IMPACTS AND MANAGEMENT OF *CENCHRUS CILIARIS* (BUFFEL GRASS) AS AN INVASIVE SPECIES IN NORTHERN QUEENSLAND

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in May 2004

For the degree of Doctor of Philosophy
In Tropical Plant Sciences
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Janice Jackson

Abstract

Cenchrus ciliaris L. (buffel grass) (Poaceae) is recognized as one of Australia's most serious environmental weeds. This introduced grass is associated with loss of native species and alteration of fire regimes. However there is considerable controversy regarding its weed status as it is also highly valued as a pasture species for arid and semi-arid zones. Quantitative studies are needed to determine its ecological effects. In addition, its spread into non-target areas, including conservation reserves, means that there is considerable interest in strategies for containing or eliminating *C. ciliaris*. These two issues, the effects of *C. ciliaris* on native species and strategies for managing *C. ciliaris*, are the focus of this thesis.

The relationship between *C. ciliaris* and herbaceous species richness was investigated in two studies at a range of scales up to 64 m^2 in open woodlands in north-eastern Queensland. In the first study, the herbaceous species composition of sites with and without *C. ciliaris* were compared. *Cenchrus ciliaris*-dominated sites had fewer herbaceous species than non-*C. ciliaris* sites at all scales investigated and this pattern was found for the major plant groups (perennial grasses, legumes and other forbs) present. In the second study, the relationship between varying levels of *C. ciliaris* biomass and species richness was investigated at one site. The relationship between varying levels of a dominant native grass, *Bothriochloa ewartiana* (Domin) C.E. Hubb. (Poaceae), and species richness was also determined for comparison with the *C. ciliaris* biomass-richness relationship. In this study, species richness was negatively associated with increasing *C. ciliaris* biomass at some scales and it appeared that *C. ciliaris* had a greater effect on richness than *B. ewartiana*. The negative association between *C. ciliaris* and species richness is consistent with the view that invasion by *C. ciliaris* poses a threat to biodiversity. However, the precise cause of the relationship has yet to be determined.

The strategic use of fire offers potential to control unwanted species. To evaluate fire as a tool for reducing *C. ciliaris* abundance, the effects of season of burning on two *C. ciliaris*-dominated communities in north Queensland were investigated. Three treatments were imposed in small plots at both sites: early dry season burn, late dry season burn and control (no burn). These treatments were selected to exploit differences in fire characteristics and vegetation responses to fire associated with different season of burning. The herbaceous species present and their cover were recorded before and after the fires and post-fire seedling emergence was monitored. To help understand the mechanisms by which fire may alter community composition, burning treatment effects on the availability of establishment sites and propagules were also investigated. Fire affects establishment site availability by reducing resident plant competition, by altering nutrient availability and by altering soil surface condition. Three studies were conducted to investigate treatment effects on establishment sites: (1) *C. ciliaris* plants were monitored to determine mortality, (2) a bioassay technique was used to assess plant nutrient availability and (3) a 'pot' experiment was conducted to examine the effects of different soil surface cover on seedling emergence to help predict the effects of litter removal on emergence patterns. Fire effects on propagule supply were investigated by monitoring flowering in *C. ciliaris*. A germination method was used to determine soil seed bank composition.

Overall, burning had little effect on these communities. The intensities of the fires were low to moderate (300-3030 kWm^{-1}). At Dalrymple there was an unexpected reversal of intensities; the mean intensity of early dry season fires was higher than that of late dry season fires. The fires caused no major changes in composition, few *C. ciliaris* plants were killed and no changes in nutrient availability or seed bank composition were detected. Although these short-term studies of single fires do not allow definitive recommendations regarding the use of fire to manage *C. ciliaris*, they provide information that will aid future research. I found that fire could kill *C. ciliaris* plants and reduce *C. ciliaris* cover. This contrasts with the positive fire feedback model generally proposed for *C. ciliaris*. *Cenchrus ciliaris* mortality was higher with early dry season burning at Dalrymple, suggesting that higher intensity fires will be more effective in eliminating *C. ciliaris* plants and/or that *C. ciliaris* plants may be more susceptible to fire at this time because they have not fully senesced. Apparent low densities of perennial grass seeds in the seed banks of these communities may be exploited: over-sowing with native perennial grasses after fire may encourage shifts in perennial grass dominance.

There is an urgent need for management strategies that reduce, prevent or contain invasive weed invasion. Further work is required to investigate the application of fire regimes in *C. ciliaris*-dominated communities. Of particular interest are differences in growth and/or phenology between *C. ciliaris* and native species in these grasslands that may be exploited to disadvantage *C. ciliaris*.

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ACKNOWLEDGEMENTS

This project would not have been possible without the support of Paul Williams, Queensland Parks and Wildlife Service. Paul provided access to field sites and assistance with field work and I thank him very much for his support and enthusiasm. Thanks also to QPWS staff Benton Haigh, Ken McMahon and Eddie Staier who assisted with the fire work and others who assisted with access to field sites and with field work including Brett Abbott, Peter Allen, Jeff Corfield, Mandy Kotzman, Brigid McCallum, Mike Nicholas, Peter O’Reagain, Ian Radford, Gary Rogers, Lynn Walker, Lindsay Whiteman and Mike Whiting. John Childs, while director of the Tropical Savanna CRC, approved funding to support some of this work. I would also like to thank him for financial support to attend a conference in Townsville and a writing course in Darwin. Thanks also to Brett Abbott for regular help with computer matters, Christy Matthes for library assistance and Chris Stokes for informative discussions regarding species area curves among other things. Many thanks to Betsy Jackes for seeing me through the university hoops. She and Tony Grice provided valuable feed back during the writing of this thesis. I would also like to thank John McIvor, John Ludwig and other reviewers for their advice on an associated manuscript that assisted with the writing of the second chapter of this thesis. The various studies were undertaken in consultation with a very patient statistician. Thank you Bob Mayer, senior biometrician with the Department of Primary Industries. Finally, I would like to thank friends, family and my husband for their support.

CHAPTER 1. GENERAL INTRODUCTION

1.1. *CENCHRUS CILIARIS* (BUFFEL GRASS) – WONDER GRASS OR WEED?

Cenchrus ciliaris L. (buffel grass) is a deep rooted, summer growing, perennial tussock grass. A native of southern Africa, India and Indonesia, it was accidentally introduced into Australia in the 1870s (Paull and Lee 1978). *C. ciliaris* is well adapted to a wide range of soils and the climate of arid and semi-arid Australia and recognition of its drought tolerance and productivity led to its uptake and development by the pastoral industry (Hall 2001). A number of cultivars have been introduced and their use promoted in arid and semi arid regions (Humphreys 1967; Cavaye 1991). *Cenchrus ciliaris* has also been used for erosion control (Albrecht and Pitts 1997) and rehabilitation of degraded and mined land (Grigg *et al.* 2000).

Today *C. ciliaris* is one of the most important pasture introductions in arid and semi-arid Australia. It is by far the most widely distributed sown pasture grass in Queensland (Cavaye 1991) and has become naturalized over large areas. It is estimated to be abundant or dominant over 30 to 50 million ha in Queensland (Woinarski 2001) and covers large areas of Western Australia, Northern Territory, South Australia and New South Wales (Pitts and Albrecht 2000; Franks and Hannah 2001). In a pastoral context *C. ciliaris* has been highly regarded, both for its value as pasture for livestock and for its soil protecting properties (Hall 2001). “Buffel grass has brought great financial benefit to many individual producers and companies…as well as supported many rural communities, because of its benefit to the pastoral industries. Its wide adaptation and tolerance of drought, fire and over-grazing have been major assets” (Hall 2001).

Recently however, the perceived negative effects of this species have gained attention. *Cenchrus ciliaris* is reported to be reducing biodiversity and altering fire regimes (Humphries *et al.* 1991; Low 1997; Franks 2002; Butler and Fairfax 2003). Its weediness derives from its dominance of native vegetation and natural dispersal ability (Hall 2001). It is a strong competitor, producing more biomass than many native perennial grass species, and its high seed yields and light fluffy seed allow it to spread readily via wind and water. In particular, *C. ciliaris* is seen as a major threat to important mesic habitats within the arid zone (Humphries *et al.* 1991). These sites are critical parts of the landscape, providing concentrations of water and nutrient resources and refugia for plants and animals. The displacement of native vegetation by *C. ciliaris* in these sites is believed to be threatening the survival of rare species and altering the food supply of native animals.

The spread of *C. ciliaris* into non-target areas has become a serious concern to non-pastoral land managers, particularly those responsible for conservation areas. *Cenchrus ciliaris* is now considered one of Australia's worst environmental weeds (State of the Environment Advisory Council 1996). In contrast to Hall's (2001) summation, Humphries *et al.* (1991) stated: "Buffel grass is one of a large number of introduced grass species which is causing insidious changes to ecosystem composition, structure and function". The spread of *C. ciliaris* into non-target areas as well as recognition of the need to manage Australia's pastoral lands for multiple uses means the status of *C. ciliaris* – weed or valued pasture plant – has become highly controversial.

Although the literature relating to biological invasions has grown considerably over the last decade (Barrow 1995), much is lacking from our understanding of the impacts and management of invasive species. In the case of *C. ciliaris,* there is a large literature dealing with this species in an agricultural context including issues such as variety development, establishment and animal production. However, there is relatively little published information relating to the impacts and management of this species as an invasive plant. Although *C. ciliaris* has been associated with reduced biodiversity and altered fire regimes, there are few studies quantifying such impacts. There is even less published information regarding management strategies for the control of *C. ciliaris.* Most of the work on these issues has focused on *C. ciliaris* in central Australia where this species is perceived to be a major problem (Griffin 1993; Pitts and Albrecht 2000). The focus of this project is the impact and management of *C. ciliaris* as an invasive species in northern Queensland. Although there is increasing concern regarding *C. ciliaris* as a threat to semi-arid habitats in north Queensland, there is relatively little published information regarding its weed status in these habitats.

1.2. THE ISSUES: IMPACTS AND MANAGEMENT

Two questions relating to invasive species require consideration. Firstly what are the impacts of invasive species on ecosystem components and processes and, secondly, how can we manage them?

