	🟩						
Cymbopogon bombycinus							🟩					
Digitaria breviglumis	🟩	🟩	🟩	🟩	🟩	🟩						
Heteropogon contortus				🟩	🟩	🟩	🟩	🟩	🟩	🟩		
Heteropogon triticeus		🟩	🟩	🟩	🟩	🟩						
Imperata cylindrica										🟩	🟩	🟩
*Melinis repens**	🟩		🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
Panicum effusum	🟩	🟩	🟩	🟩	🟩							
*Panicum maximum**				🟩								
Paspalidium rarum					🟩							
Sorghum laxiflorum					🟩							
*Sporobolus jacquemontii**	🟩	🟩	🟩	🟩								
Themeda triandra	🟩	🟩	🟩	🟩								
Non-grass monocots												
Commelina spp.	🟩	🟩	🟩	🟩		🟩	🟩				🟩	🟩
Cyperus sp.				🟩	🟩	🟩						
Dianella caerulea				🟩		🟩	🟩	🟩	🟩	🟩	🟩	🟩
Eustrephus latifolius	🟩	🟩		🟩	🟩				🟩	🟩	🟩	🟩
Fimbristylis tristachya				🟩								🟩
Scleria mackaviensis				🟩	🟩	🟩						
Tacca leontopetaloides		🟩										
Number of species with mature fruit in each month	20	21	31	46	52	41	26	18	23	27	26	27

The PCA scatter plot indicated that the species composition in seed bank samples was distinct to the composition in the floristic surveys (Figure 5.9). This distinction reflects the higher species number per survey, and the greater consistency of species presence, in the floristic surveys compared with seed bank samples. While 22 species occurred in more than half of the 180 floristic surveys, only three species were recorded in more than half of the 288 seed bank samples (Appendix 1). Most (84%) of the 64 species detected in the seed bank occurred in a lower proportion of the seed bank samples than floristic surveys. *Digitaria breviglumis*, which occurred in the greatest number of seed bank samples (61%) was present in a higher percentage of the floristic surveys (94%). *Heteropogon triticeus*, the species present in the most floristic surveys (97%), was observed in only 58% of the seed banks samples. Ten species occurred in a higher percentage of seed bank samples than floristic surveys, including the ephemeral forb *I. hirsuta*, which was present in 57% of the seed bank samples and 48% of the floristic surveys.

5.3.7 Fire effects on **Corymbia clarksoniana** *seed production*

The mean number of seeds per capsule of *Corymbia clarksoniana* was 5.0 (n = 30; s.e. = 0.33). The late dry season fire of 1999 significantly reduced seed production (as estimated by capsule density on the ground) in the following year, compared to unburnt controls ($H_{2,447} = 11.175$; $P < 0.004$; Figure 5.10). Seed production in savanna burnt during the early dry season fire was not significantly different from either unburnt or late burnt sites.

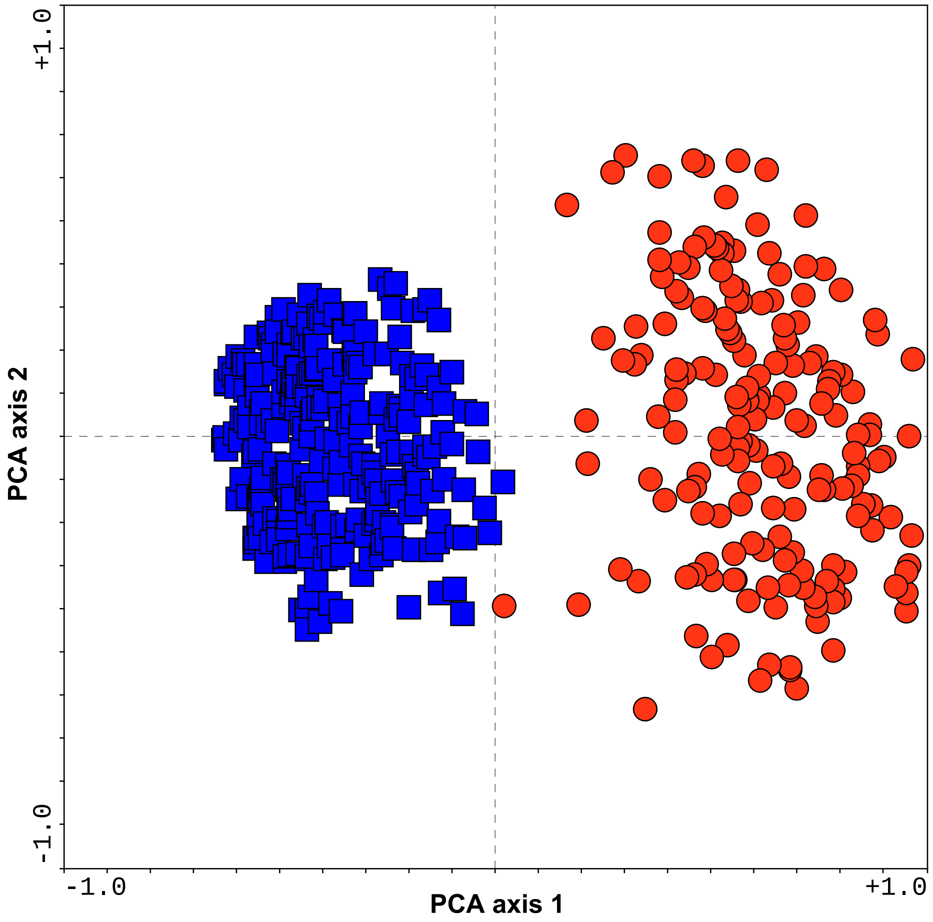


Figure 5.9. PCA scatter plot of species composition in the 288 soil seed bank samples (■); and 180 floristic surveys (●).

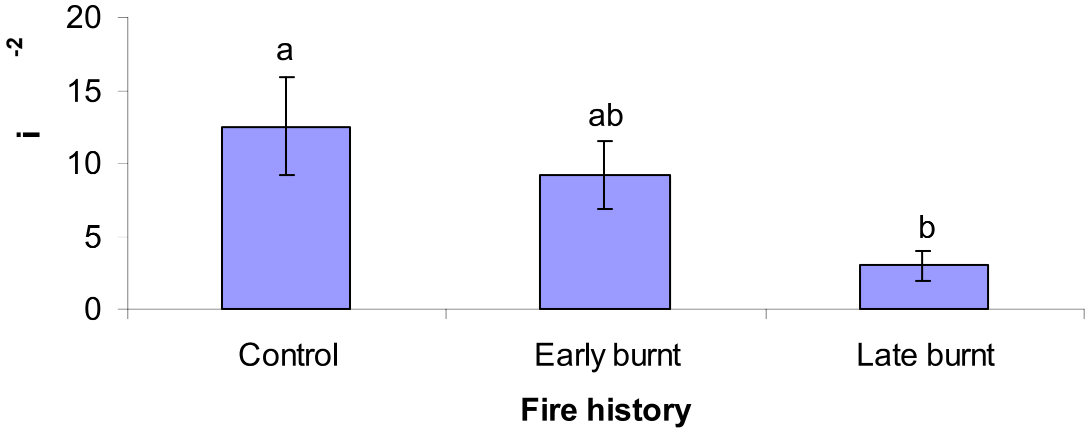


Figure 5.10. Mean (± 1 standard error) seed production of *Corymbia clarksoniana* at Cape Cleveland in December 2000, in savanna with different fire histories. Control, last burnt in July 1997; Early burnt, last burnt in May 1999; Late burnt, last burnt October 1999. Columns with different superscripts are significantly different at $P < 0.05$.

5.4 Discussion

5.4.1 The effect of fire on the balance between dormant and active soil seed banks

The germination of several individual species and species groups was significantly increased by exposure to heat shock or smoke, providing indirect evidence that fire releases seed from dormancy, and increases the active fraction of the soil seed bank (Tables 5.1, 5.3, 5.5 and 5.8). Heat shock significantly increased species richness of germinants, total density of seedlings from the seed bank, and the density of native species, exotic species, subshrubs, ephemeral and twining perennial forbs, and *Indigofera hirsuta*, *Pycnospora lutescens* and *Triumfetta rhomboidea* seed banks. Germination of grasses as a group, and the common grass *Digitaria breviglumis*, was inhibited by heat shock. These data, documenting a heat shock response by *I. hirsuta*, but not by *Glycine tomentella*, are consistent with the results of the laboratory experiments on these two forbs (Chapter 4). Heat shock has proved effective in promoting the germinable soil seed bank of a range of fire-prone communities across Australia, demonstrating its value as a treatment for assessing soil seed bank composition and importance in understanding seed dormancy mechanisms (e.g. Warcup 1980; Hopkins and Graham 1984; Skull 1992; Enright *et al*. 1997; Williams 2000).

Exposure to smoke at ambient temperature significantly increased the germination of native species, upright perennial forbs, grasses as a group and the common grasses *D. breviglumis* and *Heteropogon triticeus* from the seed bank (Table 5.8). Smoke has been reported to increase germination from the soil seed bank in a range of eucalypt woodland flora, including grasses and forbs (Enright *et al*. 1997; Roche *et al*. 1998; Lloyd *et al*. 2000; Read *et al*. 2000). In accordance with the laboratory experiment, no evidence was found that smoke plays a role in seed dormancy release for the ten legumes examined in Chapter 4.

The mid dry season fire of 1997 significantly increased the total density of the untreated seed bank, as well as the density of natives, upright perennial forbs and the common grass *H. triticeus* (Table 5.1). The late dry season fire of 1999 significantly increased the density of seedlings emerging from the untreated seed bank overall, and that of combined natives and upright perennial forbs (Table 5.7). Assessment of seedlings emerging from the untreated seed bank samples documented the active seed bank (Figure 5.1), plus seed with innate or enforced dormancy that was broken through the process of soil collection and incubation in the shadehouse. As the soil collection and incubation process was identical for samples from control, early burnt and late burnt savanna, the significant increase in seedling density from untreated seed bank collected after the mid dry season 1997, and late dry season 1999 fires provide direct evidence that these fires broke seed dormancy of a range of species, thereby increasing the active fraction of the soil seed bank. Odgers (1996) reported a similar stimulation of the seed banks of forbs by a fire in a eucalypt woodland of south-eastern Queensland. The early dry season fires of 1999 at Cape Cleveland did not significantly promote the active fraction of the total seed bank or the seed bank of any species or groups (Table 5.7).

The germination of the upright perennial forbs and *H. triticeus* was promoted by smoke rather than heat shock (Table 5.8) and therefore in addition to producing greater heat penetration into the topsoil, late dry season fires may also expose a greater proportion of the soil seed bank to smoke. Overall, these results indicate that several aspects of the passage of fire including heat shock, smoke and elevated nitrate levels (Chapter 4) combine to break seed dormancy of a range of savanna species, and that mid to late dry season fires provide a greater dormancy release stimulus than early dry season fires.

5.4.2 Distribution of seed in the topsoil

The seed bank was more abundant at soil depths of between 3 and 40 mm than in the surface 3 mm, indicating seed burial and incorporation within the topsoil occurs (Table 5.1). This may occur via a seed-based mechanism, such as the twisting action of hygroscopic awns, or through the activities of fauna, especially ants (Tothill 1969; Andrew and Mott 1983). The lower density of surface seed may also indicate greater levels of mortality of seed exposed to the elements.

5.4.3 Seed bank composition and abundance

The seed bank density of eucalypt savanna at Cape Cleveland ranged from 50 to 792 seeds m^{-2} (for samples to 5 cm depth; Tables 5.4, 5.6 and 5.9), which is a low to moderate density in comparison to other eucalypt communities across Australia (Table 5.11) and in comparison with several annual grasses that dominate the ground layer of some Australian tropical savannas. For instance, seed bank density of the annual grasses Sorghum intrans and Schizachyrium fragile have been observed at over 2000 seeds m^{-2} (Andrew 1986; Crowley and Garnett 1999). The seed bank density at Cape Cleveland is also low in comparison with a tropical savanna located approximately 50 km to the south-west, which was cleared and over-sown with exotic annual grasses and legumes, (McIvor 1987; Table 5.11). However, the bulk of seed in the tropical pasture studied by McIvor (1987) was from a few, mainly exotic, species. The Cape Cleveland seed bank contained 19 species common to McIvor's (1987) study. He found that all of these species produced average seed banks of [60 seeds m^{-2} and 14 species averaged [10 seeds m^{-2}. This suggests that the low to moderate seed bank density documented at Cape Cleveland is typical of the tropical savannas in the region that have not been over-sown with exotic pasture species.

Table 5.11. Response to soil treatments, total number of species, seed density and the most abundant growth form detected in germinable soil seed bank studies undertaken in eucalypt communities across Australia. [1] McIvor (1987); [2] Hodgkinson *et al*. (1980), seed extraction used rather than germination method; [3] Lunt (1997); [4] Read *et al*. (2000); [5] Clifford *et al*. (1996), data from 56 locations; [6] Melzer (1997); [7] Odgers (1996); [8] Vlahos and Bell (1986); [9] Enright *et al*. (1997); [10] this study; [11] Wang (1997); [12] Drake (1979); [13] Williams (2000).

Community	Region	Soil treatment "*"significant germination stimulus	Total number of species	Seed density (m^{-2})	Most abundant growth form
Pasture established from cleared eucalypt savanna [1]	North-eastern Queensland	Untreated	88	11000 - 36000	Herbs
Eucalypt woodland [2]	Western New South Wales	Untreated	47	1360 - 13800	Herbs
Eucalypt forest[3]	Victoria	Untreated	135	7989 - 11307	Herbs
Eucalypt forest [4]	New South Wales	Untreated, heated,* smoked*	85	2887 - 7578	Herbs
Eucalypt forest [5]	South-eastern Queensland	Untreated	Unknown	8 - 7432	Herbs
Eucalypt forest [6]	South-eastern Queensland	Untreated	Unknown	231 - 7021	Herbs
Eucalypt forest [7]	South-eastern Queensland	Untreated, burnt*	Unknown	436 - 1745	Herbs
Eucalypt forest [8]	Southern Western Australia	Untreated	68	377 - 1579	Subshrubs and herbs
Heathy eucalypt woodland [9]	Victoria	Untreated, ashed, heated,* smoked*	56	405 -1080	Herbs
Eucalypt savanna [10]	North-eastern Queensland	Untreated, burnt,* heated,* smoked*	64	50 - 792	Herbs
Eucalypt forest [11]	Victoria	Untreated	48	61 - 668	Herbs
Eucalypt forest [12]	South-eastern Queensland	Untreated	26	28 - 433	Herbs
Eucalypt forest [13]	North-eastern Queensland	Untreated, heated*	20	157 - 206	Herbs and pioneer rainforest trees

The PCA demonstrated that the seed bank samples at Cape Cleveland differed to that of the floristic surveys, on the basis of species composition (Figure 5.9). This was probably due to the lower species richness detected in seed bank samples, which contained only a subset of species documented in the floristic surveys. Only half of the species present in standing vegetation were detected in the soil seed bank (Appendix 1). As no species were observed to store a bradysporous seed bank, the soil seed bank data suggest that only half of the species at Cape Cleveland store seed reserves at any significant density. The detection of a low proportion of the standing vegetation in the soil seed bank has also been reported in several other studies (e.g. Vlahos and Bell 1986; Lunt 1997; Wang 1997).

The seed bank at Cape Cleveland was dominated by herbaceous species (Tables 5.4, 5.6, 5.9 and Appendix 1). The dominance of herbaceous species in the seed bank has been widely reported (Table 5.11). Most (94%) species of trees and shrubs were absent from the seed bank. The few woody species detected were subshrubs, with the exception of *Lantana camara* and the dominant tree *Corymbia clarksoniana*. The seed bank of *C. clarksoniana* was only detected in October 1998 and October 2000, and that of *L. camara* in October 2000, and both species at a very low density. In contrast, only three short-lived species (two ephemeral forbs and the single annual grass) were absent from seed bank, and all of these were only recorded in a low number (< 5%) of the floristic surveys. The scarcity of tree and shrub seed bank is in accordance with the generalisation by Higgins *et al*. (2000) that savanna trees produce short-lived seed banks and seedling recruitment may only result when appropriate environmental conditions coincide with seed fall. In fact most trees at Cape Cleveland dropped mature seed at the most appropriate time for germination, that is prior to and during the wet season (Table 5.10). This indicates a lower investment of stored reproductive potential, in the form of seed banks, for the longer lived trees and shrubs than for ephemeral species. However, the longevity of trees and many shrubs in tropical savanna provides an avenue of population persistence without regular seedling recruitment (Bond and Midgley 2001).

The most abundant seed banks were detected for the perennial grasses, *Digitaria breviglumis* and *Heteropogon triticeus*, and the ephemeral forb *Indigofera hirsuta*

(Tables 5.4, 5.6, 5.9 and Appendix 1). Ephemeral forbs in general, and especially *I. hirsuta*, displayed persistence in seed bank during the third year after fire, when there was limited abundance of standing plants (Chapter 3). This indicates the importance of soil seed banks for population persistence of these species.

5.4.4 Seasonal and annual dynamics in the soil seed bank

Seasonal fluctuations were detected in the seed bank, increasing through the dry season to a maximum, for most species, in the late dry season, and declining to a minimum by the mid wet season (Tables 5.3, 5.5 and 5.8). These results correspond with McIvor's (1987) study in a tree-cleared and over-sown pasture, 50 km from Cape Cleveland, who documented peak seed bank densities in the late dry season and at the start of the wet season. Soil seed banks of eucalypt forests in south-eastern Queensland display less distinct seasonal patterns and show strong variation between species (e.g. Drake 1979; Clifford *et al*. 1996; Melzer 1996; Odgers 1999). This may result from the reduced contrast in rainfall between seasons in south-eastern, compared with north-eastern Queensland.

The seasonal dynamics of seed banks are consistent with the timing of annual seed production at Cape Cleveland (Table 5.10). Peak seed production occurred during the early to mid dry season, so that the accumulation of seeds reached a maximum by the end of the dry season and start of the wet season. A comparison of seed production times for species that also occur at Kakadu National Park, in the Northern Territory (Brennan 1996), indicates seed production extends further into the dry season at Cape Cleveland. This may relate to the more gradual decline in rainfall at the start of the dry season on the east coast (Figure 2.2).

Soil seed banks of several tropical grasses, both annual and perennial, have been identified as transient in nature, requiring seed replenishment annually due to losses during the wet season (Andrew and Mott 1983; Mott and Andrew 1985). The strong declines recorded during each wet season in seed bank density of *H. triticeus*, and grasses as a group, indicate reliance on annual seed input to maintain seed bank density. This contrasts with the persistence of viable seeds of ephemeral forbs,

including *I. hirsuta* and the common grass *D. breviglumis* which did not display a significant decline over the wet season but a persistence of seed bank.
A lower seed density and species richness were detected in the seed bank in 1998 than in 1999 and 2000 (Table 5.3). The increase in seed bank density in 1999 and 2000, which included both native and exotic species, corresponds with the overall increase in abundance of native and exotic species after the 1997 fire (Chapter 3). Thus the seed bank was reflecting the general increase in species abundance during the study, which may have been aided by the above average rainfall in 1997 and 1998 (Table 2.1).

Fire had limited influence on the seasonal and annual dynamics of the seed bank overall (Tables 5.3, 5.5 and 5.8). However, significant interactions were demonstrated between fire and season for natives as a whole, and *D. breviglumis*, possibly due to the increase in the active component of the seed bank in savanna burnt in the late dry season. Subshrubs and non-grass monocots displayed higher seed bank density in unburnt savanna, suggesting fire depleted the seed bank through either seed mortality and/or germination. The seed bank density of the ephemeral forb, *I. hirsuta*, was highest in savanna burnt in the early dry season, which may have been enhanced by recruitment and subsequent seed production following fire.

5.4.5 Fire effects on Corymbia clarksoniana

The late dry season fires reduced seed production by the dominant tree, *C. clarksoniana* (Figure 5.10). This probably resulted from mortality of flower buds from the high scorch height produced by the late fires, which tended to singe the entire canopy. Setterfield (1997*b*) found both early and late dry season annual fires reduced seed production by the tropical eucalypts, *Eucalyptus miniata* and *E. tetrodonta*. She considered the primary cause of seed reduction from late dry season fires was the high canopy scorch produced by fires of the previous year, which killed developing flower buds. The early dry season fires caused flower abortion, thereby inhibiting seed production in the same year as the fire. She considered this was due to some canopy scorching, plus some unknown additional effect of fire, as the early dry season fires did not cause enough canopy scorch to completely destroy flower buds. Setterfield's (1997*b*) study therefore supports the conclusion that extensive canopy scorch produced by late dry season fires reduced seed production by *C. clarksoniana* in the year following burning. Her results also suggest that seed production of tropical eucalypts can be reduced by early dry season fires, and therefore seed production of *C. clarksoniana* may have been reduced by early dry season fires in 1999.

5.5 Conclusion

The use of soil treatments in this study (i.e. heat shock and smoke) were useful for enhancing the detection of germinable soil seed banks, although it is possible that direct seed extraction may have detected additional species. Seed extraction methods can be particularly useful for detecting large seeded species, although are likely to be inadequate for small seeded species and therefore both seed extraction and germination methods have advantages and disadvantages for detecting community-level seed bank dynamics (Pierce and Cowling 1991).

Fire, and the fire-related cues heat shock and smoke, have been demonstrated to break seed dormancy for a range of tropical savanna species. However early dry season fires, after a two year fire-free interval, are less effective at breaking seed dormancy than late dry season fires of the same interval, or mid dry season fires following a three year interval.

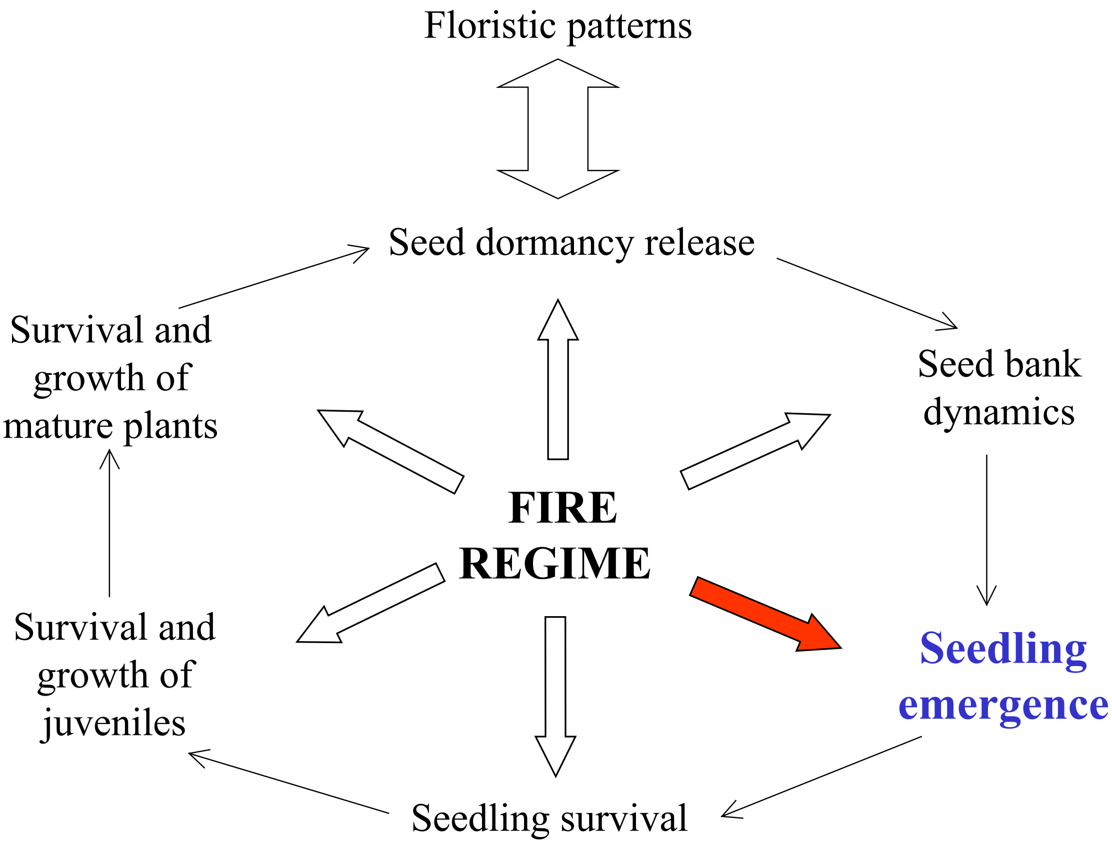
Only half of the species present in the standing vegetation were detected in the soil seed bank. The seed bank was dominated by herbaceous species and contained few seeds of trees and shrubs. This suggests the longer-lived woody species invest fewer resources in maintaining a store of reproductive potential (i.e. seeds). Seedling recruitment of these woody species would be more likely to occur when appropriate germination conditions coincided with seed fall, which is timed to occur prior to, or during the wet season. In contrast, ephemeral species displayed a persistent seed bank that maintains their populations on-site, even in the absence of standing plants.

Strong and consistent seasonal fluctuations, and some differences between years, were documented in the seed bank. Seed banks peaked in the late dry season as a culmination of seed input throughout the year. Declines in seed banks over the wet season indicate considerable annual input is required for the maintenance of seed bank density. Seed banks were lowest in 1998, the year following the 1997 fire, however a decline after the 1999 fires was only apparent for a few species, and therefore the higher seed density in 1999 and 2000 may relate to other factors such as rainfall, rather than fire.

While fire affected the balance between the proportion of dormant and active components of the seed bank, it had only limited influence on the overall seasonal and annual dynamics in soil seed banks. However, late dry season fires significantly reduced seed production of the dominant tree, *Corymbia clarksoniana*, possibly as a result of mortality of young flower buds from high canopy scorch.

Chapter 3 documented a pulse of species abundance after fire, especially those of the late dry season, in the tropical savanna at Cape Cleveland. The results from this chapter and Chapter 4 indicate fire plays a crucial role in breaking seed dormancy in a range of savanna species and that late dry season fires provide a greater stimulus than early dry season fires for releasing seed from dormancy. There are also more seeds available during the late dry season that can be affected by fire. The next chapter examines seedling emergence and assesses the relative importance of seed bank size and the capacity of fires to break seed dormancy, on patterns of seedling recruitment.

Chapter 6. The effect of fire regime on seedling emergence in a tropical savanna of north-eastern Australia.



6.1. Introduction

Seedling emergence is subject to the availability of seeds and safe sites, which provide a moisture, light and temperature regime appropriate for germination (Harper 1977). In Australian tropical savannas, seedling emergence of many annual grasses, such as *Schizachyrium* spp. and *Sorghum* spp., is linked to seasonal cycles in rainfall, with abundant recruitment occurring at the start of each wet season (Andrew and Mott 1983; Crowley and Garnett 1999). Seedling emergence of tropical savanna trees, such as eucalypts and *Melaleuca viridiflora*, is irregular and may primarily occur in years with above average rainfall (Lacey 1974; Gill *et al.* 1990; Fensham 1992; Crowley and Garnett 1998). Hence the consistency of wet season rainfall, and the quantity of rain, play a critical role in seedling emergence of many Australian tropical savanna species.

Seedling emergence in many fire-prone communities occurs primarily in the first wet season following fire. This has been documented for species of Californian chaparral (Keeley and Bond 1997), South African fynbos (Pierce and Cowling 1991), heaths of south-eastern (Bradstock 1991) and south-western Australia (Bell *et al.* 1987*b*), and temperate eucalypt forests (Ashton 1979) and woodlands (Purdie and Slatyer 1976). In tropical savannas, fire is known to enhance seedling emergence of some perennial grasses, such as *Heteropogon contortus* (Shaw 1957; Tothill 1969). Fire stimulates the release seed from dormancy, or from canopy storage, removes competitive inhibition from overstorey and grass layers, and often enhances soil nutrient availability (Whelan 1995; Bond and van Wilgen 1996).

Some tropical savanna trees recruit seedlings during intervals between fires, rather than in the immediate post-fire environment (Puyravaud *et al.* 1995; Hoffman 1996). *Eucalyptus miniata*, which co-dominates many tropical savannas across the Northern Territory and Western Australia, recruits seedlings in greater numbers in unburnt rather than recently burnt savanna (Setterfield 1997*b*).

The duration of fire intervals can influence seedling recruitment by affecting seed bank size and fire intensity (Whelan 1995). Fire intensity influences seed mortality and the proportion of seeds that are released from dormancy (Keith 1996). Fire season can affect seedling recruitment through the coincidence of fire with seasonal fluctuations in seed bank size and post-fire rainfall, and its influence on fire intensity (Whelan 1995; Bond and van Wilgen 1996).

An increase in plant abundance occurs in the year following fire in eucalypt savanna near Townsville (Chapter 3). This may result from increased vegetative growth and/or seedling emergence. In this savanna, fire breaks seed dormancy of many species, with a greater proportion of seeds released from dormancy by late rather than early dry season fires (Chapters 4 and 5). Seed bank size, and hence the density of seed available to be influenced by fire, is larger in the late dry season than the early dry season (Chapter 5).

This chapter examines the patterns of seedling emergence in eucalypt savannas near Townsville. It assesses seedling emergence after several fires, and in the absence of fire. The experimental removal of the grass layer in unburnt savanna is also examined to help understand the effect of fire on seedling emergence. Specific questions are:

1. Does seedling emergence occur primarily in the first year after fire or at similar densities throughout fire intervals?
2. Are seedling emergence patterns consistent across eucalypt savannas of the Townsville region?
3. What are the effects of fire season on seedling emergence?
4. What is the total density of seedlings that emerge over a year?
5. What level of seedling emergence is promoted by the removal of herbaceous cover?
6. What proportion of the soil seed bank germinates after fires of different seasons?
7. What is the relationship between the species composition of the seedling community, the standing vegetation and the soil seed bank?

6.2 Methods

6.2.1 Sampling methods

6.2.1a Seedling emergence surveys in the Townsville region

Seedling emergence was measured in recently burnt savanna and adjacent savanna that had not been burnt for several years, in each of three locations in the Townsville region: Mt Elliot, Castle Hill and Many Peaks Range (Figure 2.1). The aim of the surveys was to compare seedling emergence in recently burnt and longer unburnt savanna to examine whether a pulse of germination occurs after fire. The three locations were used in addition to surveys at the Cape Cleveland study site to determine whether seedling emergence patterns were consistent across the Townsville region. All locations are incorporated within a Protected Area, or local council reserve, and have been excluded from stock grazing for at least 20 years. All sites are located along the coastal floodplain at less than 150 m altitude. All sites are based on granite derived soils, with the exception of Many Peaks Range, which is based on a mixture of metamorphosed acid volcanic parent material (Paine and Smith 1972).

Mt Elliot

A fire burnt through parts of the Mt Elliot section of Bowling Green Bay National Park during September 2000. Seedling emergence surveys were undertaken at Mt Elliot in eucalypt savanna surrounding Alligator Creek (Figure 2.1). The surveys compared seedling emergence in the recently burnt savanna on the western side of Alligator Creek with that of savanna that had remained unburnt for four years on the eastern side.

On the western side of the creek, burnt in September 2000, three separate sites were located between minor creek systems, which were approximately 700 m to 2000 m apart. In each of these three sites, seedlings were surveyed across an area of approximately 1 ha. The exact location of each site was determined using a random number, between one and 100, which determined the number of paces before the corner of the survey site. The three unburnt sites were roughly opposite the burnt sites on the opposite side of Alligator Creek. Again a random number from one to 100 was used to locate the corner of each site.

The seedling surveys at Mt Elliot were carried out on the 6th December 2000, after the start of the wet season. This meant the survey was undertaken after abundant seedling emergence and whilst plants remained small enough to be easily distinguished as seedlings. Sprouting plants, and established plants in unburnt savanna, were distinguished from seedlings on the basis of swollen stem bases from which shoots emerge. Seedlings typically retained cotyledons and their identification was aided by the experience gained during the soil seed bank study (Chapter 5). Seedling counts were made within a 1m^2 quadrat, which was thrown 50 times whilst traversing up and back through each of the 1 ha sites. The quadrat was thrown in a random direction at each of the 50 points, which were five paces apart.

Many Peaks Range

On the 7th December 2000, seedling emergence surveys were undertaken in eucalypt savanna at Many Peaks Range (Figure 2.1) that was burnt in September 2000 and adjacent savanna that had remained unburnt for four years. Three 1 ha sites were assessed in each of recently burnt and longer unburnt savanna, all of which were located on the eastern side on the lower foothills (below 100 m altitude). Sites were spaced approximately 200 m apart and the starting corner of each site was determined by a random number between one and 100. The entire hillside typically burns as one unit, however active fire-protection was used for the first time in September 2000 to provide a mosaic of burnt and unburnt savanna for general habitat management. Seedling emergence surveys in 50, 1m^2 quadrats in each of the 1 ha sites was undertaken as described for the Mt Elliot seedling surveys.

Castle Hill

A fire burnt through most of the eucalypt savanna on Castle Hill (Figure 2.1) in August 1999. Seedling surveys were undertaken on relatively level ground at approximately 120 m altitude on 26th January 2000. Seedling emergence in recently burnt savanna was surveyed in 1 ha sites located on either side of the Castle Hill road. The history of recent fires on the northern side of the road is unknown, although it is likely to have received regular fires, as sections of the hill are burnt in most years. The southern side was burnt in September 1997 and again in August 1999. The corner location of both sites was determined by a random number between one and 100. Seedling counts in 50,

$1m^2$ quadrats in both of the 1 ha sites were performed as described for the Mt Elliot seedling surveys. Surveys were also undertaken in four small patches of unburnt savanna that had been protected from fire by walking tracks. These unburnt areas totalled approximately 0.15 hectares and probably had a similar fire history to the surrounding savanna and were burnt with the surrounding area in a fire on 2001 (pers. obs.). Therefore, 100 burnt and 50 unburnt $1m^2$ quadrats were sampled at Castle Hill, while 150, $1m^2$ quadrats were sampled in each of the burnt and unburnt savannas at Mt Elliot and Many Peaks Range.

6.2.1b Seedling emergence surveys at Cape Cleveland

Annual seedling emergence surveys were undertaken across the nine, 1 ha blocks at the Cape Cleveland study site (Figure 2.1) each December, from 1997 to 2000. Each annual seedling survey involved seedling counts in 50, $1m^2$ quadrats. As described for Mt Elliot, the $1m^2$ quadrat was thrown 50 times whilst walking up and back through each of the nine, 1 ha blocks. The quadrat was thrown in a random direction at each of the 50 points, which were five paces apart. Therefore a total of 36 seedling surveys (four annual surveys in each of the nine 1 ha blocks) were undertaken, each involving seedling counts in 50, $1m^2$ quadrats.

Mass seedling emergence of the dominant tree *Corymbia clarksoniana* occurred across the Cape Cleveland site immediately prior to the December 1998 seedling survey. It was noticed that considerable germination also occurred within the annually burnt fire break block, which is located adjacent to the nine, 1 ha trial blocks (Figure 2.4). The density of *C. clarksoniana* seedlings along the fire break block, burnt three months prior to the December 1998 seedling survey, was compared with that documented within the nine 1 ha blocks, which at that stage had remained unburnt for 16 months. The density of *C. clarksoniana* seedlings was also measured along the 4 m wide slashed fire line, that separates the fire break block with the nine 1 ha blocks, which was cut four months prior to the December 1998 survey. Seedlings of *C. clarksoniana* were counted within 50, $1m^2$ quadrats along both the fire break block and the adjacent slashed fire line, using the method described above, except that the 50 quadrats were spaced 10 m apart to cover the length of these narrow blocks with a single transect.

The opportunity to document seedling emergence of *C. clarksoniana* in recently burnt and slashed savanna was taken because the recruitment of this dominant species had not been observed in previous years, and seedling emergence of tropical eucalypts is considered episodic (Fensham 1992; Setterfield 1997*b*). However, replication of recently burnt and slashed treatments was not available in December 1998, so results should be interpreted within this design constraint.

6.2.1c Safe sites for Corymbia clarksoniana

The one-off mass recruitment of *C. clarksoniana* in 1998 raised questions regarding the safe-site requirements of this dominant species. The effects of fire and grass layer removal on the seedling emergence of *C. clarksoniana* were experimentally tested to assess whether the absence of grass cover, or some aspect of the ash bed, significantly increased seedling emergence. Seeds were extracted from fallen capsules collected at Cape Cleveland in October 2000, and pooled. An experiment was established to test the effect of micro-site disturbance on seedling emergence. Five replicates of 100 seeds were placed on the soil surface, within a 20 cm x 20 cm plot, in each of three micro-site disturbance treatments:

Undisturbed; seeds placed in undisturbed savanna.

Burnt; seeds placed on recently burnt ground. Each of the replicate fires was implemented across a 2 m x 3 m area on 19th October 2000, one hour prior to seed sowing.

Cut; seeds were placed in an area that had the herbaceous layer cut and removed across a circular area of 1.5 m radius.

The treatments were established along the edge of a control block, which had remained unburnt for three years. One of the edges of the three unburnt control blocks was randomly selected. Twenty-one possible plot locations were available along the 130 m length of the control block, allowing the separation distance of 6 m required for burnt treatments. Replicates of the three treatments were randomly allocated to the 21 available plot locations. Seeds were placed on the soil surface within plots on the 19th October 2000. Seedling emergence was defined by cotyledon emergence and was assessed weekly.

Seed viability was assessed by placing three replicates of 100 seeds onto moist filter paper in a petri dish, sprayed with a 2g L^{-1} solution of fungicide (Thiram ®) and incubated in a controlled temperature room at 27.5°C with a 12 h diurnal light regime. After a fortnight, ungerminated seeds were assessed for viability using a tetrazolium test (Moore 1985). A slit was made in seeds, which were then soaked in a 1% tetrazolium solution in the dark for 48 h. Seeds were then dissected under a microscope and assessed for the pink colouration that indicates a viable embryo. The number of viable seeds detected in the tetrazolium test was added to the number of seeds that germinated in the laboratory to produce a total number of viable seeds for each replicate of the control treatment.

Despite rain falling within a fortnight of establishing the experiment (Table 2.1), very limited seed germination was detected by the end of six weeks. A second experiment was established on 4th December 2000 to investigate whether shallow burial of seed, which has been documented to increase the germination of several temperate forest and woodland species (Free 1951; Clarke and Davison 2001), would promote the germination of *C. clarksoniana*. The experiment used the same micro-site disturbance treatments described above (undisturbed, burnt and cut) for both surface sown seed and buried seed. Seed burial involved covering the seed with approximately 5 mm of soil.

Each treatment was replicated three times using 25 seeds and each replicate was randomly allocated to the previously established plots in the first *C. clarksoniana* field experiment. There had been limited regrowth in the plots burnt or cut in October, so that these treatments remained useful. Seeds were placed within 20 cm x 20 cm plots which were established within the treated areas, adjacent to but not in the identical positions of the 20 cm x 20 cm plots of the initial field experiment.

6.2.1d Total seedling emergence surveys at Cape Cleveland

The seedling surveys at Cape Cleveland, Castle Hill, Many Peaks Range and Mt Elliot provided a snapshot of seedling density at the start of the wet season. However, they do not provide information on the seedling emergence that occurs over the course of a year. Therefore permanent $1m^2$ sites were established at Cape Cleveland to document the full emergence of seedlings for one year, prior to and following the 1999 fire season treatments (Chapter 2).

The effect of removal of the herbaceous layer on seedling emergence was examined to help understand fire effects, by isolating the release from competition from the herbaceous cover from the heat and chemical attributes of fire. The treatments were:

1. Undisturbed; savanna that was last burnt in July 1997 and remained undisturbed (with the exception of some minor native herbivore grazing).
2. Early burnt; savanna burnt in early dry season fires (May 1999).
3. Late burnt; savanna burnt in late dry season fires (October 1999).
4. Early cut; herbaceous layer cut and removed from unburnt plots at the time of early dry season fires, in savanna that was last burnt in July 1997.
5. Late cut; herbaceous layer cut and removed from unburnt plots at the time of late dry season fires, in savanna that was last burnt in July 1997.

The undisturbed, early cut and late cut treatments were established in the three, 1 ha control blocks, which were last burnt in July 1997 (Figure 2.4). The early burnt and late burnt treatments were established in the respective early and late burnt 1 ha blocks, which were all burnt in July 1997 and in either May 1999 (early burnt) or October 1999 (late burnt; Figure 2.4). Each treatment was represented by ten 1m^2 plots in each of three relevant 1 ha blocks at Cape Cleveland, providing a total of 30, 1m^2 plots for each of the five treatments. To facilitate re-location, each 1m^2 plot was randomly allocated to a corner of one of the four 100 m^2 plots used in the floristic surveys (Chapter 3). Plots for the cut treatment were established outside the allotted corner and the herbaceous layer was removed from an area of 1.5 m radius, to reduce shading effects on the 1m^2 plots.

6.2.2 Statistical analyses

6.2.2a Seedling emergence surveys in the Townsville region

When considered individually, the seedling emergence surveys at Mt Elliot, Many Peaks Range and Castle Hill are technically pseudo-replications of surveys of a single burnt and adjacent unburnt area at each location (Underwood 1997). Therefore, all surveys from the three locations (Mt Elliot, Many Peaks Range and Castle Hill) were pooled and analysed together, providing samples from three separate fires and adjacent longer unburnt savanna.

The intention was to compare seedling emergence in recently burnt and unburnt sites using a one-factor ANOVA, which allowed samples to be nested into the Mt Elliot, Many Peaks Range and Castle Hill sites. However, due to the many zeros in the data, the variance heterogeneity was not solved by data transformations, so the statistical significance of differences between burnt and unburnt savanna was assessed using a non-parametric Mann-Whitney *U*-test (Zar 1999). This test does not allow for nesting so seedling density within all 400 burnt $1m^2$ replicate quadrats were compared with all 350 unburnt $1m^2$ replicate quadrats.

Assessments were made for native and exotic species, growth form groups described in Chapter 3 and common species that comprised at least 1% of the total seedling emergence. Six taxa could not be identified and were excluded from the species group analyses, so that the combined species category contained six more species than the totals of the growth form groups, and natives and exotic species.