Whereas many workers cite the negative effects of invasive species, there are relatively few studies that quantify the effects of exotic plant species on natural and semi-natural environments in Australia (Humphries *et al.* 1991; Adair and Groves 1998; Vranjic *et al.* 2000). Australian and overseas studies report that exotic plants are generally associated with a decline in species richness or diversity (Adair and Groves 1998). *Cenchrus ciliaris* has been associated with reduced herbaceous species richness in Hawaii (Daehler and Carino 1998), Mexico (Saucedo-Monarque *et al.* 1997) and Australia (Fairfax and Fensham 2000; Franks 2002). However, few studies provide conclusive evidence of causal relationships between exotic plants and species richness. The impacts of such species must be determined before control programs are undertaken (Adair and Groves 1998).

“The formulation of management regimes that reduce or prevent further weed invasion and consequent loss of biological diversity is viewed as one of the most urgent tasks for all Australian natural ecosystems” (Adair and Groves 1998). Fire is one of the cheapest tools available for managing vegetation on a large scale. Fire can influence the tree-grass balance in favour of the grass layer and there is growing recognition of the value of fire for manipulating invasive shrub and tree species. Although its application for control of fire-adapted grasses such as *C. ciliaris* may initially appear inappropriate, manipulation of the fire *regime* may offer opportunities to reduce the competitive advantage of *C. ciliaris* over native species (Daehler and Carino 1998). The effects of fire are a consequence of complex interactions between the characteristics of the fire regime and of the vegetation. Research is needed to determine how fire influences interactions between native and invasive species.

1.3. THIS PROJECT

The overall aim of this project was to enhance our understanding of *C. ciliaris* as an invasive, weedy species in northern Queensland. This project focused on two issues: (1) the impacts of *C. ciliaris* on herbaceous species richness and (2) the use of fire in the management of *C. ciliaris*. These issues are covered separately in chapters two and three.

Chapter two consists of two main sections. Section 2.1 is a review of the impacts of invasive plants. The effects of invasive plants in general, and *C. ciliaris* in particular are described. The controversy surrounding plant introductions in Australia and methods used to assess invasive plant impacts are also discussed. Section 2.2 describes two field studies investigating the relationship between *C. ciliaris* and species richness in the herbaceous layer.

The aim of the first study was to compare herbaceous species richness in habitats in which *C. ciliaris* was either dominant or absent. Herbaceous species composition was surveyed in *C. ciliaris*-dominated plots and non-*C. ciliaris* plots at sites in the Dalrymple Shire, north-eastern Queensland. In such site-comparison studies it is often difficult to determine the effects of exotic plants on species richness because various factors affecting species richness, such as site differences in grazing, are often confounded with the presence of the exotic.

The aim of the second study was to investigate the relationship between *C. ciliaris* and herbaceous species richness at a single site in the absence of grazing to help minimize some of these confounding factors. Rather than comparing species richness between areas with and without *C. ciliaris*, the relationship between *C. ciliaris* and herbaceous species richness was investigated by comparing areas with varying levels of *C. ciliaris* biomass. Herbaceous species richness was surveyed in small plots that varied in composition, ranging from plots dominated by *C. ciliaris* to plots dominated by a native perennial grass, *Bothriochloa ewartiana*. The specific aims of the study were (1) to compare *C. ciliaris* and *B. ewartiana* for their effects on herbaceous species richness and (2) to investigate the effects of scale on these relationships.

Chapter three describes a series of studies investigating the effects of season of burning on two *C. ciliaris*-dominated communities in northern Queensland. The overall aim of the work was to determine the effects of season of burning on these communities to assess fire as a tool for managing *C. ciliaris*-dominated vegetation. Three burning treatments were imposed in the two communities: early dry season burn (June), late dry season burn (November) and no burn (control). The experimental sites and fire treatments are described (section 3.3) following a review of the use of fire as a tool for manipulating vegetation composition (section 3.2). Individual studies investigating burning effects on establishment site availability, propagule supply, seedling recruitment and community composition are described (sections 3.3-3.10) and the implications of the findings for using fire as a tool to manage *C. ciliaris* are discussed (section 3.11).

The final chapter of this thesis (chapter four) gives a brief summary of the findings from chapters two and three and discusses future research needs.

Several cultivars of *C. ciliaris* are established in Australia. It is not always possible to identify individual cultivars in the field and I did not determine the identity of the cultivars present at sites involved in this work. Authorities to species names are provided in appendices at the end of the relevant sections.

CHAPTER 2. *CENCHRUS CILIARIS* AS AN INVASIVE SPECIES

2.1. LITERATURE REVIEW: IMPACTS OF INVASIVE PLANTS

2.1.1. INTRODUCTION

Biological invasions are seen as one of the major threats to ecosystem integrity both in Australia and around the world (Heywood 1989; Vitousek *et al.* 1997). Invasive, exotic plants have been associated with changes in ecosystem components and processes, resulting in changes in community composition and structure. Invasive plants alter communities by direct competition and displacement of native species (Humphries *et al.* 1991). They also alter ecosystem processes such as water and nutrient cycling, geomorphological processes, micro-climate and disturbance regimes (Macdonald *et al.* 1989; D'Antonio and Vitousek 1992; Gordon 1998). Where invasions result in ecosystem-level effects, ecosystems can be irreversibly altered and their capacity to provide goods and services can be reduced (Masters and Sheley 2001). Such effects can have profound economic and cultural consequences (Vermeij 1996). Invasive plants can destroy wildlife habitat, diminish forest regeneration and production, render rangeland unsuitable for grazing, increase soil erosion, degrade streams and lakes and reduce recreational opportunities such as hunting, fishing, camping and boating (Franklin *et al.* 1999).

Exotic plants have been introduced into Australia both accidentally and intentionally. Although many accidental introductions are generally perceived as weeds, the status of deliberately introduced plants, such as those introduced for pasture improvement, is more controversial. Until recently, problems associated with such plants had received little attention (Low 1997). However, there is now growing concern about their negative effects. In particular, concern has been raised about the negative effects associated with introduced grasses (Humphries *et al.* 1991; Adair and Groves 1998). Invasion by exotic grasses has been associated with displacement of native species, changes in fire regimes and alteration of wetland structure (Low 1997).

One of the most controversial of these grasses is *Cenchrus ciliaris*, a drought and grazing tolerant perennial tussock grass that has become well established in Australia's arid and semi-arid zones. In a pastoral context, *C. ciliaris* has been highly regarded for its value as pasture for livestock and for its soil protecting properties (Hall 2001). However, its apparent negative effects on biodiversity and fire regimes are of considerable concern, particularly for management of conservation reserves. It has been associated with reduced plant (Fairfax and Fensham 2000; Franks 2002) and animal (QPWS 2001) diversity as well as an increase in the intensity and incidence of fire (Humphries *et al.* 1991; Butler and Fairfax 2003). Given these changes and its vast range, *C. ciliaris* is believed to be having a major impact on Australia's biodiversity (Humphries *et al.* 1991; Woinarski 2001).

Although there is a large literature discussing the ecological effects of invaders, much of this is purely anecdotal (Parker *et al.* 1999). This is very much the case for species such as *C. ciliaris* in Australia where there are relatively few published data quantifying the perceived negative impacts of this species. Understanding and being able to quantify the impacts of invasive species is necessary for developing appropriate management strategies (Adair and Groves 1998, Masters and Sheley 2001). Given the controversy associated with deliberately introduced species, understanding and being able to quantify plant impacts is particularly important. The status of *C. ciliaris* as a major environmental weed is highly contentious. While reported to be one of Australia's most damaging plant imports (Low 1997), it is considered by many to be a highly desirable and valuable pasture introduction. A better understanding of this species in an ecological context will provide a basis for rational debate.

2.1.1.1. This review

In this review the phenomena of biological invasions and the impacts of invasive plants are introduced. The focus is on the detrimental effects of invasive plants in natural and semi-natural ecosystems rather than invasive plant effects in urban and cropping situations. The controversy regarding deliberately introduced plants in Australia is discussed with emphasis on pasture introductions. The introduction and development of *C. ciliaris* in Australia is described followed by a review of the reported impacts of this species. Finally, the methodologies and difficulties of quantifying invasive plant impacts are discussed.

2.1.1.2. A note on terminology

In the expanding field of invasion ecology there is considerable confusion over terms used to describe various concepts (Richardson *et al.* 2000). Terms such as 'exotic', 'invasive' and 'weed' may have broadly understood meanings but detailed definitions may be more problematic. (e.g. see Kendle and Rose (2000) for a discussion of the difficulties of defining 'native' and 'exotic'). As a rule, ecological terminology is "messy" and discrete ecological categories rarely exist (Schwart 1997). However, problems with terminology are perhaps more severe in invasion ecology than in other disciplines since the notion of invasion frequently involves anthropocentric concepts such as aggression, intrusion etc. (Richardson *et al.* 2000). The usage of some invasion ecology terms is briefly described below.

What are ‘invasive’ plants? Invasive plants have been defined as naturalised plants that produce offspring, often in very large numbers, at considerable distances from parent plants and thus have the potential to spread over a considerable area (Richardson *et al.* 2000). What then are ‘naturalised’ plants? The term ‘naturalised’ has been used loosely with various meanings being implied. Although ‘naturalisation’ has been used as a synonym for ‘invasion’, Richardson *et al.* (2000) argue that these terms represent two overlapping but not identical phases in the naturalisation/invasion process. They recommend that the term ‘naturalised’ refer to alien plants that reproduce consistently, sustaining populations over many life cycles without direct intervention by humans, and that they generally recruit offspring close to adult plants and do not necessarily invade other ecosystems. The possible differences in interpretation of these definitions demonstrate the difficulties of providing precise terminology.

Many definitions of the term ‘invasion’ assume or imply negative effects. For example that of Mack (1996): “Plant invasions describe the proliferation and persistence of a species in a new range such that it has detrimental consequences (abiotic, biotic, or both)”. However, it has been suggested that the term be used without reference to any effects (Richardson *et al.* 2000). That is, invasion occurs “when an introduced species reproduces and expands its range beyond the site of introduction” (Daehler and Strong 1994). Much of the literature dealing with the effects of plant invasions focuses on detrimental effects. This is also the focus of this review. However, it is important to note that, although any successful invasion must have some consequences for the other species present, most effects are minor (Williamson 1996). In some instances the effects of invasive plants may actually be desirable or at least tolerable. For example, invader species may increase surface cover, thereby reducing soil erosion (Walker and Smith 1997). They may provide feed for livestock or nectar for honey production during periods when other species are not flowering (Sindel 2000). They may help maintain higher levels of pollinators and act as nursery plants for native species (Woods 1997). Some aquatic weeds, for example *Salvinia molesta*, are able to remove excess nutrients and other pollutants from effluent (Sindel 2000).

The term ‘environmental weed’ needs clarification since it is encountered frequently in invasive plant literature and various definitions have been proposed (refer Adair (1995) and

Csurhes and Edwards (1998)). Whereas some restrict this term to refer to weeds of areas managed for conservation (e.g. Swarbrick and Skarratt 1994), I accept a broader definition in which the label ‘environmental weeds’ refers to species that invade native and semi-native systems including areas set aside for conservation as well as areas managed for other uses. In this context, *C. ciliaris* is considered an environmental weed even when it has invaded areas that are not designated conservation reserves.

2.1.2. BIOLOGICAL INVASIONS

> “For as long as humans have travelled over and between land masses, species have been transported, deliberately or inadvertently, from their native ranges to new, previously unoccupied areas” (Manchester and Bullock 2000).

Biological invasion happens when an organism reproduces and expands beyond its previous range (Williamson 1996). Although biological invasions are generally associated with human activities, they are natural phenomena that long antedate humankind (Daehler and Strong 1994). All organisms have dispersal mechanisms that provide the potential to colonize new areas. However, today invasions represent a “new ball game” (Wagner 1993). Modern human activities have caused the breakdown of barriers to dispersal. The movement of species is now occurring at rates without precedent in the last tens of millions of years such that “taxa that evolved in isolation from each other are being forced into contact in an instant of evolutionary time” (D’Antonio and Vitousek 1992).

The invasion process involves a series of stages that have been variously defined by different authors. Vermeij (1996) described three successive stages: (1) arrival, or the dispersal of individuals to the recipient region, (2) establishment, the stage in which the new population sustains itself through local reproduction and recruitment, and (3) integration, when local species and the invader respond to each other ecologically and evolutionarily. That is, the invader modifies species in the recipient community and local species modify the invader. Groves (1986a) also divided the invasion process into three stages: (1) introduction, (2) colonisation and (3) naturalization, while Humphries *et al.* (1991) described five stages (1) introduction, (2) establishment, (3) survival, (4) production of numerous propagules and (5) widespread dispersal.

Importantly, most arrivals and colonizations do not result in biological invasions (Daehler and Strong 1994) and most invasions have little impact on the systems they enter. This generalization has been described by the ‘tens rule’ (Williamson 1996): 10% of introductions will become established or naturalised and 10% of these will become pests. Williamson (1996) noted, while that this rule is very rough and ‘pests’ are defined by human perception rather than by ecological effects, it seems to be true. Consequently, while all invasions alter the invaded ecosystem, most effects are minor and the invader may simply increase species richness (Williamson 1996).

However, the dramatic increase in the numbers of species being moved from place to place significantly increases the numbers of species that may have major impacts. Significant changes may result where ecosystem processes are sufficiently disrupted by the invasion (Masters and Sheley 2001). Invasive plants may disrupt ecosystem processes such as erosion, stream sedimentation, energy flow, nutrient and water cycling, plant regeneration patterns and fire regimes (Macdonald *et al.* 1989; D’Antonio and Vitousek 1992; Masters and Sheley 2001). These impacts can result in displacement of native species, causing significant changes in community composition and structure. Although biological invasions may be perceived as less important than other major human impacts such as climate change and deforestation, D’Antonio and Vitousek (1992) pointed out that biological invasions have caused more species extinctions than human-caused climate and atmospheric change (more so for animal invaders, see Macdonald *et al.* 1989). They also stated that, whereas changes in climate, atmosphere and land use may be reversible in hundreds to thousands of years, many of the changes associated with biological invasions must be considered irreversible.

The impacts of invasive plants vary spatially and temporally, depending on the attributes of the invasive species and the characteristics of the habitat being invaded (Csurhes and Edwards 1998). Some species, such as the aquatic fern *Salvinia molesta*, grow aggressively and disperse extensively so their impacts are relatively immediate and widespread. Other species, such as *Cyperus papyrus,* become naturalised at few sites and spread very little so that their effects are very localised (Humphries *et al.* 1991). Although many species are common and have little measurable effect on other species, it is important to note that it may take a long time for a species to change from innocuous to pest (Williamson 1996). A spectacular example is *Mimosa pigra*. This leguminous shrub was introduced into Darwin in the late 1800s but did not ‘explode’ until the late 1970s (Braithwaite *et al.* 1989). Williamson (1996) describes case studies that demonstrate how the impacts of invasive species may change over time.

Invasive plants come from different plant families and vary in life form (Williams and West 2000). However, certain families, for example the Poaceae and Asteraceae, and genera, for example *Bromus, Poa, Cirsium* and *Centaurea* contain a large proportion of the world's problem species (Mack 1996). Exotic, invasive grasses are recognized as a problem around the world, displacing native species, altering water and nutrient cycles, geomorphology and microclimate, and causing changes to fire regimes (D'Antonio and Vitousek 1992). In Australia there is increasing concern about the effects of deliberately introduced pasture grasses (Humphries *et al.* 1991; Low 1997; Adair and Groves 1998).

Serious attention was first focused on the nature and significance of biological invasions with the publication of "The ecology of invasions by animals and plants" in 1958 by C.S. Elton (Barrow 1995). Today biological invasions are recognized as one of the major threats to nearly all biogeographical regions on earth (Adair and Groves 1998), although the impacts of biological invasions are perceived to be particularly serious in North America, southern Africa, Australasia and the oceanic islands such as the Galapagos and Hawaii (Manchester and Bullock 2000). Consequently, there is a significant research effort directed at issues relating to biological invasions. These include identifying the characteristics of successful invaders and the characteristics of communities that influence their ability to be invaded, as well as determining the impacts of invasive species and developing strategies for preventing and controlling invasive species.

2.1.3. IMPACTS OF INVASIVE PLANTS

The considerable literature on the effects of invasive species includes studies detailing specific effects of particular species as well as reviews discussing invasive plant impacts in broader contexts. However, there appears to be no clear cut way to categorize invasive plant impacts. Impacts on primary productivity, water and nutrient cycling and species interactions are linked such that changes in one are likely to cause changes in others (Walker and Smith 1997). These interactions between impacts make them difficult to categorize. As noted by Williamson (1996), "ecological effects can seldom be categorized neatly into distinct classes". For example, D'Antonio and Vitousek (1992) differentiated between 'competitive effects', where the invasive plant utilized resources reducing their availability for other species, and 'ecosystem effects', where the invasive plant altered resource availability at a 'whole-system' level by altering ecosystem processes such as nutrient cycling. However, they noted that these categories were not exclusive; competitive interactions can have ecosystem level consequences and visa versa. For example, grasses may competitively exclude trees and shrubs and the resultant changes in fuel loads may alter fire regimes, affecting nutrient cycling. These ecosystem level impacts may alter competitive interactions by changing resource availability.

Different schemes have been used to categorize invasive plant impacts. For example, Walker and Smith (1997) discussed the impacts of invasive plants in terms of effects on primary productivity (vegetation structure, composition, growth and diversity), nutrient dynamics, soil moisture and salinity, disturbance regimes (fire, erosion, plant-herbivore interactions) and community dynamics (competition, stability, succession etc.). Parker *et al.* (1999) considered impacts at five levels: (1) effects on individuals (e.g. growth, mortality), (2) genetic effects, (3) population dynamic effects (abundance, growth etc.), (4) community effects (species richness, trophic structure) and (5) effects on ecosystem processes (nutrient availability primary productivity etc.). Macdonald *et al.* (1989) described the impacts of invasive plants in terms of effects on “ecosystem structure” (i.e. species composition, genetic diversity) and “ecosystem function” (e.g. nutrient cycling, hydrology, soil erosion, decomposition). In general, the specific classes proposed by one author(s) do not fit well with those used by others (Williamson 1996). For example, while D’Antonio and Vitousek (1992) distinguished between competitive and ecosystem level effects, others, for example Csurhes and Edwards (1998), included competition as an ecosystem level function.

A recurrent, broad scheme used to categorize invasive plant impacts is that which divides impacts into those affecting ecosystem structure, that is impacts on ecosystem components such as individual species and/or communities, and those affecting ecosystem function including processes such as nutrient and water cycles and disturbance regimes (as in Macdonald *et al.* 1989). However, as described above, even these two broad categories overlap and division between them is not consistent in the literature. I have used this scheme to summarize the impacts of invasive plants below.

2.1.3.1. Impacts on ecosystem structure/components

Invasive plant impacts on ecosystem structure, or ecosystem components, involve changes to biodiversity. Biodiversity can be described at three levels (genetic, species and ecosystem diversity) and invasive plants are capable of affecting biodiversity at one or more of these levels (Adair and Groves 1998).

Genetic diversity

Invasive plants may alter genetic diversity, which is the diversity within a species (Lawrence 1995), via local extinction or hybridisation effects. Invasive plants have been associated with losses of local populations and it has been suggested that such losses result in reductions in the genetic diversity of the taxa involved (Adair and Groves 1998). Exotic species may also result in ‘genetic pollution’ (Robin and Carr 1986) by hybridizing with indigenous taxa. The resultant hybrids may then out-compete indigenous populations and possibly cause their elimination (Carr 1988). Robin and Carr (1986) give examples of hybridising species in Australia, noting that some *Grevillea* and *Acacia* hybrids have become environmental weeds. By hybridizing with wild populations, invasive species introduce greater genetic variability, increasing vigour and ecological amplitude (Low 1997). Macdonald *et al.* (1989) provide examples of invasive plant hybidisation in other parts of the world.

Species diversity

The majority of studies investigating the impacts of invasive plants have focused on the effects on species diversity (Adair and Groves 1998). Species diversity is the combination of the number of species present and the way in which the individuals are distributed amongst the various species (Adair and Groves 1998). Although it is a relatively well-defined concept and is relatively easily measured, there is some debate about the usefulness of species diversity indices (Adair and Groves 1998). Many studies actually quantify invasive plant effects on species richness (the number of species in a given area) rather than on species diversity. Some studies simply document changes in abundance of specific species rather attempt to measure impacts on species diversity.