6.2.2b Seedling emergence surveys at Cape Cleveland

The difference between fire treatments was initially assessed using a repeated measures ANOVA with the main factor, fire treatment, containing three levels (control, early and late dry season burnt) and a repeated measures factor, years, with four levels (1997, 1998, 1999 and 2000). Homogeneity of variance was assessed using Cochran's test (Underwood 1997) and significant heterogeneity of variances could not be resolved with data transformations. Therefore the non-parametric Friedman ANOVA by ranks was used to test the significance of differences in seedling emergence in the four years between 1997 and 2000, separately for the three replicate blocks for each of the control, early and late burnt treatments (Figure 2.4). Where a significant difference was detected between years, a Wilcoxon's matched pair test was used as a *post-hoc* test, with a Bonferroni adjustment of the significance level for multiple comparisons (Sokal and Rohlf 1995). A Kruskal-Wallis ANOVA by ranks was used to examine differences in seedling emergence between control, early and late burnt blocks in December 1999, after the fire treatments implemented in that year. Where significant differences were detected, a Mann-Whitney *U*-test was used as a *post-hoc* test, with a Bonferroni adjustment for multiple comparisons (Sokal and Rohlf 1995). Due to the large number of analyses of the same data set, a conservative significance level ($P < 0.01$) was set to provide confidence in allocating significant fire effects.

6.2.2c Species composition of seedling emergence, soil seed bank and floristic surveys

The species composition in the seedling emergence surveys at Cape Cleveland was compared with that of the soil seed bank samples (Chapter 5) and floristic surveys (Chapter 3). The seedling composition from each set of 50, 1m^2 quadrat surveys across each 1 ha block was pooled to provide the species composition of seedlings in each annual survey of each 1 ha block, providing 36 seedling surveys (four annual surveys of the nine blocks). A Principle Components Analysis (PCA) was carried out, using the CANOCO program (ter Braak and Smilauer 1998), on a data set containing the species composition in the floristic surveys from 1997 to 2001 (Chapter 3), the soil seed bank samples collected from July 1997 to October 2000, and the seedling surveys undertaken at Cape Cleveland between 1997 and 2000. The PCA was based on species presence or absence data, as methods of estimating abundance differed between floristic surveys, soil seed bank samples and seedling surveys. The PCA analysis in CANOCO can only analyse 500 samples, and as the entire floristic surveys, soil seed bank samples and seedling surveys total 504 samples, four of the 27 soil seed bank samples that underwent the smoke treatment in 2000 were randomly selected and removed from the analyses. Restricting the elimination to the smoked treatments ensured all untreated and heated samples, which were the consistent seed bank treatments between 1997 and 2000, would remain in the PCA.

6.2.2d Safe sites for Corymbia clarksoniana

The first field germination experiment of *Corymbia clarksoniana* was initially assessed for statistically significant differences between surface sown seeds in undisturbed, burnt and cut plots using a one-factor ANOVA. Homogeneity of variances was assessed using a Cochran's test (Underwood 1997). Variance heterogeneity could not be resolved using data transformations, so treatment differences were assessed for statistical significance using a non-parametric Kruskal-Wallis ANOVA by ranks.

The second *C. clarksoniana* field germination experiment was examined using a two-factor ANOVA assessing micro-site disturbance with three levels (undisturbed, burnt and cut) and the factor seed burial (surface sown and buried seed). Data for both experiments were expressed as percentage of viable seed, as determined from the results of germination in the laboratory and the tetrazolium test.

6.2.2e Total seedling emergence surveys at Cape Cleveland

The statistical significance of differences in total seedling emergence between undisturbed, early and late burnt and early and late cut savanna were assessed using a one-factor ANOVA. Homogeneity of variance was assessed using Cochran's test (Underwood 1997). All variance heterogeneity was resolved using log (x +1) data transformations.

The data on total density of seedling emergence were used to assess the proportion of the untreated soil seed bank that emerged as seedlings. This was based on the untreated seed bank samples because they provided a closer approximation to the active seed bank than seed bank samples exposed to oven-heating and smoke, which documented many seeds that contained innate dormancy (Chapter 5). The seedlings that emerged over the dry season, between 31st July and 23rd October 1999, in the undisturbed, early burnt and early cut plots were expressed as a percentage of the untreated germinable soil seed bank collected on the 31st July 1999, the first seed bank collection after the early dry season fire (Chapter 5). The seedlings that emerged over the wet season, between 23rd October 1999 and 29th February 2000, in the undisturbed, early and late burnt and early and late cut plots were expressed as a percentage of the untreated seed bank collected on the 23rd October 1999, the first seed bank collection after the late dry season fire (Chapter 5). The seedlings that emerged over the wet season in all plots, between 23rd October 1999 and 29th February 2000, were also expressed as a percentage of the decline in untreated seed bank over that period.

A one-factor ANOVA was used to assess the statistical significance of differences between treatments for the percentage mid dry season seed bank that emerged over the dry season, the percentage late dry season seed bank that emerged over the wet season, and the wet season seedling emergence as a percentage of the decline in seed bank over the wet season (i.e. the difference between the October 1999 and February 2000 seed bank densities).

6.3 Results

6.3.1 Seedling emergence surveys around Townsville

A total of 84 species were detected within the seedling emergence surveys undertaken at Mt Elliot, Many Peaks Range and Castle Hill (Table 6.1). Seventy-six percent of these species were common to the Cape Cleveland study site, indicating that these savanna sites around Townsville were similar in composition. Herbaceous species dominated the seedling surveys, representing 81% of species and 94% of total seedling density.

Species richness and total seedling density were significantly higher in recently burnt than in longer unburnt sites, with more than six times the average number of species and 15 times the seedling density in recently burnt than longer unburnt savanna (Table 6.1). Most species and species groups were significantly more abundant in recently burnt savanna and no species or groups were more abundant in longer unburnt sites. Woodland and rainforest trees and shrubs were the only growth form groups that did not have significantly increased seedling emergence in burnt sites. The rainforest group was represented by only one *Canthium attenuatum* seedling which emerged in a recently burnt site on Castle Hill. Seedling emergence was not significantly different between recently burnt and longer unburnt sites for the common exotic subshrubs *Stachytarpheta jamaicensis* and *Triumfetta rhomboidea*, the exotic ephemeral forbs *Crotalaria goreensis* and *Hyptis suaveolens*, the native twiner *Rhynchosia minima* and an undetermined species of *Fimbristylis*.

Table 6.1. Mean (standard error) seedling density (m^{-2}) and results of the Mann-Whitney *U*-tests comparing seedling density in recently burnt, and longer unburnt eucalypt savanna of Mt Elliot, Many Peaks Range and Castle Hill, Townsville. The “combined species” category has more species than the totals species groups, because several unknown species could not be allocated to groups. * indicates exotic species.

Species and groups	Mean (s.e.) species richness or seedling density (m^{-2})		*U* statistic	*P* value
	Burnt (n = 400)	Unburnt (n = 350)		
Species richness	5.13 (0.10)	0.83 (0.56)	3271.00	< 0.001
All species (n = 84)	72.14 (6.07)	4.58 (0.98)	5915.50	< 0.001
Natives (n = 59)	33.37 (2.85)	0.85 (0.12)	2639.50	< 0.001
Weeds (n = 19)	38.28 (5.69)	3.65 (0.98)	32827.00	< 0.001
Woodland trees & shrubs (n = 4)	0.19 (0.04)	0.00 (0.00)	63525.00	> 0.05
Rainforest trees & shrubs (n = 1)	0.003 (0.003)	0.00 (0.00)	69825.00	> 0.05
Subshrubs (n = 10)	4.35 (0.99)	0.37 (0.15)	58172.00	< 0.001
*Stachytarpheta jamaicensis**	3.02 (0.84)	0.34 (0.15)	65461.00	> 0.05
*Triumfetta rhomboidea**	0.89 (0.52)	0.02 (0.01)	67450.00	> 0.05
Upright perennial forbs (n = 8)	1.00 (0.16)	0.24 (0.08)	55910.50	< 0.001
Twining perennial forbs (n = 16)	8.35 (0.61)	0.41 (0.05)	24286.00	< 0.001
Desmodium gunnii	1.01 (0.20)	0.03 (0.01)	60071.50	< 0.001
Galactia tenuiflora	4.12 (0.40)	0.16 (0.03)	43228.50	< 0.001
Rhynchosia minima	1.48 (0.43)	0.02 (0.01)	64466.00	> 0.05
Ephemeral forbs (n = 23)	37.52 (5.58)	3.28 (0.96)	16264.50	< 0.001
*Calyptocarpus vialis**	26.71 (5.42)	1.79 (0.74)	58146.50	< 0.001
*Chamaecrista absus**	2.11 (0.18)	0.15 (0.03)	42599.00	< 0.001
*Crotalaria goreensis**	4.25 (1.46)	0.00 (0.00)	63534.00	> 0.05
*Hyptis suaveolens**	0.60 (0.27)	1.11 (0.35)	67560.00	> 0.05
Tephrosia juncea	1.57 (0.12)	0.01 (0.00)	34202.00	< 0.001
Grasses (n = 11)	18.71 (2.75)	0.83 (0.06)	21780.50	< 0.001
Heteropogon contortus	15.87 (2.76)	0.07 (0.06)	49900.50	< 0.001
H. triticeus	2.26 (0.29)	0.01 (0.00)	44377.00	< 0.001
Non-grass monocots (n = 5)	1.96 (0.55)	0.17 (0.04)	57861.00	< 0.001
Commelina spp.	0.85 (0.13)	0.17 (0.04)	60535.50	< 0.001
Fimbristylis sp.	0.82 (0.52)	0.00 (0.00)	68775.00	> 0.05

6.3.2 Seedling emergence surveys at Cape Cleveland

A total of 67 species were documented in the annual seedling emergence surveys between 1997 and 2000 at Cape Cleveland (Table 6.2; Appendix 1). Species richness and total seedling density were significantly higher in recently burnt blocks, being most abundant in control blocks after the 1997 fire, and in early and late burnt blocks after both the 1997 and 1999 fires (Table 6.2). In December 1999, following the implementation of the early and late dry season fires, species richness and total seedling density were significantly higher in late burnt than early burnt blocks, and early burnt than in unburnt control blocks.

The mean seedling density and statistical significance of differences between recently burnt and longer unburnt savanna, for the species groups and common species at Cape Cleveland are presented in Table 5.2. Seedling density of native species was highest in recently burnt savanna, that is in 1997 in control blocks, and both 1997 and 1999 in early and late burnt blocks. Seedling numbers of both native and exotic species in 1999 were significantly higher in late burnt than early burnt sites, which were higher again than in unburnt control sites. There was no significant difference in exotic seedling density between surveys within the control blocks. The seedling density of exotic species in both early and late burnt blocks was significantly higher following the 1999 fires than all other years, including 1997.

Densities of seedlings of woodland trees and shrubs, and that of the dominant tree *Corymbia clarksoniana*, were significantly higher in 1998 than in any other years and there was no difference between fire treatments in 1999. The additional surveys in 1998 of *C. clarksoniana* seedlings within the fire break block, burnt three months prior to the seedling survey, and fire line slashed four months prior to the survey, indicated the recently burnt and slashed savanna contained significantly higher densities of *C. clarksoniana* seedlings than in the nine 1 ha blocks, which had not been burnt for 16 months at that stage (Figure 6.1).

Table 6.2. Mean (standard error) species richness and seedling density (m^{-2}), and results of statistical analyses of fire treatment and year of survey in eucalypt savanna at Cape Cleveland, between 1997 and 2001. ❹$^{2}{}_{3,150}$ = indicates ❹^{2} or *H* value, denominator d.f., numerator d.f.; ❹^{2} or *H* values without an asterisk (*) are not significantly different at $P > 0.01$; *$P < 0.01$; **$P < 0.001$. Results of Scheffe's *post-hoc* test are provided for differences in 1999 between C, control; E, early burnt; and L, late burnt. Means in each row with different superscripts are significantly different at $P < 0.01$.

Species and groups	Fire treatment	Mean (s.e.) species richness or seedling density in 1997 (n = 150)	Mean (s.e.) species richness or seedling density in 1998 (n = 150)	Mean (s.e.) species richness or seedling density in 1999 (n = 150)	Mean (s.e.) species richness or seedling density in 2000 (n = 150)	Friedman's ANOVA by ranks			Kruskal-Wallis ANOVA by ranks
						Control 1997 –2000 ❹$^{2}{}_{3,147}$ =	Early burnt 1997 – 2000 ❹$^{2}{}_{3,147}$ =	Late burnt 1997 – 2000 ❹$^{2}{}_{3,147}$ =	Fire treatment in 1999 $H_{2,447}$ =
Species richness	Control	2.11 (0.09) ^{a}	0.65 (0.07) ^{b}	0.59 (0.06) ^{b}	0.69 (0.07) ^{b}	163.946**	271.509**	334.153**	317.026** L > E > C
	Early burnt	2.17 (0.11) ^{p}	0.83 (0.08) ^{q}	4.24 (0.13) ^{r}	0.96 (0.09) ^{q}				
	Late burnt	2.21 (0.11) ^{x}	0.88 (0.08) ^{y}	6.05 (0.16) ^{z}	0.76 (0.08) ^{y}				
All species (n = 67)	Control	16.18 (2.35) ^{a}	0.96 (0.13) ^{b}	1.05 (0.16) ^{b}	2.03 (0.57) ^{b}	191.261**	255.499**	341.790**	362.862** L > E > C
	Early burnt	14.39 (1.72) ^{p}	1.53 (0.23) ^{q}	12.19 (0.68) ^{p}	1.63 (0.23) ^{q}				
	Late burnt	17.53 (2.96) ^{x}	1.65 (0.23) ^{y}	41.84 (2.39) ^{z}	1.23 (0.16) ^{y}				
Native species (n = 51)	Control	15.25 (2.32) ^{a}	0.82 (0.12) ^{b}	0.75 (0.15) ^{b}	1.21 (0.19) ^{b}	206.790**	241.317**	343.743**	344.757** L > E > C
	Early burnt	13.55 (1.70) ^{p}	1.29 (0.21) ^{q}	9.02 (0.54) ^{p}	1.14 (0.14) ^{q}				
	Late burnt	17.14 (2.95) ^{x}	1.31 (0.21) ^{y}	34.23 (2.32) ^{x}	0.91 (0.13) ^{y}				
Exotic species (n = 16)	Control	0.93 (0.40) ^{a}	0.14 (0.04) ^{a}	0.30 (0.06) ^{a}	0.83 (0.54) ^{a}	6.708	153.448**	238.404**	180.763** L > E > C
	Early burnt	0.84 (0.24) ^{p}	0.25 (0.05) ^{q}	3.17 (0.39) ^{r}	0.49 (0.18) $^{p\,q}$				
	Late burnt	0.39 (0.12) ^{x}	0.35 (0.09) ^{x}	7.61 (0.66) ^{y}	0.32 (0.07) ^{x}				
Woodland trees & shrubs (n = 2)	Control	0.00 (0.00) ^{a}	0.47 (0.10) ^{b}	0.00 (0.00) ^{a}	0.00 (0.00) ^{a}	96.000**	106.576**	111.000**	4.007
	Early burnt	0.00 (0.00) ^{p}	0.76 (0.18) ^{q}	0.01 (0.01) ^{p}	0.0 (0.00) ^{p}				
	Late burnt	0.00 (0.00) ^{x}	0.63 (0.17) ^{y}	0.00 (0.00) ^{x}	0.0 (0.00) ^{x}				

Table 6.2 (cont.)

Species and groups	Fire treatment	Mean (s.e.) species richness or seedling density in 1997 (n = 150)	Mean (s.e.) species richness or seedling density in 1998 (n = 150)	Mean (s.e.) species richness or seedling density in 1999 (n = 150)	Mean (s.e.) species richness or seedling density in 2000 (n = 150)	Friedman's ANOVA by ranks			Kruskal-Wallis ANOVA by ranks
						Control 1997 –2000 ❹$^{2}_{3,147}$ =	Early burnt 1997 – 2000 ❹$^{2}_{3,147}$ =	Late burnt 1997 – 2000 ❹$^{2}_{3,147}$ =	Fire treatment in 1999 $H_{2,447}$ =
Corymbia clarksoniana	Control	0.00 (0.00) ^{a}	0.47 (0.10) ^{b}	0.00 (0.00) ^{a}	0.00 (0.00) ^{a}	96.000**	114.000**	111.000**	0.000
	Early burnt	0.00 (0.00) ^{p}	0.76 (0.18) ^{q}	0.00 (0.00) ^{p}	0.00 (0.00) ^{p}				
	Late burnt	0.00 (0.00) ^{x}	0.63 (0.17) ^{y}	0.00 (0.00) ^{x}	0.00 (0.00) ^{x}				
Rainforest trees & shrubs (n = 4)	Control	0.00 (0.00) ^{a}	0.00 (0.00) ^{a}	0.02 (0.01) ^{a}	0.0 (0.00) ^{a}	6.000	9.000	12.000*	0.671
	Early burnt	0.00 (0.00) ^{p}	0.00 (0.00) ^{p}	0.03 (0.02) ^{p}	0.01 (0.01) ^{p}				
	Late burnt	0.00 (0.00) ^{x}	0.01 (0.01) ^{x}	0.03 (0.02) ^{y}	0.0 (0.00) ^{x}				
Subshrubs (n = 6)	Control	0.67 (0.39) ^{a}	0.03 (0.02) ^{b}	0.03 (0.01) ^{b}	0.65 (0.52) ^{a}	14.086*	4.843	44.354**	31.237** L > C
	Early burnt	0.30 (0.19) ^{p}	0.02 (0.01) ^{p}	0.09 (0.03) ^{p}	0.26 (0.18) ^{p}				
	Late burnt	0.17 (0.10) ^{x}	0.04 (0.02) ^{x}	0.62 (0.17) ^{y}	0.03 (0.01) ^{x}				
Triumfetta rhomboidea	Control	0.66 (0.39) ^{a}	0.01 (0.01) ^{b}	0.02 (0.01) ^{b}	0.63 (0.52) ^{a}	14.982**	1.263	37.996**	33.433** L > C
	Early burnt	0.30 (0.19) ^{p}	0.02 (0.01) ^{p}	0.05 (0.03) ^{p}	0.25 (0.18) ^{p}				
	Late burnt	0.13 (0.09) ^{x}	0.04 (0.02) ^{x}	0.55 (0.17) ^{y}	0.02 (0.01) ^{x}				
Upright perennial forbs (n = 9)	Control	0.07 (0.03) ^{a}	0.07 (0.02) ^{a}	0.02 (0.01) ^{a}	0.09 (0.04) ^{a}	9.632	41.763**	51.346**	57.082** E & L > C
	Early burnt	0.04 (0.02) ^{p}	0.17 (07) ^{p}	0.02 (0.03) ^{q}	0.12 (0.03) ^{p}				
	Late burnt	0.14 (0.06) ^{x}	0.14 (0.04) ^{x}	0.02 (0.01) ^{y}	0.12 (0.04) ^{x}				
Hybanthus spp.	Control	0.01 (0.01) ^{a}	0.05 (0.02) ^{a}	0.00 (0.00) ^{a}	0.07 (0.03) ^{a}	10.571	52.8000**	50.681**	35.188** L > C
	Early burnt	0.00 (0.00) ^{p}	0.03 (0.02) ^{p}	0.69 (0.22) ^{q}	0.05 (0.02) ^{p}				
	Late burnt	0.00 (0.00) ^{x}	0.07 (0.02) ^{x}	0.73 (0.23) ^{y}	0.08 (0.03) ^{x}				

Table 6.2 (cont.)

Species and groups	Fire treatment	Mean (s.e.) species richness or seedling density in 1997 (n = 150)	Mean (s.e.) species richness or seedling density in 1998 (n = 150)	Mean (s.e.) species richness or seedling density in 1999 (n = 150)	Mean (s.e.) species richness or seedling density in 2000 (n = 150)	Friedman's ANOVA by ranks			Kruskal-Wallis ANOVA by ranks
						Control 1997 –2000 ❹$^{2}_{3,147}$ =	Early burnt 1997 – 2000 ❹$^{2}_{3,147}$ =	Late burnt 1997 – 2000 ❹$^{2}_{3,147}$ =	Fire treatment in 1999 $H_{2,447}$ =
Twining perennial forbs (n = 20)	Control	0.35 (0.08) ^{a}	0.21 (0.04) ^{a}	0.41 (0.07) ^{a}	0.22 (0.06) ^{a}	7.175	203.306**	292.452**	241.648** L > E > C
	Early burnt	0.48 (0.10) ^{p}	0.32 (0.06) ^{p}	3.53 (0.34) ^{q}	0.35 (0.06) ^{p}				
	Late burnt	0.29 (0.05) ^{x}	0.41 (0.09) ^{x}	11.83 (0.92) ^{y}	0.30 (0.06) ^{x}				
Galactia tenuiflora	Control	0.08 (0.03) ^{a}	0.03 (0.01) ^{a}	0.03 (0.01) ^{a}	0.03 (0.02) ^{a}	2.899	74.681**	164.295**	71.988** E & L > C
	Early burnt	0.13 (0.04) ^{p}	0.09 (0.03) ^{p}	1.05 (0.18) ^{q}	0.10 (0.04) ^{p}				
	Late burnt	0.04 (0.02) ^{x}	0.03 (0.01) ^{x}	1.29 (0.20) ^{y}	0.01 (0.01) ^{x}				
Glycine tomentella	Control	0.05 (0.02) ^{a}	0.00 (0.00) ^{a}	0.07 (0.03) ^{a}	0.01 (0.01) ^{a}	9.462	36.354**	103.640**	46.847** L > C & E
	Early burnt	0.04 (0.02) ^{p}	0.05 (0.02) ^{p}	0.21 (0.04) ^{q}	0.06 (0.04) ^{p}				
	Late burnt	0.11 (0.04) ^{x}	0.05 (0.03) ^{x}	2.01 (0.46) ^{y}	0.00 (0.00) ^{x}				
Passiflora foetida	Control	0.16 (0.05) ^{a}	0.07 (0.03) ^{a}	0.22 (0.06) ^{a}	0.15 (0.05) ^{a}	5.212	151.782**	233.892**	137.683** L > E > C
	Early burnt	0.27 (0.08) ^{p}	0.11 (0.03) ^{q}	1.84 (0.29) ^{r}	0.11 (0.03) ^{q}				
	Late burnt	0.11 (0.3) ^{x}	0.22 (0.08) ^{y}	5.16 (0.55) ^{z}	0.21 (0.05) ^{y}				
Pycnospora lutescens	Control	0.00 (0.00) ^{a}	0.08 (0.02) ^{b}	0.03 (0.01) ^{ab}	0.00 (0.00) ^{a}	21.533** 17.400**	125.508**	72.608**	L > C & E
	Early burnt	0.00 (0.00) ^{p}	0.03 (0.02) ^{pq}	0.16 (0.05) ^{q}	0.07 (0.03) ^{pq}				
	Late burnt	0.00 (0.00) ^{x}	0.05 (0.02) ^{x}	2.03 (0.47) ^{y}	0.05 (0.02) ^{x}				
Ephemeral forbs (n = 14)	Control	3.90 (0.83) ^{a}	0.12 (0.03) ^{b}	0.03 (0.15) ^{b}	0.05 (0.02) ^{b}	208.521**	216.176**	283.414**	249.969** L > E > C
	Early burnt	6.42 (0.81) ^{p}	0.19 (0.05) ^{q}	3.25 (0.34) ^{p}	0.19 (0.05) ^{q}				
	Late burnt	3.51 (0.53) ^{x}	0.20 (0.06) ^{y}	11.10 (0.93) ^{x}	0.13 (0.04) ^{y}				

Table 6.2 (cont.)

Species and groups	Fire treatment	Mean (s.e.) species richness or seedling density in 1997 (n = 150)	Mean (s.e.) species richness or seedling density in 1998 (n = 150)	Mean (s.e.) species richness or seedling density in 1999 (n = 150)	Mean (s.e.) species richness or seedling density in 2000 (n = 150)	Friedman's ANOVA by ranks			Kruskal-Wallis ANOVA by ranks
						Control 1997 –2000 ❹$^{2}_{3,147}$ =	Early burnt 1997 – 2000 ❹$^{2}_{3,147}$ =	Late burnt 1997 – 2000 ❹$^{2}_{3,147}$ =	Fire treatment in 1999 $H_{2,447}$ =
Chamaecrista absus	Control	0.05 (0.04) ^{a}	0.01 (0.01) ^{a}	0.01 (0.01) ^{a}	0.01 (0.01) ^{a}	1.571	34.887**	44.966**	28.005** E > C
	Early burnt	0.15 (0.05) ^{p}	0.05 (0.02) ^{pr}	0.68 (0.20) ^{q}	0.03 (0.01) ^{r}				
	Late burnt	0.07 (0.03) ^{xy}	0.01 (0.01) ^{y}	0.45 (0.14) ^{z}	0.01 (0.01) ^{y}				
Crotalaria pallida	Control	0.00 (0.00) ^{a}	0.02 (0.01) ^{a}	0.01 (0.01) ^{a}	0.00 (0.00) ^{a}	5.400	29.632**	42.584**	24.670** L > C
	Early burnt	0.01 (0.01) ^{p}	0.03 (0.02) ^{pq}	0.33 (0.12) ^{q}	0.01 (0.01) ^{p}				
	Late burnt	0.03 (0.01) ^{x}	0.07 (0.04) ^{x}	1.27 (0.36) ^{y}	0.08 (0.04) ^{x}				
Indigofera hirsuta	Control	3.01 (0.82) ^{a}	0.00 (0.00) ^{b}	0.01 (0.01) ^{b}	0.01 (0.01) ^{b}	167.663**	178.498**	219.535**	176.349**
	Early burnt	4.63 (0.70) ^{p}	0.05 (0.02) ^{q}	1.13 (0.15) ^{r}	0.05 (0.03) ^{q}				
	Late burnt	2.45 (0.47) ^{x}	0.03 (0.02) ^{y}	8.01 (0.84) ^{z}	0.03 (0.02) ^{y}				
Tephrosia juncea	Control	0.76 (0.17) ^{a}	0.03 (0.01) ^{b}	0.01 (0.01) ^{b}	0.00 (0.00) ^{b}	97.395**	92.371**	79.850**	42.860** E & L > C
	Early burnt	1.45 (0.27) ^{p}	0.03 (0.01) ^{q}	0.61 (0.13) ^{p}	0.02 (0.01) ^{q}				
	Late burnt	0.89 (0.17) ^{x}	0.02 (0.01) ^{y}	0.79 (0.18) ^{x}	0.01 (0.01) ^{y}				
Grasses (n = 8)	Control	11.19 (2.02) ^{a}	0.01 (0.01) ^{b}	0.07 (0.04) ^{b}	0.05 (0.03) ^{b}	346.836**	209.930**	292.452**	241.648** L > E > C
	Early burnt	7.15 (1.46) ^{p}	0.02 (0.01) ^{p}	2.51 (0.30) ^{q}	0.13 (0.05) ^{p}				
	Late burnt	13.41 (2.90) ^{x}	0.04 (0.02) ^{x}	14.45 (2.07) ^{y}	0.08 (0.02) ^{x}				
Heteropogon contortus	Control	7.38 (2.00) ^{a}	0.00 (0.00) ^{b}	0.00 (0.00) ^{b}	0.00 (0.00) ^{b}	156.000**	61.274**	109.827**	38.792** L > C
	Early burnt	4.62 (1.47) ^{p}	0.00 (0.00) ^{q}	0.17 (0.08) ^{q}	0.01 (0.01) ^{q}				
	Late burnt	10.29 (2.90) ^{x}	0.01 (0.01) ^{y}	6.09 (2.06) ^{z}	0.00 (0.00) ^{y}				
H. triticeus	Control	3.71 (0.57) ^{a}	0.00 (0.00) ^{b}	0.07 (0.04) ^{b}	0.05 (0.03) ^{b}	266.402**	176.631**	283.870**	201.406** L > E > C
	Early burnt	2.52 (0.33) ^{p}	0.00 (0.00) ^{q}	2.31 (0.30) ^{p}	0.08 (0.04) ^{q}				
	Late burnt	3.08 (0.43) ^{x}	0.03 (0.02) ^{y}	8.01 (0.74) ^{z}	0.03 (0.01) ^{y}				

Table 6.2 (cont.)

Species and groups	Fire treatment	Mean (s.e.) species richness or seedling density in 1997 (n = 150)	Mean (s.e.) species richness or seedling density in 1998 (n = 150)	Mean (s.e.) species richness or seedling density in 1999 (n = 150)	Mean (s.e.) species richness or seedling density in 2000 (n = 150)	Friedman's ANOVA by ranks			Kruskal-Wallis ANOVA by ranks
						Control 1997 –2000 ❹$^{2}_{3,147}$ =	Early burnt 1997 – 2000 ❹$^{2}_{3,147}$ =	Late burnt 1997 – 2000 ❹$^{2}_{3,147}$ =	Fire treatment in 1999 $H_{2,447}$ =
Non-grass monocots (n = 4)	Control	0.00 (0.00) ^{a}	0.05 (0.02) ^{a}	0.48 (0.12) ^{b}	0.97 (0.17) ^{b}	72.863**	125.831**	108.946**	33.011** E & L > C
	Early burnt	0.00 (0.00) ^{p}	0.05 (0.02) ^{p}	1.85 (0.26) ^{q}	0.57 (0.10) ^{q}				
	Late burnt	0.01 (0.01) ^{x}	0.19 (0.07) ^{x}	2.24 (0.32) ^{y}	0.56 (0.10) ^{y}				
Commelina spp.	Control	0.00 (0.00) ^{a}	0.05 (0.02) ^{a}	0.47 (0.12) ^{b}	0.90 (0.15) ^{b}	73.539**	131.355**	94.578**	28.346** E & L > C
	Early burnt	0.00 (0.00) ^{p}	0.03 (0.02) ^{p}	1.79 (0.25) ^{q}	0.52 (0.09) ^{r}				
	Late burnt	0.01 (0.01) ^{x}	0.16 (0.06) ^{x}	2.01 (0.31) ^{y}	0.56 (0.10) ^{z}				

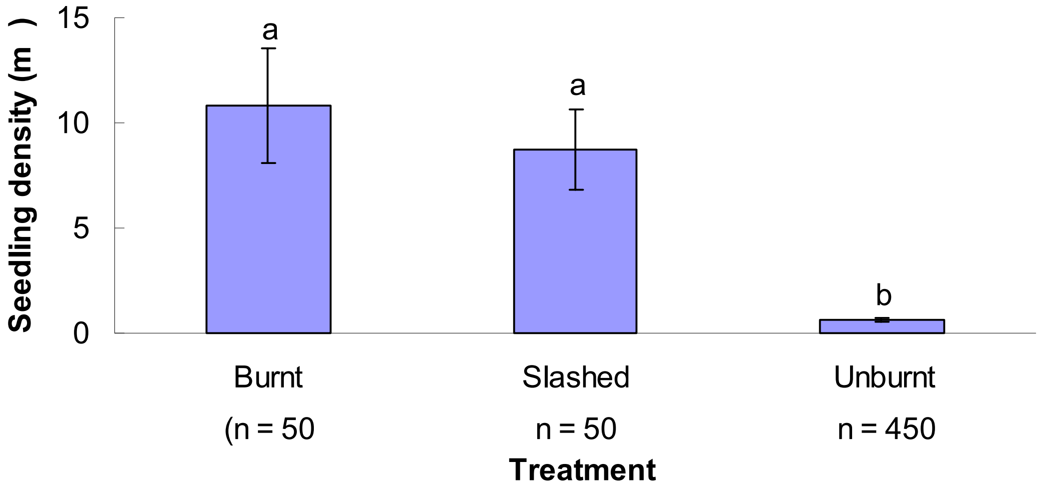


Figure 6.1. Mean (± 1 standard error) seedling density of *Corymbia clarksoniana* in eucalypt savanna in December 1999, at Cape Cleveland. Burnt, burnt two months prior to survey; Slashed, grass was cut four months prior to survey; Unburnt, savanna that was unburnt for 16 months at time of survey.

Seedling density of rainforest trees and shrubs was significantly higher in the late burnt blocks following the 1999 fires. There were no significant differences in rainforest seedlings between years in control and early burnt blocks, nor between the fire treatments of 1999.

Subshrub seedlings were significantly more abundant in late burnt than unburnt control blocks after the 1999 fire treatments. In the control blocks, subshrub seedlings were more abundant in 2000 than in 1998, and there were no significant differences between years in the early burnt blocks. Seedlings of the common subshrub *Triumfetta rhomboidea* were significantly denser after late dry season fires than in unburnt blocks in 1999. *Triumfetta rhomboidea* seedlings were more abundant in 1997 and 2000 in control blocks, and in 1999 in late burnt blocks. There were no significant differences between years in the early burnt blocks.

Both early and late dry season fires promoted seedling emergence of upright perennial forbs over unburnt controls in 1999. No significant differences were detected between years in control blocks, but seedling density of upright perennial forbs in 1999 was significantly greater in both early and late burnt blocks than other years. Seedling density of *Hybanthus* spp. (combined *H. enneaspermus* and *H. stellarioides*, which were indistinguishable at the seedling stage) were not significantly different between years in the control blocks, but seedling density in the early and late burnt blocks was significantly higher after the 1999 fires than all other years. In 1999 the late dry season fires promoted greater seedling density than occurred in the unburnt control blocks.

In 1999, the seedling density of twining perennial forbs was significantly greater in late rather than early dry season burnt savanna, which in turn was significantly greater than in unburnt savanna. No significant differences were detectable in seedling density between years in control burnt blocks. However, a significantly higher seedling density occurred in both early and late burnt blocks in 1999 than all other years, indicating the 1999 fires produced denser seedling emergence than the July 1997 fire. The seedling density of the common twiner, *Galactia tenuiflora*, was significantly higher in 1999 than in other years in both the early and late dry season burnt blocks, but not significantly different between years in control blocks, and a greater seedling density was recorded after both early and late dry season fires than in unburnt savanna in 1999. Seedlings of the common twiners *Glycine tomentella*, *Passiflora foetida* and *Pycnospora lutescens* emerged at significantly higher density in 1999 in late burnt savanna than in early burnt and unburnt savanna. Seedling density of *G. tomentella* was not significantly different between years in control blocks, but in both early and late burnt blocks, was highest following the 1999 fires. Seedlings of the exotic twiner *Passiflora foetida* were significantly more abundant in 1999 than other years in both early and late burnt blocks. Seedling density of *Pycnospora lutescens* was significantly higher in 1998 than in 1997 in control blocks and in 1999 than 1997 in early burnt blocks. In late burnt blocks, *P. lutescens* seedlings were significantly denser in 1999 than other years and in 1998 and 2000 compared to 1997, indicating poor recruitment after the July 1997 fire.

Seedling density in 1999 of ephemeral forbs, and the common forb *Indigofera hirsuta*, was significantly higher after late rather than early dry season fires, which produced significantly greater recruitment than in unburnt savanna. For ephemeral forbs, and *I. hirsuta*, significantly higher seedling density in control blocks was documented following the 1997 fire than in other years. In early burnt blocks, a significantly higher seedling density was recorded in after the 1997 fire than the 1999 fire, and more seedlings were documented in both 1997 and 1999 than 1998 and 2000. In the late burnt blocks, significantly more seedlings were detected in 1999 than 1997, and both years contained significantly higher seedling densities than 1998 and 2000.

The common ephemeral forb *Chamaecrista absus* produced significantly more seedlings in 1999 than 1998 in early burnt blocks, and in 1999 than other years in late burnt blocks. *Crotalaria pallida* produced significantly more seedlings in late burnt than unburnt blocks in 1999, and the 1999 fire produced significantly more seedlings than the 1997 fire in late burnt blocks. *Crotalaria pallida* seedlings were more abundant in 1999 than 1997 and 2000 in early burnt blocks. Seedling density of *Tephrosia juncea* was significantly higher after early and late dry season fires than in unburnt savanna in 1999. More seedling recruitment of *T. juncea* were recorded after the 1997 fire than during other years in control blocks, and seedling emergence was higher in 1997 and 1999 than 1998 and 2000 in both early and late burnt blocks.

Seedling density of grasses in 1999 was significantly greater in late than early dry season burnt savanna, which in turn was greater than unburnt savanna. In control blocks, significantly higher seedling density was recorded following the 1997 fire than in other years. In early burnt blocks, significantly more grass seedlings emerged in 1997 than 1999, and greater numbers in 1999 than in 1998 and 2000. In late burnt blocks, significantly more grass seedlings emerged following the 1999 fires than the 1997 fire, and greater densities were recorded in 1997 than in 1998 and 2000.

Seedlings of the common grass *Heteropogon contortus* were more abundant after late dry season fires than those in the early dry season and in unburnt savanna in 1999. In control and early burnt blocks, a significantly higher seedling density was recorded following the 1997 fire than in other years. Significantly more seedlings of *H. contortus* were detected in 1997 than in 1999, which in turn yielded more seedlings than 1998 and 2000, in both early and late burnt blocks.

Heteropogon triticeus produced significantly more seedlings in 1999 after late rather than early dry season fires, and in early burnt than in unburnt savanna. In control blocks, significantly more *H. triticeus* seedlings were documented following the 1997 fire than in other years. In early burnt blocks, significantly more seedlings were recorded following the 1997 fire than the 1999 fires, with less again in 1998 and 2000. In late burnt blocks, significantly more seedlings were recorded following the 1999 fires than the 1997 fire, and more in 1997 than in 1998 and 2000.

Seedling density of non-grass monocots in 1999 was significantly increased by both early and late dry season fires over unburnt savanna. In control blocks, 1999 and 2000 contained significantly greater seedling density than 1997 and 1998. In both early and late burnt blocks, significantly more seedlings were recorded in 1999 than in other years. The seedling density of the common monocot *Commelina* spp. (combined *C. diffusa* and *C. ensifolia* which were indistinguishable at the seedling stage) in 1999 was more abundant after early and late dry season fires than in unburnt savanna. Significantly more seedlings of *Commelina* spp. emerged in 1999 and 2000 than 1997 and 1998 in control blocks. In both early and late burnt blocks, significantly greater numbers of seedlings were recorded in 1999 than 2000, and more in 2000 than in 1997 and 1998.

6.3.3 Species composition of seedling emergence surveys, soil seed bank samples and floristic surveys

The four annual seedling surveys of the nine 1 ha blocks at Cape Cleveland, between 1997 and 2000 documented a total of 67 species, 12 of which were present in at least half of the surveys (Appendix 1). Seventy six percent of the species documented in the seedling surveys were common to the soil seed bank samples (Appendix 1). These included all eight grasses, while none of the four rainforest seedling species were detected in the soil seed bank. Eleven species that were documented within the soil seed bank were absent from the seedling surveys, although all were uncommon, producing < 0.5 % of the total seed bank density. Five seedling species were not recorded within the floristic surveys but mature plants of each were observed at the Cape Cleveland site, adjacent to floristic survey plots. This suggests germination originated from seed produced on site and, for approximately one quarter of the seedling species, germination originated from fresh, rather than stored seed.

Seedlings were detected for 20% of the woodland trees and shrubs recorded in the floristic surveys, 22% of the rainforest trees and shrubs, 69% of the subshrubs, 88% of the upright perennial forbs, 82% of the twining perennial forbs, 100% of the ephemeral forbs, 50% of the grasses and 31% of the non-grass monocots (Appendix 1).

The relative abundance of native and exotic species remained fairly constant across the floristic surveys, soil seed bank samples and seedling surveys. Only ephemeral forbs and grasses were more common in the seedling surveys than in the floristic surveys and soil seed bank samples. Woodland and rainforest trees and shrubs were most abundant in the floristic surveys, and more abundant in the seedling surveys than the soil seed bank samples.

The PCA scatter plot indicated that the species composition of seedling surveys was related to both the floristic surveys and the soil seed bank (Figure 6.2). It positioned points representing seedling surveys between those representing floristic surveys and soil seed bank samples. Surveys of the same blocks did not tend to be grouped together (i.e. the PCA symbols representing the seedling surveys of a certain block were usually not adjacent to those representing floristic surveys or seed bank samples of that same block). Twenty five (69%) seedling surveys were positioned nearest to a seed bank sample and 11 (31%) were positioned closest to a floristic survey. This suggests species composition of two thirds of the seedling surveys displayed a greater affinity with the soil seed bank than the floristic surveys.

The 11 seedling surveys that were positioned closest to a floristic survey were the 11 most species diverse seedling surveys, and each contained species that were not detected in the soil seed bank. Eight of these 11 seedling surveys (73%) were undertaken in recently

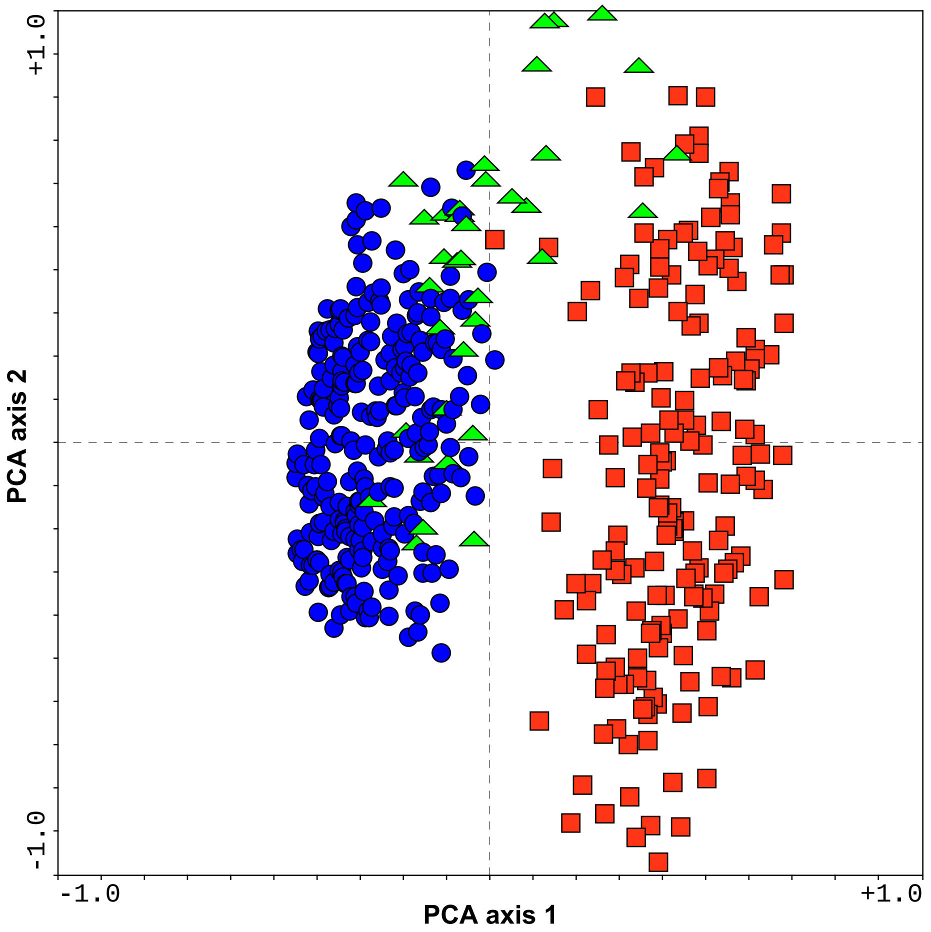


Figure 6.2. PCA scatter plot of species composition within floristic surveys (🟥); soil seed bank samples (●); and seedling emergence surveys (▲) in eucalypt savanna at Cape Cleveland.

burnt savanna, including all surveys after the early and late dry season fires of 1999. The three surveys in unburnt savanna were undertaken in 1998 or 2000 and contained common seedling species as well as several woody species that were absent (*Cajanus confertiflorus* and *Terminalia sericocarpa*) from or rare (*Breynia oblongifolia*) in the seed bank.