Few invasions cause extinctions and most invasions have little impact on species richness, apart from simply increasing local diversity (Williamson 1996). However, some invasive plants have profound impacts on diversity. Invasive plants have generally been associated with declines in species richness or diversity (Adair and Groves 1998) and negative correlations have been found between exotic species abundance and numbers of native species (Bridgewater and Blackshell 1981; McIntrye *et al.* 1988; Vlok 1988; Batianoff and Franks 1998). Plant species richness has been reduced in areas invaded by various life forms including: trees and shrubs (e.g. *Cytisus scoparius*, Smith 1994), vines (e.g. *Clematis vitalba*, Ogle *et al.* 2000), forbs (e.g. *Euphorbia esula*, Belcher and Wilson 1989), grasses (e.g. *Agropyron cristatum* and *Agropyron desertorum*, Lesica and DeLuca 1996) and aquatic plants (e.g. *Myriophyllum spicatum*, Boylen *et al.* 1999). Nineteen of 20 studies on environmental weed impact in Australia reviewed by Adair and Groves (1998) reported a decline in species richness, canopy cover or frequency of native species. The reverse has been found, where invasive plants are associated with increased species richness. This generally occurs on disturbed land where invasive plants have acted as ‘nurse plants’ for the regeneration of other species (Adair and Groves 1998).

The majority of studies investigating the impacts of invasive plants on biodiversity have focused on changes in floristic composition and less is known about invasive plant impacts on animal diversity (Adair and Groves 1998). Weed invasions may have a range of effects on the survival of native animals by altering food supply, nesting sites, cover and protection from predators (Loyn and French 1991) and both positive (Hedge and Kriwoken 2000) and negative (Usher 1986) effects of plant invasions on animal communities have been reported (Adair and Groves 1998). Some studies have found that, whereas species richness appears unchanged by plant invasion, changes in the abundance of particular taxa are evident. For example, the abundance of litter invertebrate taxa was found to differ between coastal heath with and without *Chrysanthemoides monilifera* (bitou bush) in New South Wales, although the numbers of invertebrate species were similar in these two habitats (French and Eardley 1997). The invasion of riverine woodland in central Australia by *Tamarix aphylla* was associated with changes in the trophic structure of bird assemblages and an overall decline in bird abundance but no change in bird species richness (Griffin *et al.* 1989).

In their review of environmental weed impacts, Adair and Groves (1998) concluded that most studies report negative effects of weed invasion on some measure of biodiversity. However, it is important to note that the effects of invasion can be positive, negative or neutral depending on the biotic group measured (Groves and Willis 1999). For example, in Californian shrublands the invasive perennial tussock grass *Cortaderia jubata* has been associated with reduced richness of native shrub species but increased numbers of exotic plant species such that overall plant species richness is similar to that of non-invaded areas (Lambrinos 2000). The effects of invasive species also depend on the invaded community. Belnap and Phillips (2001) found a reversal of the effects of *Bromus tectorum* invasion on soil biota between two grassland communities in Utah. Consequently, generalizations such as “plant invasions…..are typically characterized by a decline in species diversity at all trophic levels within an ecosystem” (Beerling 1995), are perhaps premature when so little is known about the impacts of invasive plants on many groups of organisms. It is also important to recognize that invasive plant impacts may change over time. For example, although invasion of temperate woodland in New South Wales by *Cytisus scoparius* (broom) is associated with reduced herbaceous species richness, in the longer term species richness may recover as the broom canopy begins to open (Smith 1994).

Although many studies document negative impacts of invasive plants on species diversity and on particular species, there is little information regarding the role of invasive plants in species extinction. (In contrast, there are many examples of animal invasions resulting in extinction particularly on islands, see Macdonald *et al.* 1989). Determining the role of invasive species in the extinction of species is difficult since (1) it is difficult to 'prove' that a species has, in fact, become extinct and (2) few species are studied in sufficient detail before they become extinct so the factors responsible for their demise are unknown (Macdonald *et al.* 1989). The evidence available suggests that, while invaders (referring here to both animal and plant invaders) often cause extinction on oceanic islands and in lakes, they rarely cause extinctions in the sea or on large land masses. Rather, they probably restrict the ecological range of native species (Vermeij 1996). Macdonald *et al.* (1989) noted that there was only one well documented case where invasions by exotic plants posed a major threat to native plant species diversity at a continental scale: the fynbos and Karoo biomes in South Africa. There have been no documented cases of continental species extinctions attributed solely to weed invasion in Australia (Adair 1995). Leigh and Briggs (1992) list weeds as a major cause in the extinction of only four plant species. However, invasive plants are currently threatening several species (Williams and West 2000). For example two endangered species, *Pterostylis arenicola* and *Pimelea spicata*, are threatened by the introduced *Asparagus asparagoides* (bridal creeper) (Groves and Willis 1999). The fragmentation and disintegration of native vegetation caused by weed invasion has lead to range contractions, reduced abundance and a decline in the diversity of native biota. In many areas, species extinctions have occurred at local and regional levels (Adair 1995). Rare plants are often threatened by extinction (Daelher and Strong 1994) and numbers of rare species have been found to be negatively correlated with the abundance of exotic species (McIntrye and Lavorel 1994).

Ecosystem diversity

Ecosystem diversity is the number of different ecosystems in a given environment (Lawrence 1995). The impacts of plant invasion on ecosystem diversity are generally not explicitly quantified since determining whether invasion-induced changes represent increases or decreases in ecosystem diversity depend on the scale of concern and how the ecosystems are defined. Rather, the threats of invasive species to particular ecosystems are recognized at various scales.

Where invasive plants threaten ecosystems, it is usually where the invading species creates a new stratum and/or where essential ecosystem functions are altered (Adair and Groves 1998). Invasive plants may have dramatic effects on vegetation structure. For example *Mimosa pigra* converts sedgeland to tall shrubland. *Acacia nilotica* converts dry grassland into tall shrubland (Panetta and Lane 1996) and is considered a threat to Mitchell grasslands Australia wide (Humphries *et al.* 1991). Vine species such as *Thunbergia grandiflora, Macfadyena unguis-cati* and *Anredera cordifolia* convert forest vegetation into vine thicket (Panetta and Lane 1996). *Cryptostegia grandiflora* (rubber vine) threatens native vine thickets, gallery forests and dry rainforest in the monsoonal belt of northern Australia (Humphries *et al.* 1991). Humphries *et al.* (1991) list a number of Australian ecosystems at risk from plant invasion. Invasive plants also affect the diversity of ecosystems elsewhere. For example, replacement of native flora in California has been so thorough that a new vegetation type 'valley grassland' has been created (Heady 1977).

2.1.3.2. Impacts on ecosystem function/processes

Invasive plants may affect ecosystem processes. These have been defined as "whole-system fluxes of energy, the amounts and pathway of inputs, outputs and cycling of materials and the ways that these vary in time" (D'Antonio and Vitousek 1992). They include water and nutrient cycling, productivity, geomorphological processes, and disturbance regimes (Williamson 1996).

Vitousek (1990) suggested that invasive species could have ecosystem-level effects where they (1) differ substantially from natives in resource acquisition or utilization; (2) alter the trophic structure of the invaded area; or (3) alter disturbance frequency and/or intensity. Invasive plants may alter ecosystem properties where they add a life form that is not well-represented in the native flora (Vitousek 1986) and/or where they add a new biological process, such as nitrogen fixation, to a system (Vitousek *et al.* 1987).

Whereas numerous studies demonstrate that biological invasions can alter population dynamics and community structure, there is much less information available regarding ecosystem-level effects (Ramakrishnan and Vitousek 1989). Vitousek (1990) considered that relatively few invasive species have ecosystem-level effects. However, Adair and Groves (1998) concluded that the numbers of species altering ecosystem functions were likely to be higher than that reported because this issue is not widely researched. Gordon (1998) also suggested that ecosystem-level effects were more common than thought, but noted that much of the current information was anecdotal. It is difficult to demonstrate ecosystem-level effects of invasive species because the impacts of invasion are often confounded with ecosystem disturbance (Ramakrishnan 1991), making it difficult to separate out the effects of exotic species from the effects of disturbance that allows the species to establish (Vitousek 1986). The impacts of environmental weeds on ecosystem processes have not been well researched in Australia (Williams and West 2000) and there are few quantitative overseas studies on ecosystem-level impacts of invasive plants (Adair and Groves 1998).

Where invasions alter ecosystem properties, there may be major changes in ecosystem structure and function. Ecosystem-level changes in fluxes of water or energy and/or the cycling and loss of material can alter conditions for life for all the organisms in an ecosystem (Ramakrishnan and Vitousek 1989). As pointed out by Vitousek (1990), exotic species that alter ecosystem properties do not merely compete with or consume native species; they alter the fundamental rules for existence for all organisms in the area. Consequently, ecosystem effects may be more serious than local extinction since they lead to the severe disruption of many species rather than the local loss of a few (Williamson 1996). In fact, some invasive plant species have been described “transformer” species since they become dominant and change the character and condition of ecosystems over substantial areas (Wells *et al.* 1986). The alteration of some ecosystem processes can have repercussions for others, thereby increasing the scale of change (Vitousek 1986). Positive ecosystem-level feedback may occur where there are changes in nutrient availability or disturbance regimes (Vitousek 1986). For example, invasion by weedy plants in Hawaii favours feral pig activity, which in turn favours the spread of the weeds via the effects of soil disturbance and seed spread (Smith 1985). Species whose invasive capacity involves such positive feedback present the greatest threats to ecological systems (Levine *et al.* 2003). The effects of invasive plants on hydrological cycles, geochemical processes, geomorphological processes, primary productivity and disturbance regimes and community dynamics are briefly described below.