The three seedling surveys furthest within the cluster of seed bank samples were the surveys undertaken in 2000 of the second control, early burnt and late burnt blocks. They each contained well below average species richness, and species commonly recorded in the seed bank samples, including *Commelina* spp., *Digitaria breviglumis*, *Galactia tenuiflora* and *Passiflora foetida*.

6.3.4 Safe sites of **Corymbia clarksoniana**

Mean seed germination of *Corymbia clarksoniana* in the laboratory was 38% (standard error = 7). The tetrazolium test found that a mean of 75% (standard error = 5) of the seeds were viable, indicating that 51% of viable seeds germinated in the laboratory within a fortnight of sowing.

Very limited seedling emergence was observed in the first experimental sowing of *C. clarksoniana* seeds, where all seeds were placed on the soil surface (Figure 6.3). Differences between treatments were not statistically significant ($F_{2,12}$; $P > 0.05$).

More seedlings emerged in the second experiment, particularly where seed was buried in cut or burnt plots (Figure 6.4). While no seedlings emerged from the undisturbed plots, differences between treatments were not statistically significant, because of inter-plot variation within treatments (Table 6.3).

6.3.5 Total seedling emergence surveys at Cape Cleveland

The majority of seedlings emerged from the permanent 1m^2 plots during November and early December 1999 (Figure 6.5), which was the start of the 1999 wet season (Table 2.1). The highest rate of seedling emergence occurred in late burnt plots in the first fortnight of November 1999, when an average of 55 new seedlings m^{-2} were recorded. A minor germination event also occurred in the early burnt and early cut sites after some rain during the first fortnight of September 1999.

The mean total seedling emergence and statistical significance of differences between treatments are presented in Table 6.4. Species richness was significantly higher in early and late burnt and cut treatments than in undisturbed savanna. Total seedling emergence was significantly higher in late burnt plots, averaging 90 seedlings m^{-2}, than all other

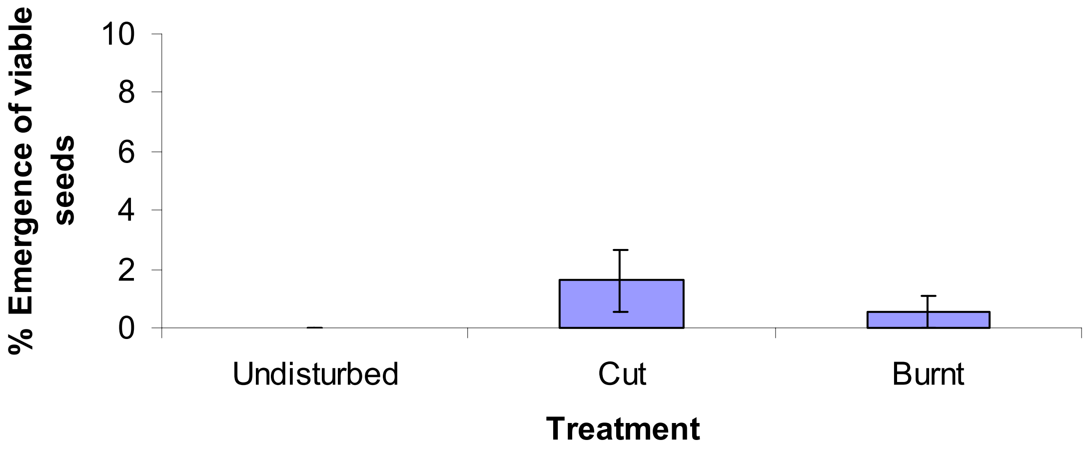


Figure 6.3. Mean (± 1 standard error) percentage seedling emergence of viable seeds of *Corymbia* clarksoniana in eucalypt savanna at Cape Cleveland. Undisturbed, savanna unburnt for three years; Cut, herbaceous layer cut and removed prior to sowing seeds in savanna unburnt for three years; Burnt, savanna burnt prior to seed sowing. Treatments were not significantly different at P > 0.05.

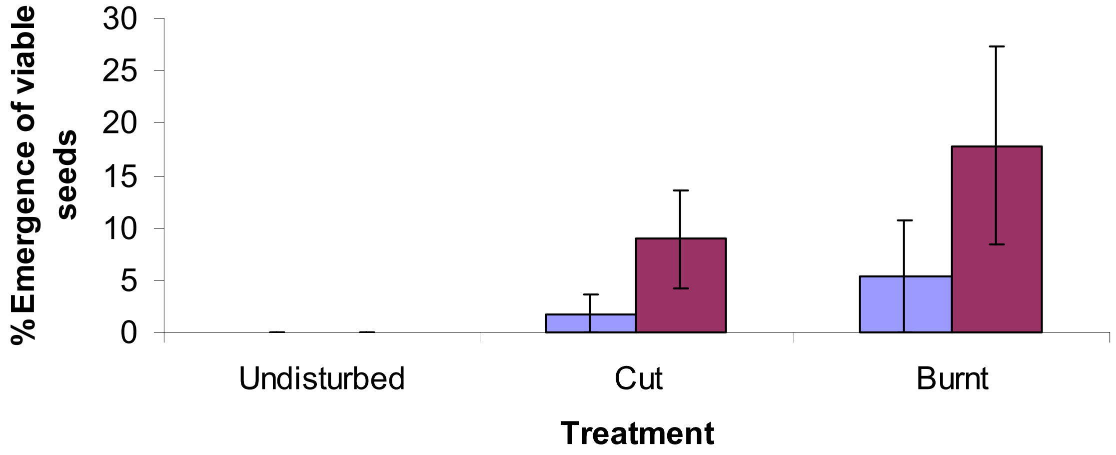


Figure 6.4. Mean (± 1 standard error) percentage seedling emergence of surface sown (🟦) and buried (🟥) viable seeds of *Corymbia clarksoniana* in eucalypt savanna at Cape Cleveland. Seeds sown on the soil surface and buried to 5 mm in Undisturbed, savanna unburnt for three years; Cut, unburnt savanna with the herbaceous layer cut and removed prior to sowing seeds; Burnt, savanna burnt prior to seed sowing.

Table 6.3. Results of two-factor ANOVA of the effect of micro-site disturbance and seed burial on seedling emergence of *Corymbia clarksoniana* in eucalypt savanna at Cape Cleveland. *F* statistic, denominator d.f., numerator d.f..

Treatment	*F* statistic	*P* value
Micro-site disturbance	$F_{2,12} = 2.822$	> 0.05
Seed burial	$F_{1,12} = 2.689$	> 0.05
Disturbance x burial	$F_{2,12} = 0.822$	> 0.05

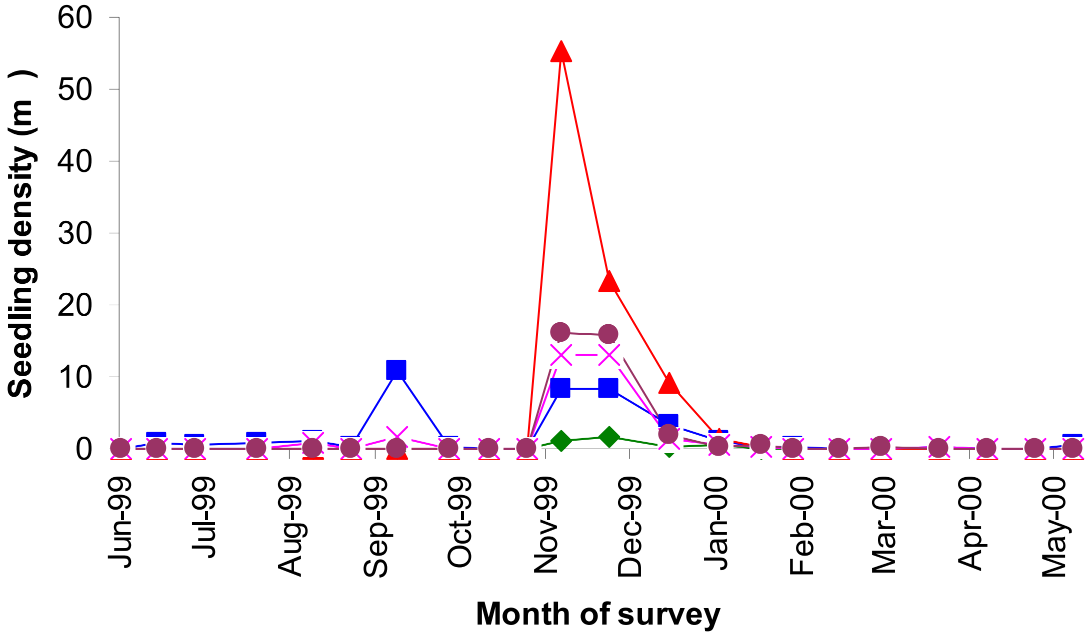


Figure 6.5. Rate of seedling emergence in eucalypt savanna at Cape Cleveland in savanna undisturbed since burning July 1997 (◆); savanna burnt early dry season (May) 1999 (■); savanna burnt late dry season (October) 1999 (▲); savanna unburnt since July 1997, with herbaceous layer cut and removed in May 1999 (X); savanna unburnt since July 1997 with herbaceous layer cut and removed in October 1999 (●). Note that the 1999/2000 wet season rainfall began at the start of November, with 186 mm in that month (see Table 2.1).

Table 6.4. Mean (standard error) species richness and total seedling density (m^{-2}), and Kruskal-Wallis ANOVA results, in undisturbed, early burnt, late burnt, early cut and late cut plots at Cape Cleveland. Total seedling density includes the sum of seedling emergence documented between May 1999 to May 2000 in undisturbed, early burnt and early cut plots; and between October 1999 and May 2000 in late burnt and late cut plots. *H* statistic, denominator d.f., numerator d.f.; *H* statistics without an asterisk (*) are not significantly different at $P > 0.01$; $*P < 0.01$; $**P < 0.001$.

Species and goups	Undisturbed (n = 30)	Early burnt (n = 30)	Late burnt (n = 30)	Early cut (n = 30)	Late cut (n = 30)	Kruskal-Wallis ANOVA $H_{4,145}$ =
Species richness	1.77 (0.24) ^{a}	7.83 (0.54) ^{bc}	8.63 (0.36) ^{c}	6.30 (0.45) ^{b}	6.87 (0.32) ^{bc}	76.859**
All species (n = 49)	1.60 (0.61) ^{a}	37.00 (3.53) ^{b}	90.23 (11.41) ^{c}	31.57 (3.31) ^{b}	35.10 (4.09) ^{b}	96.063**
Native species (n = 39)	2.40 (0.43) ^{a}	31.87 (3.36) ^{b}	79.80 (11.19) ^{c}	24.83 (3.20) ^{b}	25.00 (3.90) ^{b}	95.754**
Exotic species (n = 10)	1.70 (0.49) ^{a}	5.13 (1.24) ^{b}	10.43 (1.37) ^{c}	6.73 (1.01) ^{bc}	10.10 (1.50) ^{c}	49.448**
Rainforest trees and shrubs (n = 5)	0.03 (0.03) ^{a}	0.03 (0.03) ^{a}	0.03 (0.03) ^{a}	0.13 (0.10) ^{a}	0.03 (0.03) ^{a}	0.736
Subshrubs (n = 4)	0.63 (0.40) ^{a}	0.87 (0.63) ^{a}	1.43 (0.50) ^{ab}	2.60 (0.72) ^{b}	1.87 (0.54) ^{ab}	18.912**
Triumfetta rhomboidea	0.63 (0.41) ^{a}	0.73 (0.63) ^{a}	1.37 (0.49) ^{ab}	2.17 (0.58) ^{b}	1.80 (0.52) ^{ab}	22.756**
Upright perennial forbs (n = 6)	0.13 (0.08) ^{a}	4.93 (1.84) ^{b}	4.63 (2.18) ^{b}	1.60 (0.50) ^{b}	2.50 (0.90) ^{b}	23.821**
Hybanthus spp.	0.10 (0.07) ^{a}	3.30 (1.51) ^{a}	1.63 (0.73) ^{a}	0.90 (0.40) ^{a}	1.40 (0.48) ^{a}	11.529
Spermacoce brachystema	0.03 (0.03) ^{a}	0.17 (0.84) ^{a}	2.50 (1.55) ^{a}	0.60 (0.33) ^{a}	1.07 (0.69) ^{a}	5.818
Twining perennial forbs (n = 13)	1.37 (0.31) ^{a}	9.83 (1.62) ^{bd}	17.47 (3.05) ^{c}	7.27 (1.32) ^{d}	13.40 (1.77) ^{bc}	62.869**
Galactia tenuiflora	0.27 (0.12) ^{a}	4.53 (1.34) ^{b}	2.37 (0.63) ^{b}	0.93 (0.30) ^{ab}	1.10 (0.34) ^{ab}	20.248**
Glycine tomentella	0.00 (0.00) ^{a}	1.70 (0.50) ^{b}	5.17 (2.78) ^{b}	0.50 (0.21) ^{ab}	1.13 (0.36) ^{b}	24.020**
Macroptilium atropurpureum	0.27 (0.10) ^{a}	0.27 (0.11) ^{a}	0.27 (0.13) ^{a}	0.40 (0.22) ^{a}	0.67 (0.26) ^{a}	1.546
Passiflora foetida	0.73 (0.27) ^{a}	2.20 (0.56) ^{ac}	6.73 (1.08) ^{b}	3.30 (0.69) ^{c}	6.83 (1.29) ^{bc}	51.146**
Pycnospora lutescens	0.10 (0.07) ^{a}	0.77 (0.39) ^{a}	1.77 (0.77) ^{a}	2.13 (0.96) ^{a}	3.17 (1.18) ^{a}	10.622
Ephemeral forbs (n = 11)	0.13 (0.06) ^{a}	5.33 (0.80) ^{bc}	12.70 (2.45) ^{c}	3.00 (0.63) ^{bd}	2.33 (0.59) ^{d}	56.717**
Crotalaria pallida	0.00 (0.00) ^{a}	1.00 (0.49) ^{a}	1.40 (0.60) ^{a}	0.10 (0.07) ^{a}	0.40 (0.21) ^{a}	11.737
Indigofera hirsuta	0.03 (0.03) ^{a}	1.70 (0.44) ^{b}	8.37 ^{c} (1.93)	1.00 ^{b} (0.28)	1.23 ^{b} (0.54)	45.205**
Tephrosia juncea	0.03 (0.03) ^{a}	1.23 (0.43) ^{ab}	1.83 (0.84) ^{b}	0.13 (0.08) ^{ab}	0.03 (0.03) ^{a}	18.868**
Grasses (n = 6)	0.23 (0.20) ^{a}	11.77 (1.72) ^{b}	45.20 (10.65) ^{c}	8.83 (2.00) ^{d}	5.20 (0.93) ^{d}	91.262**
Heteropogon contortus	0.00 (0.00) ^{a}	0.03 (0.03) ^{ab}	17.00 (10.18) ^{b}	1.27 (1.27) ^{ab}	0.07 (0.05) ^{ab}	19.411**
H. triticeus	0.23 (0.20) ^{a}	11.07 (1.72) ^{b}	27.43 (3.13) ^{c}	7.40 (1.77) ^{bd}	4.97 (0.94) ^{d}	86.943 **
Non-grass monocots (n = 4)	0.77 (0.20) ^{a}	4.23 (1.08) ^{ab}	8.87 (2.21) ^{b}	8.13 (2.23) ^{b}	9.77 (2.35) ^{b}	31.453**
Commelina spp.	0.77 (0.20) ^{a}	4.07 (1.09) ^{ab}	8.70 (2.21) ^{b}	7.90 (2.24) ^{b}	9.53 (2.37) ^{b}	29.751**

treatments. The early burnt, early cut and late cut treatments produced significantly more seedlings than undisturbed plots.

Total seedling emergence of native species was significantly less in undisturbed plots than all other treatments. Late burnt plots contained significantly higher native seedling densities than early burnt, early cut and late plots. Seedlings of exotic species were more abundant in burnt and cut plots than undisturbed plots. Late burnt and early cut plots contained significantly higher seedling densities of exotic species than early burnt plots.

No seedlings of woodland trees and shrubs were observed within the plots. There were no significant differences between seedling emergence of rainforest trees and shrubs across the treatments. Total seedling emergence of subshrubs and the common subshrub *Triumfetta rhomboidea*, was significantly higher in early cut than early burnt plots.

All burnt and cut treatments produced significantly higher total seedling emergence of upright perennial forbs than undisturbed savanna. No significant differences were detected for the common upright perennial forbs *Hybanthus* spp. and *Spermacoce brachystema*.

Seedling emergence of twining perennial forbs was significantly increased by burning and cutting in both the early and late dry seasons. Late burning and cutting promoted seedlings of twining perennial forbs over early cutting, while late burnt plots contained significantly more seedlings than early burnt plots. No significant effects could be detected for the common twiners *Macroptilium atropurpureum* and *Pycnospora lutescens*. Early and late burnt plots contained significantly more seedlings of *Galactia tenuiflora* than undisturbed plots. Early and late burning and late cutting enhanced emergence of *Glycine tomentella* seedlings over undisturbed savanna. *Passiflora foetida* seedlings were more abundant in late burnt and late cut plots than undisturbed plots, and late burning promoted seedlings over early burning and cutting.

Total seedling emergence of ephemeral forbs was significantly lower in undisturbed savanna than all other treatments. Burning during both the early and late dry seasons promoted the emergence of ephemeral forb seedlings relative to late cutting, and late burnt plots contained more seedlings than early cut plots. No significant differences could be detected for the common ephemeral forb *Crotalaria pallida*. *Indigofera hirsuta* seedlings were significantly more abundant after burning and cutting than in undisturbed savanna, and late burnt plots contained more seedlings than early burnt, and early and late cut plots. *Tephrosia juncea* seedlings were significantly more abundant in late burnt than early burnt and early cut plots.

Total grass seedling emergence was significantly lower in undisturbed plots than all other treatments. Early and late burning increased seedling emergence more than early and late cutting. The common grass *Heteropogon contortus* produced significantly more seedlings after late dry season fires than in undisturbed savanna. Significantly more *H. triticeus* seedlings emerged from savanna burnt and cut in the early and late dry seasons than in undisturbed savanna. Early and late burnt plots contained significantly more seedlings than late cut, and late burnt more than early burnt and early cut plots.

Seedling emergence of non-grass monocots, including *Commelina* spp., was significantly greater in late burnt, and early and late cut plots than in undisturbed savanna.

6.3.6 Total seedling emergence as a proportion of the soil seed bank

Up to 3% of the untreated soil seed bank collected in the mid dry season (July) of 1999, emerged as seedlings between July and October 1999. A significantly higher proportion of the seed bank emerged in the early burnt plots than in early cut plots, and in early cut plots than in undisturbed plots (Figure 6.6a; $H_{4,10} = 7.261$; $P < 0.027$).

Up to 14% of the untreated soil seed bank collected in the late dry season (October) of 1999, emerged as seedlings over the wet season (23rd October 1999 to 29th February 2000; Figure 6.6b). The percentage seedling emergence was significantly higher in late burnt, early cut and late cut plots than undisturbed plots (Figure 6.6b; $F_{4,10} = 13.238$;

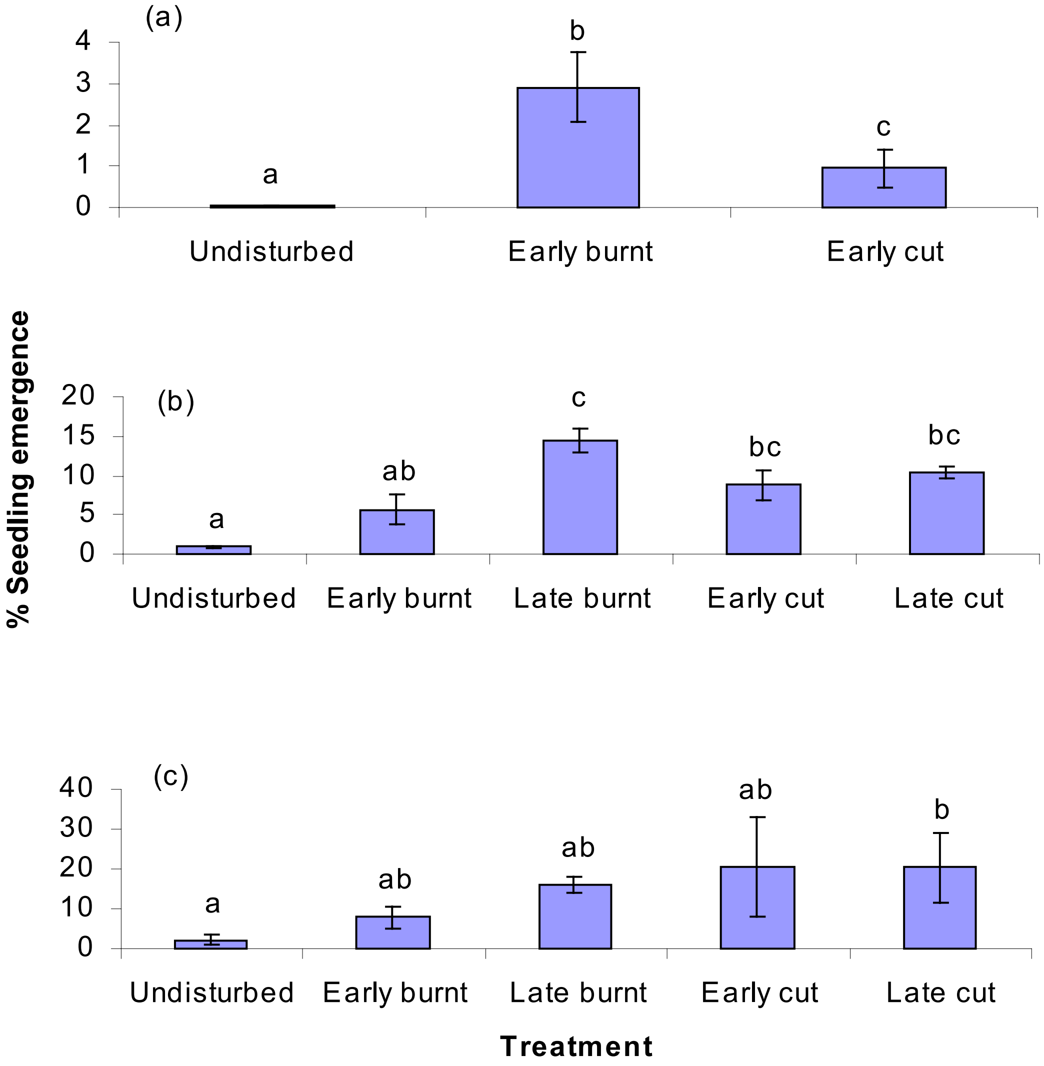


Figure 6.6. Mean (± 1 standard error) percentage seedling emergence of soil seed bank at Cape Cleveland. (a) seedling emergence between 31 July and 23 October 1999 as a percentage of untreated soil seed bank collected 31 July 1999; (b) seedling emergence between 23 October 1999 and 29 February 2000 as a percentage of the untreated soil seed bank collected 23 October 1999; (c) seedling emergence between 23 October 1999 and 29 February 2000 as a percentage of the decline in soil seed bank over the same period. Undisturbed, savanna that was last burnt July 1997; Early burnt, savanna burnt in July 1997 and May 1999; Late burnt, savanna burnt in July 1997 and October 1999; Early cut, the herbaceous layer cut and removed in the early dry season (May) 1999, from savanna that was last burnt July 1997; Late cut, the herbaceous layer cut and removed in the late dry season (October) 1999, from savanna that was last burnt July 1997.

$P < 0.001$). Late burnt plots also had a higher percentage emergence than early burnt plots.

Seedling emergence, as a percentage of the decline in the untreated soil seed bank over the wet season (23rd October 1999 to 29th February 2000), was up to 20% (Figure 6.6c). It was significantly higher in the late cut than the undisturbed plots ($F_{4,10} = 4.112$; $P < 0.032$).

6.4 Discussion

6.4.1 Seedling emergence surveys

Surveys of eucalypt savanna at four sites across the Townsville region indicated that seedling emergence occurs primarily in the first year after fire (Tables 6.1 and 6.2). At Mt Elliot, Castle Hill and Many Peaks Range, species richness of seedlings, total seedling density and seedling density of native and exotic species, most growth form groups and common species, were significantly higher in recently burnt than unburnt savanna (Table 6.1). Woodland and rainforest trees and shrubs were the only growth form groups that did not show not significantly enhanced seedling emergence following fire, being observed at low densities in both burnt and unburnt sites. Four exotic species, *Crotalaria goreensis*, *Hyptis suaveolens*, *Stachytarpheta jamaicensis* and *Triumfetta rhomboidea*, the native twiner *Rhynchosia minima* and an unidentified species of *Fimbristylis*, were the only common species that did not show a significant response to fire. Seedling emergence of these species in unburnt savanna was high in areas disturbed by feral pigs at one of the sites (Many Peaks Range). In this study, no species or species groups produced seedlings in significantly higher densities in unburnt compared to burnt savanna. This contrasts with patterns of seedling emergence of some other tropical savanna species, including *Eucalyptus miniata* which recruits seedlings at highest density in unburnt savanna (Setterfield 1997*b*). Annual grasses that dominate many tropical eucalypt savannas, such as *Schizachyrium* spp. and *Sorghum* spp., germinate in high densities in both burnt and unburnt savanna (Andrew and Mott 1983; Crowley and Garnett 1999).

Fire, especially late dry season fire, significantly increased the richness of seedling species and the density of seedlings of most groups and common species at Cape

Cleveland (Table 6.2). A significant increase in seedling density by late dry season fires over unburnt savanna was documented for native and exotic species, subshrubs, the common subshrub *Triumfetta rhomboidea*, all herbaceous growth form groups, and the common herbaceous species *Crotalaria pallida*, *Galactia tenuiflora*, *Glycine tomentella*, *Indigofera hirsuta*, *Heteropogon contortus*, *H. triticeus*, *Passiflora foetida, Pycnospora lutescens* and *Tephrosia juncea*. The late dry season fires also increased seedling emergence compared with early dry season fires for native and exotic species, twining perennial forbs, the common twiners *Galactia tenuiflora*, *Glycine tomentella*, *Passiflora foetida* and *Pycnospora lutescens*, ephemeral forbs and the common ephemeral *Indigofera hirsuta*, grasses, and the dominant grass *Heteropogon triticeus*.

The late dry season fires of 1999 produced significantly higher species richness and higher seedling emergence than the 1997 mid dry season fire for native and exotic species, subshrubs, *Triumfetta rhomboidea*, all herbaceous species groups, and the common herbs *Chamaecrista absus*, *Crotalaria pallida*, *Galactia tenuiflora*, *Glycine tomentella*, *Indigofera hirsuta*, *Heteropogon triticeus*, *Passiflora foetida*, *Pycnospora lutescens* and *Tephrosia juncea* (Table 6.2). The 1997 mid dry season fire promoted significantly greater seedling density than the 1999 early dry season fires for ephemerals, *I. hirsuta* and *H. contortus*.

The increased seedling density of *Chamaecrista absus*, *Crotalaria pallida*, *Galactia tenuiflora* and *Glycine tomentella* following late dry season fires, compared with unburnt savanna, indicates that burning plays a role in releasing seeds of these species from a state of dormancy, despite the inability of laboratory and shadehouse experiments to detect significant effects of heat shock and smoke (Chapters 4 and 5). Further assessment of the seed germination ecology of these species is therefore required.

Differences in seedling density with fire season are often reported where rainfall is strongly seasonal. Late dry season (i.e. autumn) fires tend to produce greatest recruitment in some fire-prone communities of Mediterranean climates, such as shrubby forests and woodlands of south-western Australia (Bell *et al*. 1987*b*; Hobbs and Atkins 1990). However, Noble (1989) found that annual forbs in mallee vegetation of New South Wales emerged at greatest density after early dry season (i.e. spring) fires. Roche *et al*. (1998) demonstrated that smoke application in unburnt *Banksia* woodland of south-western Australia in the late dry season (i.e. autumn) also produced greatest seedling recruitment compared with other seasons. Seedling density of *H. contortus* has been reported at highest densities after late dry season fires in south-eastern Queensland (Tothill 1969). Regions with lower seasonal differences in rainfall or less consistency in seasonal variation, such as the Sydney region, may display less variation in recruitment with fire season (Bradstock and Bedward 1992). However in these areas, low intensity fires, regardless of season, tend to produce fewer seedlings than higher intensity fires (Clark 1988; Bradstock and Auld 1995). The use of repeated low intensity fires may reduce populations of species that rely on fire-triggered germination (Keith 1996).

Bond and van Wilgen (1996) argued that differences in seedling recruitment with fire season may be due to the size of seed banks at the time of fire, or variation in soil heating, which affects seed mortality and dormancy release. It has been demonstrated that heat penetrates to a greater depth, and therefore affects a larger proportion of the soil seed bank, during late rather than early dry season fires in savanna at Cape Cleveland (Chapter 4). The large number of seeds released from seed dormancy compensated for the higher seed mortality produced by elevated soil temperatures, resulting in significantly denser seedling emergence of *Indigofera hirsuta* after late rather than early dry season fires (Chapter 4). It has also been demonstrated that the soil seed bank is significantly larger in the late rather than early dry season, so that a greater density of seed is available to be influenced by late dry season fires (Chapter 5). Therefore the more abundant seedling recruitment after late, rather than early, dry season fire appears to be the result of both greater heat penetration into the topsoil and the larger seed bank present during that season.

Bond and van Wilgen's (1996) discussion on variation in seedling density with variation in the heat penetration of the topsoil during fires, may be expanded to include other fire cues. The significantly denser seedling recruitment after late dry season fires of species released from seed dormancy by smoke, i.e. upright perennial forbs, grasses and the dominant grass *Heteropogon triticeus*, indicates that greater numbers of seed were exposed to smoke. While seed banks were larger in the late dry season (Chapter 5), it may be that, in the same way that heat shock penetrates a greater volume of soil during late dry season fires, the chemical stimulant present in smoke may also penetrate to a greater depth in the topsoil. This may result from the greater percentage combustion of fine fuels (Chapter 3) and the proximity of rainfall that follows within weeks of the late dry season fires. Further research is needed to examine whether chemical stimulants in smoke penetrate to the greatest depth during late dry season fires.

Seedling emergence of trees and shrubs differed from that of herbaceous species. While seedling emergence of herbs was concentrated during the first wet season after fire, the recruitment of several trees and shrubs was linked to particular years. For instance seedling emergence of rainforest trees and shrubs was higher in 1999 than any other year (Table 6.2). The limited recruitment of rainforest species in Townsville savannas contrasts with that recorded in some savanna studies, such as in South America (Hoffman 1996), and wet sclerophyll forests of north-eastern Australia (Harrington and Sanderson 1994; Williams 2000), but is consistent with many Australian tropical savanna studies (e.g. Bowman *et al*. 1988; Bowman and Panton 1993; Russell-Smith *et al*. in press).

Seedling emergence of the dominant tree, *Corymbia clarksoniana*, was observed exclusively in 1998, indicating irregular recruitment events (Table 6.2). The density of *C. clarksoniana* germination resulted in the seedling density of woodland trees and shrubs as a group also being significantly higher in 1998 than other years. Gill *et al*. (1990) suggested long-term episodic establishment events of tropical eucalypts may result from a combination of particularly abundant seed set and an extended wet season. This may explain the emergence of *C. clarksoniana* seedling exclusively in 1998, which had above average annual rainfall, with unusually high rain in August to October, coinciding with seed fall and seedling emergence of *C. clarksoniana* (Table 2.1). This pattern of episodic seedling emergence resembles that of many tropical rainforest trees. For instance Connell and Green (2000) documented six episodes of dense seedling emergence over 32 years, in tropical rainforest on the Atherton Tableland in north-eastern Australia.

Seedling surveys of *C. clarksoniana* in 1998 indicated that while this species does germinate in savanna that has remained unburnt for 16 months, seedlings emerged in recently burnt and slashed savanna at 14 to 17 times the density of unburnt savanna (Figure 6.1). These results should be considered in the light of the fact that the data were collected from only a single slashed and recently burnt block, and differences may have resulted from a separate factor linked with the recently burnt and slashed areas. However, given the proximity of these areas to the unburnt 1 ha blocks, the results provide evidence that seedling emergence of *C. clarksoniana* is enhanced in burnt savanna, and sites with low herbaceous cover.

6.4.2 Safe sites for **Corymbia clarksoniana**

Due to low and variable germination, experimental manipulation of micro-site did not provide conclusive proof that seedling emergence of *C. clarksoniana* is increased in recently burnt savanna or where the ground cover is removed. No seedlings emerged from seed sown in undisturbed savanna, while slightly higher recruitment occurred from buried rather than surface sown seeds in burnt or cut savanna (Figure 6.4). The absence of seedlings from at least one replicate of each treatment can be linked with the failure to detect significant differences between treatments. However, the increased seedling emergence documented in the seedling surveys in recently burnt and slashed savanna, coupled with the absence of recruitment from seeds experimentally sown onto undisturbed plots, combine to provide good evidence that *C. clarksoniana* seedling emergence is enhanced where the herbaceous cover is thin, and particularly when seeds fall onto recently burnt ground.

Late dry season fires reduce seed production in *C. clarksoniana* (Chapter 5). The low proportion of viable *C. clarksoniana* seed that germinated in the experimental plots indicates that the reduction in seed fall produced by late fires may have a significant effect on seedling emergence.

Further examination is warranted to assess the possibility that shallow seed burial, which may be provided by ants or animal digging, also enhances seedling emergence. Seed burial has been demonstrated to enhance seedling emergence in temperate eucalypt forests and woodlands in south-eastern Australia (Free 1951; Clarke and

Davison 2001). Ant removal of experimentally sown tropical eucalypt seeds can be considerable (Setterfield 1997*b*) and this may have affected the emergence of seedlings in this experiment. The fact that only 51% of the viable seeds germinated in the laboratory suggests further experimentation is needed to understand the germination requirements of *C. clarksoniana*.

Seedling recruitment of eucalypts has been reported in both recently burnt and longer unburnt sites (Bowman and Kirkpatrick 1986; Gill 1997). *Eucalyptus marginata* of south-western Australia can germinate in both burnt and unburnt forest, however seedlings have been documented at more than twice the density in burnt forest (Whelan and Main 1979). Germination of *E. regnans* has also been documented in the absence of fire, although seedling survival is poor in unburnt forest (Ashton and Chinner 1999).

The possibility that *C. clarksoniana* germination is higher in recently burnt savanna contrasts with *E. miniata* in the Northern Territory, which recruits seedlings at greater density in unburnt savanna (Setterfield 1997*b*). These differences may reflect different micro-site environments in the savanna investigated by Setterfield (1997*b*), which experiences an annual dry season senescence of much of the herbaceous layer, in contrast to the savanna at Cape Cleveland, which is dominated by a perennial herbaceous layer.

6.4.3 Comparative species composition of seedling emergence surveys, soil seed bank samples and floristic surveys

No species that were absent from the standing vegetation, emerged as seedlings at Cape Cleveland (Appendix 1). This suggests that seedlings germinated from seed that was produced on-site, which is typical of many species of fire-prone communities (Whelan 1986). Three quarters of the seedling species recorded in the surveys were also detected in the soil seed bank, suggesting most seedlings originated from stored seed and highlighting the value of soil seed banks in this community. The remaining quarter of the species observed as seedlings probably originated from freshly fallen seed or very short-lived seed banks, although it is possible that some may have produced a persistent but undetected soil seed bank. No species produced a bradysporous seed bank.

6.4.4 Total seedling emergence

Total seedling emergence between May 1999 and May 2000 was significantly enhanced by fire, particularly late dry season fires (Table 6.4). Most seedlings emerged within the first six weeks of the initial rain of the post-fire wet season, between November and December 1999 (Figure 6.5; Table 2.1).

The seedling density documented during surveys in December 1999 (Table 6.2) was approximately one third to one half of the total seedlings that emerged from the early and late burnt blocks (Table 6.4). Differences between total seedling density and the snapshot provided by the seedling surveys at the start of December, would most likely be due to additional seedlings emerging after the surveys and seedling mortality prior to the surveys (Chapter 7). This indicates that the estimate of seedling density provided by the seedling surveys was a moderate proportion of the total seedlings that emerged over the year, and that the surveys displayed the same overall trends in regards to fire-enhanced seedling emergence.

Burning and cutting in both the early and late dry seasons significantly promoted the number of seedling species, total seedling density, and seedling emergence of native and exotic species, upright and twining perennial forbs, ephemeral forbs, the common ephemeral *I. hirsuta*, grasses and the dominant grass *H. triticeus* (Table 6.4).

Early and late dry season fires both promoted seedling density of grasses over cutting in both seasons. Late burnt plots contained significantly more seedlings overall, and more seedlings of natives, grasses and *Indigofera hirsuta*, than plots burnt early in the dry season and cut in either season.

The removal of the grass layer in both the early and late dry season promoted seedling emergence that was not significantly different from that of burning in the early dry season, for total seedling density and seedlings of rainforest trees and shrubs, upright perennial forbs, including *Hybanthus* spp. and *Spermacoce brachystema*, twining perennial forbs, and the common twiners *Galactia tenuiflora*, *Glycine tomentella*, *Passiflora foetida* and *Pycnospora lutescens*, the common ephemeral forbs *Crotalaria pallida*, *I. hirsuta* and *Tephrosia juncea*, the common grass *H.*, non-grass monocots and

*Commelin*a spp. Of these species, upright forbs, *P. lutescens*, ephemeral forbs, *I. hirsuta*, and *T. juncea* showed significant fire-related dormancy release (Chapters 4 and 5). This suggests that early dry season fires did not promote the full potential recruitment of several species and species groups.

Cutting in each season produced seedling emergence that was not significantly different from that under late dry season fires for exotic species, rainforest trees and shrubs, upright forbs, *Hybanthus* spp., *Spermacoce brachystema*, *Galactia tenuiflora*, *Glycine tomentella*, *Pycnospora lutescens*, *Crotalaria pallida*, *Heteropogon contortus*, non-grass monocots and *Commelina* spp. Of these, only upright perennial forbs, whose seed germination is enhanced by exposure to smoke, and *P. lutescens,* which is promoted by heat shock (Chapter 5), have displayed significant fire-related heat or chemical cues for dormancy release. This indicates that most species with seed dormancy broken by heat shock or smoke, germinated at greater density after late fires than cutting treatments. It also confirms that late dry season fires release a larger number of species from a state of seed dormancy than early dry season fires.

These data indicate that part of the role of fire in enhancing seedling emergence operates through removing the competitive inhibition provided by the dense herbaceous cover. Shaw (1957) also found that cutting and removing the grass layer produced a seedling density of *Heteropogon contortus* that was intermediate between that of burnt and undisturbed treatments. This inhibition may be due to competition for light, or be linked to soil temperatures, which can increase after the removal of grass cover (Shaw 1957; Tothill 1969).

Total seedling emergence, with a maximum mean density in one year of 90 seedlings m^{-2} (Table 6.4), is higher than that recorded by Purdie and Slatyer (1976) in a temperate eucalypt woodland in south-eastern Australia, where total seedling emergence levels ranged from 7.5 to 25 m^{-2}. However, it is lower than that recorded in some fire-prone communities. For instance, the fire-killed shrub *Beaufortia elegans* in south-western Australia, can produce an average of 235 seedlings m^{-2} after autumn fires (Bell *et al.* 1987*b*). Annual grasses of tropical savannas can also recruit seedlings at higher densities than recorded in this study. For example, the annual grass *Schizachyrium* *fragile* can produce 2560 seedlings m^{-2} (Crowley and Garnett 1999), and *Sorghum intrans* 253 m^{-2} (Andrew and Mott 1985).

6.4.5 Total seedling emergence as a proportion of untreated soil seed bank

Seedling emergence between July and October 1999, accounted for up to 3% of the untreated soil seed bank collected in the mid dry season, and was significantly higher in early burnt than in undisturbed and early cut plots (Figure 6.6a). Seedling emergence over the wet season, between October 1999 and February 2000, accounted for up to 14% of the untreated soil seed bank collected in the late dry season, and was significantly higher in late burnt, early and late cut plots than in undisturbed plots, and in late burnt than early burnt plots (Figure 6.6b). While this is a larger proportion of the seed bank than recruited during the dry season, it remains only a small fraction of the seed bank that was available for germination. These data suggest that a proportion of the untreated seed bank that germinates in the shadehouse, may possess an enforced dormancy (Chapter 5). Auld *et al*. (2000) suggested enforced seed dormancy produced by darkness and inappropriate temperatures may be responsible for the seed bank persistence of viable seed that lacked an innate dormancy. There is evidence that darkness may have enforced dormancy onto a proportion of the seed bank at Cape Cleveland, as the removal of shading from the herbaceous layer significantly enhanced the percentage germination from the seed bank (Figure 6.6).

The low percentage germination of the seed bank indicates that while late dry season fires promote greater recruitment than early dry season fires, the potential for further seedling emergence remains. However, the density of seeds that germinate but fail to emerge above the soil surface may be considerable and Murray (1998) demonstrated seed germination can be density-dependent, which suggests an upper threshold exists for potential density of emerging seedlings.

Seedling emergence accounted for up to 20% of the decline in untreated soil seed bank over the wet season, and was significantly higher in late cut than undisturbed plots (Figure 6.6c). This indicates that only a low proportion of the seeds that are lost from the seed bank during the wet season reach the emerged seedling stage, the majority presumably either rot or are eaten.

Several recruitment studies have documented a low proportion of the seed bank emerging as seedlings (e.g. Keeley 1977; Grice and Westoby 1987; Moreno and Oechel 1991; Pierce and Cowling 1991). While seedling recruitment in eucalypt savanna at Cape Cleveland was primarily limited by the occurrence of fire required to break seed dormancy (Chapters 4 and 5), it may be concluded that the low to moderate density of the soil seed bank (Chapter 5) was a contributing factor that limited seedling emergence.

The limited or episodic seedling emergence of woody species in savannas around Townsville is consistent with other trees and shrubs of tropical savannas (e.g. Lacey 1974; Burrows and Burrows 1992). The low seedling emergence of trees and shrubs may represent a trade-off for the resources. Sprouting species tend to put greater resources into vegetative growth and maintenance of meristematic tissue than seed production, resulting in lower seedling densities than associated fire-killed species (Pate *et al*. 1990; Kruger 1997; Bell 2001; Bond and Midgley 2001). Allocating resources to ensure the longevity of individual plants is a successful strategy that can buffer against the effects of frequent burning and provide population persistence (Bond and Midgley 2001). This is reflected in the stability in composition and abundance of woody species documented over five years in the floristic surveys at Cape Cleveland (Chapter 3).

Climatic conditions, and their effects on other factors such as fire frequency and intensity, may be influential in the development of life history strategies. For example, van Rensberg *et al*. (1999) found that populations of *Themeda triandra* from regions with high and predictable rainfall relied less on seedling recruitment and more on vegetative reproduction, than populations in regions with lower and less predictable rainfall. This reflects the low seedling emergence of *T. triandra*, which was < 1% of the total seedling density, in the high rainfall region of Townsville. It also supports Bond and Midgley's (2001) hypothesis that regular burning promotes persistent species with less seedling recruitment, as fires tend to be more frequent in regions with higher and predictable rainfall (Higgins *et al*. 2000).

6.5 Conclusion

Seedling emergence in the eucalypt savannas around Townsville, in north-eastern Australia, is dominated by herbaceous species, reflecting the dominance of herbs in the soil seed bank (Chapter 5). Seedling recruitment of these species occurs primarily at the start of the first wet season following fire. The removal of the herbaceous layer has been demonstrated to significantly increase seedling emergence. This indicates that there are multiple fire-related cues that promote germination in this savanna, including exposure to heat shock, smoke, enhanced nitrate levels (Chapters 4 and 5), and the removal of competition from the herbaceous layer.

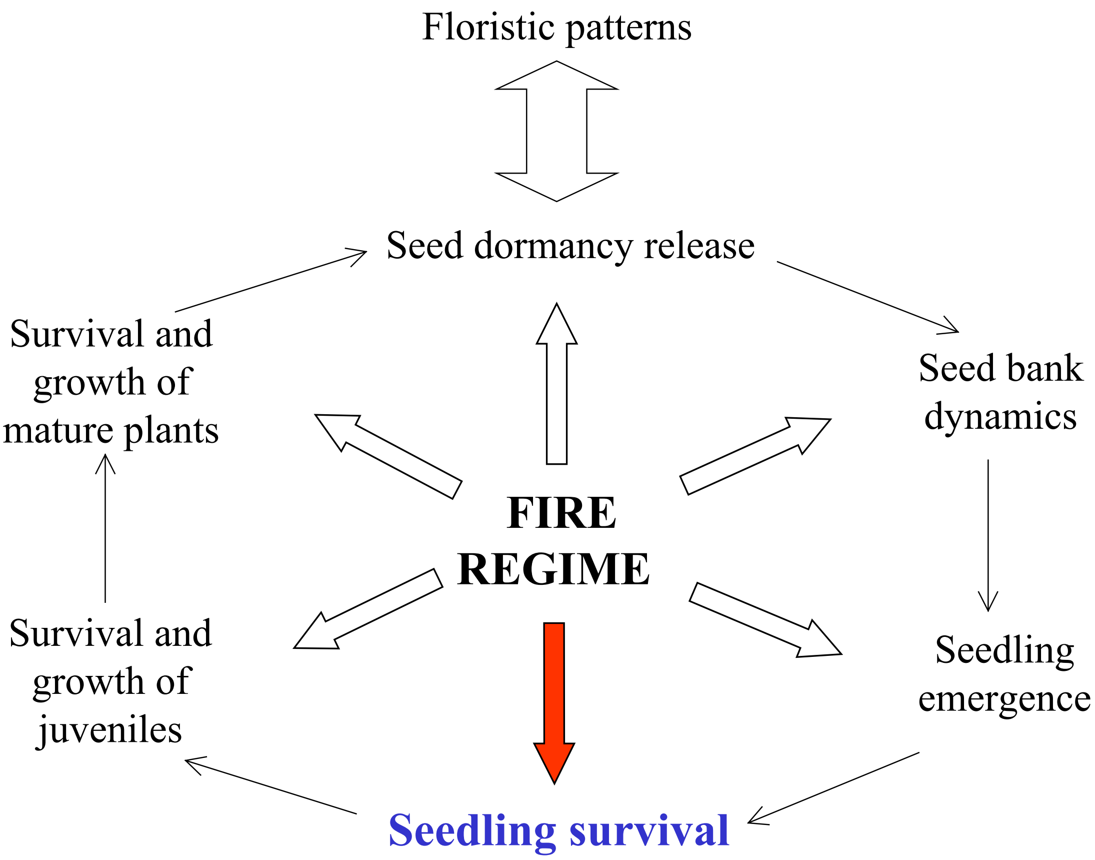
Late dry season fires promote a greater density of seedling emergence than early dry season fires. This is consistent with reports from other fire-prone communities that high intensity, late dry season fires promote the emergence of more seedlings than early dry season fires, or low intensity fires in general for regions with a poor distinction between wet and dry seasons. It contrasts with the seedling recruitment of annual grasses that dominate some tropical savannas of northern Australia, which can recruit seedlings at high densities in the absence of fire (Andrew 1986; Crowley and Garnett 1999). The greater seedling density after late, rather than early, dry season fires at Cape Cleveland accounts for the larger increase in species abundance after late dry season fires, documented in the floristic surveys (Chapter 3).

Bond and van Wilgen (1996) proposed that differences in seedling recruitment after fires of different seasons may be due to variation in either the size of the seed bank, or the heat of fire in causing seed mortality and dormancy release. Chapters 4 and 5 have demonstrated that late dry season fires produce greater heat penetration and release from seed dormancy than early dry season fires. Soil seed banks are also larger during the late rather than early dry season, so that a greater density of seeds is available to be affected by fire in the late dry season. It appears from these data that both the greater dormancy-release stimuli of late dry season fires, and the higher seed bank density in the late dry season, combine to promote the greatest seedling emergence. Further experimental work involving the manipulation of seed bank density and fire stimuli is required to elucidate the relative contributions of each factor.

Seedling emergence of some trees and shrubs is episodic. Rainforest trees and shrubs recruited a low density of seedlings, primarily in 1999, in both unburnt and recently burnt savanna. The dominant eucalypt, *C. clarksoniana*, was observed to recruit seedlings only in 1998, which may have been the result of the high rainfall and early start to the wet season in that year. Seedling emergence of *C. clarksoniana* was documented in both recently burnt and longer unburnt savanna. However, there is evidence that the density of seedling emergence of this tree may be increased when seeds fall onto recently burnt ground, or at least in areas with low herbaceous cover.

Seedling emergence is therefore a critical life event that mainly occurs in brief pulses, either at the start of the first wet season following fire for most herbs and subshrubs, or more irregularly for the dominant eucalypt and other trees. The survival of seedlings is another critical stage in a plant's life cycle and ultimately determines the success of recruitment events. The next chapter examines the survival of seedlings that emerged after different fire treatments and the fire-tolerance of seedlings of common species.

Chapter 7. The effect of fire regime on seedling survival in a tropical savanna of north-eastern Australia.



7.1 Introduction

Seedling survival is as critical to the recruitment of new plants as the density of seedling emergence (Keith 1996), and the conditions that produce dense seedling emergence can differ from those resulting in highest seedling survival (Lamont *et al.* 1993; Mustart and Cowling 1993; Stoneman and Dell 1994).

There is considerable variation in seedling survival between species. For instance, Vaughton (1998) documented very high seedling survival (91%) two years after germination for *Grevillea barklyana*, a shrub of coastal heath and woodland in New South Wales; whereas in semi-arid woodland of western New South Wales, survival of *Acacia victoriae* and *Senna* spp. (synonym *Cassia*) seedlings can be very low one year after germination (< 1% and 2.1% survival respectively; Grice and Westoby 1987). The low seedling survival of *Acacia victoriae* and *Senna* spp. lead Grice and Westoby (1987) to consider seedling survival the critical life event that limits population growth in those species.

Seedling survival can be a critical life event that limits the distribution of a species to certain habitats. For example, seedlings of the rainforest tree, *Sterculia quadrifida*, showed greater survival one year after transplanting within rainforest than after transplanting within adjacent savanna (Bowman and Panton 1993); although three and a half years after transplanting, the rainforest trees *Aglaia rufa* and *Diospyros maritima* displayed similar seedling survival in rainforest and savanna (Bowman 1993).

Seedling survival can also vary significantly within habitats, at the micro-site scale. For instance, the Tasmanian shrub *Epacris stuartii* displays greater survival of seedlings growing in soil rather than on rocks, although the converse is true for seedling emergence (Keith 2002). Lamont *et al.* (1993) found survival of *Banksia* and *Hakea* seedlings in south-western Australia was higher in bare sand than amongst leaf litter, whereas seedling survival of *Eucalyptus obliqua* in south-eastern Australia can be enhanced by leaf litter (Facelli *et al.* 1999).

Seedling mortality can be caused by competition for resources, especially competition for moisture, nutrients and light; and includes both inter- and intra-specific interactions

(Harper 1977). Other mechanisms of seedling mortality include herbivory, disease, and disturbance, and different mortality processes may operate during different seasons (Whelan 1995). Herbivory, disease and competition for resources can be density-dependent processes (Bond and van Wilgen 1996), that is, the proportion of seedlings affected varies with seedling density. Evidence for density-dependent seedling mortality has been documented for seedlings of the semi-arid shrub *Senna artemisioides* (synonym *Cassia eremophila*; Hodgkinson 1991). Experimental thinning of seedlings of the annual grass, *Sorghum intrans*, has provided evidence of significant density-dependent effects on seedling growth and seed production, but not seedling survival (Andrew 1986).

Established plants may compete with, or facilitate, seedling establishment. Survival of *Eucalyptus marginata* seedlings is limited by competition with canopy trees (Stoneman *et al*. 1994). Seedling survival of herbs in Victorian grassland is higher in gaps than underneath *Themeda triandra* tussocks (Morgan 1998). Establishment of rainforest seedlings in tropical savannas may be facilitated by established trees and shrubs (Kellman 1985; Bowman and Fensham 1991). Noble (1980) documented both competitive and facilitative interactions between tussock grasses and *Eucalyptus pauciflora* seedlings. Competition from grass tussocks (*Poa* spp.) prevented the survival of *E. pauciflora* seedlings within 4 cm of a tussock. However, grasses provided some benefits to nearby seedlings, as the tallest *E. pauciflora* seedlings were those closest to tussocks, but outside the 4 cm zone.

Seedling survival is often higher on burnt rather than unburnt ground (Pate *et al*. 1985; Bradstock 1991). This may result from various factors, including enhanced nutrient and light availability (Ashton and Chinner 1999) and reduced competition (Bond and van Wilgen 1996). Herbivory from invertebrates can be reduced in recently burnt communities (Whelan and Main 1979; Tozer and Bradstock 1997), while herbivory by vertebrates can increase after burning, especially after small scale fires (Whelan 1995).

Seedling survival is affected by various aspects of fire. Fire interval is important because seedlings of fire-killed species need to produce seed, and seedlings of resprouting species need to develop the ability to survive the next fire. Variation in fire intensity may affect the ability of a seedling to survive the passage of fire and patchy low intensity fires can enable the survival of seedlings in unburnt areas. Fire intensity can influence the survival of seedlings that emerge following the fire, through its effect on ground layer combustion and therefore micro-site environment (Keith 1996).

Fire season affects seedling survival through its relationship with fire intensity, and the timing of fires with seasonal phases in plant resource allocation, seed abundance and the post-fire climate (Whelan 1995). Early to mid wet season fires in tropical savannas kill seedlings of annual *Sorghum* spp. before they set seed, causing population declines (Stocker and Sturtz 1966; Lonsdale *et al*. 1998; Williams and Lane 1999). Baird (1977) concluded that the greater seedling survival in eucalypt woodland after mid dry season (i.e. summer) fires than early dry season fires (i.e. spring) in south-western Australia was due to the limited rain following early dry season fires. In contrast, higher mortality of *Banksia* seedlings was documented after late dry season fires (i.e. autumn) than early dry season fires (i.e. spring) in *Banksia* woodland of south-western Australia (Enright and Lamont 1989). They considered this was due to more safe sites provided by early dry season fires, with the unconsumed leaf litter protecting seedlings from desiccation.

Seedlings of obligate seeders often show higher percentage survival than seedlings of associated sprouters (Pate *et al*. 1990; Benwell 1998). For sprouting species, the period required to develop the capacity to tolerate fire is of equivalent functional importance to the time required for seedlings of obligate seeders species to set seed (i.e. primary juvenile period, Gill 1975; Keith 1996).

Fires, particularly those in the late dry season, promote seedling emergence in tropical savannas of Townsville (Chapter 6). This chapter examines the effect of fire on seedling survival. It assesses the survival of seedlings that emerged after early and late dry season fires, as well as the survival of seedlings that recruited prior to burning. Specific questions addressed are:

1. Is percentage survival higher for seedlings that emerged from recently burnt than longer unburnt savanna?

2. Is seedling survival enhanced by the removal of herbaceous cover?
3. Does the season of burning, or removal of herbaceous cover, influence the survival of post-disturbance seedlings?
4. Can seedlings develop the capacity to survive fire within a year?
5. What is the effect of fire season on pre-fire seedlings?
6. Is there evidence of density-dependent seedling survival in this savanna?

7.2 Methods

7.2.1 Sampling methods

7.2.1a Survival of seedlings emerging from burnt, cut and undisturbed savanna

The 1m^2 permanently marked plots that were established at Cape Cleveland in 1999 to examine seedling emergence (Chapter 6), were used to assess the effects of burning, and the removal of the herbaceous layer from unburnt savanna, in both the early and late dry seasons, on the survival of seedlings. The treatments were:

1. Undisturbed; savanna that was last burnt in July 1997, and remained undisturbed.
2. Early burnt; savanna burnt in early dry season fires (May 1999).
3. Late burnt; savanna burnt in late dry season fires (October 1999).
4. Early cut; herbaceous layer cut and removed from unburnt plots in the early dry season (May 1999), in savanna that was last burnt in July 1997.
5. Late cut; herbaceous layer cut and removed from unburnt plots in the late dry season (October 1999), in savanna that was last burnt in July 1997.

Each treatment was represented by ten 1m^2 plots in each of three 1 ha blocks at Cape Cleveland, providing a total of 30, 1m^2 plots for each of the five treatments (Chapter 6). Seedlings that emerged between May 1999 (October 1999 for late burnt and late cut) and May 2000, were tagged by placing fencing wire, that was twisted into various shapes to distinguish common species, into the soil two or three centimetres from the base of the seedlings (Chapter 6). The survival of tagged seedlings was examined for survival in October 2001, two years after the late dry season fires. This provided data on seedling survival for at least 18 months following germination of all seedlings and, as most emerged in November and early December 1999 (Figure 6.5), it represents 23 months since the germination of most seedlings.

7.2.1b Ability of seedlings to survive fire within one year of germination

Prior to burning along the fire break block (Figure 2.4) in September 1998, ten 1m^2 plots were established to examine seedling emergence and survival in annually burnt savanna. These plots document the ability of post-fire seedlings to tolerate a follow up fire within one year of germination.

Random numbers were used to determine the distance of the 1m^2 plots along the 700 m length of the fire break block. Seedling emergence was assessed every month after the September 1998 fire, and seedlings were tagged by placing fencing wire in the soil, two or three centimetres from the base of the seedlings. The number of tagged seedlings that sprouted after the May 1999 fire was assessed in August 1999, three months following fire. No seedlings were simultaneously tagged in unburnt savanna, and therefore no direct comparison can be drawn between survival in burnt and unburnt savanna between September 1998 and August 1999. Conclusions from these data are also limited by the assessment of only one burnt area, and it is possible that seedlings which were alive three months after fire subsequently died before the onset of the wet season in November. Nevertheless, the data are useful for documenting sprouting capabilities of seedlings.

7.2.1c The effect of fire season on the survival of Corymbia clarksoniana *seedlings that emerged prior to fire*

In November 1998, within one month of the mass seedling emergence of *Corymbia clarksoniana* at Cape Cleveland, 50 seedlings were tagged in each of the nine, 1 ha blocks (Figure 2.4). Seedlings were easily distinguished from established plants by the presence of broad cotyledons. The seedlings examined were those that emerged along the edges of the 100m^2 plots used in the floristic surveys (Chapter 3) to allow ease of relocation. In each of the nine, 1ha blocks, one of the four edges was randomly selected from each of the four 100m^2 plots for the examination of seedlings. Additional plot edges were selected where needed. Seedlings were tagged by placing fencing wire in the soil, two or three centimetres from the base of the seedlings and twisting the top of the wire into a Z shape to identify as the location of a *C. clarksoniana* seedling in the event of seedling mortality. The seedlings were assessed for survival, and heights measured, seven months (prior to the May 1999 fire), 19 months (May 2000) and 36 months (October 2001) after germination.

7.2.2 Statistical analyses

7.2.2a Survival of seedlings emerging from burnt, cut and undisturbed savanna

The influence of disturbance treatments on seedling survival was assessed using percentage survival figures, as final seedling numbers varied with the density of seedling emergence. The percentage survival of seedlings of each species was calculated for each replicate $1m^2$ plot, by dividing the total number of seedlings that emerged between May 1999 and May 2000 (Chapter 6), by the number surviving in October 2001 and multiplying by 100. As the life span of the ephemeral species is less than the period for which survival was assessed, the seedling emergence of ephemeral species was not included in the calculation of overall percentage seedling survival. The statistical significance of differences in percentage seedling survival between undisturbed, early and late burnt and early and late cut savanna was assessed using a one-factor ANOVA. Analyses were performed for total seedling survival, and that of native and exotic species, the growth form groups defined in Chapter 3, and common species with at least 5% of the surviving seedlings. As the overall seedling survival was low, species with less than 5% of surviving seedlings were highly variable within treatments and were not analysed.

The ten, $1m^2$ plots from each of the three replicate 1 ha blocks used in each treatment were considered nested within the disturbance treatments (undisturbed, early or late burnt, early or late cut). The nested plots were treated as random factors, with treatment as a fixed factor. Where the variation between treatment replicates of separate blocks was low
($P > 0.25$) the plot replicates were pooled to increase the power of the ANOVA (Underwood 1997).

Homogeneity of variance was assessed using Cochran's test (Underwood 1997). Variance heterogeneity was resolved for most species and species groups using arcsine data transformation (Underwood 1997). Due to the large number of analyses, a significance level of $P < 0.01$ was used to reduce the probability of incorrectly attributing a significant difference (i.e. alpha; Zar 1999). Where significant differences were detected, a Scheffe's *post-hoc* test was used to determine where differences lay (Underwood 1997). Where data transformation did not resolve significant variance heterogeneity, the non-parametric Kruskal-Wallis ANOVA by ranks was used, and a Mann-Whitney *U*-test used as a *post-hoc* test with a Bonferroni adjustment of the significance level for multiple comparisons (Sokal and Rohlf 1995).

The presence of density-dependent mortality was assessed using the total seedling survival data. As variances were strongly heterogeneous, the non-parametric Spearman's rank correlation was used to assess a relationship between the density of seedling emergence and the percentage seedling survival in each of undisturbed, early burnt, late burnt, early cut and late cut plots (Sokal and Rohlf 1995). Seedling emergence data for ephemeral species were not included in the calculation of percentage seedling survival, as their life span is less than the period for which survival was assessed. However, the seedling emergence density used in the correlation with seedling survival did include ephemeral species, due to the role of all seedlings in influencing density-dependent processes.

7.2.2b Ability of seedlings to survive fire within one year of germination

Seedling survival following the early dry season fire along the fire break block was calculated for the four most common sprouter species that emerged between September 1998 and May 1999. In each of the 1m^2 plots, percentage seedling survival was calculated for the total numbers of seedlings that emerged between the September 1998 fire and the May 1999 fire. Percentage survival was also calculated for the number of seedlings that were alive one week prior to the May 1999 fire. No comparative data were collected for survival of these seedlings in unburnt savanna and therefore no analyses of survival in burnt and unburnt were performed. Inter-species differences were not analysed as the seedlings were tagged within the same plots and were not independent of each other (Underwood 1997).

7.2.2c The effect of fire season on the survival of pre-fire Corymbia clarksoniana *seedlings*

The statistical significance of differences between seedling survival of *Corymbia clarksoniana* in control, early and late dry season burnt blocks was compared using a one-factor ANOVA. The intention was to perform a repeated measures ANOVA on the percentage seedling survival at seven months (prior to the May 1999 fires), 19 and 36 months folowing germination. A Cochran's test (Underwood 1997) indicated variance heterogeneity for the 36 month survival data could not be resolved with data transformations. Therefore a repeated measures ANOVA was performed on the survival data at seven and 19 months, with a separate non-parametric Kruskal-Wallis ANOVA by ranks used to assess significance of differences between fire treatments at 36 months after germination (Sokal and Rohlf 1995; Zar 1999).

To examine the statistical significance of differences in seedling heights between fire treatments, an independent *t*-test was performed on the heights of seedlings surviving at 36 months in the control and early burnt blocks, as no seedlings remained in the late burnt blocks (Zar 1999).

7.3 Results

7.3.1 Survival of seedlings emerging from burnt, cut and undisturbed savanna

The rainfall during the period of assessment was above average during the first year (i.e. 2000) but below average during the second year following seedling emergence (i.e. 2001; Figure 2.2 and Table 2.1). Seedling emergence between May 1999 and May 2000 ranged from 1.6 seedlings m^{-2} in the undisturbed savanna to 90.2 seedlings m^{-2} in the late burnt savanna (Table 6.4). An average of approximately four seedlings m^{-2} survived in late burnt and two seedlings m^{-2} in early dry season burnt savanna by October 2001. Negligible seedlings survived in undisturbed ($0.1m^{-2}$), early cut ($0.8m^{-2}$) and late dry season cut savanna ($0.4m^{-2}$).

The percentage of species that survived until October 2001 in the $1m^2$ plots was significantly higher in early and late dry season burnt savanna than in undisturbed and late dry season cut savanna ($F_{4,145} = 218.13$; $P < 0.001$; Figure 7.1a). Percentage survival of species was also significantly higher in late dry season burnt than early dry season cut savanna. The percentage survival of all seedlings combined was significantly higher in early and late dry season burnt savanna than in undisturbed and early and late dry season cut savanna ($F_{4,10} = 8.26$; $P < 0.003$; Figure 7.1b).

The mean percentage survival and statistical significance of species groups and common species is presented in Table 7.1. The percentage survival of native seedlings was significantly higher in early and late dry season burnt savanna than in undisturbed and early and late dry season cut savanna. There were no significant differences between treatments for exotic seedlings.

No seedlings of trees and shrubs, ephemerals or non-grass monocots were alive by October 2001, at least 18 months after seedling emergence. A higher percentage of subshrub seedlings survived in late dry season burnt savanna than undisturbed savanna. There were no significant differences between treatments for the common subshrub *Triumfetta rhomboidea*, which possessed the highest percentage seedling survival of any individual species, at 19%.

There were no significant differences in percentage seedling survival between treatments for the upright perennial forbs, grasses or the common grasses *Heteropogon contortus* and *H. triticeus*; although there was significant variation in the survival of *H. triticeus* seedlings between blocks, which suggests edaphic factors were influencing survival.

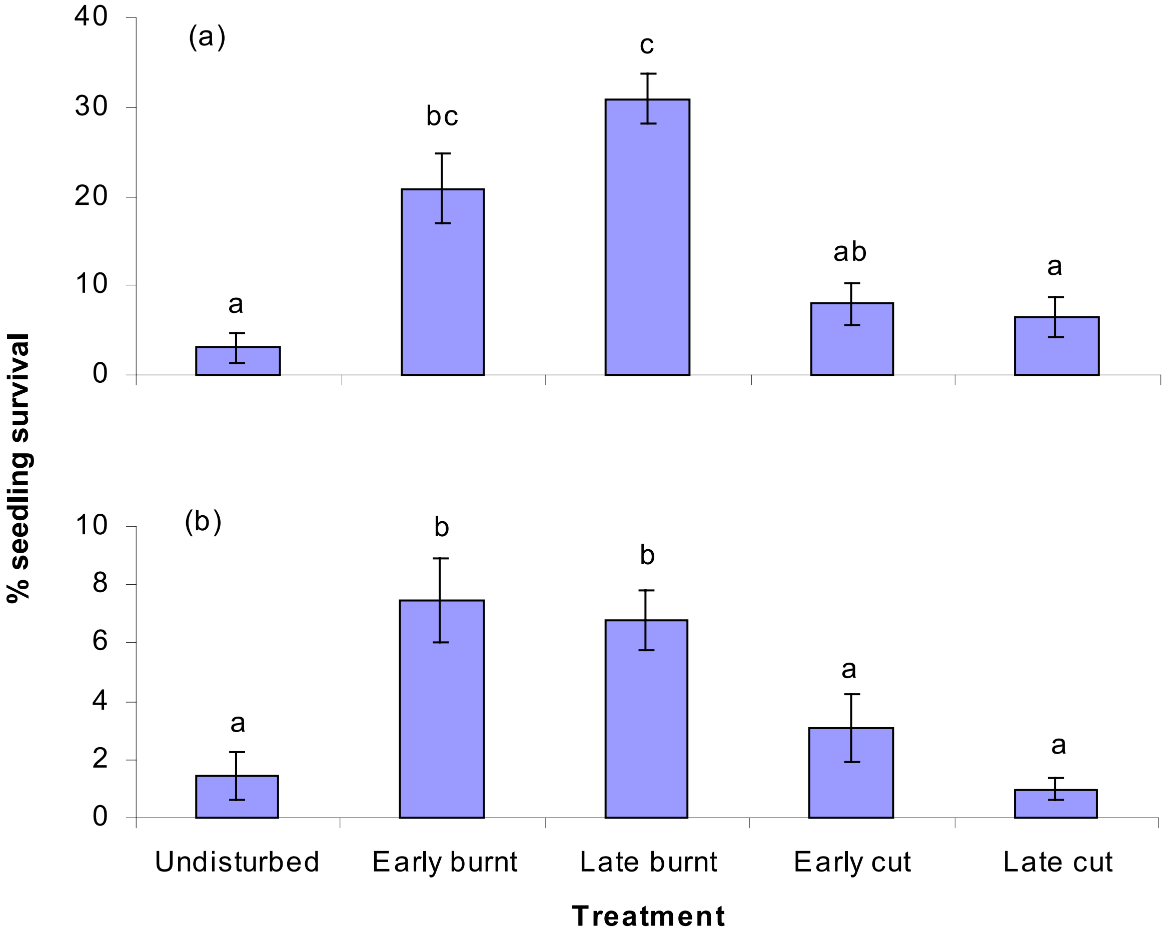


Figure 7.1. Mean (± 1 standard error) percentage (a) species survival and (b) seedling survival in October 2001, 18 to 24 months after seedling emergence in eucalypt savanna at Cape Cleveland. Undisturbed, savanna unburnt since July 1997 and remained undisturbed; Early burnt, savanna burnt early dry season (May) 1999; Late burnt, savanna burnt late dry season (October) 1999; Early cut, savanna unburnt since July 1997 with the herbaceous layer cut and removed in May 1999; Late cut, savanna unburnt since July 1997 with the herbaceous layer cut and removed in October 1999. Columns with the same superscript are not significantly different at $P < 0.01$.

Table 7.1. Mean (standard error) percentage survival after at least 18 months, and ANOVA results, of seedlings of native and exotic species, growth form groups and common species emerging from eucalypt savanna at Cape Cleveland. Undisturbed, savanna unburnt since July 1997 and remained undisturbed; Early burnt, savanna burnt early dry season (May) 1999; Late burnt, savanna burnt late dry season (October) 1999; Early cut, savanna unburnt since July 1997 with the herbaceous layer cut and removed in May 1999; Late cut, savanna unburnt since July 1997 with the herbaceous layer cut and removed in October 1999. $H_{4,145}$, H value, denominator d.f., numerator d.f.; H values without an asterisk (*) are not significantly different at $P > 0.01$; *$P < 0.01$; **$P < 0.001$. *Arcsine*, arcsine transformation before analysis to resolve heterogeneity of variances; *Pooled*, blocks replicates pooled where $P > 0.25$. *Block*, a significant difference between blocks at $P < 0.01$. Means with the same superscript are not significantly different at $P < 0.01$.

	Control	Early burnt	Late burnt	Early cut	Late cut	ANOVA results
Native species (n = 11)	8.10 (5.72) ^{a}	15.83 (3.56) ^{b}	8.73 (1.35) ^{b}	4.77 (2.28) ^{a}	2.90 (0.96) ^{a}	$H_{4,145} = 69.837$**
Exotic species (n = 2)	3.33 (3.33) ^{a}	8.28 (3.86) ^{a}	18.44 (3.56) ^{a}	5.85 (2.92) ^{a}	3.97 (0.28) ^{a}	*Arcsine* $F_{4,145} = 4.005$
Subshrubs (n = 2)	0.00 (0.00) ^{a}	6.67 (6.67) ^{ab}	18.52 (6.89) ^{b}	4.65 (2.39) ^{ab}	0.48 (0.48) ^{ab}	*Arcsine, Pooled* $F_{4,145} = 4.687$**
Triumfetta rhomboidea	0.00 (0.00) ^{a}	3.51 (3.33) ^{a}	18.61 (6.89) ^{a}	5.04 (2.47) ^{a}	0.48 (0.48) ^{a}	$H_{4,145} = 12.713$
Upright perennial forbs (n = 3)	0.00 (0.00) ^{a}	3.54 (3.33) ^{a}	3.39 (3.33) ^{a}	3.33 (3.33) ^{a}	1.67 (1.67) ^{a}	$H_{4,145} = 2.391$
Twining perennial forbs (n = 5)	2.50 (1.84) ^{a}	9.35 (2.00) ^{ab}	11.63 (2.06) ^{b}	1.31 (1.12) ^{a}	1.07 (0.52) ^{a}	*Pooled* $F_{4,145} = 9.335$**
Galactia tenuiflora	2.36 (2.36) ^{ab}	19.23 (5.99) ^{b}	14.57 (5.72) ^{ab}	3.85 (2.67) ^{ab}	0.00 (0.00) ^{a}	$H_{4,145} = 20.572$**
Passiflora foetida	3.33 (3.33) ^{a}	7.44 (3.83) ^{a}	15.51 (3.56) ^{b}	0.26 (0.26) ^{a}	0.42 (0.42) ^{a}	$H_{4,145} = 48.293$**
Grasses (n = 3)	0.56 (0.56) ^{a}	7.28 (1.86) ^{a}	5.45 (1.18) ^{a}	1.44 (0.78) ^{a}	3.64 (2.36) ^{a}	*Arcsine* $F_{4,145} = 4.590$
Heteropogon contortus	0.00 (0.00) ^{a}	3.33 (3.33) ^{a}	7.44 (3.92) ^{a}	0.09 (0.09) ^{a}	6.67 (4.63) ^{a}	$F_{4,145} = 1.710$
H. triticeus	0.56 (0.56) ^{a}	7.50 (2.03) ^{a}	3.40 (0.96) ^{a}	1.35 (0.78) ^{a}	1.43 (0.93) ^{a}	*Block* $F_{4,145} = 1.520$

A significantly greater percentage of twining perennial forb seedlings survived in late dry season burnt savanna than undisturbed savanna, and early and late dry season cut plots. Seedling survival of the common twiner *Galactia tenuiflora* was significantly higher in early dry season burnt than late dry season cut savanna. A significantly higher percentage of *Passiflora foetida* seedlings survived in late dry season burnt savanna than in all other treatments.

Evidence of density-dependent seedling mortality was detected in late burnt plots, with a significant negative correlation between percentage seedling survival and density (Figure 7.2). No significant correlation was found between seedling survival and density for other treatments.

7.3.2 Ability of seedlings to survive fire within one year of germination

Half (56%) of the *Galactia tenuiflora* seedlings that were alive prior to the May 1999 fire had developed the ability to sprout after the early dry season fire, despite being less than eight months old (Figure 7.3). The lowest seedling survival was of *Corymbia clarksoniana* with survival of only 5% of the seedlings that were alive one week prior to the fire. This represents only 1% of the total *C. clarksoniana* seedlings that emerged between September 1998 and May 1999.

Survival of *Heteropogon triticeus* and *Pycnospora lutescens* seedlings that were alive one week prior to the May 1999 fire was 38% for both species (Figure 7.3). The higher pre-fire mortality of *H. triticeus* seedlings that emerged between September 1998 and May 1999 meant that total seedling survival was lower than that of *P. lutescens*.

7.3.3 The effect of fire season on the survival of pre-fire **Corymbia clarksoniana** *seedlings*

Only 5% of *Corymbia clarksoniana* seedlings survived in undisturbed savanna in control blocks and no seedlings remained alive in late burnt blocks 36 months after germination (Figure 7.4). No statistically significant differences were detected in percentage seedling survival between fire treatments (Table 7.2). The inability to detect a significant difference, even though no seedlings survived in late burnt savanna after

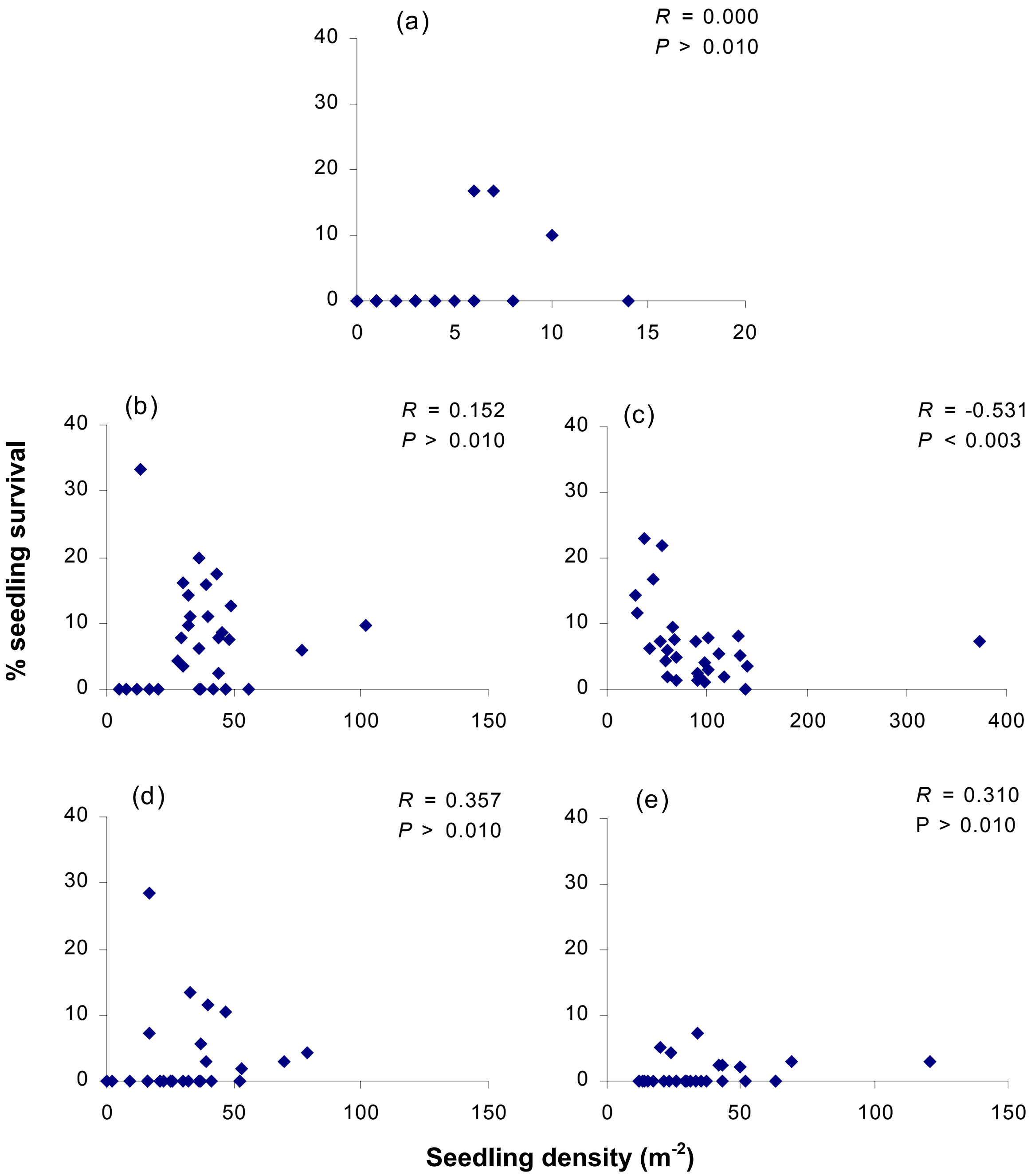


Figure 7.2. Correlation between percentage seedling survival and seedling density for (a) undisturbed savanna, unburnt since July 1997; (b), savanna burnt early dry season (May) 1999; (c), savanna burnt late dry season (October) 1999; (d), savanna unburnt since July 1997 with the herbaceous layer cut and removed in May 1999; (e), savanna unburnt since July 1997 with the herbaceous layer cut and removed in October 1999. Spearman's rank coefficient *R* and *P* value indicated.

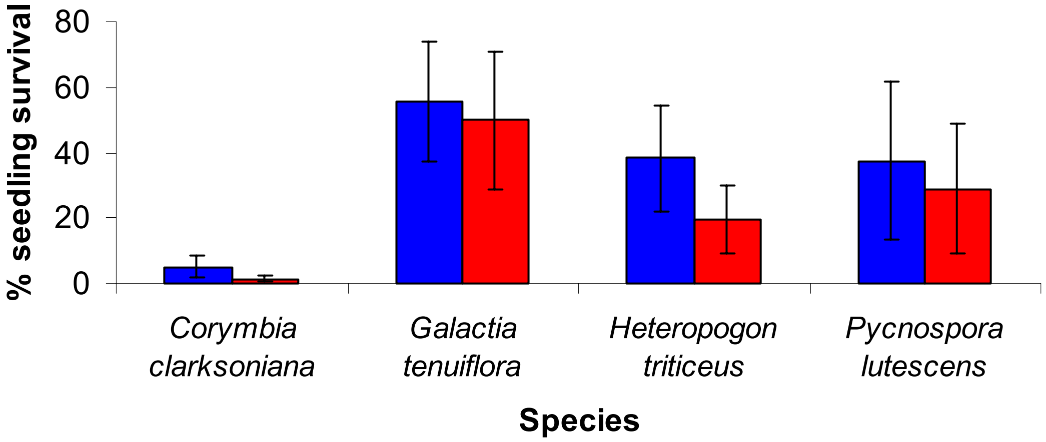


Figure 7.3. Mean (± 1 standard error) percentage survival of seedlings, less than eight months old, following an early dry season fire (May 1999) in eucalypt savanna at Cape Cleveland. Percentage survival calculated from the number of seedlings alive one week prior to fire (🟦); percentage survival calculated from the total number of seedlings that emerged between the September 1998 and May 1999 fires (🟥).

36 months, was probably a result of the variation in survival in unburnt savanna, where one of the three replicate blocks possessed no seedling survival after 36 months. However, a significant age effect was detected in the repeated measures ANOVA for seven and 19 months since germination, indicating a significant decline in seedling survival with time since establishment of cohort (Table 7.2). Eight percent of *C. clarksoniana* seedlings that were alive in early burnt blocks prior to the May 1999 fires sprouted following those burns, which is a similar percentage to that recorded for seedlings tagged along the fire break block (Figure 7.3).

Growth of *C. clarksoniana* seedlings levelled off after 19 months, with no additional height recorded by 36 months. The mean height of *C. clarksoniana* seedlings after 36 months was not significantly different between control and early burnt blocks (t_9 = 0.995; $P > 0.05$).

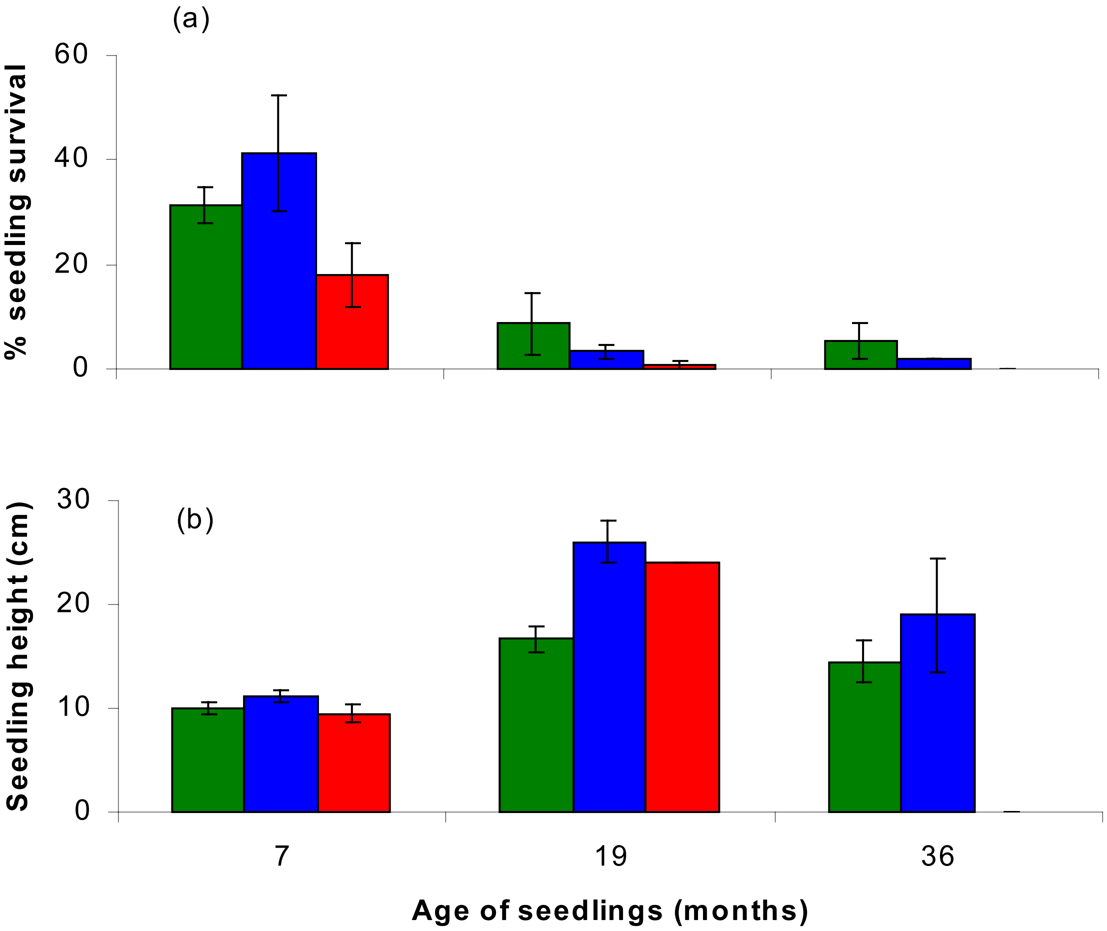


Figure 7.4. Mean (± 1 standard error) percentage (a) seedling survival and (b) seedling height with age of *Corymbia clarksoniana* in eucalypt savanna at Cape Cleveland. Savanna last burnt July 1997 (🟩); savanna burnt in the early dry season (May) 1999 (seven months after germination) and July 1997 (🟦); savanna burnt in the late dry season (October) 1999 (11 months after germination) and July 1997 (🟥).