Hydrological cycles

Some invasive species alter water distribution. For example, *Orbea variegata,* an exotic plant invading chenopod shrublands in South Australia, has a dense root system that is thought to trap water in the surface soil, reducing movement to lower layers (Dunbar and Facelli 1999). Changes in transpiration rates associated with invasive species may also affect hydrology. Sites dominated by the exotic grass *Andropogon virginicus*, which has invaded tropical rainforest in Hawaii, become water logged as this grass has much lower transpiration rates than the original native forest vegetation (Mueller-Dombois 1973). Some broadleaf, invasive plants have lower leaf areas than the annual and perennial grasses they are replacing and this can alter water capture at invaded sites. Surface water runoff and stream sediment yields were 56 and 196% higher respectively in a *Centaurea maculosa*-dominated site compared with adjacent native perennial grassland (Lacey *et al.* 1989). In contrast, invasive species with much higher water usages than the native species they have replaced can reduce water tables and dry up water holes. For example, *Tamarix* spp., which have invaded water courses in North America (Vitousek 1986) and Australia (Griffin *et al.* 1989), have deep penetrating roots and can tap into the water table throughout much of the year. The resulting high transpiration rates can lower water tables (Loope *et al.* 1988).

Geochemical processes (nutrient cycling)

Invasion by woody and herbaceous species has been associated with altered nutrient cycling and distribution patterns. Invasion of grasslands by woody plants may create patches of higher fertility. The deeper root systems of trees and shrubs, together with their relative longevity, enable them to extract nutrients from soil layers beyond the rooting depth of herbaceous species. Nutrient and organic matter levels beneath their canopies are increased via litter drop, canopy drip and stem flow (Johnson 1986). Alternatively, it has been suggested that the deep root systems of some invasive plants mean that they contribute less organic matter near the soil surface (Olson 1999). Invasion by nitrogen fixing plants in particular may result in altered nutrient cycling and soil nitrogen status (e.g. *Myrica faya*, Vitousek and Walker 1989).

Effects on nutrient cycles have been attributed to changes in litter quality and quantity associated with invasive plants. Invasion of exotic *Acacia* spp. in the South African fynbos increases soil phosphorus levels since the *Acacia* spp. have higher phosphorus levels in their litter, greater litter accumulation and more rapid litter turn over rates than the native species (Witkowski and Mitchell 1987). The invasive grass *Bromus tectorum* has been associated with reduced inorganic nitrogen availability. This grass produces more litter than native species and its significantly higher C:N and lignin:N ratios decreases N mineralization rates (Evans *et al.* 2001).

Invasive plants may affect soil biota as well as soil physical and chemical properties and these changes interact to affect nutrient cycling and the soil environment. For example

Mesembryanthemum crystallinum (iceplant), an invasive species in South Australia and California, accumulates salt in its tissues and leachate from its residues raises the salinity of the top soil, creating an unfavourable environment for the establishment or growth of other species (Kloot 1983). Allelopathic effects have been attributed to some invasive plants (e.g. *Pittosporum undulatum* (Gleadow and Ashton 1981) and *Lantana camara* (Achhireddy and Singh (1984)).

Geomorphological processes

Some species have landscape transforming abilities via their effects on geomorphological processes. Both woody and herbaceous invasive species can have major impacts on the physical environment by altering sediment deposition patterns. Aquatic habitats may be transformed by species such as *Hymenachne amplexicaulis* (Houston and Duivenvoorden 2002) that tend to form dense, monospecific stands (Macdonald and Frame 1988). Invasive *Tamarix* spp. may alter river courses as they form dense stands that increase sedimentation rates by trapping and stabilizing sediments (Griffin *et al.* 1989). *Spartina* spp. (cord grasses) can rapidly alter the character of estuaries by increasing sediment deposition. Their growth along river banks and tidal channels can restrict water flow and cause widening of the flood plain (Asher 1991).

Invasive species also alter the geomorphological dynamics of beaches and dunes. For example, invasion by the European beach grass *Ammophila arenaria* has been found to alter dune formation processes in North America (Mooney *et al.* 1986) and Australia (Heyligers 1985). The Australasian tree *Casuarina equisetifolia* has also been found to affect dune dynamics in subtropical coastal regions of North America (Barbour and Johnson 1977).

Primary productivity and disturbance regimes

Invasive species may increase, decrease or have neutral effects on primary productivity (Walker and Smith 1997). Plant invasion may increase productivity by providing new life forms, new phenological patterns and/or new modes of resource acquisition. For example, productivity has increased dramatically in young volcanic sites in Hawaii that have been invaded by the nitrogen fixing tree *Myrica faya* (Walker and Smith 1997). Whereas the vigorous growth of many invasive species increases productivity (e.g. *Spartina* spp., Daehler and Strong 1996), slower growth or growth at a similar rate to the native species may lead to negative or neutral effects on productivity (Walker and Smith 1997).

Invasive species that alter disturbance regimes can have significant ecosystem-level consequences (Vitousek 1990) and probably the most dramatic impact of invasive species is their alteration of fire regimes (Woods 1997). Invasive species can alter the rate of spread, the probability of occurrence, and the intensity of fire, and where they do, they generally increase fire frequency and/or intensity (D'Antonio 2000).

Invasive species affect fire regimes by altering primary productivity, and thus fuel loads. Invasive species often produce more biomass than native species, providing higher fuel loads (Woods 1997). Fire regimes may also be altered by differences in the flammability, phenology or structure of the invaded community compared with the native vegetation (D'Antonio 2000). For example, differences in phenology between native and exotic species increase the fire risk in desert shrublands in Nevada where, in contrast to the native vegetation, the invasive grass *Bromus rubens* is able to germinate in spring and produce biomass that provides fuel throughout summer (Beatley 1966). The invasion of fire-tolerant, exotic plants often results in positive feedback loops between fire and weed invasion: as the weed becomes more abundant, fire frequency and intensity increases, fire-sensitive native species decline and the exotic species increases in abundance, further altering the fire regime (Vitousek *et al.* 1997; Rossiter *et al.* 2003). These invasive species are sometimes referred to as 'fire weeds' due their promotion of fire (Wilson and Mudita 2000).

Fire regimes are affected by various plant life forms. However, increased fire frequency and intensity have been particularly associated with invasion by exotic grasses (D'Antonio and Vitousek 1992; D'Antonio 2000). Many studies report increased fire frequency and/or intensity in association with invasion by exotic grasses (refer D'Antonio 2000). For example, invasion of *Artemisia* rangelands in the United States by *Bromus tectorum* (downy brome) has led to a reduction in fire interval from 60 to 110 years before invasion to less than five years after invasion (Whisenant 1990a). Exotic grasses that behave this way in Australia include *Andropogon gayanus, C. ciliaris, Melinis minutiflora* and *Pennisetum polystachion* (Low 1997).

Other plant growth forms have also been associated with altered fire regimes. In Africa, the vine *Chromolaena odoratum*, which rapidly smothers all types of native vegetation and is prominent in ecotones between forest and grassland, burns readily even when green and can allow fire to penetrate forest canopies that would otherwise not burn (Macdonald 1983). Invasion of dry rainforest remnants in Queensland by *Lantana camara* alters fuel characteristics and increases the flammability of these systems (Fensham 1996). In contrast, van Wilgen and Richardson (1985) concluded that invasive shrubs decrease the frequency and intensity of fire in South African fynbos under normal conditions. D'Antonio (2000) listed some tree and shrub species also considered to have the potential to decrease fire frequency.

Altered fire regimes may lead to significant changes in community composition as some species are favoured by the modified fire regime while others may suffer recruitment failure or are killed (Csurhes and Edwards 1998). Changes in fire regime can result in major structural changes such as the conversion of forest to savanna or grassland or of Mediterranean-climate shrubland to grassland (refer Woods 1997). Invasive plant-fire interactions have been reviewed by D'Antonio and Vitousek (1992) and D'Antonio (2000).

Plant invasions may also affect other disturbance processes including the frequency and intensity of wind throw, erosion and herbivory (Woods 1997). Invasive vines can change the likelihood of windfall by binding trees together and weighting their canopies (Thomas 1980). The establishment of *Larrea tridentata* (creosote bush) in desert communities in New Mexico reduces perennial herbaceous cover and soil aggregate stability, leading to soil loss by wind and water (Whitford *et al.* 2001). The invasive grass *Agropyron cristatum* also increases the erosion risk as it is associated with fewer water-stable aggregates and greater amounts of exposed soil than native prairie (refer Lesica and DeLuca 1996). Erosion may be promoted where invasive trees are shallow rooted or more susceptible to burning than the species they replace (Versfeld and van Wilgen 1986). Invasive plants may also alter plant-herbivore interactions through changes in plant density, chemistry and seed production (Walker and Smith 1997).

Community dynamics (competitive interactions, recruitment processes and succession)

Invasive plants may alter species interactions including competition and facilitation as well as community stability and successional pathways (Walker and Smith 1997).

Woods (1997) identified two main types of competition associated with invasive plants. Invasion could initiate competition between species of similar life history, resulting in the reduction or displacement of one or a few directly competing species. Alternatively, the invading species may have broad competitive effects on species of different guilds. In this case, the competitive effects may lead beyond floristic replacement to alteration of community structure. Invasive plants are often superior competitors for soil nutrients and water (D'Antonio and Vitousek 1992). Shading by invasive species, which inhibits growth and prevents regeneration, is also significant (Leigh *et al.* 1984) and many studies suggest that shading is the predominant mechanism responsible for invasive plant effects (Braithwaite *et al.* 1989; Downey and Smith 2000). Recruitment patterns may be affected by altered litter quantity and quality. Greater litter production by invasive species has been associated with altered recruitment patterns as germinants are smothered or the flammability characteristics of a site are altered (Vranjic *et al.* 2000).

The vigorous growth of invasive species such as *Spartina* spp. (Daehler and Strong 1996) and *Clematis vitalba* (Ogle *et al.* 2000) can smother native vegetation and reduce or prevent the establishment of native species. However, invasive species may affect recruitment and successional processes via mechanisms other than direct competition. For example, *M. faya* forms dense forests that may alter wind dispersal of propagules (Walker and Smith 1997). Some invasive species act as hosts for insect and fungal pests that attack native plants (Leigh *et al.* 1984) while others alter successional processes via allelopathic effects (Rice 1972). Shifts in successional pathways may be difficult to detect since they generally occur over considerable periods of time (Adair and Groves 1998).

2.1.3.3. Mechanisms underlying invasive plant impacts

Processes such as competition, allelopathy and production of flammable biomass have been defined as 'mechanisms' that generate invader impacts such as reduced diversity and increased fire frequency (Levine *et al.* (2003), although, as noted earlier, the differentiation between invasive plant effects and mechanisms producing effects is not clear cut. In general, the role of these processes in producing invasive plant impacts is poorly understood (Levine *et al.* 2003).

Relatively few studies investigating invasive plant impacts on plant community structure attempt to determine the mechanisms by which such effects are occurring (Levine *et al.* 2003). However, they often assume competitive effects. "Commonly introduced species are inferred to be superior competitors to natives for resources" and many studies simply "report a correlation between increased prominence of the alien and decreased native species population size, diversity, or vigour" (Daehler and Strong 1994). Competitive effects are often difficult to verify (Woods 1997) and are usually not investigated. Studies investigating invasive plant effects on higher trophic levels are generally also comparative (that is comparing invaded versus non-invaded areas), but are more likely to suggest a mechanism responsible for the observed effect (Levine *et al.* 2003). For example, Griffin *et al.* (1989) suggested that the reduced numbers of birds and reptiles associated with *Tamarix aphylla* invasion of river habitat in central Australia was due to lack of food supply and nesting holes, which made conditions less suitable for birds, and reduced numbers of logs and litter and a change in litter type, which made tamarisk-invaded areas less suitable for reptiles.

Whereas studies on the impacts of invasive plants on community structure rarely investigate the mechanisms of impact, studies examining invasive plant effects on ecosystem processes are generally more mechanistic, often attributing impacts to differences in functional traits between the invader and the resident species (Levine *et al.* 2003). For example, the importance of photosynthetic rates, water relations and growth of invasive African grasses in affecting ecosystem processes has been discussed by Williams and Baruch (2000). Other examples are given in Levine *et al.* (2003).

2.1.4. GRASSES: A FAMILY OF PROBLEM PLANTS

Grasses are a particularly problematic group of invading species. From work by Holm *et al.* (1977), Heywood (1989) identified the grass family (Poaceae) as one of three families (the others being Asteraceae and Papilionaceae) containing notable concentrations of invasive species of agriculture. The Poaceae is also over-represented among natural area invaders (Daehler 1998). Of the 18 species listed by Holm *et al.* (1977) as the world’s worst agricultural weeds 10 were grasses. Of the 18 species listed as Australia’s worst environmental weeds, six were grasses (Humphries *et al.* 1991).

Invasive grasses have been associated with reduced biodiversity (Houston and Duivenvoorden 2002; D’Antonio and Vitousek 1992; Lesica and DeLuca 1996). They are good competitors against both herbaceous and woody species (refer D’Antonio and Vitousek 1992) and may displace native species, forming monocultures (Humphries *et al.* 1991). They effectively compete for water and nutrients (D’Antonio and Vitousek 1992) and rapidly growing grasses can reduce light levels at the soil surface (refer D’Antonio and Vitousek 1992) and alter light quality, affecting the growth of other plants (Thompson and Harper 1988). Some invasive grasses have been reported to have allelopathic effects (Rice 1972).

As well as directly out-competing native species, invasive grasses affect ecosystem processes including water (Mueller-Dombois 1973) and nutrient (Ley and D’Antonio 1998) cycling, geomorpholocial processes such as wetland sedimentation (Daehler and Strong 1996) and dune formation (Heyligers 1985), as well as microclimate and disturbance regimes (D’Antonio and Vitousek 1992; Williams and Baruch 2000).

By out-competing native species and/or by altering ecosystem processes, invasive grasses may have ecosystem-level effects resulting in major changes in community composition and structure. Species such as *Hymenachne amplexicaulis* (Houston and Duivenvoorden 2002) and *Spartina* spp. (Daehler and Strong 1996) out-compete and smother native vegetation, changing wetland structure. *Brachiaria mutica* (Para grass) may cause changes in topography by accumulating large amounts of organic matter (Brown and Ramsay 1999). In arid and semi-arid habitats grasses are strong competitors against woody species (D’Antonio *et al.* 1998). By suppressing woody seedling survival, invasion by exotic grasses may result in conversion of woodland into grassland.

Probably the most significant impacts of exotic grasses are their effects on fire regimes (D’Antonio and Vitousek 1992). Invasion by grasses is associated with increased fuel loads and altered fire regimes in habitats around the world (Csurhes and Edwards 1998). Invasive grasses have introduced fire into areas where it was previously rare or absent (Smith 1985) and, in habitats where fire is already a natural occurrence, grass invasion may result in increased fire frequency and intensity (Levine *et al.* 2003).

Many exotic grasses have evolved with fire and have mechanisms for surviving and recovering rapidly after fire (Daubenmire 1968; Vogl 1975). Where exotic grasses are fire-adapted, they may be promoted by fire at the expense of less fire-adapted native species. For example, fires promote the noxious, perennial grass *Imperata cylindrica* by stimulating rhizome sprouting and by preventing the growth of native species that would otherwise shade it (Friday *et al.* 1999).

In addition to being adapted to fire, many invasive grasses actually promote fire and various attributes explain why this is so. The greater biomass production of invasive grasses compared with native species is often cited as a causal factor (Williams and Baruch 2000; Rossiter *et al.* 2003). Grass fuel distribution and flammability are also important. For example, the Asian grass *Imperata cylindrica*, which has invaded sand hills in Florida, provides a more continuous and higher fuel bed than the native vegetation, resulting in higher fire intensities (Lippincott 2000). Fire-promoting grasses such as *Melinis minutiflora*, *Andropogon virginicus* and *Schizachyrium condensatum* that have invaded Hawaiian ecosystems maintain very high dead:live biomass ratios throughout most of the year and burn at very high moisture contents, thereby providing a continuous fuel supply (Hughes *et al.* 1991). Differences in community structure due to grass invasions may also affect fire regimes. For example, wind speed, which directly affects fire characteristics, may be higher over grassland than over woodland (Freifelder *et al.* 1998).

Changes in fire frequency and intensity can have profound effects on community composition and structure. The seedlings of many woody species are susceptible to fire (Dyer *et al.* 1997) and invasive grass-induced changes to fire regimes can reduce or eliminate woody species. For example, the increased fire frequency associated with *Bromus tectorum* invasion in the Great Basin of North America has resulted in changes in vegetation structure with decline in shrub species (Billings 1990). Fires promoted by invasive grasses in seasonal sub-montane areas in Hawaii have resulted in reduced cover and diversity of shrubs and trees (Hughes *et al.* 1991). Altered fire regimes may have impacts on other ecosystem components and processes such as nutrient cycling and erosion processes.

Grass species have been moved both actively and accidentally around the world, resulting in some of the most destructive and widespread invasions (refer D'Antonio *et al.* 1998). In fact, grass invasions are considered widespread and effective enough to alter regional and even global aspects of ecosystem function (D'Antonio and Vitousek 1992). In their review on invasive grasses, D'Antonio and Vitousek (1992) suggested that at a regional scale invasive grasses may cause changes to climate, via conversion of forest to grassland, and changes to atmospheric composition, via changes in fire regime. They suggested that, at a global scale, grass invasions could contribute to functional change if exotic grass-fuelled fires added significantly to concentrations of greenhouse or ozone destroying gases, although they noted that this contribution appeared to be relatively small.

Grass invasions can be found on all continents, although examples from Eurasia and Africa are relatively rare (D'Antonio and Vitousek 1992). In North America, invasion has been most severe in the arid and semi-arid west and invasive species include European annual grasses and perennial bunchgrasses of African, Eurasian and South American origin. Although introductions of many European species were largely unplanned, perennial species have been deliberately introduced for pasture and for soil protection (D'Antonio and Vitousek 1992; Lesica and DeLuca 1996). Tropical Africa has been the centre of origin for a number of sown forage grasses that, once introduced into America, "have proven to be explosively aggressive, invading and holding vast areas wherever they have received minimal support by man" (Parsons 1972). Grasses of African origin, also introduced for pasture, have invaded savannas in Central and South America (D'Antonio and Vitousek 1992) and have become a problem in nature reserves in Brazilian savannas (Pivello *et al.* 1999). Exotic perennial grasses of African origin are also common throughout Oceania (D'Antonio and Vitousek 1992) and various species have had major impacts on Hawaiian native communities (Hughes *et al.* 1991). In Australia, there are about 310 exotic grass species (Michael 1994) with European annuals and African bunch grasses predominating (D'Antonio and Vitousek 1992).

2.1.5. INVASIVE PLANTS IN AUSTRALIA

The history of plant introductions into Australia prior to European settlement is unclear, although it is believed that at least three plant species (*Datura leichhardtii*, *Solanum erianthum* and *Centratherum punctatum*) were introduced prior to European settlement (Jacobs 1981). Undoubtedly most plant introductions have occurred since 1788 and these have been both accidental and intentional (Leigh *et al.* 1984). Groves (1986b) and Fox (1995) have reviewed exotic introductions into Australia.

The rate of plant introductions into Australia is unknown and the numbers of naturalised plants in Australia are also difficult to determine (Michael 1994). It is estimated that at least 1226 species have become naturalised in Queensland (refer Csurhes and Edwards 1998). However, despite the fact that only a small percentage of plant introductions become invasive weeds, exotic plants represent a significant threat to many Australian ecosystems (Humphries *et al.* 1991; Adair and Groves 1998). Williams and West (2000) stated that environmental weeds affect virtually all vegetation communities in Australia.

The majority of Australia's most serious weeds have been intentionally introduced (Panetta and Scott 1995). Many new species of grasses, legumes and other fodder species have been imported for pasture 'improvement' with inadequate consideration given to their potential impact on native ecosystems (Csurhes and Edwards 1998). In his review of grass and legume pasture introductions in northern Australia, Lonsdale (1994) reported that, of 463 introductions, 60 species (13%) became listed as weeds. Only 21 species (5%) were useful but some of these were also considered weedy (e.g. *C. ciliaris*), such that only four species (less than 1%) were useful and not weedy. The issue of deliberate plant introductions has attracted recent attention as problems associated with such species have become apparent and it is now recognized that a significant proportion of introduced species has weed potential.

Introduced grasses in particular have become the focus of attention for government agencies and others involved with resource management, particularly those managing land for conservation purposes. In their review of environmental weeds in Australia, Humphries *et al.* (1991) considered grasses to be an insidious and serious problem. They noted that grass invasions are inconspicuous and the mechanism of altering ecosystem structure and function is gradual so the process is easily overlooked. Adair and Groves (1998) stated that “Exotic grasses can alter ecosystem functions thereby causing substantial and often irreversible changes to native biotic communities”.