Table 7.2. ANOVA results of fire season treatments on the survival of *Corymbia clarksoniana* seedlings that emerged seven months prior to the early dry season fire. $F_{4,145}$, *F* or *H* value, denominator d.f., numerator d.f.

Analysis	*F* or *H* Statistic	*P* value
Repeated measures ANOVA at seven and 19 months:		
Fire	$F_{2,6} = 2.184$	> 0.05
Age of seedling	$F_{1,6} = 55.051$	< 0.001
Fire x Age	$F_{2,6} = 0.459$	> 0.05
Kruskal-Wallis ANOVA at 36 months	$H_{2,6} = 4.300$	> 0.05

7.4 Discussion

7.4.1 Survival of seedlings emerging from burnt, cut and undisturbed savanna

Seedlings that emerged after fire displayed a higher percentage survival than seedlings in unburnt savanna (Figure 7.1). The number of species that survived was also highest when seedlings emerged after fires, especially those of the late dry season. Seven percent of seedlings survived in burnt savanna, which meant that by October 2001, approximately two years after germination, four seedlings m^{-2} survived in late and two in early dry season burnt savanna. Seedling establishment in unburnt savanna was negligible.

Seven percent seedling survival after approximately two years in eucalypt savanna at Cape Cleveland, with highest survival of an individual species at 19% for *Triumfetta rhomboidea*, is low compared to that recorded in some other communities. For instance, Abbott (1985) found seedling survival of *Banksia grandis* in Western Australia ranged from 74 to 86% after two years and Vaughton (1998) found 91% of *Grevillea barklyana* seedlings in coastal New South Wales were alive after two years. In tropical savannas, survival to maturity of seedlings of the annual grasses *Sorghum intrans* and *S. stipoideum* is 30 to 60% (Andrew and Mott 1983). Seedling survival in *Eucalyptus* and *Banksia* dominated woodland of south-west Western Australia was

15% in woodland, 2.5 years following fire (Whelan and Main 1979). Purdie and Slatyer (1976) documented between three and 88%, and Clarke (in press) recorded between 0 and 25%, seedling survival after one year in temperate eucalypt woodlands in south-eastern Australia.

Enhanced seedling survival after fire has been reported in shrubby and open eucalypt woodlands and forests of south-eastern Australia (Purdie 1977; Bradstock 1991; Ashton and Chinner 1999) and south-west Western Australia (Whelan and Main 1979; Pate *et al.* 1985). The greater survival after fire may be a result of higher nutrient and light availability, lower competition for resources and reduced herbivory (Whelan and Main 1979; Noble 1980; Stoneman *et al.* 1994; Ashton and Chinner 1999). The similar levels of seedling survival documented in undisturbed and cut savanna (Figure 7.1), indicates competition for light soon after seedling emergence is probably not the primary factor limiting seedling survival in the tropical savanna at Cape Cleveland, and seedling herbivory, disease and competition for nutrients and moisture require assessment. The mechanisms causing seedling mortality may differ between burnt and unburnt areas. For instance, Tozer and Bradstock (1997) found herbivory was the primary cause of seedling mortality in the absence of fire, and desiccation in burnt sites.

Late dry season fires enhanced seedling survival over all other treatments for twining perennial forbs and the common twiner, *Passiflora foetida,* while subshrubs displayed significantly greater percentage survival in late burnt over undisturbed savanna, and *Galactia tenuiflora* in early burnt over late cut savanna (Table 7.1). Seasonal differences in seedling survival may result from variation in the post-fire climate (Baird 1977; Whelan 1995). All seedling emergence following late dry season fires occurred during the wet season (Chapter 6), and therefore those seedlings received substantially greater rain following emergence than the seedlings that emerged during the dry season following early fires. Variation in seedling survival following different fire season may also result from different micro-site environments. While late dry season fires produced complete combustion of the herbaceous layer, some unconsumed grass stalks remained after early dry season fires (Chapter 3), and this variation in herbaceous cover may have influenced seedling survival, including the greater survival of *G. tenuiflora* in early burnt savanna. Leaf litter remaining unconsumed after fire can enhance seedling survival of *Banksia* spp. of Western Australia (Enright and Lamont 1989) and *Eucalyptus obliqua* in forests of south-eastern Australia (Facelli *et al*. 1999).

Evidence of density-dependent seedling mortality was found in late dry season burnt savanna, which contained the highest density of seedling emergence (Figure 7.2). This data suggests competition, herbivory and/or disease, may have a proportionately greater influence on seedling mortality at the higher seedling densities that are only recorded after late dry season fires. However, experimental manipulation of seedling density is required to gain a better understanding of density-dependent processes operating in this savanna.

Many seedlings, across all treatments, were observed to be in an advanced state of wilting prior to death. This suggests competition for soil moisture was the primary mechanism of seedling mortality, as identified in other communities (e.g. Baird 1977; Lamont *et al*. 1993). However, disease and invertebrate damage to roots and stems may also have caused wilting and therefore the cause of seedling mortality remains unconfirmed.

7.4.2 Ability of seedlings to survive fire within one year of germination

Some seedlings of all four species examined along the fire break block survived the early dry season fire in May 1999, although survival varied between 5% for *Corymbia clarksoniana* and 56% for *Galactia tenuiflora* (Figure 7.3). While the extrapolation of these data is limited because it documents only a single burnt area, the results indicate seedlings of these common sprouting species are capable of surviving fire within a year of germination. The ability of seedlings to rapidly develop a tolerance of fire is critical for population persistence in frequently burnt communities (Keith 1996). The higher survival in herbaceous species may reflect the differences between the dominating tree *C. clarksoniana* and the herbs in plant longevity, with greater seedling survival, and hence recruitment success, of shorter-lived herbaceous species that require more regular replacement of individuals to maintain populations.

The period required before seedlings develop the ability to survive fire varies between species. For instance, in heathy woodlands of south-eastern Australia, seedlings of *Banksia serrata* require approximately six years before they can sprout after fire and those of *Isopogon anemonifolius* require around 13 years (Bradstock and Myerscough 1988). Seedlings of *Allosyncarpia ternata*, a rainforest tree of the Northern Territory, develop the ability to sprout after approximately three years (Fordyce *et al*. 1997). Seedlings of several common tropical savanna and rainforest trees can survive fire within one year of germination, at least when initially raised in a shadehouse and transplanted into the field (Williams 1998).

The ability of seedlings of fire-killed species to set seed before a subsequent fire is functionally similar to the ability of seedlings of sprouting species to survive fire (Keith 1996). Seedlings of ephemeral species at Cape Cleveland were all observed to set seed within a year (*pers*. *obs*.), whereas the tagged seedlings of perennial species did not set seed during their first year, and only a few species, for example *Pycnospora lutescens*, produced seed in their second year (*pers*. *obs*.). This suggests that seedlings of sprouting species allocate more resources towards developing the ability to sprout after fire than producing seed, while seedlings of ephemerals allocate more resources towards seed production. Both strategies enable some population resilience to fires that occur in the first year following germination. However, the low percentage of seedlings that survive fire for some perennial species, such as *C. clarksoniana*, suggests populations of sprouting, perennial species may be more sensitive to annual fires than fire-killed, ephemeral species.

7.4.3 The effect of fire season on the survival of pre-fire **Corymbia clarksoniana** *seedlings*

A minor number of *Corymbia clarksoniana* seedlings sprouted after late dry season fires that occurred one year after germination, however no seedlings remained alive in late burnt savanna three years after germination (Figure 7.4a). Five percent of seedlings survived in unburnt savanna after three years, while one percent survived in savanna burnt in the early dry season, six months after germination. While this suggests greater survival for seedlings that remained unburnt for three years, differences between fire treatments were not statistically significant due to variation within treatments (Table

7.2). The variation in seedling survival within unburnt savanna suggests differences with micro-site and further experimentation is required to examine the effect of fire on seedling survival of *C. clarksoniana*. While the results of this study are not conclusive, they provide some evidence that fire may enhance the number of safe sites, thus increasing seedling density (Chapter 6), and that fire in the year following germination reduces seedling survival.

The fire-sensitivity of *C. clarksoniana* corresponds with results of a study of *Eucalyptus miniata* seedlings in tropical savanna of the Northern Territory by Setterfield (1997*b*). She found seedling survival of *E. miniata* was significantly greater in unburnt savanna, with 11% of seedlings alive after 1.5 years. No *E. miniata* seedlings survived a late dry season fire within a year of germination. Three percent of *E. miniata* seedlings initially sprouted after early dry season fires, but all subsequently died the following month (Setterfield 1997*b*).

Low levels of seedling survival may be common among eucalypts. Fensham (1992) found very low (< 5%) seedling survival of *E. miniata* and *E. tetradonata* seedlings in unburnt tropical savanna. Seedling survival of eucalypts in southern Australia is also typically low (i.e. < 10%) after two or three years (e.g. Withers 1978; Bowman and Kirkpatrick 1986).

7.5 Conclusion

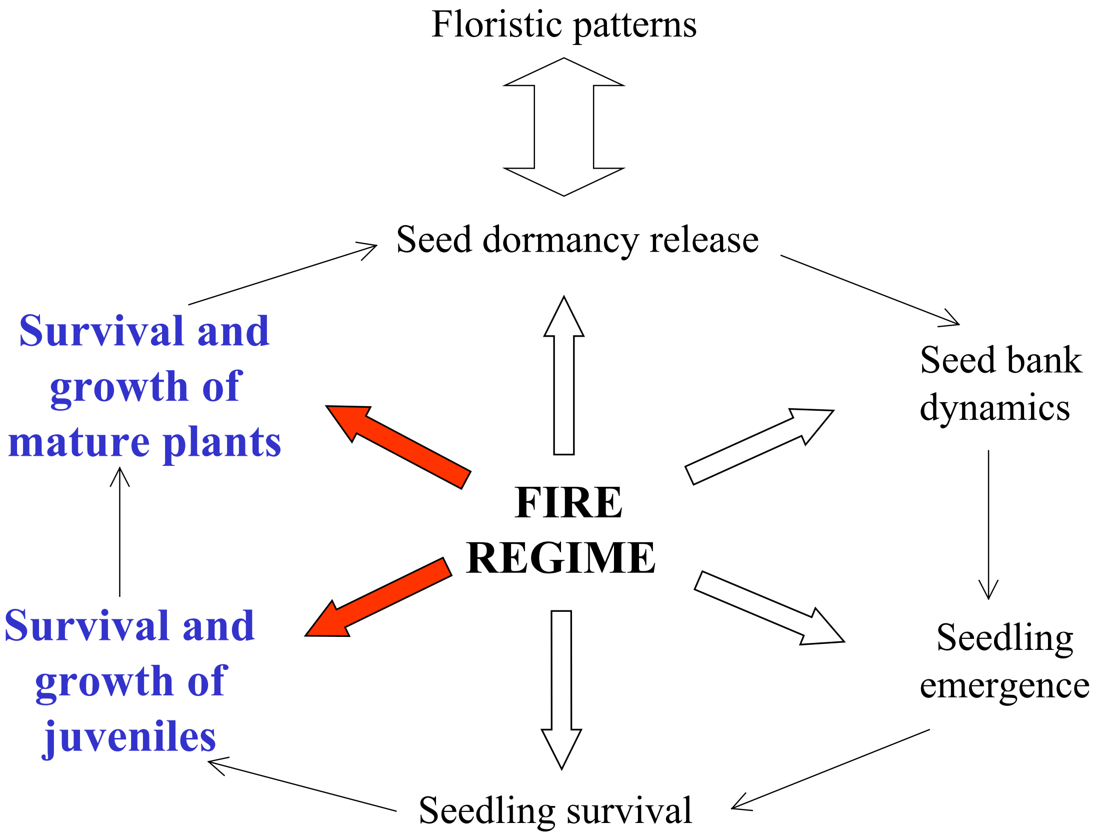
Seedling survival was higher for those seedlings that emerged in recently burnt rather than unburnt savanna. The removal of the herbaceous cover in unburnt savanna did not significantly increase seedling survival, suggesting aspects of fire other than the removal of shade, such as enhanced nutrients or reduced invertebrate herbivory or disease, are the primary factors promoting seedling survival. Some species displayed variation in seedling survival between early and late dry season fires, which may have resulted from differences in post-fire climate and micro-site environments. Only late dry season fires promoted sufficient seedlings for density-dependent mortality to be detected.

Only four seedlings m^{-2} (of all species pooled) survived in late burnt, two seedlings m^{-2} survived in early burnt, and negligible numbers of seedlings survived in unburnt savanna, approximately two years following germination. Further work is required to determine the survival until maturity of ephemeral species. Data is also needed on the density of established seedlings, and the frequency of recruitment, required to maintain stable populations of savanna species. Details of the longevity of species, the primary juvenile periods and how long it takes for seedlings of each species to develop the capacity to sprout after fire are also required.

The density of soil seed banks in the eucalypt savanna at Cape Cleveland is low to moderate and seedling emergence is correspondingly low to moderate compared with other communities (Chapter 5 and 6). This chapter has demonstrated that seedling survival is low compared with other species and communities. While 14% of the soil seed bank emerged as seedlings after late dry season fires (Chapter 5) only 7% of perennial seedlings were alive two years later. Together these data indicate that seed supply, seedling emergence and seedling survival are all critical life events that limit the recruitment of new plants.

Chapter 8 examines the effect of fire on the survival and growth of juveniles and mature plants in eucalypt savanna at Cape Cleveland. It documents the fire response of each species and assesses the influence of fire season on plant survival.

Chapter 8. The effect of fire regime on the survival and growth of juveniles and mature plants.



8.1 Introduction

Plant growth in Australian tropical savannas is linked with the seasonal patterns in rainfall (Mott *et al*. 1985). Trees typically produce a flush of new leaves during the transition between the end of the dry season and start of the wet season (Williams *et al*. 1997). The growth of tree girths occurs primarily during the wet season (Mucha 1979), as does the growth of grasses and forbs (Andrew and Mott 1983; Mott *et al*. 1985).

Plant growth is limited by climate, competition for resources, disease, herbivory and disturbance (Harper 1977). Soils of many Australian tropical savannas are low in nutrients (Morgan *et al*. 2000; Jackson and Ash 2001). Competition for soil nutrients limits the growth of the annual grasses *Sorghum intrans* and *S. stipoideum* that dominate some savannas of northern Australia (Cook and Andrew 1991). Competition for soil moisture during the annual dry season may also limit plant growth in tropical savannas (Bowman 1988).

Herbaceous and woody species differ in life span. Through an assessment of seasonal growth rings, Mucha (1979) suggested eucalypts of the Darwin region in the Northern Territory occasionally reach 100 years in age. Fensham and Bowman (1992) pointed out that this calculation did not include the years spent as stunted saplings, less than 2 m in height, which are described hereafter as “juveniles,” that may remain stunted for decades. Perennial grasses of tropical savannas may live for approximately eight years, or more, under low stock grazing pressure (Mott 1978; Mott *et al*. 1985). Species that complete their life cycle in one or two years (ephemeral herbs) are also common in Australian tropical savannas (Crowley and Garnett 1999; Russell-Smith *et al*. in press; Chapter 3).

Fire is a frequent disturbance in tropical savannas (Walker 1985; Higgins *et al*. 2000). The majority of woody species of tropical savannas are capable of sprouting after full canopy scorch (Walker 1985; Williams *et al*. 1999*b*; Midgley and Bond 2001; Russell-Smith *et al*. in press). Many perennial herbs of tropical savannas are also capable of sprouting after fire (Shaw 1957; Mott and Andrew 1985). Sprouting can originate from buds located below the soil at the base of the stem and along roots and rhizomes, and for woody species, also epicormically from buds on branches and trunks (Gill 1981).

Re-growth from roots and rhizomes can provide stem multiplication and is common to a range of herbs and woody species (e.g. Lacey 1974; Russell-Smith *et al.* in press).

The ability to sprout after fire can vary with life stage, or plant size, and the type of fire. In tropical savannas, medium sized trees (20 to 30 cm diameter at breast height) show greater survival through fires than larger and smaller trees (Williams *et al.* 1999*b*). For many woody species, the ability to epicormically sprout from stems and branches is only apparent in plants taller than approximately 1.5 to 2 m, with plants below this height being reduced to sprouting from basal buds below the soil surface (Trollope 1996; Williams *et al.* 1999*b*). Frequent fires may therefore keep juvenile trees below 2 m in height, holding them within a “fire-trap” and maintaining an open savanna structure (Midgley and Bond 2001). Suppression below 2 m in height of juveniles of non-eucalypt trees has been documented in tropical savannas of northern Australia. Fire intervals of at least two years are required to allow the growth of stunted juveniles of some *Acacia* and broadleaf species, such as *Gardenia megasperma* (Bowman *et al.* 1988), and at least three years for the release of *Melaleuca viridiflora* juveniles from the fire-trap (Crowley and Garnett 1998). Eucalypt juveniles do not always grow rapidly beyond 2 m in height in the absence of fire, and a proportion may die-back to ground level during the dry season (Prior *et al.* 1997). While stunted juveniles of *Eucalyptus tetrodonta* have been documented to grow above the fire-trap in the absence of fire, *E. miniata* juveniles can remain stunted with fire exclusion for two decades (Fensham 1990; Bowman and Panton 1995; Russell-Smith *et al.* in press). Insect attack on eucalypt juveniles can be severe, however, Fensham (1994) demonstrated herbivory by insects is not the primary process that suppresses juveniles. Evidence has been found that competition for resources with canopy trees is an important process suppressing the growth of *E. miniata* juveniles (Fensham and Bowman 1992).

Frequent fires may exhaust a plant’s capacity to sprout, and the intensity and season of fire may also affect survival (Keith 1996). High intensity, late dry season fires significantly reduce the survival of trees in tropical savannas of the Northern Territory (Williams *et al.* 1999*b*). Noble (1989) also reported higher survival of mallee eucalypts after repeated early dry season (i.e. spring) rather than late dry season (i.e. autumn) fires in New South Wales.

Variation in survival after fires of different intensities and seasons may be due to differences in the survival of regenerative buds and/or the quantity of stored carbon reserves (Bond and van Wilgen 1996). Bud survival depends on the location and protection of buds, heat from the fire and residence time of flames (Whelan 1995). Carbon reserves fluctuate seasonally and percentage survival is likely to be greatest when stored reserves are high and while plants are dormant, or when there is sufficient growing season following fire to allow replacement of reserves (Bond and van Wilgen 1996). The effect of fire season on plant recovery has been demonstrated on perennial grasses, with poorest recovery after burning grasses during the growing season, while culms are elongating (Tainton 1981, cited in Bond and van Wilgen 1996).

Vegetative survival through fire provides plant persistence and therefore stability of populations in frequently burnt communities (Bond and Midgley 2001). The ability to sprout after fire requires a trade-off in resource allocation, with sprouters allocating fewer resources to seed production than non-sprouters (Bellingham and Sparrow 2000; Bell 2001).

Fire may affect plant growth through its impact on soil nutrient dynamics, damage to buds and depletion of plant reserves (Whelan 1995). The basal area of trees at the Kapalga research station in the Northern Territory remained stable over five years with fire exclusion and annual early dry season burning, but declined with annual late dry season fires, primarily as a result of stem mortality (Williams *et al.* in press). Overall basal area of trees at nearby Munmarlary increased over 21 years in annually and biennially burnt savanna, and particularly in unburnt savanna (Russell-Smith *et al.* in press). The greatest increase in basal area of *Eucalyptus miniata* trees at Munmarlary occurred in savanna burnt annually in the early dry season, while no change in basal area was recorded for *E. tetrodonta* (Russell-Smith *et al.* in press).

In dry sclerophyll forest of south-eastern Queensland, annual burning in the mid dry season for 44 years produced no effect on the growth rates of *Eucalyptus acmenoides* and *E. drepanophylla*, but enhanced the growth of *E. tereticornis* in comparison to unburnt forest (Guinto *et al.* 1999). In an associated wet sclerophyll forest, fire intervals of two to three years, with low fire intensities (< 500 kWm^{-1}) enhanced the growth of *Lophostemon confertus* but inhibited growth of *Syncarpia glomulifera*, compared to unburnt forest (Guinto *et al*. 1999).

Chapter 3 documented community resilience to a series of fires in eucalypt savanna at Cape Cleveland. Population persistence in a frequently burnt savanna can be provided by vegetative survival and/or seedling recruitment. Chapters 4 to 7 examined seedling recruitment, which was most abundant for herbaceous rather than woody species, and occurred primarily after fire. This chapter examines vegetative survival and growth to complete the assessment of mechanisms that can provide resilience to species composition in a frequently burnt savanna. The ability of species to survive fire is documented, and a quantitative assessment of survival during fire is made for juvenile and mature individuals of common species.

Specific questions addressed are:

1. Which species are capable of sprouting after fire and is fire response consistent across eucalypt savanna sites of the Townsville region?
2. What is the effect of fire season and time since fire on the survival and growth of juveniles and mature individuals of common tree species?
3. Does the density of sprouting stems differ after burning and cutting, and with season of disturbance?
4. Does the percentage survival of common herbs vary with burning and cutting in the early and late dry seasons?

8.2 Methods

8.2.1 Sampling

8.2.1a Regenerative capacity of savanna species

The ability of plants to sprout after fire was documented following burns at Cape Cleveland, Mt Elliot, Many Peaks Range and Castle Hill (Figure 2.1). Sprouting stems originating from below the soil surface were distinguished from seedlings by the attachment of shoots to a burnt stem, thickened bases or roots. Documentation of plant regeneration followed Gill and Bradstock's (1992) classification, and only species that were fully scorched in fires were included in the assessment.

8.2.1b Survival and growth of trees

To assess the effect of fire on tree survival, the number of trees > 2m in height was counted in each of the 36, permanently marked 100m^2 plots at Cape Cleveland (Chapter 3) in March to May, in each of 1997 to 2001. The circumference at breast height of trees was recorded in each annual survey from 1998 to 2001, to assess the influence of fire on tree basal area.

8.2.1c Survival and growth of Corymbia clarksoniana *juveniles*

Survival and growth of *Corymbia clarksoniana* juveniles (defined as individuals < 2m in height) were compared between unburnt, early (May 1999) and late dry season (October 1999) burnt savanna. Heights were recorded for all *C. clarksoniana* juveniles within the 36, 100m^2 plots at Cape Cleveland in March to May 1999, prior to the implementation of the early dry season fires. The juveniles were tagged and re-measured at the same time of year in 2000 and 2001.

8.2.1d Stem regeneration after burning and cutting in the early and late dry seasons

An assessment was made of the effect of different disturbances (burning and cutting) and the season of disturbance (early and late dry seasons), on the number of sprouting stems of the common subshrub, *Breynia oblongifolia*. This shrub was assessed because of its capacity to regenerate from root-suckers, hence its value for assessing the effect of fire on vegetative regeneration. The permanent 1m^2 plots used to document total seedling emergence (Chapter 6) were used to assess the effects of disturbance type and season of disturbance on stem survival and growth. The experiment assessed the impacts of a single set of fires or cutting treatments. These were:

1. Undisturbed; savanna that was last burnt in July 1997 and remained undisturbed.
2. Early burnt; savanna burnt in early dry season fires (May 1999).
3. Late burnt; savanna burnt in late dry season fires (October 1999).
4. Early cut; herbaceous layer cut and removed from unburnt plots at the time of early dry season fires, in savanna that was last burnt in July 1997.
5. Late cut; herbaceous layer cut and removed from unburnt plots at the time of late dry season fires, in savanna that was last burnt in July 1997.

Prior to the implementation of burning and cutting treatments in May 1999 and October 1999, the number of *B. oblongifolia* stems was recorded within the permanent 1m^2 plots. The number of surviving stems were recorded in May 2000.

8.2.1e Survival of mature herbs

An assessment was made of the effect of burning and cutting, in the early and late dry seasons, on the percentage survival of common grasses and forbs. The permanent 1m^2 plots established to document total seedling emergence (Chapter 6) were used to assess the effects of disturbance type and season of disturbance on stem survival and growth. The five treatments are outlined above in section *8.2.1d*. Assessments were made when the plots were established in May and October 1999, and survival was re-surveyed one month after the early and late dry season fires.

Density counts of common grasses and forbs were attempted when the 1m^2 plots were established. However, the density of plants could not be calculated accurately due to the multiple stems of many common forbs, and the clumping nature of grasses. Post-disturbance assessments indicated that pre-fire counts were inaccurate (i.e. two or three distinct clumps sprouted where a pre-treatment count documented a single clump). In the case of *Heteropogon triticeus*, not only were pre-fire clumps difficult to count, but post-fire re-growth emerged from several distinct sections of individual clumps, making distinction and therefore estimating post-fire density inaccurate.

As a result of the inaccuracies of density measurements, the assessment of plant survival was based on the presence or absence of a species within a 1m^2 plot, pre- and post-treatment. A percentage survival figure was calculated for each of the three replicate 1 ha blocks, based on the percentage of 1m^2 plots in which a species remained present. This is less sensitive to changes in plant density than counts of individual plants and, depending on the number of plants per plot, may lead to an over- or underestimate of percentage survival.

8.2.2 Statistical analyses

8.2.2a Regenerative capacity of savanna species

Records of post-fire regeneration of all species encountered were tabulated. Observations from the four savanna sites across Townsville were listed separately to provide confirmation of regenerative capabilities across the region. No quantitative data were collected and therefore no statistical analyses were performed.

8.2.2b Survival and growth of trees

The influence of fire treatments on the density and basal area of trees (> 2m in height) was analysed for combined tree species and the four most abundant species, as other species were present at very low densities. A repeated measures ANOVA was performed for fire treatment, with three levels (control, early burnt and late burnt) and year of survey as the repeated measure. The repeated measure factor “year” contained five levels (1997 to 2001) for the tree density analyses and four levels (1998 to 2001) for basal area analyses, as circumference measurements were only available from 1998 to 2001. Due to the small number of trees within each of the 100m^2 plots, data from the four 100m^2 plots were pooled for each replicate 1 ha per block to reduce variance.

*8.2.2c S*urvival and growth of* Corymbia clarksoniana *juveniles*

The influence of fire regime on the growth and survival of *C. clarksoniana* juveniles was assessed using a one-factor ANOVA to test the statistical significance of differences in survival and heights of juveniles with time since last fire. The differences in survival and heights of juveniles between fire treatments (control, early and late burnt) was assessed using a repeated measures ANOVA, with the repeated measure factor “year” containing three levels (1999 to 2001). Individuals that were < 2 m in height during the initial 1999 survey that grew > 2 m by 2001 remained in the analyses to ensure accuracy in assessment of the changes in survival and height.

8.2.2d Stem regeneration after burning and cutting in the early and late dry seasons

The statistical significance of differences in the number of *B. oblongifolia* stems between treatments (undisturbed, early and late burnt, early and late cut) was assessed using a one-factor analysis of co-variance (ANCOVA) of the final survey data collected in May 2000, using the initial stem density data collected in 1999 as a covariate.

8.2.2e Survival of mature herbs

A one-factor ANOVA was initially used for determining the statistical significance of differences in percentage survival following treatments (undisturbed, early and late burnt, early and late cut) for each of the five most common herbs. However a Cochran's test (Underwood 1997) indicated significant variance heterogeneity could not be resolved with data transformations. Therefore a non-parametric Kruskal-Wallis ANOVA by ranks was used to test the statistical significance of differences between treatments for each species.

8.3 Results

8.3.1 Regenerative capacity of savanna species

Post-fire regeneration observations were documented for a total of 160 species (Appendix 2). Eighty one percent (130 species) were observed to sprout after fires in Townsville eucalypt savannas and fire response for individual species was consistent between sites.

While nearly all trees and shrubs were consistently able to sprout after fire (Table 8.1; Appendix 2), the ability to sprout from epicormic rather than basal buds was restricted to the eucalypts, *Canarium australianum* and *Planchonia careya*. The ability to epicormically sprout was size-dependent, with epicormic sprouting of eucalypts and *Planchonia careya* only observed for plants greater than 1.5 m to 2 m in height. The tallest *Canarium australianum* tree, of 8 m in height, was also able to epicormically sprout after full canopy scorch during both the July 1997 and October 1999 fires, while all other *C. australianum* plants sprouted from the stem base.

Obligate seeders were primarily ephemeral forbs that were observed to produce seed within one year of germination (Table 8.1; Appendix 2). Obligate seeder perennials were the shrubs *Acacia holosericea* and *A. umbellata*, the twining forb *Cassytha filiformis* and the subshrubs *Triumfetta rhomboidea* and *Urena lobata*. A single *Vitex trifolia* shrub present at Cape Cleveland was killed by the 1997 fire and until further observations are made, it must be assumed to be an obligate seeder. *Acacia umbellata*, *Cassthya filiformis*, *Triumfetta rhomboidea* and *Urena lobata* produce seed in the second year after germination, but the juvenile period of *A. holosericea* and *V. trifolia* are unknown.

Table 8.1. Summary of post-fire regeneration of growth form groups in eucalypt savanna in the vicinity of Townsville.

Growth form group	Number of species	% sprouters	% obligate seeders	% sprouting ability unknown
Woodland trees and shrubs	32	91	9	0
Rainforest trees and shrubs	20	95	0	5
Subshrubs	15	93	0	7
Upright perennial forbs	14	93	0	7
Twining perennial forbs	26	100	0	0
Ephemeral forbs	20	0	100	0
Grasses	18	89	11	0
Non-grass monocots	15	100	0	0

8.3.2 Survival and growth of trees

The density of all trees (> 2m in height) increased between 1997 and 2001 with a significant interaction between fire and year (Table 8.2; Figure 8.1). Tree density increased in control sites, unburnt since 1997, but declined in late burnt sites after the October 1999 fire. Although *Canarium australianum* and *Corymbia tessellaris* displayed slight increases in tree density in control sites, and a *Corymbia tessellaris* tree was killed in a late dry season fire, no statistically significant differences between fire treatments, or year of survey, were found for any of the four most abundant trees over the five years of investigation (Table 8.2; Figure 8.1).

Table 8.2. Repeated measures ANOVA results for the effect of fire on the density of all trees (> 2m height) and the four most abundant trees, between 1997 to 2001 at Cape Cleveland. No *Canarium australianum* trees > 2m in height were present in early burnt blocks, hence analyses were restricted to comparisons of control and late burnt blocks. $F_{2,6}$, *F* value, denominator d.f., numerator d.f.; *F* values without an asterisk (*) are not significantly different at $P > 0.05$; $^*P < 0.05$; $^{**}P < 0.01$. Scheffe's *post-hoc* test results are provided for differences between years.

Species	Fire	Year	Fire x Year
Combined trees (n = 10 species; 199 plants)	$F_{2,6} = 3.131$	$F_{4,24} = 4.929^{**}$ (2001 > 1997 & 1998)	$F_{8,24} = 2.507^{*}$
Canarium australianum (n = 16 plants)	$F_{1,4} = 2.896$	$F_{4,16} = 2.804$	$F_{4,16} = 2.804$
Corymbia clarksoniana (n = 61 plants)	$F_{2,6} = 0.138$	$F_{4,24} = 1.758$	$F_{8,24} = 1.030$
Corymbia tessellaris (n = 25 plants)	$F_{2,6} = 0.311$	$F_{4,24} = 1.714$	$F_{8,24} = 0.643$
Planchonia careya (n = 60 plants)	$F_{2,6} = 1.333$	$F_{4,24} = 0.000$	$F_{8,24} = 1.500$

There were no significant fire effects on tree basal area (Figure 8.2; Table 8.3), even though tree density differed between fire treatments (Table 8.2). This is because the increase in tree density resulted from the growth of saplings above the 2 m height, which added little to the overall basal area compared to the larger trees. The basal area of the dominant tree *Corymbia clarksoniana* significantly increased over the course of the study (Figure 8.2; Table 8.3). No other statistically significant differences in basal area were detected for the four most abundant trees, despite the decline in basal area in *C. tessellaris* in late burnt sites in 2000 and 2001 due to the death of a large tree in a late dry season fire.

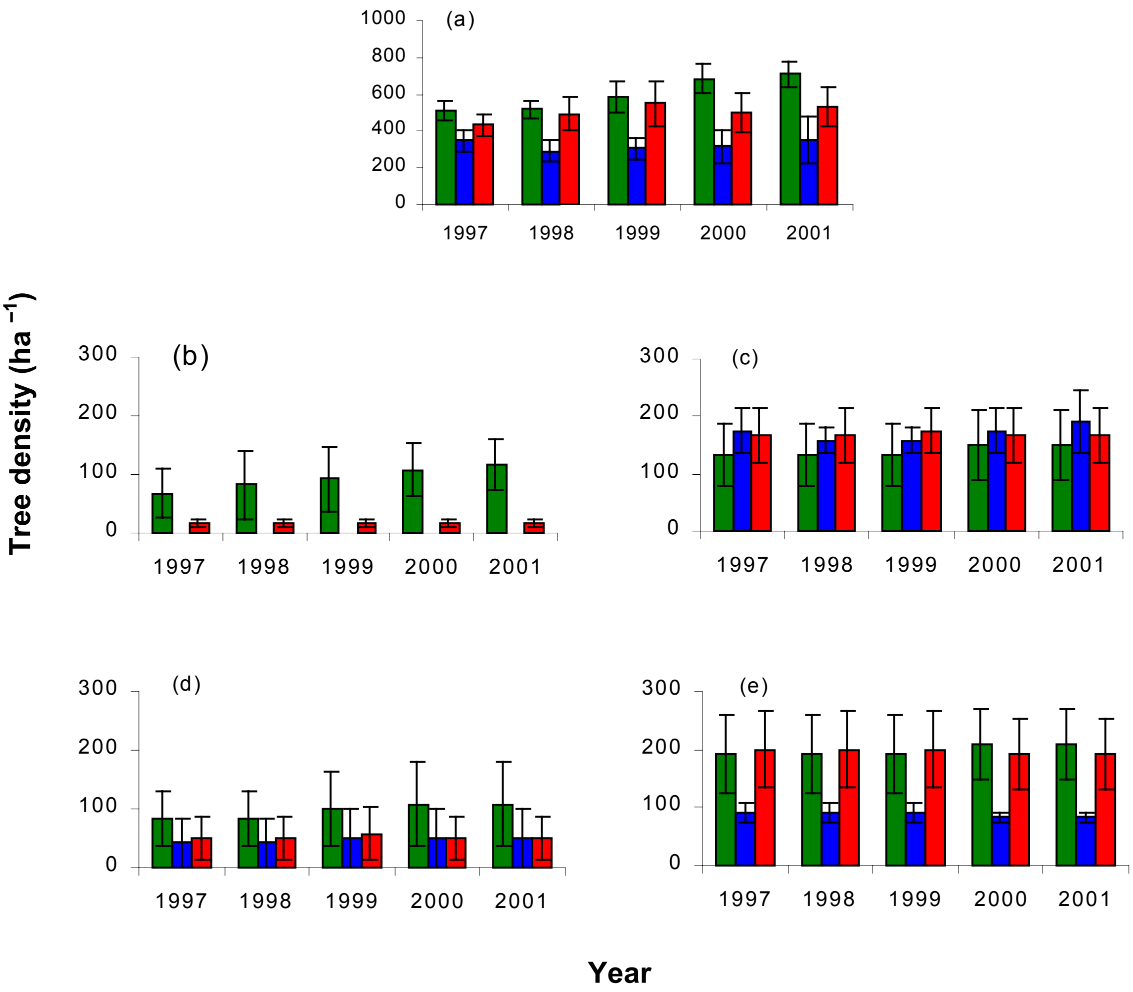


Figure 8.1. Mean (± 1 standard error) tree density in control (🟩), early (🟦) and late dry season burnt (🟥) eucalypt savanna at Cape Cleveland, between 1997 and 2001 for (a) combined trees; (b) *Canarium australianum*; (c) *Corymbia clarksoniana*; (d) *Corymbia tessellaris*; (e) *Planchonia careya*.

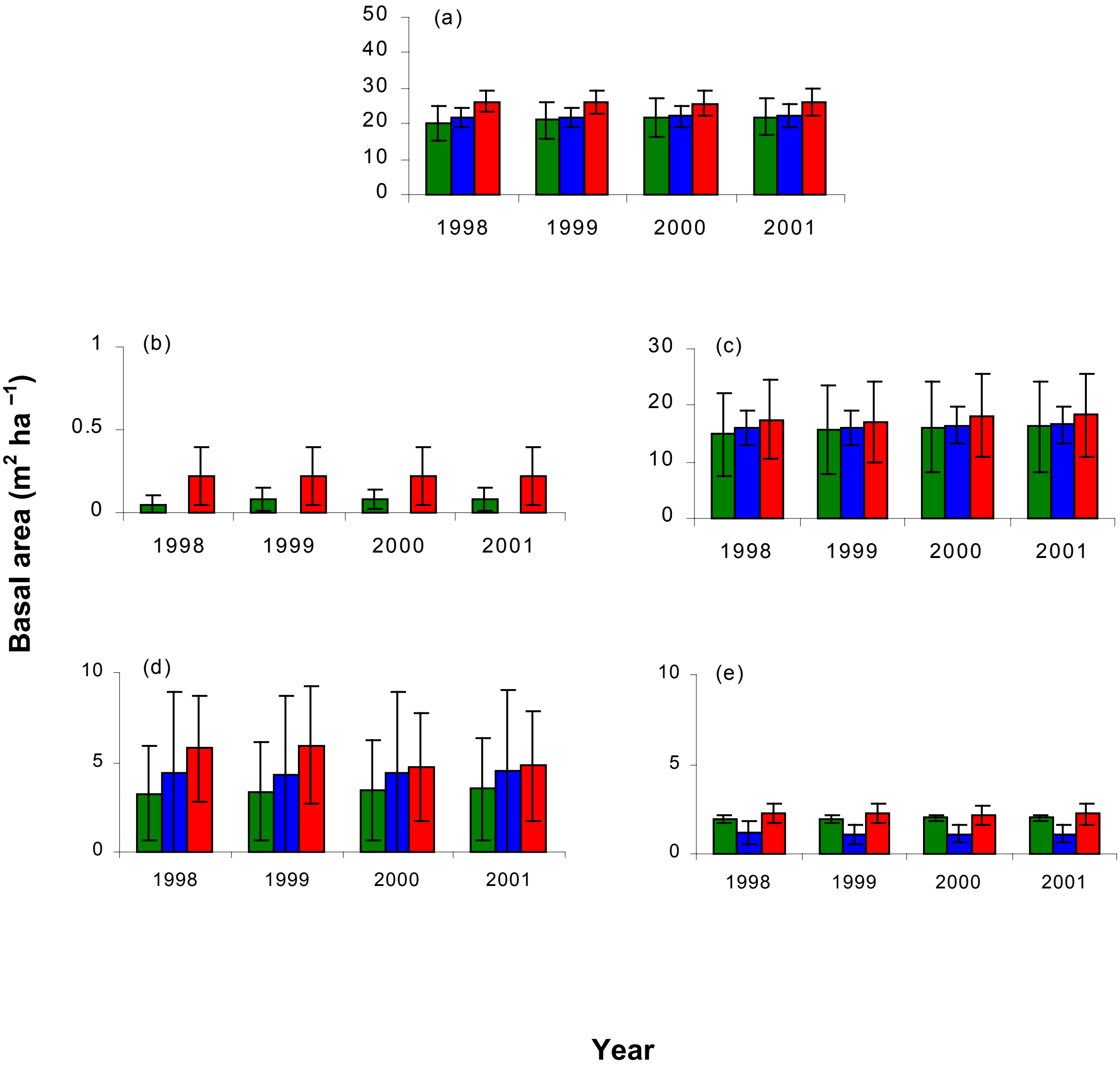


Figure 8.2. Mean (± 1 standard error) tree basal area in control (🟩), early burnt (🟦) and late dry season burnt (🟥) eucalypt savanna at Cape Cleveland between 1997 and 2001 for (a) combined trees; (b) *Canarium australianum*; (c) *Corymbia clarksoniana*; (d) *Corymbia tessellaris*; (e) *Planchonia careya*.

Table 8.3. Repeated measures ANOVA results for the effect of fire (control, early burnt, late burnt) on the basal area of all trees (> 2m height) and the four dominant species, between 1998 to 2001 at Cape Cleveland. No *Canarium australianum* trees > 2 m in height were present in early burnt blocks, hence analyses were restricted to comparisons of control and late burnt blocks. $F_{2,6}$, F value, denominator d.f., numerator d.f.; F values without an asterisk (*) are not significantly different at $P > 0.05$; *$P < 0.05$; **$P < 0.01$. Scheffe's *post-hoc* test results are provided for differences between years.

Species	Fire	Year	Fire x Year
Combined trees (n = 10 species; 199 plants)	$F_{2,6} = 0.440$	$F_{3,18} = 1.396$	$F_{6,18} = 1.572$
Canarium australianum (n = 16 plants)	$F_{1,4} = 0.685$	$F_{3,12} = 1.813$	$F_{3,12} = 1.813$
Corymbia clarksoniana (n = 61 plants)	$F_{2,6} = 0.026$	$F_{3,18} = 5.148$** (2001 > 1998)	$F_{6,18} = 0.919$
Corymbia tessellaris (n = 25 plants)	$F_{2,6} = 0.077$	$F_{3,18} = 0.369$	$F_{6,18} = 0.765$
Planchonia careya (n = 60 plants)	$F_{2,6} = 1.615$	$F_{3,18} = 0.292$	$F_{6,18} = 2.324$

8.3.3 Survival and growth of **Corymbia clarksoniana** *juveniles*

No significant fire by year interaction, which would indicate an effect of the 1999 fires, was detected for the density or heights of *Corymbia clarksoniana* juveniles (Table 8.4). However, a significant block effect was found for both density and heights, with fewer juveniles in the third block of control, early and late burnt sites. A significant year effect for height indicated growth of *C. clarksoniana* juveniles between 1999 and 2001 consistent across all treatments (Figure 8.3; Table 8.4). A significant positive correlation was detected between the height of juveniles and years since last fire, indicating an overall increase between one year and four years after fire (n = 1080; Spearman's $R = 0.090$; $P < 0.003$; Figure 8.4).