The impacts of invasive grasses have been described above (section 2.1.4) and have been reviewed in an Australian context by Humphries *et al.* (1991) and Low (1997). Low (1997) considered the two outstanding problems associated with introduced pasture grasses in Australia to be (1) the impacts of terrestrial species on fire regimes which cause habitat change and (2) the impacts of semi-aquatic species on wetland structure. Many introduced grasses are highly productive and produce more biomass than the native species they are replacing. In addition, they may be highly flammable (e.g. *Melinus minutiflora*, Paul Williams, *pers comm*.) and/or cure later (e.g. *Pennisetum polystachyon*, Gill *et al.* 1990), creating the potential for severe, late season fires. They regenerate quickly after fire and can form dense monocultures, displacing native species and can become dominant over large areas (Low 1997). The vigorous growth of semi-aquatic species also displaces native species and can alter wetland structure (e.g. *Brachiaria mutica*, Brown and Ramsay 1999 and *Hymenachne amplexicaulis*, Houston and Duivenvoorden 2002). Some introduced grasses considered to be problematic in Australia are listed in Table 2.1.

Attempts to deal with the threat of intentionally introduced species must address conflicts of interest within society (Panetta and Scott 1995). For example, introductions involving ornamental or aquarium plants involve conflicts between commercial and environmental interests. However, the most difficult conflicts to resolve are those involving the introduction of species for the purpose of increasing primary production (Panetta and Scott 1995).

Table 2.1. Some introduced grasses considered to be problematic in Australia.

Achnatherum spp.
Andropogon gayanus (Gamba grass)
Agrostis capillaries (Brown-top vent)
Ammophila arenaria (Marrum grass)
Anthoxanthum odoratum (Sweet vernal)
Avena spp.
Brachiaria decumbens
Brachiaria mutica (Para grass)
Briza maxima (Large quaking grass)
Bromus diandrus (Great brome)
Cenchrus cililaris (Buffel grass)
Cortaderia spp. (Pampas grasses*)*
Echinochloa polystachya (Aleman grass)
Eragrostis curvula
Ehrharta calycina (Veldt grasses)
Glyceria maxima
Hymenachne amplexicaulis
Hyparrhena hirta (Tambookie grass)
Melinus minutiflora (Molasses grass)
Nassella spp.*/ N. trichotoma* (Serrated tussock)
Panicum maximum (Guinea grass)
Pennisetum clandestinum (Kikuyu)
Pennisetum polystachyon (Mission grass)
Spartina spp. (Cord grass)
Sorghum halepense (Johnson grass)
Stenotaphrum secundatum (Buffalo grass)
Sporobolus pyramidalis (Giant rats tail grass)
Themeda quadrivalvis (Grader grass)

(Source: Humphries *et al.* 1991; Gardener and Sindel 1998; Parsons and Cuthbertson 2001; CRC for the Sustainable Development of Tropical Savannas web site).

2.1.5.1. Weeds or wonder plants

> "Conflicts are likely to arise where plant introductions with high potential value to rural industries may have an undesirable impact on native ecosystems" (Adair 1995).

Exotic plants have been introduced into many countries to enhance livestock productivity. Any negative consequences of such introductions were generally unforeseen or were overshadowed by the perceived benefits of these species. The enthusiasm for such introductions was significant. One observer commenting on the introduction of *Panicum maximum* (guinea grass) to Columbia called *P. maximum* "a true miracle grass" and suggested that the unknown person responsible for its introduction into the Magdalena Valley in the 1830s deserved a statue "as high as New York's Statue of Liberty, illuminated by night….so as to be visible throughout the vast area of the new haciendas of the *tierra calienta* that it had made productive" (Rivas 1946).

In Australia during the mid 1900s considerable effort was made to source and establish exotic pasture species (Mott 1986). More recently however, the enthusiasm for introduced species has been dampened by recognition of their potential negative effects. There is now considerable debate about the value of pasture introductions (Lonsdale 1994; Low 1997; McIvor *et al.* 2000).

Many introductions were promoted before their negative effects became apparent. For example, the invasive tree *Tamarix aphylla* was “widely and heartily recommended” for ornamental and shade planting in central Australia (Griffin *et al.* 1989). However, some species have been actively promoted by particular agencies despite concerns being raised by other groups. For example, Low (1997) reported that while there were concerns that *Hymenachne amplexicaulis* was “behaving badly” and that, as a high-risk species, it should be declared a noxious weed, it was being promoted by the Queensland Department of Primary Industries. *Andropogon gayanus* was promoted by agencies in northern Australia who initially ignored warnings regarding its detrimental effects and continued to promote its use despite considerable opposition (Whitehead and Wilson 2000).

The fact that many pasture introductions have the potential to become weeds should come as no surprise since some of the characteristics they were selected for, as desirable pasture species, parallel those suggested as being characteristics of an ideal weed (Mott 1986). Resilience to disturbance, ability to invade new sites and to out-compete native plants under grazing conditions are highly valued characteristics, which at the same time put native systems at risk (Whitehead and Wilson 2000). As summed up by Panetta and Scott (1995): “Herein lies the crux of the problem: some of the characteristics that make a species useful in an agronomic context also predispose it to invasive behaviour”.

It is not unusual for an introduction to be welcomed by some interests while condemned by others (Williamson 1996). For example, in Australia *Echium plantagineum* takes over grazing lands and is known as ‘Paterson’s curse’ to graziers. However it is valued by bee keepers who refer to it as ‘Salvation Jane’ (Williamson 1996). The invasive, stoloniferous grass *Bothriochloa pertusa* (Indian couch), which has become naturalised in north Queensland, is variously regarded as a useful forage grass and a weed of pastoralism (Grice 2000).

Cenchrus ciliaris is a particularly controversial introduced grass. “It seems that some people love it and others hate is and there are very few in between” (White 1997). It is recognized as one of the most important pasture introductions for arid and semi-arid Australia and has been called “the outstanding improved pasture grass in the drier areas of Queensland” (Paull and Lee 1978). It is very drought-tolerant, can withstand heavy grazing once established, and is able to establish, persist and produce under harsh climatic conditions (Paull and Lee 1978). It is a strong competitor, producing more biomass than native perennial grasses and high yields of light, fluffy seeds that are readily spread by wind and water (Hall 2001). However, these very characteristics give it its weed potential. It has spread into non-target areas (Griffin

1993; Woinarski 2001) and has been reported to form monocultures, displacing native species and altering fire regimes (Humphries *et al.* 1991; Franks *et al.* 2000).

Consequently, different interest groups have very different perceptions of the value of this species. While ‘Landcare’ supports the pastoral industry to meet its sustainable industry goals by rehabilitating land with *C. ciliaris*, a few kilometres away conservation agencies are concerned with the impact of *C. ciliaris* in parks (Stafford Smith 1994). The following transcript from the ABC daily National Rural News program (18 August 1997, www.abc.net.au/rural/news_states/nrn/nrn-18aug1997-2.htm) illustrates how emotive the *C. ciliaris* issue can be.

> Cattle producers are outraged at news of a research study underway in Western Australia that they claim is looking into the possibility of finding a biological control agent to eradicate buffel grass……. Richard Golden from the Cattlemens Union … says buffel grass has an estimated worth of $1.5 billion. Richard Golden**:** *We do have to accept the fact that buffel grass is of vital economic importance to this entire Australian community, we're not just talking pastoralism here, we're talking about something which, if it was biologically eradicated, stands a chance of destroying profitable pastoralism across a whole heap of this country.*

2.1.6. *CENCHRUS CILIARIS*

The genus name *Cenchrus* is derived from ‘kenchros’ which is the Greek name of a small millet or one of the cereals used by the ancient Greeks that resembled small millet (Wagner *et al.* 1990). There are about 30 *Cenchrus* species world wide, found mainly in warm, dry regions of Africa, America and south west Asia (Harden 1993). Eleven species are listed by Sharp and Simon (2002) as being present in Australia. These are: *C. biflorus* (=*C. barbatus*), *C. brownii*, *C. caliculatus* (=*C. australis*, Hillside burrgrass), *C. ciliaris*, *C. echinatus* (Mossman River grass), *C. elymoides*, *C. incertus* (=*C. pauciflorus*, *C. tribuloides*, Spiny burrgrass), *C. longispinus* (=*C. pauciflorus*, *C. tribuloides*, Gentle Annie, Innocent weed), *C. pennisetiformis* (Cloncurry buffel, (Paull and Lee 1978)), *C. robustus* and *C. setiger* (Birdwood grass). Only *C. caliculatus*, *C. elymoides* and *C. robustus* are native (Sharp and Simon 2002).

2.1.6.1. Origin, introduction and establishment in Australia

Cenchrus ciliaris is native to north tropical and south Africa, India and Indonesia (Humphreys 1974). It is believed to have first been introduced into Australia accidentally, being brought to Wallal in the north-west of Western Australia as a contaminant of Afghan camel harness between 1870 and 1880 (Marriott 1955). It rapidly became naturalised there (Humphreys 1974) and its spread to other areas was systematically encouraged (Humphreys 1967). In 1910, seed was spread at Port Hedland and, after World War I, the Western Australian Department of Agriculture distributed lines of *Cenchrus* sent by General Birdwood from Afghanistan (Humphreys 1967). This was the source of the first *Cenchrus* in Queensland, arriving in the 1920s (Hall 2001). The early history of *C. ciliaris* is described by Humphreys (1967) and its spread in Queensland is described by Cavaye (1991).

Cenchrus ciliaris has been the subject of agricultural extension activity in northern Australia since the 1920s (Humphries 1967). In the 1950s *C. ciliaris* became the prominent sown pasture grass for the more arid zones of northern Australia and was well researched for its potential to improve pastures across Queensland, Western Australia and the Northern Territory (Hall 2001). Most plantings have taken place since the late 1950s (Paull and Lee 1978). It has also been used for soil stabilization and erosion control (Albrecht and Pitts 1997; Grigg *et al.* 2000), although in some situations it fails to provide effective surface cover (Harwood *et al.* 1999).