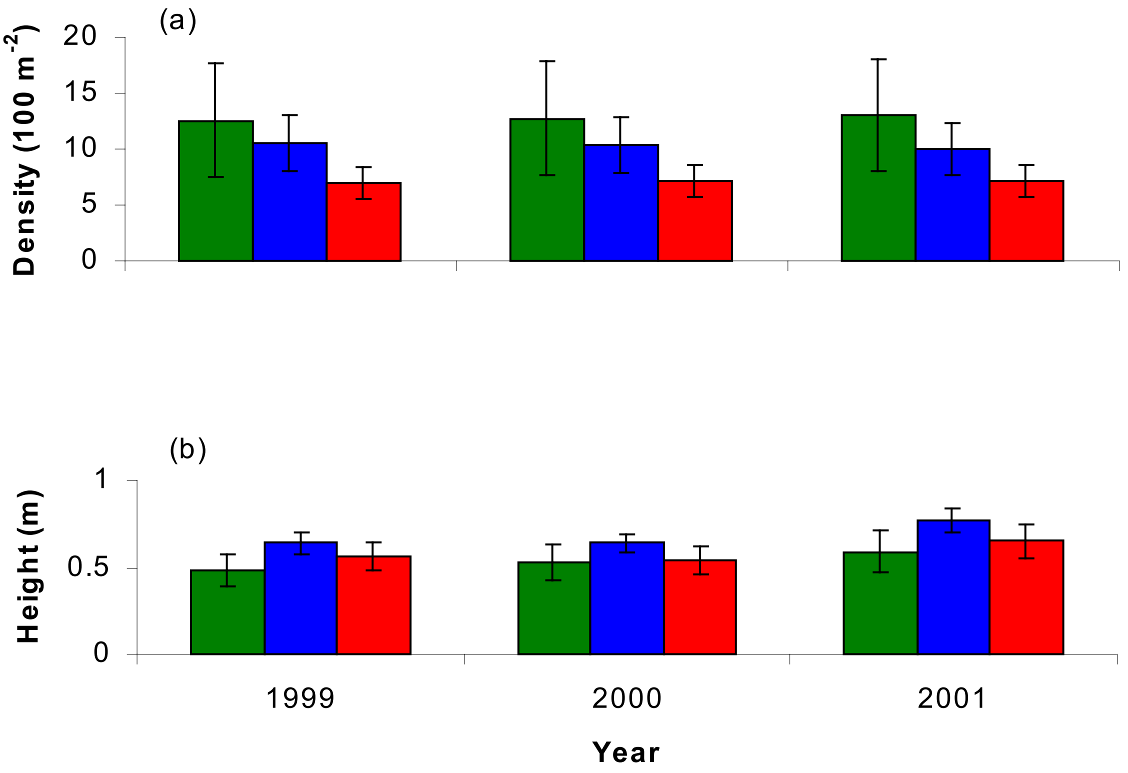


Figure 8.3. Mean (± 1 standard error) (a) density and (b) height of *Corymbia clarksoniana* juveniles between 1999 and 2000 in control (🟩), early (🟦), and late dry season burnt (🟥) savanna at Cape Cleveland.

Table 8.4. Repeated measures ANOVA results of *Corymbia clarksoniana* juvenile density and height between 1999 and 2001 in control, early and late burnt blocks. $F_{2,6}$, F value, denominator d.f., numerator d.f.; F values without an asterisk (*) are not significantly different at $P > 0.05$; *$P < 0.05$; **$P < 0.01$; *** $P < 0.001$.

Species	Fire	Block	Year	Fire x Year
Density	$F_{2,6} = 0.146$	$F_{6,27} = 4.989$***	$F_{2,12} = 0.191$	$F_{4,12} = 2.989$
Height	$F_{2,6} = 0.310$	$F_{6,27} = 4.137$**	$F_{2,12} = 17.181$***	$F_{4,12} = 0.850$

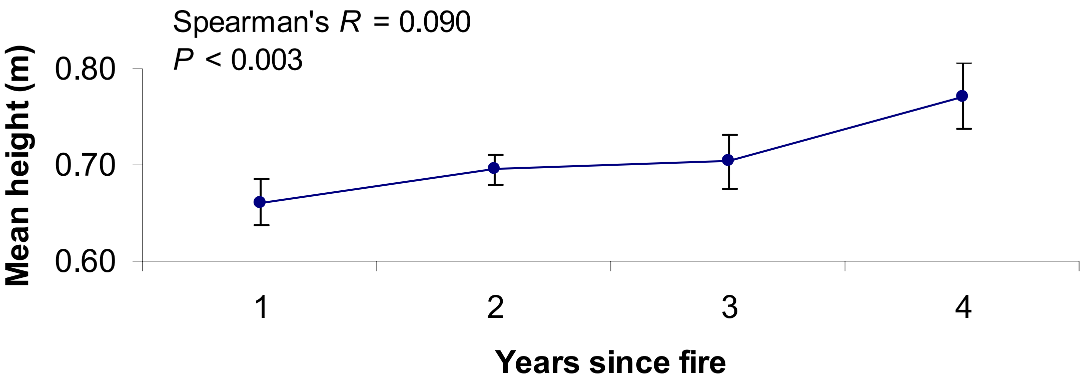


Figure 8.4. Mean (± 1 standard error) growth of *Corymbia clarksoniana* juveniles (< 2 m tall in 1999) with years since fire in eucalypt savanna at Cape Cleveland. Results of Spearman rank correlation are provided.

8.3.4 Stem regeneration after burning and cutting in the early and late dry seasons

The density of *Breynia oblongifolia* stems increased between May 1999 and May 2000 in all treatments, except late cut savanna (Figure 8.5). Burning in both the early and late dry seasons significantly increased stem density over both early and late cut treatments ($F_{4,23} = 4.006$; $P < 0.013$). Although not specifically quantified, stems rapidly re-grew to pre-disturbance heights of approximately 30 to 60 cm after both burning and cutting.

8.3.5 Survival of mature herbs

All five common herbaceous species assessed displayed some mortality in burnt or cut treatments, but differences between treatments were not statistically significant (Table 8.5; Figure 8.6). Some *Galactia tenuiflora* died after fires in both seasons, but no mortality was observed after cut treatments. Mortality of *Heteropogon triticeus* was only detected in late burnt plots. Some *Passiflora foetida* died after burning and cutting in both seasons. Mortality of *Pycnospora lutescens* was detected after fires in both seasons and cutting in the early dry season. These results indicate that although the common herbaceous species sprout after fire, burning and cutting kills some plants.

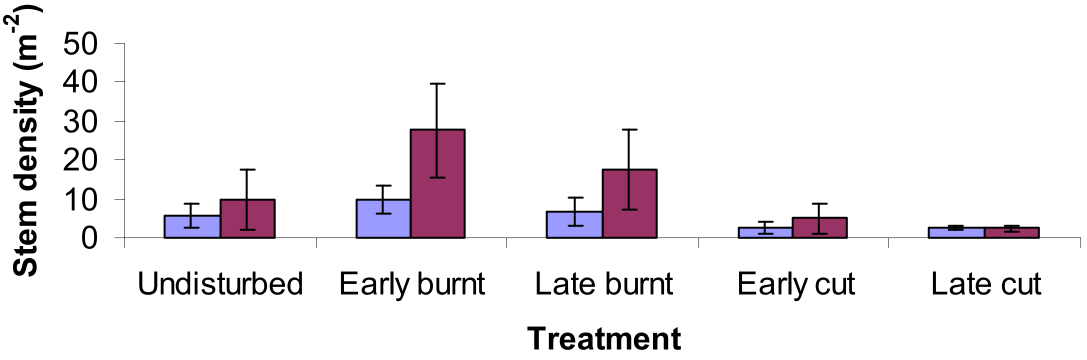


Figure 8.5. Mean (± 1 standard error) *Breynia oblongifolia* stem density before (🟦), and after (🟥) treatments in eucalypt savanna at Cape Cleveland. Undisturbed, savanna that was last burnt July 1997; Early burnt, savanna burnt in July 1997 and May 1999; Late burnt, savanna burnt in July 1997 and October 1999; Early cut, herbaceous layer cut and removed in May 1999, from savanna that was last burnt July 1997; Late cut, herbaceous layer cut and removed in October 1999, from savanna that was last burnt July 1997.

Table 8.5. Kruskal-Wallis ANOVA by ranks statistical results for the percentage survival of common herbaceous species after burning and cutting in the early and late dry seasons in eucalypt savanna at Cape Cleveland.

Species	denominator d.f., numerator d.f.	*H* statistic	*P* value
Galactia tenuiflora	4,10	3.238	> 0.05
Glycine tomentella	3,7	5.867	> 0.05
Heteropogon triticeus	4,10	4.000	> 0.05
Passiflora foetida	4,10	3.399	> 0.05
Pycnospora lutescens	3,7	4.516	> 0.05

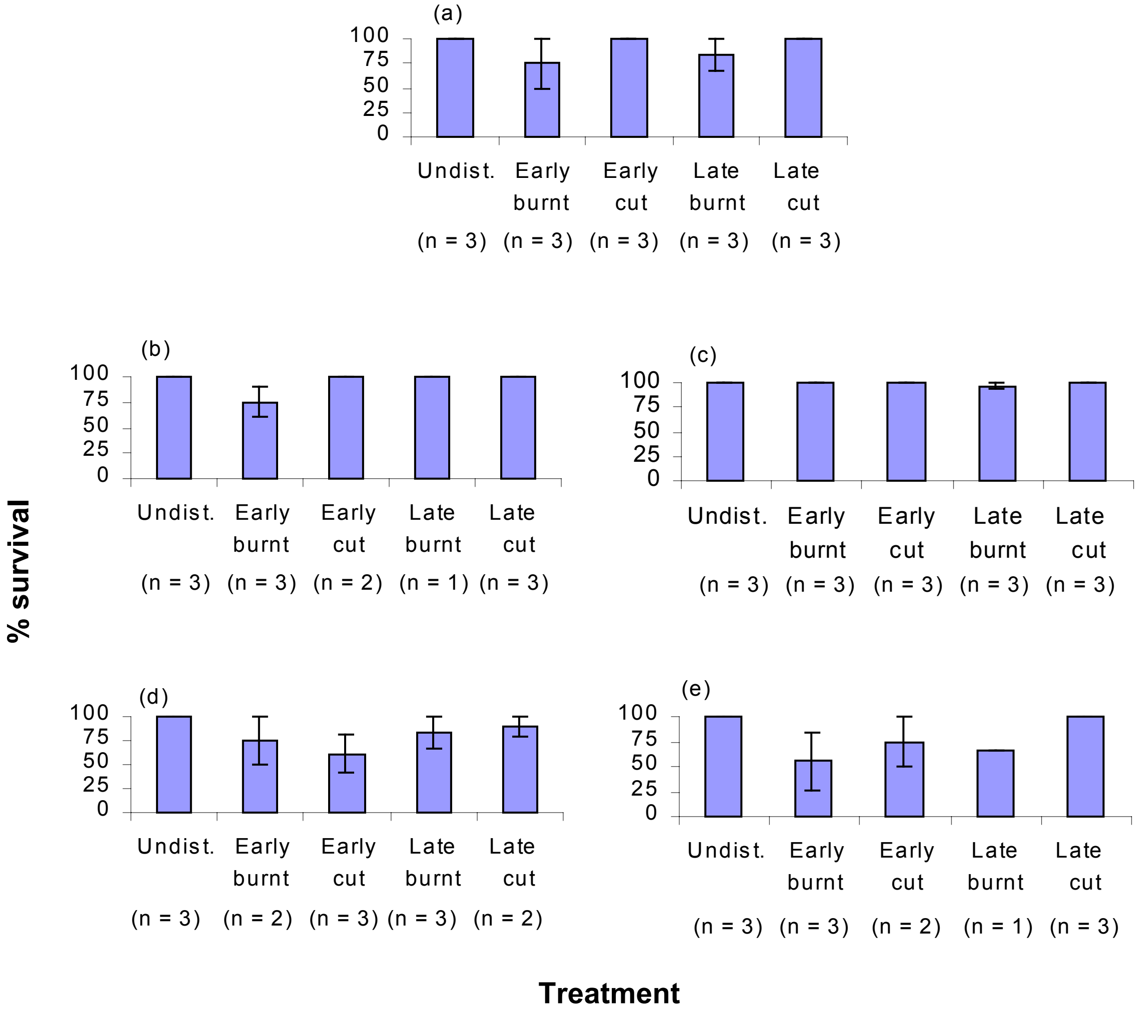


Figure 8.6. Mean (± 1 standard error) % survival of (a) *Galactia tenuiflora*, (b) *Glycine tomentella*, (c) *Heteropogon triticeus*, (d) *Passiflora foetida*, (e) *Pycnospora lutescens* in eucalypt savanna at Cape Cleveland. Undist., savanna that was last burnt July 1997 and remained undisturbed; Early burnt, savanna burnt in July 1997 and May 1999; Late burnt, savanna burnt in July 1997 and October 1999; Early cut, herbaceous layer cut and removed in May 1999, from savanna that was last burnt July 1997; Late cut, herbaceous layer cut and removed in October 1999, from savanna that was last burnt July 1997; n = the number of 1 ha blocks the species was present within.

8.4 Discussion

8.4.1 Regenerative capacity of savanna species

Eighty one percent of species in eucalypt savannas around Townsville were observed to be capable of sprouting after fire (Appendix 2). The proportion of sprouting species in Townsville savannas is high compared to many Australian heath, woodland and forest communities (Table 8.6). The higher proportion of sprouters in tropical forests and savannas than in most temperate heaths, woodlands and forests (Table 8.6) agrees with Bond and Midgley's (2001) generalisation that sprouters are more abundant in the tropical communities. Although the high percentage of sprouters in alpine woodland may appear to be an anomaly to this conclusion, this community is subjected to frequent insect attack and frost damage (Wahren *et al*. 1999). Hence the post-fire sprouting ability of many species may be in response to frequent disturbances rather than frequent fire (Wahren *et al*. 1999).

The capacity of individuals to live through several fires reduces plant turn over, providing population stability (Bond and Midgley 2001). The abundance of sprouting species in the eucalypt savannas of Townsville provides resilience to community composition with regular burning. This explains the stability of species composition documented in annual floristic surveys at Cape Cleveland, and the greater importance of intrinsic plot differences than fire regimes in explaining the variation in species composition and abundance (Chapter 3). The persistence provided by sprouting after fire is therefore a critical mechanism maintaining the composition of eucalypt savannas in northern Australia.

Sprouting species in Townsville savannas displayed variation in their mode of re-growth, with many species re-shooting from buds located below the soil surface at the base of the plant, while some woody species were able to epicormically sprout from the trunk and branches (Appendix 2). For species that were capable of epicormic sprouting, this ability was size dependent, with epicormic sprouting apparent only for plants greater than 1.5 m to 2 m in height (and > 8 m for *Canarium australianum*). Size-dependent variation in sprouting is common in tropical savanna trees (e.g. Lonsdale and Braithwaite 1991; Trollope 1996; Williams *et al*. 1999*b*), and is probably due to the

Table 8.6. Comparison of the percentage of sprouting species within a range of Australian vegetation types. ACT, Australian Capital Territory; NSW, New South Wales; NT, Northern Territory; QLD, Queensland; VIC, Victoria; WA, Western Australia. Sources: [1] Clarke and Knox (2002); [2] Bradstock *et al*. (1997); [3] Russell-Smith *et al*. 1998; [4] Keith (2002); [5] van der Moezel *et al*. (1987); [6] Wahren *et al*. (1999); [7] Williams (2001); [8] Williams (1995); [9] Ashton (1981); [10] Cary and Morrison (1995); [11] Bell and Koch (1980); [12] Purdie and Slatyer (1976); [13] this study.

Vegetation	Number of species assessed	% sprouting species
Heaths and shrubby communities		
Granite outcrop heath, NSW [1]	58	10
Coastal heath, NSW [2]	62	52
Tropical heath and savanna mosaic, NT [3]	152	53
Montane dry heath, NSW [4]	135	60
Shrubby temperate forest, NSW [1]	111	73
Sandplain shrubland, southern WA [5]	192	73
Alpine heath, VIC [6]	70	81
Heathy tropical savanna, QLD [7]	64	83
Montane wet heath, NSW [8]	87	84
Wet sclerophyll forests		
Temperate forest, VIC [9]	101	37
Tropical forest, QLD [7]	58	90
Dry sclerophyll forests, woodlands and savanna		
Temperate woodland, NSW [10]	118	52
Temperate forest, WA [11]	93	69
Temperate woodland, ACT [12]	91	73
Temperate forest, NSW [1]	54	81
Tropical savanna, QLD [13]	160	81
Alpine woodland, VIC [6]	56	95

development of bud protection. Burrows (2002) has demonstrated that the capacity of many eucalypts to re- shoot from the trunk and branches is linked to greater protection of meristematic tissue, which is located within the vascular cambium rather than the outer bark, as in many other species.

Bellingham and Sparrow (2000) predicted basal sprouting should be more common than epicormic sprouting with severe and frequent disturbance. This concept may be applied to the contrast between canopy trees, which are capable of epicormic sprouting, and juvenile trees and shrubs, which are reduced to basal sprouting. Mature trees in Townsville savannas do not experience full canopy scorch during every fire, only partial scorching during many low intensity early to mid dry season fires (*pers. obs.*). The lower height of shrubs and tree juveniles ensures full canopy scorch during most fires, and therefore shrubs and tree juveniles receive more frequent full canopy disturbance than taller trees of the same community.

Several woody species in Townsville savannas sprouted from the roots after fire (Appendix 2). Vegetative spread of woody species via root and rhizome suckering has been reported for a range of tropical species and may be a significant source of stem replacement and multiplication (Lacey 1974; Lacey and Whelan 1976; Hoffman 1998; Williams 2000; Russell-Smith *et al.* in press).

The "persistence niche" (Bond and Midgley 2001), provided by sprouting and plant longevity, is important for maintaining population stability and species co-existence. Various modes of post-fire sprouting may also allow species co-existence. For instance, root-suckering species of Townsville savannas are primarily subshrubs and herbs, and regeneration from roots tends to promote horizontal spread, whereas epicormic sprouting allows continued vertical growth, and has been observed only in canopy species. Root regeneration is therefore a mechanism that allows species to efficiently exploit a spatial niche near the soil surface and to co-exist with taller, epicormic sprouting species.

Obligate seeders in Townsville savannas are primarily ephemeral species that produce seed within one year of germination. Four of the six perennial obligate seeders require only two years after germination to produce seed. The rapid seed production of obligate seeders is a mechanism that allows population persistence with frequent fires. This contrasts with the many obligate seeder shrubs of heaths and heathy savannas in the Northern Territory and western Queensland which require more than five years to produce seed and whose populations may decline with fire intervals of less than five years (Russell-Smith *et al*. 1998; Williams *et al*. 2002*b*). It is possible that fire regimes of less than five years in Townsville savannas may have removed obligate seeders that require more than five years to mature.

8.4.2 Survival and growth of trees

The total density of trees taller than 2 m significantly increased with a four year absence of fire at Cape Cleveland, although this was not significant for any individual species (Table 8.2). The increase in tree density resulted from the growth of saplings above 2 m in height. Burning during the early and late dry seasons inhibited an increase in tree density over the course of the study. However, the increase in tree density in the absence of fire was not associated with a significant increase in basal area, because the growth of saplings above the 2 m height category added little to the overall basal area (Figure 8.2; Table 8.3).

Fire season can affect sprouting ability, with poor recovery often reported after burning during rapid growth periods (Whelan 1995). Noble (1989) found that fire season affected survival of mallee eucalypts, with greater survival after annual spring (i.e. early dry season) fires, which coincide with the start of the growing season, than annual autumn (i.e. late dry season) fires. Fire intensity can also affect stem survival, as high intensity, late dry season fires produce the highest mortality in tropical savanna trees of the Northern Territory (Williams *et al*. 1999*b*). No significant fire season effect was detected at Cape Cleveland, although the late dry season fires did cause the mortality of one *Corymbia tessellaris* tree. The absence of distinct fire season differences in survival may be because all Cape Cleveland fires were of a lower intensity than the late dry season fires that caused significant mortality in the study by Williams *et al*. (1999*b*).

Higgins *et al*. (2000) suggested variation in fire intensity is a key factor governing tree density in savannas, with the escape of stunted juveniles from the "flame zone" depending on fire frequency and intensity. Data from Cape Cleveland provide evidence that fire frequency influences the release of stunted juveniles. However no evidence was found that fire intensity affected juvenile release, as juveniles of various tree species were reduced to sprouting from the base after both high intensity late dry season fires and low intensity early and mid dry season fires. As a result, tree density did not increase in early burnt sites that experienced only low intensity fires during the study.

8.4.3 Survival and growth of **Corymbia clarksoniana** *juveniles*

The density of *Corymbia clarksoniana* juveniles remained stable in all fire regimes between 1999 and 2001. *Corymbia clarksoniana* juveniles were not killed by fire and rapidly re-grew after both early and late dry season fires to return to their pre-fire heights within one year of burning (Figure 8.3). While no significant interaction between fire treatment and year could be detected, a significant block effect indicated variation between plots prior to the implementation of this study, and which may be caused by species interactions or edaphic factors (Table 8.4). A significant year effect resulted from growth of *C. clarksoniana* juveniles between 1999 and 2001, which was consistent across all fire regimes. While the interaction between fire and year was not significant in the repeated measures ANOVA, a significant correlation between juvenile height and time since fire was detected, with a steady increase in height with time after fire. This apparent inconsistency in statistical results can be explained by the fact that the comparisons between burnt and unburnt plots in the repeated measures analyses did not compare juvenile heights at the extreme range in time since fire, namely one and four years post-fire, as the 2000 comparison assessed one and three years after fire, and the 2001 data compared two and four years post-fire. The data suggest that the absence of fire does lead to the growth of *C. clarksoniana* juveniles, although the growth is slow and it may take many years before many juveniles grow beyond 1.5 to 2 m in height, and become capable of epicormic sprouting and can therefore continue vertical growth.

The escape of stunted juvenile savanna trees from the flame zone has been repeatedly documented in tropical savannas experiencing infrequent fires (Higgins *et al*. 2000). This includes many non-eucalypt trees of northern Australia, with intervals greater than two or three years allowing the release of stunted juveniles (Bowman *et al*. 1988; Crowley and Garnett 1998; Russell-Smith *et al*. in press). The growth of tropical eucalypt juveniles beyond the flame zone may require longer fire intervals than many non-eucalypt species. While the growth of *Eucalyptus tetrodonta* juveniles can occur with several years without fire, *E. miniata* remain stunted after the absence of fire for 21 years, and may require release from competitive suppression by canopy trees (Fensham and Bowman 1992; Russell-Smith *et al.* in press).

8.4.4 Stem regeneration after burning and cutting in the early and late dry seasons

Burning in both the early and late dry seasons significantly increased the density of stems originating from root suckers in the subshrub *Breynia oblongifolia*, compared with cutting back to ground level in unburnt savanna (Figure 8.5). This vegetative stem reproduction explains the increase in the abundance of *B. oblongifolia* following fire, documented in the annual floristic surveys (Chapter 3). The data provide evidence that vegetative regeneration is affected by the type of disturbance but not the season of disturbance. Bond and van Wilgen (1996) suggested that increased stem mortality after burning, rather than cutting, indicated the fate of regenerative buds, rather than carbon reserve size, is the primary mechanism controlling regeneration. In this instance, cutting led to the regeneration of stem density similar to pre-disturbance numbers, while burning increased the density of stems. Following Bond and van Wilgen's (1996) argument, these data suggest that the fate of regenerative buds, or meristematic tissue within the roots, control the density of regenerating stems to a greater extent than carbon reserve size, with fire triggering an increase in stem re-growth. This may result from a stimulus to the roots from heat penetration into the topsoil during fire. While late dry season fires produced greater heat penetration into the topsoil than early dry season fires (Chapter 4), no significant differences between early and late fires were detected in *B. oblongifolia* stem density.

Asexual reproduction is a common and important strategy in frequently burnt savannas, and stems arising from root suckers show greater survival, growth and earlier production of seeds than seedlings of the same species (Hoffman 1998). The strength of the conclusion, that the density of regenerating stems of *B. oblongifolia* is governed to a greater extent by the fate of buds than carbon reserves, is limited by the low number of *B. oblongifolia* plants assessed, and by the indirect means of assessment. Further research is required to directly examine the carbon reserve size and the influence of fire on bud regeneration in a larger number of plants of *B. oblongifolia* and co-existing root-suckering species, such as *Grewia retusifolia*, and *Cajanus confertiflorus*.

8.4.5 Survival of mature herbs

Burning and cutting produced some mortality in the five common herbaceous species assessed, although differences between undisturbed, burnt and cut treatments were not significant (Figure 8.6; Table 8.5). This indicates that, while these species may be classified as sprouters, burning can kill plants. In *Galactia tenuiflora* and *Heteropogon triticeus*, mortality was only detected after burning and not after cutting unburnt plants. This suggests that, similar to *B. oblongifolia*, the fate of regenerative buds may be more important than reserve size for controlling vegetative regeneration of these herbs (Bond and van Wilgen 1996).

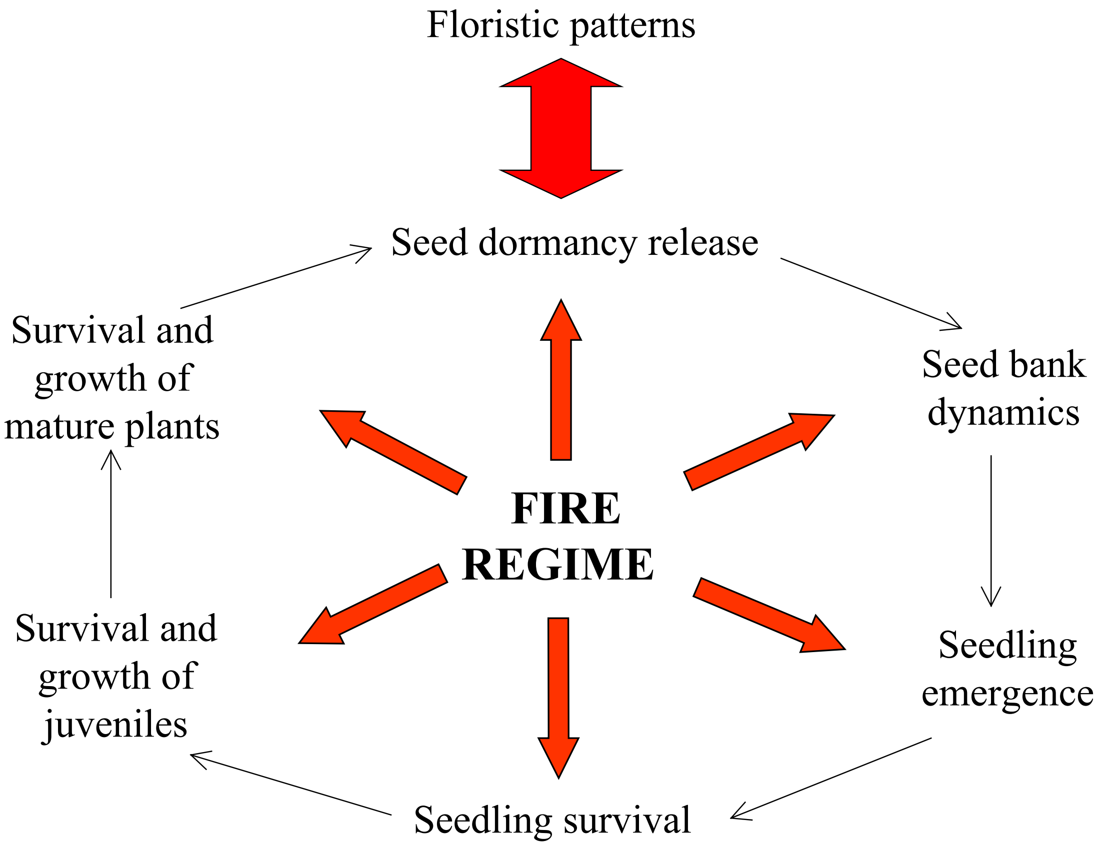
Further research is required to accurately examine the effect of fire on the level of mortality of herbaceous species in Townsville savannas. The method used in this study does not detect the survival of individual plants and can either over- or underestimate the percentage survival, depending on the number of individuals present in the plots. An improved method for use in further studies of survival of adult grass and forbs could involve tagging plants with a wire ring that encircles the plants, as described by Crowley and Garnett (2001).

8.5 Conclusion

The ability to sprout after fire is an important mechanism that promotes population resilience in regularly burnt communities (Bond and Midgley 2001). The high proportion of sprouting species in Townsville eucalypt savannas enables the persistence of individual plants and explains the stability of species composition detected in this savanna after two fires over five years (Chapter 3). However, some trees and common herbs were killed by fire, indicating that burning does affect the number of standing plants through mortality, as well as germination (Chapter 6).

There is evidence that frequent fires are responsible for suppressing juvenile trees from growing beyond 2 m in height. However, the growth of juveniles of *C. clarksoniana* may require many years of fire exclusion before a significant number of juveniles reach 2 m in height and are thus released from the fire trap. The release of some juvenile trees with fire-free intervals of four years is consistent with Higgins' *et al.* (2000, p. 226) hypothesis that “grass-tree coexistence is driven by the limited opportunities for tree seedlings to escape both drought and the flame zone into the adult stage.” Midgley and Bond (2001) suggested, for high rainfall areas, that the growth of tall grasses allows fires to inhibit juvenile tree release to the canopy. This is supported by data from Cape Cleveland, where the increase in tree density coincided with the decline in abundance of the dominant tall grass *Heteropogon triticeus* after four years (Chapter 3).

Chapter 9. Summary and conclusions.



9.1 Thesis objectives

The influence of fire on Australian tropical savannas has been the subject of debate (e.g. Bowman *et al*. 1988; Lonsdale and Braithwaite 1991). It has been argued that the long history of fire in tropical savannas has produced communities that are well adapted to regular fire and that current fire regimes have little influence on species composition and abundance, which are primarily governed by edaphic factors (Wilson and Bowman 1987; Bowman *et al*. 1988). Yet research has provided evidence that variation in fire regime can significantly affect species abundance within tropical savannas (e.g. Lonsdale and Braithwaite 1991; Williams and Lane 1999). Fire may also play a critical role in maintaining savanna structure (Bowman and Panton 1995), and ultimately the co-existence of trees and grasses (Higgins *et al*. 2000).

The purpose of this research was to examine the influence of fire regime on species composition and abundance, i.e. floristic patterns, within a tropical savanna of north-eastern Australia. Floristic patterns respond to a complex interaction of biotic, climatic, edaphic and fire variables, so that the ability to predict the effect of a specific fire regime requires analysis of the processes that determine patterns (Whelan *et al*. 2002). Therefore, a further objective of this research was to provide an understanding of the mechanisms determining floristic patterns through an investigation into the effects of fire on critical events in a plant's life cycle, i.e. critical life events. Fire may differentially affect critical life events (Gill 1975), and the effect of fire on one or more life events may limit population growth. For instance, Higgins *et al*. (2000) and Midgley and Bond (2001) proposed that seedling emergence, governed by rainfall, and the release of stunted juvenile trees to the canopy, controlled by fire, may be critical events limiting tree density in savannas. Population stability in frequently burnt savannas may rely on the persistence of established plants (Bond and Midgley 2001).

To examine the effect of fire on tropical savannas of north-eastern Australia, an assessment was made of a series of fires in eucalypt savannas in the vicinity of Townsville. To focus directly on the impacts of fires and reduce the confounding effects of landscape and climatic variation between locations, this study was primarily based on a manipulative experiment within a 10 ha eucalypt savanna site at Cape Cleveland, 25 km east of Townsville (Figures 2.1 and 2.4). Annual surveys of permanent plots were used to document the effect of fire on changes in species composition and abundance over time. The influence of fire on critical life events was assessed using further surveys of seedlings and plant survival, as well as field and laboratory experiments. Seedling emergence and vegetative regeneration after fire were also assessed at three additional sites in the vicinity of Townsville, at Castle Hill, Many Peaks Range and Mt Elliot (Figure 2.1), to examine the consistency in fire-response in the eucalypt savannas around Townsville.

The experimental fire regimes implemented at Cape Cleveland were:
1. Control; after the initial floristic survey, the savanna was burnt in the mid dry season (July) 1997, and remained unburnt for the rest of the study.
2. Early burnt; savanna burnt in both the mid dry season 1997 and early dry season (May) 1999.
3. Late burnt; savanna burnt in both the mid dry season 1997 and late dry season (October) 1999.

9.2 Summary of results

9.2.1 The effect of fire regime on floristic patterns

Fuel loads in eucalypt savanna at Cape Cleveland rapidly re-establish after fire, reaching approximately ten tonnes per hectare two years after fire, with no further gains in biomass in the third and fourth years following fire. It is probable that fuel loads remain static at approximately ten tonnes per hectare for many years, as documented in eucalypt savannas unburnt for several decades on adjacent Magnetic Island (Sandercoe 1989) and in the Northern Territory (Russell-Smith *et al.* in press). Fire intensity, after a two year interval, was higher during the late rather than early dry season, which is consistent with that recorded in other tropical eucalypt savannas (e.g. Williams et al. 1999*b*). As fuel loads reach a maximum after two years in Townsville savannas, the season of burning will have a greater influence on fire intensity than the number of years since last fire in all but annually burnt savanna.

Multivariate analyses of survey data documented a high level of resilience in floristic composition and abundance in response to fire regimes, however significant floristic patterns were detected over the five year period. Cluster analyses of species composition alone, and species composition and abundance data, grouped many of the annual surveys of the same plots. This suggests that many of the pre-existing floristic differences between plots were not greatly altered by fire regimes between 1997 and 2001, but that some floristic dynamics did occur in response to fire.

Redundancy analyses also indicated that while distinct changes in community composition and abundance were attributable to fire regime and interactions between fire, year and plot, the intrinsic differences between plots were of more value in explaining species variation amongst surveys than fire regimes. That is, pre-existing plot differences, and small changes within each plot that were irrespective of fire treatment, accounted for species variation to a greater extent than the fire regime over five years. The stability of species composition through various fire regimes has been repeatedly documented in Australian tropical savannas (e.g. Bowman *et al*. 1988; Lonsdale and Braithwaite 1991; Russell-Smith *et al*. in press; Williams *et al*. in press). This highlights the value of repeated surveys of permanently marked plots to document floristic changes over time and thus reduce the confounding effects of edaphic and climatic factors that would confuse the interpretation of floristic patterns from one-off surveys of savannas that differ in recent fire history.

Subtle floristic changes after fires were detected using principle components analyses, which displayed a consistency in floristic patterns across plots prior to the 1999 fire treatments. The early and late dry season burnt savanna then responded differently from savanna that remained unburnt.

Species richness at the 1 m^2 scale significantly increased in the year following late dry season fires. This reflects an increase in plant density, rather than in the number of species in the savanna, as no corresponding effect was detected at the 100 m^2 scale (Whelan 1995).

A significant pulse in plant abundance was detected in the first year after fire, particularly following late dry season fires, for several species and growth form groups. The influence of fire on floristic patterns was most evident in the herbaceous layer, particularly in promoting ephemeral forbs and the two most abundant growth form groups, twining perennial forbs and grasses. The dominant grass *Heteropogon triticeus* declined after a fire interval of four years.

The promotion of herbaceous species' abundance by fire is consistent with results for other tropical savanna studies. Regular fires promote many tropical grasses, such as the annuals *Schizachyrium fragile* (Bowman *et al*. 1988) and *Sorghum intrans* (Russell-Smith *et al*. in press); and perennials *Heteropogon contortus* (Shaw 1957; Walker *et al*. 1989), *H. triticeus* (Sandercoe 1989; Fensham 1990; Russell-Smith *et al*. in press) and *Themeda triandra* (Trollope 1996). Fire also promotes the abundance of many perennial forbs, including *Glycine* spp. and *Kennedia* spp. (Lamb *et al*. 1989) and ephemeral forbs, such as *Crotalaria* spp. (Fensham 1990) and *Hyptis suaveolens* (Sandercoe 1989).

9.2.2 The effect of fire regime on seed dormancy release

Exposure to temperatures between 80°C and 100°C breaks seed dormancy in a range of forbs, particularly legumes, while exposure to 120º C for five minutes proved lethal. These temperatures were documented in a narrow band of topsoil during the passage of early and late dry season fires, with greater heat penetration during late fires. The depth of germination of two common forbs, *Galactia tenuiflora* and *Indigofera hirsuta*, was correlated with heat penetration into the topsoil and these data suggested that exposure to 60°C may also increase seed germination of these species. Late dry season fires were found to provide greater release from heat-related seed dormancy than early dry season fires.

While no evidence was found that exposure to smoke at ambient temperature enhanced seed germination of legumes, the combined effects of exposure to 80°C and a nitrate solution increased the germination of two species, *Crotalaria lanceolata* and *Indigofera hirsuta*. Smoke significantly increased the germination of upright perennial forbs, grasses as a group and the common grasses *Digitaria breviglumis* and *Heteropogon triticeus*.

9.2.3 The effect of fire regime on soil seed bank dynamics

The germinable soil seed bank at Cape Cleveland was dominated by grasses and forbs. No species produced a bradysporous seed bank, and the soil seed banks of woody species were scarce and short-lived, which is consistent with many other communities (e.g. Drake 1979; Vlahos and Bell 1986; Melzer 1996; Clark *et al*. 1999). There were more seeds between 3 and 40 mm soil depth than in the surface 3 mm, indicating that burial mechanisms, such as the twisting action of hygroscopic awns, or the activities of fauna, possibly ants, may incorporate seed within the topsoil.

The germinable soil seed bank displayed strong and consistent seasonal fluctuations, increasing through the dry season to a maximum in the late dry season, and declining to a minimum by the mid wet season. While many species showed reliance on annual seed input to maintain seed bank density, the common grass *Digitaria breviglumis* and the common ephemeral forb *Indigofera hirsuta* had a persistent soil seed bank, with densities remaining high through the wet season. The seasonal dynamics of the germinable soil seed bank were consistent with annual seed production, which is greatest during the early to mid dry season, so that seeds accumulate in the soil through the dry season.

Total seed density and species richness of the seed bank were lower in 1998 than 1999 and 2000. The increase in seed bank in 1999 and 2000 corresponds with a general increase in plant abundance over that period and may be linked with the above average rainfall of 1998 and 2000.

Late dry season fires reduced seed production of the dominant tree *Corymbia clarksoniana* in the year following burning, probably as a result of high canopy scorch causing mortality of flower buds. However, fire had less influence on the seasonal and annual dynamics of the soil seed bank, enhancing the seed bank of the ephemeral forb *Indigofera hirsuta*, and decreasing the overall seed bank of subshrubs and non-grass monocots. Late dry season fires increased the germinable seed bank density of untreated soil, confirming the importance of fire on seed dormancy release. The limited impact of fire on soil seed banks was probably due to the shallow heat penetration into the topsoil and the heavy decline in seed bank density over each wet season, so that seed banks were at a low density towards the end of the wet season, irrespective of burning. Total seed bank density was lower than in many other fire-prone communities (e.g. Clark *et al*. 1999; Read *et al*. 2000). Thus the data suggest seed bank density limits population growth of savanna species.

9.2.4 The effect of fire regime on seedling emergence

Seedling emergence in eucalypt savanna near Townsville is dominated by herbaceous species, reflecting the dominance of herbs in the soil seed bank. Data from four locations in eucalypt savannas around Townsville, at Mt Elliot, Castle Hill, Many Peaks Range and Cape Cleveland, indicated seedling emergence of herbaceous species occurred primarily at the onset of the post-fire wet season. Laboratory and shadehouse experiments indicated multiple fire-related factors were responsible for the pulse of seedling emergence, including heat, nitrate and smoke. The removal of the dense herbaceous cover also increased seedling emergence.

Seedling density was highest following late dry season fires. This resulted from both a greater dormancy-breaking stimulus, particularly heat penetration into the topsoil, and the greater seed reserves available to be influenced by fire in the late dry season. The increased germination of smoke-triggered species, *Digitaria breviglumis* and *Heteropogon triticeus*, after late dry season fires suggests greater soil penetration of chemicals found in smoke during late rather than early dry season fires. This is probable as greatest combustion of ground fuels occurred during late dry season fires.

Seedling emergence of trees and shrubs differed to that of herbaceous species, with the limited seedling recruitment of woody species linked to a particular year. The most abundant woody species amongst emerging seedlings was the dominant tree, *Corymbia clarksoniana*, which emerged on mass after high rainfall in 1998, suggesting seedling emergence of trees may be restricted to years of above average rainfall, and/or with an early start to the wet season (Higgins *et al*. 2000). While considerable numbers of *C. clarksoniana* seedlings emerged in savanna that was unburnt for one year, seedling emergence in a single recently burnt site was 17 times the density of unburnt savanna. Evidence that seedling emergence of *C. clarksoniana* is enhanced in recently burnt savanna or where the ground cover is removed was not conclusive. However, the combined data of increased germination in a single burnt site, coupled with the lack of seedling emergence from undisturbed experimental plots, provides a strong case that the density of seedling emergence of *C. clarksoniana* is increased where seed falls onto recently burnt or bare ground. This contrasts with the germination ecology of *Eucalyptus miniata* in tropical Australia (Setterfield 1997*b*) but is consistent with a range of eucalypts from southern Australia (Gill 1997).

The density of seedling emergence of Cape Cleveland species was low compared with that of species of other communities (e.g. Bell *et al.* 1987; Crowley and Garnett 1999). Total seedling emergence accounted for a low proportion of the soil seed bank available in the late dry season (< 15%), and of the seed bank decline over the wet season (< 21%), indicating that seedling emergence is an event that limits population growth in Townsville savannas.

Seedlings appeared to germinate from seed that was produced on-site, rather than seed dispersed from adjacent areas. Three quarters of the species recorded in the seedling surveys were also detected in the soil seed bank, suggesting most seedlings originated from stored seed. The remaining quarter of seedling species probably originated from freshly fallen seed or very short-lived seed banks. This highlights the value of soil seed banks in the ecology of tropical eucalypt savannas.

9.2.5 The effect of fire regime on seedling survival

Seedling survival was a life event that limited population growth. Only 7%, or less, of seedlings of perennial species that emerged after the 1999 dry season survived until October 2001. Seedlings that emerged from recently burnt savanna displayed significantly greater survival than those emerging from undisturbed savanna, and unburnt savanna with the herbaceous layer removed. Some aspect other than the removal of the herbaceous layer is therefore responsible for the enhanced survival in burnt savanna. This requires further research but may be linked to an increased availability of nutrients after fire, or reduced herbivory or disease.

These data indicate that little seedling recruitment occurs in the absence of fire, as seedling emergence is low in unburnt savanna and very few of the seedlings that do emerge survive to maturity. That is, seedling recruitment, at least of herbaceous species, is primarily limited to the post-fire environment, and is greatest after late dry season fires.

Seedlings of common sprouter species developed the capacity to survive fire within one year of germination, although survival varied between 5% for *Corymbia clarksoniana* and 56% for *Galactia tenuiflora*. The ability to rapidly acquire the capacity to survive fire provides stability to populations in frequently burnt communities, although the moderate to low level of survival indicates annual fires may limit seedling establishment.

Only 5% of *C. clarksoniana* seedlings survived three years in unburnt savanna, while 1% survived in savanna burnt in the early dry season, and none survived in late burnt savanna. Population growth of this dominant tree is therefore limited by seedling recruitment, which may be rainfall driven. Late dry season fire may reduce seed production in the year following burning, while fire immediately prior to seed fall may improve seed bed conditions to increase seedling recruitment in the same year as burning. Burning after seedling emergence may reduce seedling survival.

9.2.6 The effect of fire regime on the survival and growth of juveniles and mature plants

Townsville eucalypt savannas contain a large proportion of sprouting species. This enables the persistence of individual plants and therefore provides stability to populations in a frequently burnt environment. Some mortality of both trees and common herbs was documented after fires, indicating that fire can affect the number of standing plants through mortality as well as germination.

Evidence was found that frequent fires may suppress the growth of juvenile trees towards the canopy, limiting tree density (Higgins *et al*. 2000). However, many years of fire exclusion may be required before a significant number of *C. clarksoniana* juveniles grow to 2 m in height and thus escape the fire trap.

Vegetative regeneration of the root-sprouting subshrub *Breynia oblongifolia* was affected by the type of disturbance, with burning, rather than cutting, promoting stem multiplication. These data suggest that burning stimulates the stem production from meristematic tissue along the roots, and that the fate of regenerative buds may control the density of regenerating stems to a greater extent than carbon reserve size, although a more direct assessment of carbon reserves is required to confirm this hypothesis.

9.3 Functional ecology of Townsville eucalypt savannas

This research has demonstrated that fire regime does influence floristic patterns in eucalypt savannas of north-eastern Australia. The investigation of critical life events has provided an understanding of the processes causing floristic patterns. The pulse of seedling emergence following fire, triggered by seed dormancy release from heat, smoke, nitrate and the removal of the herbaceous cover, and the increase in stem density of root-sprouting subshrubs, explains the pulse of plant abundance in the first year after fire, especially following late dry season fires. Late rather than early dry season fires increased seedling emergence because late fires provided a greater dormancy release stimulus, and there were more seed reserves available in the late dry season to be affected by fire. The short lifespan of ephemeral forbs and the high seedling mortality of perennial species explains the decline in plant abundance in the second year following fire. The growth of juvenile trees beyond 2 m in height in the absence of fire accounts for the increase in tree density in savanna unburnt for four years. The capacity of the majority of species to sprout after fire, with rapid seed production by fire-killed species, explains the stability in species composition documented in the annual floristic surveys.

Total seed bank density, seedling emergence and seedling survival in Townsville savannas are low compared to those of many other communities. The opportunities for seed dormancy release are primarily restricted to fire events. Together these processes govern seedling recruitment and limit population growth (Figure 9.1).

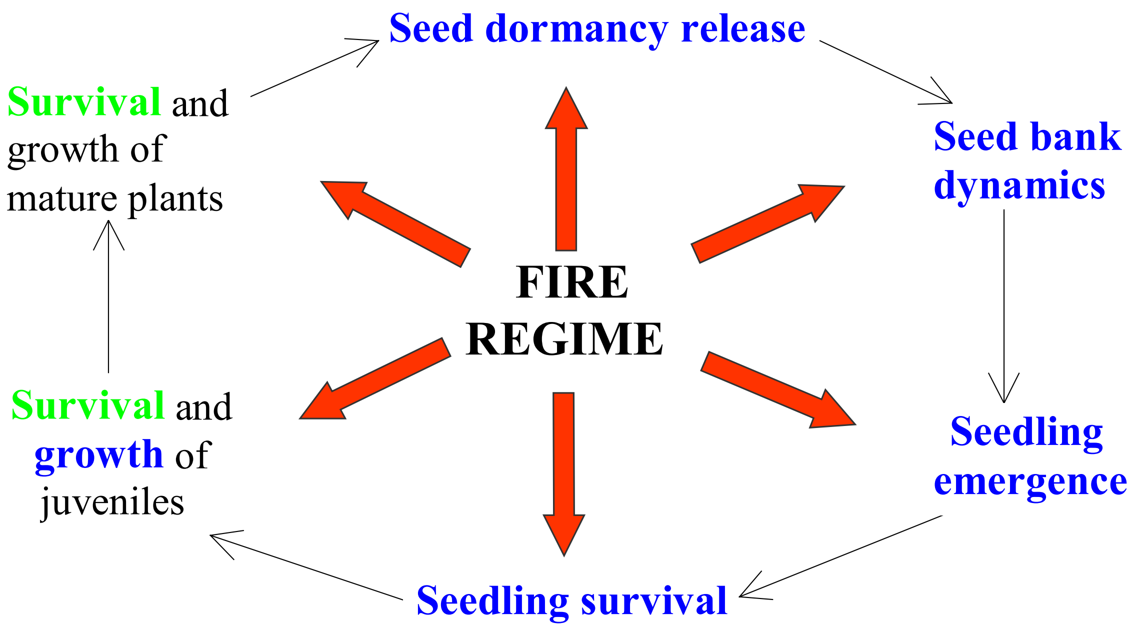


Figure 9.1. Critical life events that limit population growth (displayed in blue) and provide stability to populations (displayed in green). Note that soil seed banks also provide population stability to ephemeral species.

The high proportion of sprouting species enables plant persistence in this frequently burnt savanna. Juvenile and mature plant survival are therefore life events that provide population stability (Figure 9.1). For ephemeral species, persistent soil seed banks provide provide population resilience. Growth of juvenile trees to the canopy, and hence to reproductive maturity, requires fire free intervals of several years. Therefore, the growth of juvenile trees is an event that is restricted by fire and limits population growth.

Woody and herbaceous species have different regeneration and persistence niches (Grubb 1977; Bond and Midgley 2001) in Townsville savannas. Herbs have a shorter lifespan than most woody species, with most individuals of the former expected to senesce within a decade (Mott *et al*. 1985). Seedling recruitment of herbaceous species is concentrated within the wet season following fire and therefore occurs every few years in frequently burnt savanna. Fire intervals of more than four years could be associated with a population decline in many grasses and forbs. Short-lived ephemerals and the dominant perennial grass *Heteropogon triticeus* tend to produce the most abundant seedling recruitment. The declines in abundance of *H. triticeus* with the absence of fire for four years, indicates that individual clumps may have a fairly short lifespan in the absence of disturbance. The longevity of seed banks of ephemeral species is unknown, but both ephemeral forbs and *H. triticeus* may rely on regular seedling recruitment events to maintain population density.

Woody species can live for many decades and therefore the required rate of replacement of individuals is low in comparison with herbaceous species. Recruitment of woody species in Townsville savannas is sparse and episodic, a pattern that has been reported for many long-lived sprouters of frequently burnt communities (e.g. Lacey 1974; Midgley and Cowling 1993; Bond and Midgley 2001). The recruitment of some woody species in Townsville savannas may be enhanced by fire but is not restricted to the post-fire environment, nor does it occur after each fire, and appears to be primarily linked to years of above average rainfall and with early wet season rain. Asexual reproduction of stems may be important for several species, including the subshrub *Breynia oblongifolia*, and appears to be promoted by fire.

This study contributes to our understanding of the influence of fire regime on the maintenance of savanna structure and the balance between woody and herbaceous species. It suggests that fire intervals of four or more years may affect the balance between grasses and trees. This may result from the growth of saplings into the canopy layer, given release from overstorey competition (Fensham and Bowman 1992), and a decline in the abundance of the dominant grass, *Heteropogon triticeus*. The current regime of frequent fires may also preclude the presence of obligate seeders that require greater than two or three years to mature, and a fire regime with late dry season fires following a fire-free period of two years may be particularly beneficial to many of the ephemeral forbs of this community.

Issues that have emerged from this study that require further research include:

1. What is the longevity of soil seed banks, particularly of ephemeral species?
2. What is the longevity of individual plants of perennial herbs and wood species, and what density and frequency of seedling recruitment is required to maintain populations?
3. Does fire increase the density of safe sites for seedling recruitment of eucalypts?
4. Do late dry season fires provide a greater penetration of smoke into the soil seed bank than early dry season fires?
5. Is the density of the seed bank more important than the dormancy-release stimuli provided by fire, in determining the density of seedling emergence?
6. What is the influence of scale and patchy fires on plant recruitment?
7. What is the percentage survival of herbaceous species during various fires?
8. Is the fate of regenerative buds of greater importance in determining sprouting success than the availability of carbon reserves?
9. How do variations in fire intervals, with a constant fire season and intensity, influence floristic patterns and plant processes?
10. What are the soil nutrient dynamics in relation to fire in eucalypt savannas around Townsville, and what is the contribution of ephemeral legumes in the maintenance of nitrogen levels?
11. What is the effect of predicted climate change on the coexistence of trees and herbs?
12. How appropriate is the recommended fire regime to maintaining populations of local fauna?

9.4 Management implications and further research

This research has examined several fire regimes over five years, during a period when both above and below average annual rainfall were experienced. While five years is a brief period of time, most of the floristic responses detected over 21 years of research in eucalypt savanna at Munmarlary, Northern Territory, were evident within the first five years of the study (Russell-Smith *et al.* in press). The assessment of critical life events has identified the causes of floristic dynamics, and therefore allows some predictions regarding the floristic response to fire regimes that were not specifically addressed.

The results of this research have broad applicability across northern Australia, as many of the common species, such as the tree *Planchonia careya*, the shrub *Ficus opposita*, the grasses *Heteropogon contortus*, *H. triticeus*, and *Themeda triandra*, and forbs *Crotalaria calycina*, *C. montana*, *Galactia tenuiflora*, *Glycine tomentella* and *Indigofera hirsuta*, have a wide distribution across northern Queensland, the Northern Territory and several extend into northern Western Australia (Fensham 1990; Bowman *et al*. 1991; Craig 1997; Henderson 1997; Crowley and Garnett 1998). Much of the research into the fire ecology of tropical eucalypt savannas in Australia to date has focused on savannas dominated by annual grasses, such as *Schizachyrium* spp. and *Sorghum* spp. (e.g. Crowley and Garnett 1998; Russell-Smith *et al*. in press; Williams *et al*. in press), which do not rely on fire for seedling recruitment (Andrew and Mott 1983; Crowley and Garnett 1998). This thesis therefore provides much needed data for eucalypt savannas of northern Australian that are dominated by perennial grasses.

The season of fire is implicitly linked to fire intensity and these two elements of the fire regime affect floristic patterns in eucalypt savanna at Cape Cleveland. High intensity, late dry season fires promote greater seedling recruitment of herbaceous species than do fires in the early dry season. However, late dry season fires reduce seed production in the dominant tree *Corymbia clarksoniana*, and can kill established trees.

While fire frequency was not specifically examined within the manipulative experiment at Cape Cleveland, an understanding of processes allows some predictions regarding fire intervals. The rapid fuel accumulation allows frequent fires with intervals of one to two years. Seedlings of common perennials can develop the capacity to survive fire within a year of germination, although annual fires are expected to reduce the already low seedling survival rate. There is some evidence that the absence of fire for three years after germination can increase seedling survival of *Corymbia clarksoniana*. Fire intervals of four years can allow the growth of stunted juvenile trees beyond the fire trap to recruit to the canopy. The dominant grass *Heteropogon triticeus* declines in abundance with fire intervals of four years. Information on the persistence of seed banks of ephemeral forbs will be required to predict the decline in abundance of these short-lived species with increasing fire intervals.

Management of these savannas should take into account the contrasting effects of different fire regimes. For instance, while repeated late dry season fires every two or three years may promote seedling recruitment of many herbaceous species, it may lead to a reduced abundance of woody species, and stunt the growth of juvenile trees. Regular early dry season fires may not impact on woody species to the same degree, although probably stunt juvenile trees. Late dry season fires also burn more extensive areas of savanna and are harder to control than earlier fires (Gill *et al.* 1996). Early dry season fires will promote seedling recruitment of grasses and forbs, but not to the same density as late dry season fires, and repeated early fires may not promote enough seedling recruitment to maintain populations of some species. Fire intervals of four or more years may lead to increased tree densities, through sapling growth, but also to declines in herbaceous species, especially the dominant grass *H. triticeus*, and possibly some ephemeral species depending on the longevity of their seed banks.

Clearly, variation in fire regime is required to maintain species diversity and structure, and no single fire regime will suit all sites (Williams et al. 2002*a*). While the fire treatments assessed in this study cover regimes that are realistic to the local area, further research and monitoring will be necessary to determine the effects of different combinations of elements of the fire regime. The most appropriate fire regime to maintain plant diversity may involve primarily early to mid dry season fires, creating a patchily burnt landscape that allows the implementation of occasional late dry season fires for maximum herbaceous regeneration. As this study assessed only two fires over five years, longer-term assessments will further our understanding of the ecology and hence management of this widespread system. However, the most suitable fire regime to maintain the diversity of both woody and herbaceous species would appear to involve the fluctuation of most fire intervals between two and five years, with the occasional use of longer intervals to allow the growth of stunted juvenile trees. Fire exclusion for several years following germination of eucalypt seedlings may allow the replenishment of the sapling bank, which may aid population resilience at sites with a low density of eucalypt juveniles. Further research into the fire ecology of native fauna is required to test whether this regime would be appropriate for fauna of north-eastern Australia. A similar regime is recommended for fauna and flora management in tropical savannas of the Northern Territory (Andersen 2000).

References.

Abbott I. (1985) Recruitment and mortality in populations of *Banksia grandis* Willd. in Western Australian forest. *Australian Journal of Botany* **33**, 261-270.

Andersen A. N. (1991) Responses of ground-foraging ant communities to three experimental fire regimes in a savanna forest of tropical Australia. *Biotropica* **23**, 575-585.

Andersen A. N. (2000) Synthesis and management implications. In: *Fire and Biodiversity. CSIRO's Kapalga Fire experiment, Kakadu National Park*. pp. 13-13. CSIRO, Darwin.

Andrew M. H. and Mott J. J. (1983) Annuals with transient seed banks: the population biology of indigenous *Sorghum* species of tropical north-west Australia. *Australian Journal of Ecology* **8**, 265-276.

Andrew M. H. (1986) Population dynamics of the tropical annual grass *Sorghum intrans* in relation to local patchiness in its abundance. *Australian Journal of Ecology* **11**, 209-217.

Andrew M. H. (1986) Selection of plant species by cattle grazing native monsoon tallgrass pasture at Katherine, N. T. *Tropical Grasslands* **20**, 120-127.

Ashton D. H. (1979) Seed harvesting by ants in forests of *Eucalyptus regnans* F. Muell. in central Victoria. *Australian Journal of Ecology* **4**, 265-277.

Ashton D. H. (1981) Fire in tall open forests (wet sclerophyll forests). In: *Fire and the Australian Biota*. (eds A. M. Gill, R. H. Groves, and I. R. Noble) pp. 339-366. Australian Academy of Science, Canberra.

Ashton D. H. and Chinner J. H. (1999) Problems of regeneration of the mature *Eucalyptus regnans* F. Muell. (The Big Ash) forest, in the absence of fire at Wallaby Creek, Victoria, Australia. *Australian Forestry* **62**, 265-280.

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

Auld T. D. and Bradstock R. A. (1996) Soil temperatures after the passage of fire: Do they influence the germination of buried seeds? *Australian Journal of Ecology* **21**, 106-109.

Auld T. D. (1996) Ecology of the Fabaceae in the Sydney region: fire, ants and the soil seedbank. *Cunninghamia* **4**, 531-756.

Auld T. D. and Tozer M. G. (1999) How well do post-fire indicators provide insights into the degree of soil heating during the passage of fires? In: *Bushfire 1999. Proceedings of the Australian Bushfire Conference*. (eds B. Lord, M. Gill and R. Bradstock) pp. 25-32. Charles Sturt University, Albury.

Auld T. D., Keith D. A. and Bradstock R. A. (2000) Patterns in longevity of soil seedbanks in fire-prone communities of south-eastern Australia. *Australian Journal of Botany* **48**, 539-548.

Baird A. M. (1977) Regeneration after fire in King's Park, Perth, Western Australia. *Journal of the Royal Society of Western Australia* **60**, 1-22.

Barbour M. G., Burk J. H., and Pitts W. D. (1987) *Terrestrial Plant Ecology*. Benjamin/Cummings, California.

Battaglia M. (1996) Effects of seed dormancy and emergence time on the survival and early growth of *Eucalyptus delegatensis* and *E. amygdalina*. *Australian Journal of Botany* **44**, 123-137.

Baxter B. J. M., van Staden J., Granger J. E. and Brown N. A. C. (1994) Plant-derived smoke and smoke extracts stimulate seed germination of the fire-climax grass *Themeda triandra*. *Environmental and Experimental Botany* **34**, 217-223.

Beardsell D. and Mullett J. (1984) Seed germination of *Eucalyptus pauciflora* Sieb. ex Spreng. from low and high altitude populations in Victoria. *Australian Journal of Botany* **32**, 475-480.

Bebawi F. F. and Campbell S. D. (2000) Effects of fire on germination and viability of rubber vine (*Cryptostegia grandiflora*) seeds. *Australian Journal of Experimental Agriculture* **40**, 949-957.

Belbin L. (1995) *Technical Reference: PATN Pattern Analysis Package*. CSIRO, Canberra.

Bell D. T. (1999) Turner review no. 1. The process of germination in Australian species. *Australian Journal of Botany* **47**, 475-517.

Bell D. T. (2001) Ecological syndromes in the flora of southwestern Western Australia: Fire resprouters versus reseeders. *The Botanical Review* **67**, 417-440.

Bell D. T., King L. A. and Plummer J. A. (1999) Ecophysiological effects of light quality and nitrate on seed germination in species from Western Australia. *Australian Journal of Ecology* **24**, 2-10.

Bell D. T. and Koch J. M. (1980) Post-fire succession in the northern jarrah forest of Western Australia. *Australian Journal of Ecology* **5**, 9-14.

Bell D. T., Plummer J. A. and Taylor S. K. (1993) Seed germination ecology in southwestern Western Australia. *The Botanical Review* **59**, 24-69.

Bell D. T., van der Moezel P. G., Delfs J. C. and Loneragan W. A. (1987*b*) Northern sandplain kwongan: effect of fire on *Hakea obliqua* and *Beaufortia elegans* population structure. *Journal of the Royal Society of Western Australia* **69**, 139-143.

Bell D. T., Vlahos S. and Watson L. E. (1987*a*) Stimulation of seed germination of understorey species of the northern Jarrah forest of Western Australia. *Australian Journal of Botany* **35**, 593-599.

Bell D. T. and Williams D. S. (1998) Tolerance of thermal shock in seeds. *Australian Journal of Botany* **46**, 221-233.

Bellingham P. J. and Sparrow A. D. (2000) Resprouting as a life strategy in woody plant communities. *Oikos* **89**, 409-416.

Benwell A. S. (1998) Post-fire seedling recruitment in coastal heathland in relation to regeneration strategy and habitat. *Australian Journal of Botany* **46**, 75-101.

Bond W. J. and Midgley J. J. (2001) Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution* **16**, 45-51.

Bond W. J. and van Wilgen B. W. (1996) *Fire and Plants*. Chapman and Hall, London.

Bowman D.M.J.S. (1988) Stability amid turmoil?: towards an ecology of north Australian eucalypt forests. *Proceedings of the Ecological Society of Australia* **15**, 149-158.

Bowman D.M.J.S. (1993) Establishment of two dry monsoon forest tree species on a fire-protected monsoon forest-savanna boundary, Cobourg Peninsula, north Australia. *Australian Journal of Ecology* **18**, 235-237.

Bowman D.M.J.S. (1994) Why the skillful use of fire is critical for the management of biodiversity in northern Australia. In: *Country in Flames: Proceedings of the 1994 Symposium on Biodiversity and Fire in Northern Australia*. (ed. D. B. Rose). pp. 103-109. Department of Sport and Territories, Canberra.

Bowman D.M.J.S. (2000) *Australian Rainforests. Islands of green in a land of fire*. Cambridge University Press, Cambridge.

Bowman D.M.J.S. and Fensham R. J. (1991) Response of a monsoon forest-savanna boundary to fire protection, Weipa, northern Australia. *Australian Journal of Ecology* **16**, 111-18.

Bowman D.M.J.S. and Kirkpatrick J. B. (1986) Establishment, suppression and growth of *Eucalyptus delegatensis* R. T. Baker in multiaged forests. I. The effects of fire on mortality and seedling establishment. *Australian Journal of Botany* **34**, 63-72.

Bowman D.M.J.S. and Panton W. J. (1993) Factors that control monsoon-rainforest seedling establishment and growth in north Australian *Eucalyptus* savanna. *Journal of Ecology* **81**, 297-304.

Bowman D.M.J.S. and Panton W. J. (1995) Munmarlary revisited: Response of a north Australian *Eucalyptus tetradonta* savanna protected from fire for 20 years. *Australian Journal of Ecology* **20**, 526-531.

Bowman D.M.J.S., Wilson B. A. and Woinarski J. C. Z. (1991) Floristic and phenological variation in a northern Australian rocky *Eucalyptus* savanna. *Proceedings of the Royal Society of Queensland* **101**, 79-90.

Bowman D.M.J.S., Wilson B. A. and Hooper R. J. (1988) Response of *Eucalyptus* forest and woodland to four fire regimes at Munmarlary, Northern Teritory, Australia. *Journal of Ecology* **76**, 215-232.

Bradstock R. A. (1991) The role of fire in establishment of seedlings of serotinous species from the Sydney region. *Australian Journal of Botany* **39**, 347-356.

Bradstock R. A. and Auld T. D. (1995) Soil temperatures during experimental bushfires in relation to fire intensity: consequences for legume germination and fire management in south-eastern Australia. *Journal of Applied Ecology* **32**, 76-84.

Bradstock R. A. and Bedward M. (1992) Simulation of the effect of season of fire on post-fire seedling emergence of two *Banksia* species based on long-term rainfall records. *Australian Journal of Botany* **40**, 75-88.

Bradstock R. A. and Myerscough P. J. (1988) The survival and population response to frequent fires of two woody resprouters *Banksia serrata* and *Isopogon anemonifolius*. *Australian Journal of Botany* **36**, 415-431.

Bradstock R. A., Tozer M. G. and Keith D. A. (1997) Effects of high frequency fire on floristic composition and abundance in a fire-prone heathland near Sydney. *Australian Journal of Botany* **45**, 641-655.

Brennan K. (1996) *Flowering and fruiting phenology of native plants in the Alligator Rivers Region with particular reference to the Ranger uranium mine lease area*. Supervising Scientist, Canberra.

Burrows D. M. and Burrows W. H. (1992) Seed production and litter fall in some eucalypt communities in Central Queensland. *Australian Journal of Botany* **40**, 389-403.

Burrows G. E. (2002) Epicormic strand structure in *Angophora*, *Eucalyptus* and *Lophostemon* (Myrtaceae) - implications for fire resistance and recovery. *New Phytologist* **153**, 111-131.

Byram G. M. (1959) Combustion of forest fuels. In: *Forest Fire: Control and Use*. (ed. K. P. Davis) pp. 61-89. McGraw-Hill, New York.

Campbell S. D., Bahnisch L. M. and Orr D. M. (1996) Fire directly promotes the germination of dormant speargrass (*Heteropogon contortus*) seed. *Tropical Grasslands* **30**, 162.

Cary G. J. and Morrison D. A. (1995) Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: combinations of inter-fire intervals. *Australian Journal of Ecology* **20**, 418-426.

Cheney, P., Gould, J., and McCaw, L. (2001). The dead-man zone - a neglected area of firefighter safety. *Australian Forestry* **64**, 45-50.

Clark J. S., Beckage B., Camill P., Cleveland B., HilleRisLambers J., Lichter J., McLachlan J., Mohan J. and Wyckoff P. (1999) Interpreting recruitment limitation in forests. *American Journal of Botany* **86**, 1-16.

Clark S. S. (1988) Effects of hazard-reduction burning on populations of understorey plant species on Hawkesbury sandstone. *Australian Journal of Ecology* **13**, 473-484.

Clarke P. J. (in press) Experiments on tree and shrub establishment in temperate grassy woodlands: seedling survival. *Austral Ecology* **27**, *in press*.

Clarke P. J. and Davison E. A. (2001) Experiments on the mechanism of tree and shrub establishment in temperate grassy woodlands: Seedling emergence. *Austral Ecology* **26**, 400-412.

Clarke P. J., Davison E. A. and Fullon L. (2000) Germination and dormancy of grassy woodland and forest species: effects of smoke, heat, darkness and cold. *Australian Journal of Botany* **48**, 687-700.

Clarke P. J. and Knox K. J. E. (2002) Post-fire response of shrubs in the tablelands of eastern Australia: do existing models explain habitat differences? *Australian Journal of Botany* **50**, 53-62.

Clifford H. T., Rogers R. W. and Kahler C. (1996) Seasonal variation in the germinable seed banks of southern Queensland eucalypt forests. *Proceedings of the Royal Society of Queensland* **105**, 1-5.

Cook G. D. (1994) The fate of nutrients during fires in a tropical savanna. *Australian Journal of Ecology* **19**, 359-356.

Cook G. D. and Andrew M. H. (1991) The nutrient capital of indigenous *Sorghum* species and other understorey components of savannas in north-western Australia. *Australian Journal of Ecology* **16**, 375-384.

Craig A. B. (1997) A review of information on the effects of fire in relation to the managment of rangelands in the Kimberley high-rainfall zone. *Tropical Grasslands* **31**, 161-187.

Crowley G. M. (1995) *Fire on Cape York Peninsula*. Office of the Co-ordinator General of Queensland and Department of Environment, Sport and Territories, Canberra.

Crowley G. M. and Garnett S. T. (1998) Vegetation change in the grasslands and grassy woodlands of east-central Cape York Peninsula, Australia. *Pacific Conservation Biology* **4**, 132-148.

Crowley G. M. and Garnett S. T. (1999) Seeds of the annual grasses *Schizachyrium* spp. as a food resource for tropical granivorous birds. *Australian Journal of Ecology* **24**, 208-220.

Crowley G. M. and Garnett S. T. (2000) Changing fire management in the pastoral lands of Cape York Peninsula of northeast Australia, 1623 to 1996. *Australian Geographical Studies* **38**, 10-26.

Crowley G. M. and Garnett S. T. (2001) Growth, seed production and effect of defoliation in an early flowering perennial grass, *Alloteropsis semialata* (Poaceae), on Cape York Peninsula, Australia. *Australian Journal of Botany* **49** , 735-743.

Dixon K. W., Roche S. and Pate J. S. (1995) The promotive effect of smoke derived from burnt native vegetation on seed germination of Western Australian plants. *Oecologia* **101**, 185-192.

Drake W. E. (1979) *Seed populations and regeneration potential of coastal Eucalyptus forest of south-east Queensland*. PhD thesis, University of Queensland, Brisbane.

Duff G. A. and Braithwaite R. W. (1989) Fire and top end forests - past, present and future research. In: *Fire Research in Rural Queensland. Selected papers from the Queensland fire research workshop series 1980 – 1989*. (ed. B. R. Roberts) pp. 84-97. University of Southern Queensland, Toowoomba.

Enright N. J., Goldblim D., Ata, P. and Ashton D. H. (1997) The independent effects of heat, smoke and ash on emergence of seedlings from the soil seed bank of a heathy *Eucalyptus* woodland in Grampians (Gariwerd) National Park, western Victoria. *Australian Journal of Ecology* **22**, 81-88.

Enright N. J. and Lamont B. B. (1989) Seed banks, fire season, safe sites and seedling recruitment in five co-occurring *Banksia* species. *Journal of Ecology* **77**, 1111-1122.

Facelli J. M., Williams R., Fricker S., and Ladd B. (1999) Establishment and growth of seedlings of *Eucalyptus obliqua*: interactive effects of litter, water, and pathogens. *Australian Journal of Ecology* **24**, 484-494.

Faith D. P., Minchin P. R. and Belbin L. (1987) Compositional dissimilarity as a robust measure of ecological distance: a theoretical model and computer simulations. *Vegetatio* **69**, 57-68.

Fensham R. J. (1990) Interactive effects of fire frequency and site factors in tropical *Eucalyptus* forest. *Australian Journal of Ecology* **15**, 255-266.

Fensham R. J. (1992) The establishment of Eucalypt seedlings in tropical savanna forest. *Northern Territory Naturalist* **13**, 30-36.

Fensham R. J. (1994) Phytophagous insect-woody sprout interactions in tropical eucalypt forest. I. Insect herbivory. *Australian Journal of Ecology* **19**, 178-188.

Fensham R. J. and Bowman D.M.J.S. (1992) Stand structure and the influence of overwood on regeneration in tropical eucalypt forest on Melville Island. *Australian Journal of Botany* **40**, 335-352.

Fensham R. J. and Holman J. E. (1999) Temporal and spatial patterns in drought-related tree dieback in Australian savanna. *Journal of Applied Ecology* **36**, 1035-1050.

Floyd A. G. (1976) Effect of burning on regeneration from seeds in wet sclerophyll forest. *Australian Forestry* **39**, 210-220.

Fordyce I. R., Eamus D., Duff G. A. and Williams R. J. (1997) The role of seedling age and size in the recovery of *Allosyncarpia ternata* following fire. *Australian Journal of Ecology* **22**, 262-269.

Franklin D. C. and Noske R. A. (2000) Nectar sources used by birds in monsoonal north-western Australia: a regional survey. *Australian Journal of Botany* **48**, 461-474.

Free R. A. (1951) Germination and emergence of eucalypt seed when sown at depth. *Australian Forestry* **15**, 115-119.

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

Gill A. M. (1981) Adaptive responses of Australian vascular plant species to fires. In: *Fire and the Australian Biota*. (eds A. M. Gill, R. H. Groves and I. R. Noble) pp. 243-272. Australian Academy of Science, Canberra.

Gill A. M. (1997) Eucalypts and fires: interdependent or independent? In: *Eucalypt ecology: individuals to ecosystems*. (eds J. E. Williams and J. C. Z. Woinarski) pp. 151-167. Cambridge University Press, Cambridge.

Gill A. M. and Bradstock R. A. (1992) A national register for the fire responses of plant species. *Cunninghamia* **2**, 653-660.

Gill A. M., Hoare J. R. L. and Cheney N. P. (1990) Fires and their effects in the Wet-Dry Tropics of Australia. In: *Fire in the Tropical Biota: Ecosystems, Processes and Global Changes*. (ed. J. G. Goldammer) pp. 159-178. Springer – Verlag, Berlin.

Gill A. M. and Knight I. K. (1991) Fire measurements. In: *Proceedings of the Conference on Bushfire Modelling and Fire Danger Ratings Systems*. (eds N. P. Cheney and A. M. Gill) pp.137-146. CSIRO, Canberra.

Gill A. M., Moore P. H. R. and Williams R. J. (1996) Fire weather in the wet-dry tropics of the World Heritage Kakadu National Park, Australia. *Australian Journal of Ecology* **21**, 302-308.

Gill A. M., Ryan P. G., Moore P. H. R. and Gibson M. (2000) Fire regimes of World Heritage Kakadu National Park, Australia. *Austral Ecology* **25**, 616-625.

Gilmour C. A., Crowden R. K. and Koutoulis A. (2000) Heat shock, smoke and darkness: partner cues in promoting seed germination in *Epacris tasmanica* (Epacridaceae). *Australian Journal of Botany* **48**, 603-609.

Grant C. D., Loneragan W. A., Koch J. M. and Bell D. T. (1997) Fuel characteristics, vegetation structure and fire behaviour of 11 - 15 year-old rehabilitated bauxite mines in Western Australia. *Australian Forestry* **60**, 147-157.

Green R. H. (1993) Application of repeated measures designs in environmental impact and monitoring studies. *Australian Journal of Ecology* **18**, 81-98.

Grice A. C. (1996) Seed production, dispersal and germination in *Cryptostegia grandiflora* and *Ziziphus mauritiana*, two invasive shrubs in tropical woodlands of northern Australia. *Australian Journal of Ecology* **21**, 324-331.

Grice A. C. and Westoby M. (1987) Aspects of the dynamics of the seed-banks and seedling populations of *Acacia victoriae* and *Cassia* spp. in arid western New South Wales. *Australian Journal of Ecology* **12**, 209-215.

Grubb P. J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review* **52**, 107-145.

Guinto D. F., House A. P. N., Xu Z. H. and Saffigna P. G. (1999) Impacts of repeated fuel reduction burning on tree growth, mortality and recruitment in mixed species eucalypt forests of southeast Queensland, Australia. *Forest Ecology and Management* **115**, 13-27.

Hansman D. J. (2001) Floral biology of dry rainforest in north Queensland and a comparison with adjacent savanna woodland. *Australian Journal of Botany* **137**, 137-153.

Harden G. J. (ed.) (1990) *Flora of New South Wales*. *Vol. 1*. New South Wales University Press, Sydney.

Harper J. L. (1977) *Population Biology of Plants*. Academic Press, London.

Harrington G. N. and Sanderson K. D. (1994) Recent contraction of wet sclerophyll forest in the Wet Tropics of Queensland due to invasion by rainforest. *Pacific Conservation Biology* **1**, 319-327.

Henderson R. J. F. (ed.) (1997) *Queensland Plants. Names and Distribution*. Queensland Herbarium, Department of Environment, Brisbane.

Higgins S. I., Bond W. J. and Trollope W. S. W. (2000) Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* **88**, 213-229.

Hoare J. R. L., Hooper R. J., Cheney N. P. and Jacobsen K. L. S. (1980) *A report on the effects of fire in tall open forest and woodland with particular reference to fire management in Kakadu National Park in the Northern Territory*. Australian National Parks and Wildlife Service, Canberra.

Hobbs R. J. and Atkins L. (1990) Fire-related dynamics of a *Banksia* woodland in south-western Western Australia. *Australian Journal of Botany* **38**, 97-110.

Hodgkinson K. C. (1991) Shrub recruitment response to intensity and season of fire in a semi-arid woodland. *Journal of Applied Ecology* **28**, 60-70.

Hodgkinson K. C. and Oxley R. E. (1990) Influence of fire and edaphic factors on germination of the arid zone shrubs *Acacia aneura*, *Cassia nemophila* and *Dodonaea viscosa*. *Australian Journal of Botany* **38**, 269-279.

Hoffman W. A. (1996) The effects of fire and cover on seedling establishment in a neotropical savanna. *Journal of Ecology* **84**, 383-393.

Hoffman W. A. (1998) Post-burn reproduction of woody plants in a neotropical savanna: the relative importance of sexual and vegetative reproduction. *Journal of Applied Ecology* **35**, 422-433.

Hopkins M. S., Ash A. J., Graham A. W., Head J., and Hewett R. H. (1993) Charcoal evidence of the spatial extent of the *Eucalyptus* woodland expansions and rainforest contractions in north Queensland during the Pleistocene. *Journal of Biogeography* **20**, 357-372.

Hopkins M. S. and Graham A. W. (1984) Viable soil seed banks in disturbed lowland tropical rainforest sites in North Queensland. *Australian Journal of Ecology* **9**, 71-79.

House S. M. (1997) Reproductive biology of eucalypts. In: *Eucalypt ecology: individuals to ecosystems*. (eds J. E. Williams and J. C. Z. Woinarski) pp. 30-55. Cambridge University Press, Cambridge.

Jackson J. and Ash A. J. (1998) Tree-grass relationships in open eucalypt woodlands of northeastern Australia: influence of trees on pasture productivity, forage quality and species distribution. *Agroforestry Systems* **40**, 159-176.

Jackson J. and Ash A. J. (2001) The role of trees in enhancing soil nutrient availability for native perennial grasses in open eucalypt woodlands of north-east Queensland. *Australian Journal of Agricultural Research* **52**, 377-386.

Jhurree B., Bellairs S. M. and Hetherington S. E. (1998) Germination and dormancy release of seeds of Australian native understorey species used for mine site rehabilitation. *Seed Science and Technology* **26**, 587-601.

Keeley J. E. (1977) Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and nonsprouting chaparral shrubs. *Ecology* **58**, 820-829.

Keeley J. E. and Bond W. J. (1997) Convergent seed germination in South African fynbos and Californian chaparral. *Plant Ecology* **133**, 153-167.

Keith D. A. (1996) Fire-driven extinction of plant populations: a synthesis of theory and review of evidence from Australian vegetation. *Proceedings of the Linnean Society of New South Wales* **116**, 37-78.

Keith D. A. (1997) Combined effects of heat shock, smoke and darkness on germination of *Epacris stuartii* Stapf., an endangered fire-prone Australian shrub. *Oecologia* **112**, 340-344.

Keith D. A. (2002) Population dynamics of an endangered heathland shrub, *Epacris stuartii* (Epacridaceae): Recruitment, establishment and survival. *Austral Ecology* **27**, 67-76.

Keith D. A., McCaw W.L. and Whelan R. J. (2002) Fire regimes in Australian heathlands and their effects on plants and animals. In: *Flammable Australia: the Fire Regimes and Biodiversity of a Continent.* (eds R. A. Bradstock, J. Williams, and A. M. Gill) pp. 199-237. Cambridge University Press, Cambridge.

Kellman M. (1985) Forest seedling establishment in Neotropical savannas: transplant experiments with *Xylopia frutescens* and *Calophyllum brasiliense*. *Journal of Biogeography* **12**, 373-379.

Kenny B. J. (2000) Influence of multiple fire-related germination cues on three Sydney *Grevillea* (Proteaceae) species. *Austral Ecology* **25**, 664-669.

Kershaw A. P., Baird J. G., D'Costa D. M., Edney P. A., Peterson J. A. and Strickland K. M. (1991) A comparison of the long Quaternary pollen records from the Atherton and Western Plains volcanic provinces, Australia. In: *The Cainozoic in Australia. A Reappraisal of the Evidence*. (eds M. A. J. Williams, P. De Decker, and A. P. Kershaw) pp. 288-301. Geographical Society of Australia, Sydney.

Kruger L. M., Midgley J. J., and Cowling R. M. (1997) Resprouters *vs* reseeders in South African forest trees; a model based on forest canopy height. *Functional Ecology* **11**, 101-105.

Lacey C. J. (1974) Rhizomes in tropical Eucalypts and their role in recovery from fire damage. *Australian Journal of Botany* **22**, 29-38.

Lacey C. J. and Whelan P. I. (1976) Observations on the ecological significance of vegetative reproduction in the Katherine-Darwin region of the Northern Territory. *Australian Forestry* **39**, 131-139.

Lamb D., Landsberg J. and Foot P. (1989) Effect of prescribed burning on nutrient cycling in *Eucalyptus maculata* forest. In: *Fire Research in Rural Queensland. Selected papers from the Queensland fire research workshop series 1980 – 1989*. (ed. B. R. Roberts) pp. 502-506. University of Southern Queensland, Toowoomba.

Lamont B. B., Le Maitre D. C., Cowling R. M. and Enright N. J. (1991) Canopy storage in woody plants. *The Botanical Review* **57**, 277-317.

Lamont B. B., Witkowski E. T. F. and Enright N. J. (1993) Post-fire litter microsites: safe for seeds, unsafe for seedlings. *Ecology* **74**, 501-512.

Lloyd M. V., Dixon K. W. and Sivasithamparam K. (2000) Comparative effects of different smoke treatments on germination of Australian native plants. *Austral Ecology* **25**, 610-615.

Lonsdale W. M. and Braithwaite R. W. (1991) Assessing the effects of fire on vegetation in tropical savannas. *Australian Journal of Ecology* **16**, 363-374.

Lonsdale W. M., Braithwaite R. W., Lane A. M. and Farmer J. (1998) Modelling the recovery of an annual savanna grass following a fire-induced crash. *Australian Journal of Ecology* **23**, 509-513.

Lunt I. D. (1997) Germinable soil seed banks of anthropogenic native grasslands and grassy forest remnants in temperate south-eastern Australia. *Plant Ecology* **130**, 21-34.

Martin R. E. and Cushwa C. T. (1966) Effects of heat and moisture on leguminous seed. *Proceedings of the Annual Tall Timbers Fire Ecology Conference* **5**, 159-175.

Martin R. E., Miller R. L. and Cushwa C. T. (1975) Germination response of legume seeds subjected to moist and dry heat. *Ecology* **56**, 1441-1445.

McArdle B. (2001) *Multivariate Analysis: a Practical Guide for Biologists*. University of Auckland, Auckland.

McIvor J. G. (1987) Changes in germinable seed levels in soil beneath pastures near Townsville, North Queensland. *Australian Journal of Experimental Agriculture* **27**, 282-289.

McIvor J. G. and Gardener C. J. (1985) Germination of introduced pasture species in the semi-arid tropics. In: *Ecology and Management of the World's Savannas*. (eds J. C. Tothill and J. J. Mott) pp. 277-279. Australian Academy of Science, Canberra.

McIvor J. G. and Howden S. M. (2000) Dormancy and germination characteristics of herbaceous species in the seasonally dry tropics of northern Australia. *Austral Ecology* **25**, 213-222.

McIvor J. G., Jones R. M. and Taylor J. A. (1993) Tropical pasture establishment. 4. Population dynamics of sown species in developing pastures. *Tropical Grasslands* **27**, 302-313.

Melzer R. (1996) *The influence of canopy cover and grazing on soil seed-banks in savanna communities in subtropical south-east Queensland*. PhD thesis, University of Queensland, Brisbane.

Midgley J. J. and Bond W. J. (2001) A synthesis of the demography of African acacias. *Journal of Tropical Ecology* **17**, 871-886.

Midgley J. J. and Cowling R. M. (1993) Regeneration patterns in Cape subtropical transitional thicket - where are all the seedlings? *South African Journal of Botany* **59**, 496-499.

Moore R. P. (1985) *Handbook on Tetrazolium Testing*. The International Seed Testing Association, Zurich.

Mordelet P., Cook G., Abbadie L., Grably M. and Mariotti A. (2002) Natural ^{15}N abundance of vegetation and soil in the Kapalga savanna, Australia. *Australian Journal of Ecology* **21**, 336-340.

Moreno J. M. and Oechel W. C. (1991) Fire intensity effects on germination of shrubs and herbs in southern California chaparral. *Ecology* **72**, 193-2004.

Morgan G., Lorimer M., Morrison A. and Dahl T. (2000) *The Desert Uplands draft bioregional conservation strategy*. Environmental Protection Agency, Townsville.

Morgan J. W. (1998) Importance of canopy gaps for recruitment of some forbs in *Themeda triandra*-dominated grasslands in south-eastern Australia. *Australian Journal of Botany* **46**, 609-627.

Morgan J. W. and Lunt I. D. (1999) Effects of time-since-fire on the tussock dynamics of a dominant grass (*Themeda triandra*) in a temperate Australian grassland. *Biological Conservation* **88**, 379-386.

Morris E. C. (2000) Germination response of seven east Australian *Grevillea* species (Proteaceae) to smoke, heat exposure and scarification. *Australian Journal of Botany* **48**, 179-189.

Morrison D. A., Auld T. D., Rish S., Porter C. and McClay K. (1992) Patterns of testa-imposed seed dormancy in native Australian legumes. *Annals of Botany* **70**, 157-163.

Morrison D. A., Cary G. J., Pengelly S. M., Ross D. G., Mullins B. J., Thomas C. R. and Anderson T. S. (1995) Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: Inter-fire interval and time-since-fire. *Australian Journal of Ecology* **20**, 239-247.

Morrison D. A. and Morris E. C. (2000) Pseudoreplication in experimental designs for the manipulation of seed germination treatments. *Austral Ecology* **25**, 292-296.

Mott J. J. (1978) Dormancy and germination in five native grass species from savannah woodland communities of the Northern Territory. *Australian Journal of Botany* **26**, 621-631.

Mott J. J. and Andrew M. H. (1985) The effect of fire on the population dynamics of native grasses in tropical savannas of north-west Australia. *Proceedings of the Ecological Society of Australia* **13**, 231-239.

Mott J. J., Williams J. and Andrew M. H. (1985) Australian savanna ecosystems. In: *Ecology and Management of the World's Savannas*. (eds J. C. Tothill and J. J. Mott) pp. 56-82. Australian Academy of Science, Canberra.

Mucha S. B. (1979) Estimation of tree ages from growth rings of eucalypts in northern Australia. *Australian Forestry* **42**, 13-16.

Murray B. R. (1998) Density-dependent germination and the role of seed leachate. *Australian Journal of Ecology* **23**, 411-418.

Mustart P. J. and Cowling R. M. (1993) The role of regeneration strategies in the distribution of edaphically restricted fynbos Proteaceae. *Ecology* **74**, 1490-1499.

Noble I. R. (1980) Interactions between tussock grass (*Poa* spp.) and *Eucalyptus pauciflora* seedlings near the tree line in south-eastern Australia. *Oecologia* **45**, 350-353.

Noble I. R. and Slatyer R. O. (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* **43**, 5-21.

Noble J. C. (1989) Fire regimes and their influence on herbage and mallee coppice dynamics. In: *Mediterranean Landscapes in Australia. Mallee ecosystems and their management*. (eds J. C. Noble and R. A. Bradstock) pp. 168-180. CSIRO, Melbourne.

Norman M. J. T. (1963) The short term effects of time and frequency of burning on native pastures at Katherine, N. T. *Australian Journal of Experimental Agriculture and Animal Husbandry* **3**, 26-29.

Odgers B. M. (1996) Fire, buried germinable seed banks and grass species establishment in an urban eucalypt forest reserve. *Australian Journal of Botany* **44**, 413-419.

Odgers B. M. (1999) Seasonal variation in buried germinable seed banks of grass species in an urban Eucalypt forest reserve. *Australian Journal of Botany* **47**, 623-638.

Orr D. M., McKeon G. M. and Day K. A. (1991) Burning and exclosure can rehabilitate degraded black speargrass (*Heteropogon contortus*) pastures. *Tropical Grasslands* **25**, 333-336.

Paine A. G. L. and Smith J. (1972) *Geology and Minerals of the Burdekin-Townsville Region*. Geographic section, Department of Development, Canberra.

Pannell J. R. and Myerscough P. J. (1993) Canopy-stored seed banks of *Allocasuarina distyla* and *A. nana* in relation to time since fire. *Australian Journal of Botany* **41**, 1-9.

Pate J. S., Casson N. E., Rullo J. and Kuo J. (1985) Biology of fire ephemerals of the sandplains of the Kwongan of south-western Australia. *Australian Journal of Plant Physiology* **12**, 641-655.

Pate J. S., Froend R. H., Bowen B. J., Hansen A. and Kuo J. (1990) Seedling growth and storage characteristics of seeder and resprouter species of mediterranean-type ecosystems of S. W. Australia. *Annals of Botany* **65**, 585-601.

Pettit N. E. and Froend R. H. (2001) Availability of seed for recruitment of riparian vegetation: a comparison of a tropical and a temperate river ecosystem in Australia. *Australian Journal of Botany* **49**, 515-528.

Phelps D. (2001) Burning to control feathertop wiregrass. In: *Savanna burning. Understanding and using fire in northern Australia*. (eds R. Dyer, P. Jacklyn, I. Partridge, J. Russell-Smith, and R. Williams) p. 55. Tropical Savannas CRC, Darwin.

Pierce S. M. and Cowling R. M. (1991) Dynamics of soil-stored seed banks of six shrubs in fire-prone dune fynbos. *Journal of Ecology* **79**, 731-747.

Pressland A. J., Scanlan J. C. and McLennan S. (1989) The role of fire in the grazing lands of Queensland. In: *Fire Research in Rural Queensland. Selected papers from the Queensland fire research workshop series 1980 – 1989*. (ed. B. R. Roberts) pp. 237-250. University of Southern Queensland, Toowoomba.

Price O. and Bowman D.M.J.S. (1994) Fire-stick forestry: a matrix model in support of skilful fire management of *Callitris intratropica* R. T. Baker by north Australian Aborigines. *Journal of Biogeography* **21**, 573-580.

Pryor L. D., Eamus D. and Duff G. A. (1997) Seasonal and diurnal patterns of carbon assimilation, stomatal conductance and leaf water potential in *Eucalyptus tetradonta* saplings in a wet-dry savanna in northern Australia. *Australian Journal of Botany* **45**, 241-258.

Purdie R. W. (1977) Early stages of regeneration after burning in dry sclerophyll vegetation. II. Regeneration by seed germination. *Australian Journal of Botany* **25**, 35-46.

Purdie R. W. and Slatyer R. O. (1976) Vegetation succession after fire in sclerophyll woodland communities in south-eastrn Australia. *Australian Journal of Ecology* **1**, 223-236.

Puyravaud J. P., Shridhar D., Gaulier A., Aravajy S. and Ramalingam S. (1995) Impact of fire on a dry deciduous forest in the Bandipur National Park, southern India: Preliminary assessment and the implications for management. *Current Science* **68**, 745-751.

Read T. R., Bellairs S. M., Mulligan D. R. and Lamb D. (2000) Smoke and heat effects on soil seed bank germination for the re-establishment of a native forest community in New South Wales. *Austral Ecology* **25**, 48-57.

Roberts H. A. (1981) Seed banks in soils. *Advances in Applied Biology* **6**, 1-55.

Roche S., Dixon K. W. and Pate J. S. (1997) Seed aging and smoke: partner cues in the amelioration of seed dormancy in selected Australian native species. *Australian Journal of Botany* **45**, 783-815.

Roche S., Dixon K. W. and Pate J. S. (1998) For everything a season: Smoke-induced seed germination and seedling recruitment in a Western Australian *Banksia* woodland. *Australian Journal of Ecology* **23**, 111-120.

Rogers R. W. (2000) Weeds in the germinable seed populations from the Heron Island National Park, Great Barrier Reef. *Proceedings of the Royal Society of Queensland* **109**, 131-134.

Russell-Smith J., Hoare J. R. L., Whitehead P. J., Cook G. D. and Brooks K. (in press) Response of *Eucalyptus* open-forest and woodland savanna to four experimental fire regimes, 1973-1996, at Munmarlary, Monsoonal Northern Australia. *in press*.

Russell-Smith J., Ryan P. G. and Cheal D. C. (2002) Fire regimes and the conservation of sandstone heath in monsoonal northern Australia: frequency, interval, patchiness. *Biological Conservation* **104**, 91-106.

Russell-Smith J., Ryan P. G. and Durieu R. (1997) A LANDSAT MSS-derived fire history of Kakadu National Park, monsoonal northern Australia, 1980-94: seasonal extent, frequency and patchiness. *Journal of Applied Ecology* **34**, 748-766.

Russell-Smith J., Ryan P. G., Klessa D., Waight G., and Harwood R. (1998) Fire regimes, fire-sensitive vegetation and fire management of the sandstone Arnhem Plateau, monsoonal northern Australia. *Journal of Applied Ecology* **35**, 829-846.

Russell-Smith J. and Stanton P. (2002) Fire regimes and fire management of rainforest communities across northern Australia. In: *Flammable Australia: the Fire Regimes and Biodiversity of a Continent*. (eds R. A. Bradstock, J. Williams and A. M. Gill) pp. 329-350. Cambridge University Press, Cambridge.

Sandercoe C. S. (1988) An aerial photographic study of the long-term effect of wildfires on Magnetic Island. *Proceedings of the Ecological Society of Australia* **15**, 161-165.

Sandercoe C. S. (1989) Towards a fire management strategy for Magnetic Island. In: *Fire Research in Rural Queensland. Selected papers from the Queensland fire research workshop series 1980 – 1989*. (ed. B. R. Roberts) pp. 439-453. University of Southern Queensland, Toowoomba.

Scholes R. J. and Archer S. R. (1997) Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* **28**, 517-544.

Setterfield S. A. and Williams R. J. (1996) Patterns of flowering and seed production in *Eucalyptus miniata* and *E. tetradonta* in a tropical savanna woodland, northern Australia. *Australian Journal of Botany* **44**, 107-122.

Setterfield S. A. (1997*a*) The impact of experimental fire regimes on seed production in two tropical eucalypt species in northern Australia. *Australian Journal of Ecology* **22**, 279-287.

Setterfield S. A. (1997*b*) *Factors affecting seedling regeneration of woody species in a northern Australian tropical savanna*. PhD thesis, Northern Territory University, Darwin.

Shaw N. H. (1957) Bunch spear grass dominance in burnt pastures in south-eastern Queensland. *Australian Journal of Agricultural Research* **8**, 325-334.

Shea S. R., McCormick J. and Portlock C. C. (1979) The effect of fires on the regeneration of leguminous species in the northern jarrah (*Eucalyptus marginata* Sm.) forest of Western Australia. *Australian Journal of Ecology* **4**, 195-205.

Skowno A. L., Midgley J. J., Bond W. J. and Balfour D. (1999) Secondary succession in *Acacia nilotica* (L.) savanna in the Hluhluwe Game Reserve, South Africa. *Plant Ecology* **145**, 1-9.

Skull S. D. (1992) Fire-related aspects of succession in tropical lowland forests. In: *Fifth Queensland Fire Research Workshop*. (eds B. R. Roberts and M. Schulz) pp. 87-101. University of Southern Queensland, Toowoomba.

Smith M. A., Loneragan W. A., Grant C. D. and Koch J. M. (2000) Effect of fire on the topsoil seed banks of rehabilitated bauxite mine sites in the jarrah forest of Western Australia. *Ecological Management and Restoration* **1**, 50-60.

Sokal R. R. and Rohlf F. J. (1995) *Biometry: the Principles and Practice of Statistics in Biological Research*. W. H. Freeman and Company, New York.

Stanton P. and Roeger L. (2001) Monitoring vegetation change. In: *Savanna Burning. Understanding and using fire in northern Australia*. (eds R. Dyer, P. Jacklyn, I. Partridge, J. Russell-Smith, and R. Williams) p. 106. Tropical Savannas CRC, Darwin.

StatSoft (1999) *STATISTICA for windows*. StatSoft, Tulsa.

Stocker G. C. and Sturtz J. D. (1966) The use of fire to establish Townsville lucerne in the Northern Territory. *Australian Journal of Experimental Agriculture and Animal Husbandry* **3**, 277-279.

Stoneman G. L. and Dell B. (1994) Emergence of *Eucalyptus marginata* (jarrah) from seed in Mediterranean-climate forest in response to overstorey, site, seedbed and seed harvesting. *Australian Journal of Ecology* **19**, 96-102.

Stoneman G. L., Dell B. and Turner N. C. (1994) Mortality of *Eucalyptus marginata* (jarrah) seedlings in Mediterranean-climate forest in response to overstorey, site, seedbad, fertilizer appilication and grazing. *Australian Journal of Ecology* **19**, 103-109.

Tainton N. M. (ed.) (1981) *Veld and Pasture Management in South Africa*. Shuter and Shooter, Natal.

Ter Braak C. J. F. and Prentice I. C. (1988) A theory of gradient analysis. *Advances in Ecological Research* **18**, 93-138.

Ter Braak C. J. F. and Smilauer P. (1998) *CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4)*. Microcomputer Power, New York.

Ter Braak C. J. F. and Wiertz J. (1994) On the statistical analysis of vegetation change: a wetland affected by water extraction and soil acidification. *Journal of Vegetation Science* **5**, 361-372.

Thanos C. A. and Rundel P. W. (1995) Fire-followers in chaparral: nitrogenous compounds trigger seed germination. *Journal of Ecology* **83**, 207-216.

Thompson K. and Grime J. P. (1979) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology* **67**, 893-921.

Tothill J. C. (1969) Soil temperatures and seed burial in relation to the performance of *Heteropogon contortus* and *Themeda australis* in burnt native woodland pastures in eastern Queensland. *Australian Journal of Botany* **17**, 269-275.

Tothill J. C. (1977) Flowering phenology of some native perennial tropical grasses from north-eastern Australia. *Australian Journal of Ecology* **2**, 199-205.

Tozer M. G. and Bradstock R. A. (1997) Factors influencing the establishment of seedlings of the mallee, *Eucalyptus luehmanniana* (Myrtaceae). *Australian Journal of Botany* **45**, 997-1008.

Trapnell C. G. (1959) Ecological results of woodland burning experiments in northern Rhodesia. *Journal of Ecology* **47**, 129-165.

Trollope W. S. W. (1982) Ecological effects of fire in South African savannas. In: *Ecology of Tropical Savannas*. (eds B. J. Huntley and B. H. Walker) pp. 292-306. Springer-Verlag, Berlin.

Trollope W. S. W. (1996) Behaviour, effect and use of fire in the savanna areas of southern Africa. In: *Fire in the management of northern Australian pastoral lands*. (eds A. C. Grice and S. M. Slatter). Tropical Grasslands Society, Townsville.

Underwood A. J. (1997) *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge.

van der Moezel P. G., Loneragan W. A. and Bell D. T. (1987) Northern sandplain kwongan: regeneration following fire, juvenile period and flowering phenology. *Journal of the Royal Society of Western Australia* **69**, 123-132.

Van Rensberg S. J., Stock, W. D. and Bond W. J. (1999) Ecological significance of ecotypic variation in *Themeda triandra* Forssk. In: *People and Rangelands Building the Future. Proceedings of the VI International Rangelands Congress. Vol. 2.* (eds D. Eldridge and D. Freudenberger) pp. 938-939. VI International Rangelands Congress, Townsville.

Vaughton G. (1998) Soil seed bank dynamics in the rare obligate seeding shrub, *Grevillea barklyana* (Proteaceae). *Australian Journal of Ecology* **23**, 375-384.

Vlahos S. and Bell D. T. (1986) Soil seed-bank components of the northern jarrah forest of Western Australia. *Australian Journal of Ecology* **11**, 171-179.

Wahren C-H. A., Papst W. A. and Williams R. J. (1999) Post-fire regeneration in Victorian alpine and sub-alpine vegetation. In: *Bushfire 1999. Proceedings of the Australian Bushfire Conference*. (eds B. Lord, M. Gill and R. Bradstock) pp. 425-430. Charles Sturt University, Albury.

Walker B. H. (1985) Structure and function of savannas: an overview. In: *Ecology and Management of the World's Savannas*. (eds J. C. Tothill and J. J. Mott) pp. 83-91. Australian Academy of Science, Canberra.

Walker J. (1981) Fuel dynamics in Australian vegetation. In: *Fire and the Australian Biota*. (eds A. M. Gill, R. H. Groves, and I. R. Noble) pp. 101-127. Australian Academy of Science, Canberra.

Walker J., Malafant K. and Edwards J. (1989) The effects of fire on a *Themeda-Heteropogon* grassland near Rockhampton. In: *Fire Research in Rural Queensland. Selected papers from the Queensland fire research workshop series 1980 – 1989*. (ed. B. R. Roberts) pp. 280-287. University of Southern Queensland, Toowoomba.

Wang L. (1997) The soil seed bank and understorey regeneration in *Eucalyptus regnans* forest, Victoria. *Australian Journal of Ecology* **22**, 404-411.

Warcup J. H. (1980) Effect of heat treatment of forest soil on germination of buried seed. *Australian Journal of Botany* **28**, 567-571.

Watkinson A. R., Lonsdale W. M. and Andrew M. H. (1989) Modelling the population dynamics of an annual plant *Sorghum intrans* in the wet-dry tropics. *Journal of Ecology* **77**, 162-181.

Wellington A. B. (1989) Seedling regeneration and the population dynamics of eucalypts. In: *Mediterranean Landscapes in Australia. Mallee ecosystems and their management*. (eds J. C. Noble and R. A. Bradstock) pp. 155-167. CSIRO, Melbourne.

Whelan R. J. (1986) Seed dispersal in relation to fire. In: *Seed Dispersal*. (ed. D. R. Murray) pp. 237-271. Academic Press, Sydney.

Whelan R. J. (1995) *The Ecology of Fire*. Cambridge University Press, Cambridge.

Whelan R. J. and Main A. R. (1979) Insect grazing and post-fire plant succession in south-west Australian woodland. *Australian Journal of Ecology* **4**, 387-398.

Whelan R. J., Rogers R. W., Dickman C. R. and Sutherland E. F. (2002) Critical life cycles of plants and animals: developing a process-based understanding of population changes in fire-prone landscapes. In: *Flammable Australia: the Fire Regimes and Biodiversity of a Continent*. (eds R. A. Bradstock, J. Williams, and A. M. Gill) pp. 94-124. Cambridge University Press, Cambridge.

Williams P. R. (1995) *Floristic patterns within and between sedge-heath swamps of Gibraltar Range National Park, New South Wales*. BSc (Hons) thesis, University of New England, Armidale.

Williams P. R. (1998) Post fire regeneration of tree seedlings in a revegetation site at Townsville, north Queensland. *Proceedings of the Royal Society of Queensland* **107**, 89-92.

Williams P. R. (2000) Fire-stimulated rainforest seedling recruitment and vegetative regeneration in a densely grassed wet sclerophyll forest of north-eastern Australia. *Australian Journal of Botany* **48**, 651-658.

Williams P. R. (2001) Contrasts in post-fire regeneration and management of three eucalypt habitats in tropical Queensland, north-eastern Australia. In: *Bushfire 2001 Proceedings*. (eds G. Pearce and L. Lester) pp. 280-284. 2001. New Zealand Forest Research Institute, Christchurch.

Williams P. R., Cumming R. J. and Ball D. (2002*b*) Post-fire regeneration of eucalypt savanna flora at Lawn Hill National Park, north western Queensland. *Ecological Management and Restoration* **3**, 61-63.

Williams R. J., Cook G. D., Gill A. M. and Moore P. H. R. (1999*b*) Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Australian Journal of Ecology* **24**, 50-59.

Williams R. J., Griffiths A. D. and Allan G. E. (2002*a*) Fire regimes and biodiversity in the savannas of northern Australia. In: *Flammable Australia: the Fire Regimes and Biodiversity of a Continent*. (eds R. A. Bradstock, J. Williams, and A. M. Gill) pp. 281-304. Cambridge University Press, Cambridge.

Williams R. J. and Lane A. M. (1999) Wet season burning as a fuel management tool in wet-dry tropical savannas: applications at Ranger Mine, Northern Territory, Australia. In: *People and Rangelands Building the Future. Proceedings of the VI International Rangelands Congress. Vol. 2.* (eds D. Eldridge and D. Freudenberger) pp. 972-977. VI International Rangelands Congress, Townsville.

Williams R. J., Myers B. A., Muller W. J., Duff G. A. and Eamus D. (1997) Leaf phenology of woody species in a north Australian tropical savanna. *Ecology* **78**, 2542-2558.

Williams R. J., Myers B. A., Eamus D. and Duff G. A. (1999*a*) Reproductive phenology of woody species in a north Australian tropical savanna. *Biotropica* **31**, 626-636.

Williams R. J., Muller W. J., Wahren C.-H. and Setterfield S. A. (in press) Vegetation. In: Kapalga. *in press*.

Wilson B. A. and Bowman D.M.J.S. (1987) Fire, storm, flood and drought: The vegetation ecology of Howards Peninsula. Northern Territory, Australia. *Australian Journal of Ecology* **12**, 165-174.

Withers J. R. (1978) Studies on the status of unburnt *Eucalyptus* woodland at Ocean Grove, Victoria. II. The differential seedling establishment of *Eucalyptus ovata* Labill. and *Casuarina littoralis* Salisb. *Australian Journal of Botany* **26**, 465-483.

Witkowski E. T. F., Lamont, B. B. and Connell S. J. (1991) Seed bank dynamics of three co-occurring Banksias in south coastal Western Australia: the role of plant age, cockatoos, senescence and interfire establishment. *Australian Journal of Botany* **39**, 385-397.

Woinarski J. C. Z. (1990) Effects of fire on the bird communities of tropical woodlands and open forests in northern Australia. *Australian Journal of Ecology* **15**, 1-22.

Woinarski J. C. Z. (1999) Prognosis and framework for the conservation of biodiversity in rangelands: building on the north Australian experience. In: *People and Rangelands Building the Future. Proceedings of the VI International Rangelands Congress. Vol. 2.* (eds D. Eldridge and D. Freudenberger) pp. 639-645. VI International Rangelands Congress, Townsville.

Woinarski J. C. Z. and Fisher A. (1995) Wildlife of lancewood (*Acacia shirleyi*) thickets and woodlands in northern Australia. 1. Variation in vertebrate species composition across the environmental range occupied by lancewood vegetation in the northern Territory. *Wildlife Research* **22**, 379-411.

Zammit C. A. and Zedler P. H. (1988) The influence of dominant shrubs, fire, and time since fire on soil seed banks in mixed chaparral. *Vegetatio* **75**, 175-187.

Zar J. H. (1999) *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, N. J.

Appendix 1. Species composition of floristic surveys, soil seed bank samples and seedling emergence surveys. *, exotic species, as defined by Henderson (1997); Woodland, woodland trees and shrubs; Rainforest, rainforest trees and shrubs; Subshrub, subshrubs; Up forb, upright perennial forbs; Twiner, twining perennial forbs; Ephem, ephemeral forbs; Grass, grasses; Monocot, non-grass monocots.

Species	Growth form group	% presence in floristic surveys (n = 180)	% presence in seed bank samples (n = 288)	% presence in seedling emergence surveys (n = 36)
Abelmoschus moschatus	Subshrub	3.89	0.35	2.78
Abutilon sp.	Subshrub	0.00	0.69	0.00
Acacia crassicarpa	Woodland	9.44	0.00	0.00
Albizia procera	Woodland	22.22	0.00	0.00
Alloteropsis semialata	Grass	16.11	2.08	2.78
Alphitonia excelsa	Woodland	30.56	0.00	0.00
*Alysicarpus vaginalis**	Twiner	0.00	0.00	2.78
Anisomeles malabarica	Subshrub	7.78	0.69	11.11
*Argyreia nervosa**	Twiner	0.00	0.00	2.78
Aristida queenslandica	Grass	20.56	1.04	5.56
Aristolochia sp.	Twiner	18.89	0.35	11.11
Boerhavia sp.	Up forb	0.00	0.00	5.56
Bothriochloa bladhii	Grass	12.22	0.00	0.00
Breynia oblongifolia	Subshrub	74.44	3.13	19.44
Cajanus confertiflorus	Subshrub	5.56	0.00	2.78
Canarium australianum	Rainforest	66.67	0.00	5.56
Canthium attenuatum	Rainforest	1.11	0.00	0.00
Cassthya filiformis	Twiner	21.67	0.00	0.00
*Chamaecrista absus**	Ephemeral	30.00	5.56	63.89
C. mimosioides	Ephemeral	5.00	11.11	27.78
*Chamaesyce hirta**	Up forb	3.89	3.82	5.56
Chionanthus ramiflora	Rainforest	0.56	0.00	2.78
Cissus opaca	Twiner	3.33	0.00	0.00
Cochlospermum gillivraei	Woodland	0.56	0.00	0.00
Commelina spp.	Monocot	94.44	31.60	75.00
Corchorus aestuans	Subshrub	0.00	3.82	0.00
Corymbia clarksoniana	Woodland	81.11	2.08	25.00
C. tessellaris	Woodland	10.56	0.00	0.00
Crinum flaccidum	Monocot	0.56	0.00	0.00
Crotalaria brevis	Up forb	20.56	2.43	22.22
C. calycina	Ephemeral	16.67	5.90	36.11
*C. goreensis**	Ephemeral	7.22	0.69	16.67
*C. laburnifolia**	Ephemeral	3.89	0.00	2.78
C. lanceolata	Ephemeral	0.00	4.86	5.56
C. montana	Ephemeral	20.56	7.64	41.67
*C. pallida**	Ephemeral	17.22	10.42	50.00
Cryptocarya triplinervis	Rainforest	0.56	0.00	0.00
Cupaniopsis anacardioides	Rainforest	2.22	0.00	0.00
Curculigo ensifolia	Monocot	77.22	1.04	0.00
Cymbopogon bombycinus	Grass	0.56	0.00	0.00
Cyperus sp.	Monocot	6.67	4.51	0.00
Desmodium gangeticum	Twiner	25.00	1.04	5.56
D. gunnii	Twiner	5.00	1.74	5.56
D. rhytidophyllum	Twiner	4.44	0.00	0.00
D. sp.	Twiner ?	0.00	0.69	0.00
D. varians	Twiner	13.33	0.69	2.78

Appendix 1. (cont.)

Species	Growth form group	% presence in floristic surveys (n = 180)	% presence in seed bank samples (n = 288)	% presence in seedling emergence surveys (n = 36)
Dianella caerulea	Monocot	31.11	0.00	0.00
Digitaria breviglumis	Grass	93.89	61.46	36.11
Diospyros geminata	Rainforest	1.11	0.00	0.00
Drypetes deplanchei	Rainforest	0.56	0.00	0.00
*Emilia sonchifolia**	Ephemeral	20.00	25.69	33.33
Eucalyptus platyphylla	Woodland	4.44	0.00	0.00
Euroschinus falcata	Rainforest	3.33	0.00	5.56
Eustrephus latifolius	Monocot	58.33	0.00	8.33
Evolvulus alsinoides	Twiner	31.67	11.11	36.11
Ficus opposita	Woodland	26.11	0.00	0.00
Fimbristylis tristachya	Monocot	8.89	4.86	0.00
Fimbristylis sp.	Monocot	2.78	0.00	0.00
Flemingia parviflora	Twiner	76.11	0.00	22.22
Flueggea virosa	Woodland	5.56	0.00	0.00
Galactia tenuiflora	Twiner	94.44	30.56	83.33
Glochidion sp.	Rainforest	1.11	0.00	0.00
Glycine tomentella	Twiner	73.89	38.19	69.44
Grewia retusifolia	Subshrub	43.33	0.00	0.00
Garuga floribunda	Rainforest	0.56	0.00	0.00
Helicretes semiglabra	Subshrub	2.78	0.00	0.00
Heteropogon contortus	Grass	98.33	16.32	38.89
Heteropogon triticeus	Grass	96.67	53.82	72.22
Hibiscus meraukensis	Subshrub	14.44	0.35	11.11
Hybanthus spp.	Up forb	67.78	32.29	58.33
*Hyptis suaveolens**	Ephemeral	4.44	0.00	5.56
Imperata cylindrica	Grass	11.11	0.00	0.00
Indigofera hirsuta	Ephemeral	48.33	57.29	72.22
Jagera pseudorhus	Rainforest	10.56	0.00	0.00
Jasminum didymum	Twiner	51.67	0.00	16.67
*Lantana camara**	Woodland	15.00	0.35	2.78
Larsenaikia ochreata	Woodland	47.22	0.00	0.00
Livistona decipiens	Woodland	14.44	0.00	0.00
Lomandra sp.	Monocot	1.11	0.00	0.00
Macaranga tanarius	Rainforest	2.22	0.00	0.00
*Macroptilium atropurpureum**	Twiner	57.22	5.21	38.89
Mallotus philippensis	Rainforest	9.44	0.00	0.00
Melia azedarach	Rainforest	2.22	0.00	0.00
*Melinis repens**	Grass	33.89	5.90	8.33
*Merremia quinquefolia**	Twiner	6.11	0.00	2.78
Mnesithea rottboellioides	Grass	0.56	1.04	0.00
Panicum effusum	Grass	24.44	2.08	0.00
*Panicum maximum**	Grass	2.22	0.00	0.00
Parsonsia lanceolata	Twiner	2.78	0.00	0.00
Paspalidium rarum	Grass	44.44	21.88	2.78
*Passiflora foetida**	Twiner	95.00	31.94	100.00
Phyllanthus virgatus	Up forb	33.89	6.94	13.89
Planchonia careya	Woodland	62.22	0.00	0.00
Pleiogynium timorense	Rainforest	3.33	0.00	0.00
Pogonolobus reticulatus	Woodland	5.00	0.00	0.00
Polygala linariifolia	Ephemeral	4.44	0.35	5.56
Pterocaulon sphacelatum	Up forb	0.00	2.08	0.00
Proiphys amboinensis	Monocot	0.56	0.00	0.00
Pycnospora lutescens	Twiner	70.56	45.14	47.22
Rhynchosia minima	Twiner	18.33	1.04	16.67

Appendix 1. (cont.)

Species	Growth form group	% presence in floristic surveys (n = 180)	% presence in seed bank samples (n = 288)	% presence in seedling emergence surveys (n = 36)
Rostellularia adscendens	Up forb	58.33	1.74	44.44
Scleria mackaviensis	Monocot	84.44	23.96	13.89
*Sida acuta**	Subshrub	6.11	0.69	0.00
Sida cordifolia	Subshrub	11.11	4.17	13.89
Sida subspicata	Subshrub	5.00	0.00	0.00
Sorghum laxiflorum	Grass	1.11	0.00	0.00
Spermacoce brachystema	Up forb	31.67	31.25	52.78
*Sporobolus jacquemontii**	Grass	5.00	0.69	0.00
Stephania japonica	Twiner	17.22	0.00	5.56
Sterculia quadrifida	Rainforest	0.56	0.00	0.00
*Stylosanthes humilis**	Ephemeral	0.56	1.74	2.78
Tabernaemontana orientalis	Rainforest	7.22	0.00	0.00
Tacca leontopetaloides	Monocot	17.78	0.35	27.78
Tephrosia juncea	Ephemeral	37.78	16.32	69.44
Terminalia sericocarpa	Rainforest	4.44	0.00	2.78
Themeda triandra	Grass	73.33	3.13	25.00
Tricoryne anceps	Monocot	3.33	0.00	0.00
*Tridax procumbens**	Twiner	0.00	0.35	0.00
*Triumfetta rhomboidea**	Subshrub	72.78	29.86	80.56
Uraria lagopodioides	Twiner	18.33	0.00	2.78
*Urena lobata**	Subshrub	1.11	0.00	0.00
Vernonia cinerea	Up forb	3.33	1.39	13.89
Vigna radiata	Twiner	15.00	6.94	11.11
Vitex trifolia	Woodland	0.56	0.00	0.00
Waltheria indica	Subshrub	1.11	0.00	0.00
Xenostegia tridentata	Twiner	1.11	0.35	0.00
Zornia sp.	Twiner	0.00	0.35	5.56

Appendix 2. Post-fire regeneration observations from eucalypt savanna at Cape Cleveland, Castle Hill, Many Peaks Range and Mt Elliot. Regeneration codes from Gill and Bradstock (1992): 2, killed by fire & regenerates by seed germination from soil stored seedbank; 4, sprouting from roots or rhizomes; 5, sprouting from base of plant; 6, sprouting from stem or branch. Additional codes: s, post-fire seed germination observed for sprouting species or species whose ability to sprout unknown; *, exotic species.

Species	Family	Cape Cleveland	Castle Hill	Mt Elliot	Many Peaks Range
Abelmoschus moschatus	Malvaceae	5, s			5, s
Abutilon sp.	Malvaceae	5			
Acacia bidwilli	Mimosaceae			5	
A. crassicarpa	Mimosaceae	5, 6	5, 6	5	5
A. flavescens	Mimosaceae		5, 6, s		
A. holosericea	Mimosaceae			2	
A. simsii	Mimosaceae		5	5	
A. spirorbis	Mimosaceae		5		
A. umbellata	Mimosaceae		2		
*Ageratum conyzoides**	Asteraceae			s	
Albizia procera	Mimosaceae	5		5	5
Alloteropsis semialata	Poaceae	5, s	5, s	5, s	5, s
Alphitonia excelsa	Rhamnaceae	5	5	5	5
*Alysicarpus vaginalis**	Fabaceae	5			
Anisomeles malabarica	Lamiaceae	5		5, s	
Aristida queenslandica	Poaceae	5	5		
Aristolochia sp.	Aristolochiaceae	5, s	5, s	s	
Boerhavia sp.	Nyctaginaceae	s			
Bothriochloa bladhii	Poaceae	5			
Breynia oblongifolia	Euphorbiaceae	4, 5, s	4, 5	4, 5, s	4, 5
Bursaria incana	Pittosporaceae		5	5	
Cajanus confertiflorus	Fabaceae	4, 5			
*Calyptocarpus vialis**	Asteraceae			s	s
Canarium australianum	Burseraceae	5, 6, s	5, 6	5	5
Canthium attenuatum	Rubiaceae	5	5, s		
Cassthya filiformis	Lauraceae	2			
*Chamaecrista absus**	Caesalpiniaceae	s	s	s	s
C. mimosioides	Caesalpiniaceae	s	s	s	s
*Chamaesyce hirta**	Euphorbiaceae	5	5	5	
Chionanthus ramiflora	Oleaceae	5, s		5	
Cissus opaca	Vitaceae	5			
Cleome viscosa	Capparaceae		s		
Cochlospermum gillivraei	Bixaceae	5, 6, s	5, 6	5, 6, s	5, 6, s
Commelina diffusa	Commelinaceae	5, s	5, s	5, s	5, s
Commelina ensifolia	Commelinaceae	5, s	5	5	5
Corchorus aestuans	Tiliaceae	5	5, s	s	5, s
Corymbia clarksoniana	Myrtaceae	5, 6, s	5, 6	5, 6	5, 6
C. dallachiana	Myrtaceae		5, 6	5, 6	5, 6
C. erythrophloia	Myrtaceae		5, 6	5, 6	
C. tessellaris	Myrtaceae	5, 6	5, 6, s	5, 6	5, 6
Crinum flaccidum	Liliaceae	5	5	5	
Crotalaria brevis	Fabaceae	5, s	5, s	s	

Appendix 2. (cont.)

Species	Family	Cape Cleveland	Castle Hill	Mt Elliot	Many Peaks Range
C. calycina	Fabaceae	2	s	s	s
*C. goreensis**	Fabaceae	2	s	s	
*C. laburnifolia**	Fabaceae	s			
C. lanceolata	Fabaceae	s			
C. medicaginea	Fabaceae		s		
C. montana	Fabaceae	2	s		
*C. pallida**	Fabaceae	2	s	s	s
Cryptocarya triplinervis	Lauraceae	5			
Cupaniopsis anacardioides	Sapindaceae	5		5	
Curculigo ensifolia	Liliaceae	5		5	
Cymbopogon bombycinus	Poaceae	5	5		5
C. refractus	Poaceae		5		
Cyperus sp.	Cyperaceae	5			
Dactyloctenium radulans	Poaceae		s		
Desmodium gangeticum	Fabaceae	5, s		5	5, s
D. gunnii	Fabaceae	5	5, s	5, s	
D. rhytidophyllum	Fabaceae	5			
*D. tortuosum**	Fabaceae	S	s	s	
D. varians	Fabaceae	5			
Dianella caerulea	Liliaceae	5	5	5	5
Digitaria breviglumis	Poaceae	5	5	5	
Diospyros geminata	Ebenaceae	5		5	5
Drypetes deplanchei	Euphorbiaceae	5			5
*Emilia sonchifolia**	Asteraceae	s	s	s	s
Erythrina vespertilio	Fabaceae		5, 6	5, 6	
Eucalyptus drepanophylla	Myracteae		5, 6	5, 6	5, 6
E. platyphylla	Myrtaceae	5, 6	5, 6	5, 6	5, 6
Euroschinus falcata	Anacardiaceae	5, s	5	5	5
Eustrephus latifolius	Smilaceae	5, s	5	5	5
Evolvulus alsinoides	Convolvulaceae	2	s	s	
Ficus opposita	Moraceae	5	5	5	5
Fimbristylis tristachya	Cyperaceae	5			
Fimbristylis sp.	Cyperaceae	5			
Flemingia parviflora	Fabaceae	5, s	5	5	5
Flueggea virosa	Euphorbiaceae	5	5	5	5
Galactia tenuiflora	Fabaceae	5	5	5	5
Garuga floribunda	Burseraceae	5			
Glochidion sp.	Euphorbiaceae	5			
Glycine tomentella	Fabaceae	5, s	5	5	5
Grevillea parallela	Proteaceae		5, 6	5, 6	
Grewia retusifolia	Tiliaceae	4, 5	4, 5	4, 5	4, 5
Haemodorum coccineum	Haemodoraceae		5		
Helicretes semiglabra	Sterculiaceae	4, 5		4, 5	
Heteropogon contortus	Poaceae	5, s	5, s	5, s	5, s
Heteropogon triticeus	Poaceae	5, s	5, s	5, s	5, s
Hibiscus meraukensis	Malvaceae	5, s	s	5, s	5, s
Hybanthus enneaspermus	Violaceae	5, s	5	5, s	5, s
Hybanthus stellarioides	Violaceae	5, s			
*Hyptis suaveolens**	Lamiaceae	s	s	s	s
Imperata cylindrica	Poaceae	5		5	5
Indigofera hirsuta	Fabaceae	2	s	s	s
Jagera pseudorhus	Sapindaceae	5			5

Appendix 2. (cont.)

Species	Family	Cape Cleveland	Castle Hill	Mt Elliot	Many Peaks Range
Jasminum didymum	Oleaceae	5, s		5	
*Lantana camara**	Verbenaceae	5, s	5	5, s	5
Larsenaikia ochreata	Rubiaceae	5	5	5	5
Livistona decipiens	Arecaceae	5, s			
Lomandra sp.	Xanthorrhoeaceae	5			
Lophostemon grandiflorus	Myrtaceae		5, 6		5, 6
Macaranga tanarius	Euphorbiaceae	5			
*Macroptilium atropurpureum**	Fabaceae	5, s		5, s	
Macrotyloma uniflorum	Fabaceae		5, s		
Mallotus philippensis	Euphorbiaceae	5		5	5
Maytenus disperma	Celastraceae		5		5
Melaleuca nervosa	Myrtaceae			5, 6	
M. viridiflora	Myrtaceae		5, 6	5, 6	5, 6
Melia azedarach	Meliaceae	5			
*Melinis repens**	Poaceae	5, s	5	5	5
*Merremia quinquefolia**	Convolvulaceae	5			
Mnesithea rottboellioides	Poaceae	5	5	5	5
Panicum effusum	Poaceae	5			
*Panicum maximum**	Poaceae	5	5	5	5
Parsonsia lanceolata	Apocynaceae	5			
Paspalidium rarum	Poaceae	5, s			
*Passiflora foetida**	Passifloraceae	5, s	5, s	5, s	5, s
*Passiflora suberosa**	Passifloraceae		5	s	
Persoonia falcata	Proteaceae	5, 6	5, 6	5, 6	5, 6
Phyllanthus virgatus	Euphorbiaceae	5, s		5	
Planchonia careya	Lecythidaceae	5, 6, s	5, 6	5, 6	5, 6
Pleiogynium timorense	Anacardiaceae	5	5	5	5
Pongamia pinnata	Fabaceae		5		
Pogonolobus reticulatus	Rubiaceae	5	5	5	
Polygala linariifolia	Polygalaceae	s		s	
Pterocaulon sphacelatum	Asteraceae	5	5		5
Proiphys amboinensis	Liliaceae	5			
Pycnospora lutescens	Fabaceae	5, s		5, s	5, s
Rhynchosia minima	Fabaceae	5, s		5	5
Rostellularia adscendens	Acanthaceae	5, s	5	5	5, s
Scleria mackaviensis	Cyperaceae	5, s		5	5
*Sida acuta**	Malvaceae	5		5, s	
Sida cordifolia	Malvaceae	5, s	5		5, s
Sida subspicata	Malvaceae	5			
Sorghum laxiflorum	Poaceae	s			
Spermacoce brachystema	Rubiaceae	5, s	5, s	5, s	5, s
*Sporobolus jacquemontii**	Poaceae	5, s		5	5
*Stachytarpheta jamaicensis**	Verbenaceae			5	5
Stephania japonica	Menispermaceae	5, s		5	5
Sterculia quadrifida	Sterculiaceae	5		5	5
*Stylosanthes humilis**	Fabaceae	s	s		s
Tabernaemontana orientalis	Apocynaceae	5		5	
Tacca leontopetaloides	Taccaceae	5, s			
Tephrosia filipes	Fabaceae		s		
Tephrosia juncea	Fabaceae	2	s	s	s

Appendix 2. (cont.)

Species	Family	Cape Cleveland	Castle Hill	Mt Elliot	Many Peaks Range
Terminalia sericocarpa	Combretaceae	s		5	
Themeda triandra	Poaceae	5, s	5, s	5, s	5, s
Trichodesma zeylanicum	Boraginaceae		5		5
Tricoryne anceps	Liliaceae	5			
*Tridax procumbens**	Asteraceae	5			5
*Triumfetta rhomboidea**	Tiliaceae	2		s	s
Uraria lagopodioides	Fabaceae	5, s			
*Urena lobata**	Malvaceae	s			
Vernonia cinerea	Asteraceae	5, s	5, s	5, s	5, s
Vigna radiata	Fabaceae	5, s	5, s	5, s	5, s
Vitex trifolia	Verbenaceae	8			
Waltheria indica	Sterculiaceae	5		5	
Wedelia spilanthoides	Asteraceae				5
Xenostegia tridentata	Convolvulaceae	5			
*Ziziphus mauritiana**	Rhamnaceae		5		5
Zornia sp.	Fabaceae	5, s			