There have been 580 direct official *Cenchrus* accessions introduced to Australia from 35 countries (Hall 2001). Nine cultivars are described in the Register of Australian Herbage Plant Cultivars (Oram 1990). These are usually categorized on the basis of height. Tall varieties (up to 1.7 m) include 'Biloela' and 'Nunbank', medium height varieties (up to 1 m) include 'Gayndah' and 'American' and short varieties (up to 0.4 m) include 'West Australian' (Paull and Lee 1978). 'Gayndah', 'American' and 'Biloela' are the most widely sown varieties (Cavaye 1991).

Today *C. ciliaris* is well established in arid and semi-arid zones in Western Australia, South Australia, New South Wales and in the MacDonnell Ranges bioregion, Northern Territory (Pitts and Albrecht 2000; Franks and Hannah 2001). It is by far the most widely distributed, sown pasture grass in Queensland (Cavaya 1991) and is estimated to be abundant or dominant over 30 to 50 million ha (Woinarski 2001). In north Queensland, *C. ciliaris* forms extensive stands in the Desert Uplands bioregion (Sattler and Williams 1999) and is a prevalent species in the Dalrymple Shire (Roger Lawes *pers. comm.*).

2.1.6.2. Physical description and growth characteristics

Cenchrus ciliaris is a summer growing, perennial, C_4 tussock grass. It grows up to 1.7 m tall, depending on variety and growing conditions, and has a large, deep root system with some cultivars having short rhizomes (Paull and Lee 1978). Its stems are erect to somewhat prostrate, often kneed towards the base, and are extensively branched (Cunningham *et al.* 1981). Leaves are basal and cauline, with blades 3-25 cm long and 4-10 mm wide (Sharp and Simon 2002). It has a cylindrical 'foxtail' seed head, 2.5-15 cm long and 8-16 mm in diameter. The rachis of the seed head is a serrated stalk to which clusters of one to three spikelets are attached by very short stalks. Each cluster, or fascicle, is surrounded by a cup-shaped circle of bristles (involucre) (Paull and Lee 1978) and may contain one to five seeds (Humphreys 1981). *Cenchrus ciliaris* produces seed apomictically so cultivars breed true to type. However, odd plants do reproduce sexually and these have been used for cultivar development (Paull and Lee 1978).

Cenchrus ciliaris is grown in regions receiving 300 to 1000 mm average annual rainfall (Humphreys and Partridge 1995). It is less productive than other species in higher rainfall, coastal areas and its growth is checked by frost (Paull and Lee 1978). Its drought and grazing tolerance are associated with its deep spreading root system and its characteristic of stem bud development being slightly below ground level (Marriott 1955). It also has swollen stem bases that accumulate carbohydrates, allowing it to survive drought and fire, and to green up more rapidly than other species after rain (Humphreys 1974). *Cenchrus ciliaris* does not have day length requirements for flowering, which is promoted by rain (Humphreys and Partridge 1995). There is a long period of head production during the growing season (Humphreys 1981) and it produces abundant seed (Franks *et al.* 2000; Hall 2001).

Cenchrus ciliaris is adaptable in its soil requirements. It grows in soils of moderate fertility but with variable textures, preferring lighter textured soils but it still grows well on self-mulching soils (Humphreys 1974). Although it is not as demanding of nutrients as some other introduced species (Humphreys and Partridge 1995), establishment is quicker and drought tolerance superior on high phosphorus soils (Paull and Lee 1978). It has only moderate salt tolerance and is sensitive to water logging (Anderson 1972; Humphreys 1974).

Cenchrus ciliaris is recognised as strongly competitive once established. However, its spread and colonising ability is more contentious (McIvor 2003). Spread of *C. ciliaris* from established pastures has often been low or non-existent and is less than for some other introduced grasses (Hacker 1989; McIvor 2003). In contrast, as an invasive weed *C. ciliaris* has been reported to be a highly successful invader and its ease of spread and invasive nature is cited as a serious problem (Latz 1991; Griffin 1993). The spread of *C. ciliaris* appears related to the degree to which disturbance reduces competition from existing flora (Humphries 1976; Cavaya 1991). McIvor (2003) pointed out that competition from resident plants is critical to controlling the spread of *C. ciliaris*: it is able to colonise bare areas but is unable to invade dense vegetation.

2.1.6.3. *Cenchrus ciliaris* – valuable pasture species or destructive invader?

In a pastoral context, *C. ciliaris* is highly valued for its wide adaptation, productivity under grazing and, particularly, its drought tolerance (Hall 2001). It “has converted low producing shrublands to highly productive grazing lands” (Paull and Lee 1978) and “brought great financial benefit to many individual producers and companies” (Hall 2001). It is well adapted to a wide range of soils and the climate of arid and semi-arid Australia (Hall 2001) and has become one of the most important pasture introductions for this region. In fact, in many inland areas it is the only suitable sown grass (Cavaya 1991).

However, while the spread and persistence of *C. ciliaris* have long been valued by the pastoral industry, its domination of native vegetation and the associated changes in species richness and fire regimes are of concern to non-pastoral land managers, particularly those responsible for conservation areas. Low (1997) considered *C. ciliaris* to be “perhaps the most destructive” of Australia’s introduced pasture grasses. It has been associated with lower plant diversity both in Australia (Fairfax and Fensham 2000; Franks 2002) and overseas (Saucedo-Monarque *et al.* 1997; Daehler and Carino 1998). It displaces native vegetation, for example *Triodia* spp. (Spinifex) and Aboriginal food plants in Western Australia (Keighery 1991). It may also affect other biota and has been associated with reduced invertebrate (Best 1998) and vertebrate (QPWS 2001) diversity. In central Queensland, Ludwig *et al.* (2000) found that Delicate Mouse (*Pseudomys delicatulus*) numbers declined as *C. ciliaris* cover increased. *Cenchrus ciliaris* is an aggressive coloniser of moist habitats, such as river levees and alluvial pans, where it forms dense monocultures (Humphries *et al.* 1991). It is a major threat to key mesic areas in the arid zone where it has spread rapidly during periods of high rainfall and flooding (Griffin 1993). These mesic habitats are critical parts of the landscape where rare and relic native species occur and colonization of *C. ciliaris* in these sites is believed to threaten the survival of these species (Humphries *et al.* 1991).

Cenchrus ciliaris is also considered to be altering local fire regimes. It produced more biomass and cures later than the native perennial grasses, causing hotter fires later in the season and an increased incidence of fire (Humphries *et al.* 1991; Latz 1991). It is a threat to dry rainforest remnants as it grows along the edges and within the remnants, carrying hot fires that progressively destroy the rainforest (Fensham 1996). It appears that there is positive feedback between *C. ciliaris* and fire. *Cenchrus ciliaris* increases the risk of fire and the abundance of *C. ciliaris* has been found to increase after fire (Butler and Fairfax 2003). It has also been suggested that *C. ciliaris* has allelopathic effects (Cheam 1984ab; Nurdin and Fulbright 1990).

Many *Cenchrus* species have traditionally been considered weeds as their burrs contaminate wool and their barbed spines damage skin (Harden 1993). As early as 1906 *C. australis* R. BR. (Australian) (hillside burr grass) was included in “The weeds and suspected poisonous plants of Queensland” (Bailey 1909). Today the environmental impacts of *C. ciliaris* in particular are recognized and it is included in various weed lists for Australia (e.g. the “CSIRO’s handbook of Australian weeds”, Lazarides *et al.* 1997) and overseas (e.g. Hawaii, Smith 1985). Although acknowledged as one of Australia’s worst environmental weed (Humphries *et al.* 1991), *C. ciliaris* is not currently listed as a weed of national significance (www.weeds.org.au/natsig.htm).

Despite the assertion, in conservation management circles at least, that *C. ciliaris* has negative impacts on biodiversity and fire regimes, there is little evidence of these impacts, in terms of quantitative data, in the literature. The impacts of *C. ciliaris* are often stated without supporting data. For example, the report by Humphries *et al.* (1991) is a commonly cited reference to *C. ciliaris* impacts. However, no data are provided in this report and the authors acknowledge that the information given is anecdotal. Although some published studies do provide quantitative data, these generally report comparisons between invaded and non-invaded areas (e.g. Fairfax and Fensham 2000). There are difficulties in determining the impacts of invasive species using this approach since the data are essentially correlative and do not provide evidence of cause and effect (Wheeler and Giller 1982). Consequently, in addition to the need for more quantitative data describing this species in an ecological context, studies are required to investigate the mechanisms underlying *C. ciliaris* effects. Determining the impacts of invasive plants is problematic. Issues relating to investigating invasive plant effects and techniques available are briefly discussed below.

2.1.7. MEASUREMENT AND ASSESSMENT OF INVASIVE PLANT IMPACTS

Determining the impacts of invasive plants is problematic on three fronts. Firstly, what should be measured? Invasive plant impacts may vary depending on what is measured and at what scale it is measured. Secondly, measurement of plant impacts is often difficult technically, complicated by the fact that pre-invasion data are often not available and invasive plant effects are often confounded with disturbance effects. The third issue is how to assess any measurement of impact.

2.1.7.1. What to measure

Invasions may be deemed positive or negative depending on what is investigated. For example, the invasive tree *Tamarix aphylla* has been associated with lower numbers of reptiles and most birds, but it has a positive effect on numbers of aerial, insectivorous birds (Griffin *et al.* 1989). D’Antonio *et al.* (2000) noted that their data suggested that the “impacts of exotic species on community composition are both species and context dependent”. In their study of the impacts of exotic grasses on native plant composition in Hawaii they found that not all grasses had the same impact, the impact of a particular species varied over the range in which it was found, and the species varied in their ranges.

The population dynamics of the invader and response of the community vary over space and time. Therefore, in addition to determining what should be measured, the spatial and temporal scales of measurement are important (Parker *et al.* 1999). For example, McIvor (1998) reported oversowing native pastures with a mixture of exotic legumes and grasses reduced the total number of species recorded on a plot basis but increased the numbers found at a smaller scale. The detected effects of invasive species may vary considerably depending on the timing of measurements also. For example, the cover of perennial grasses and annual plants is reduced under newly established *Larrea tridentata* shrubs in New Mexico. However, the highest cover of perennial grasses is found under their canopies once they are mature (Whitford *et al.* 2001).

Adair and Groves (1998) recommended measuring a broad range of environmental parameters to determine invasive plant impacts on diversity, ecosystem-level functions and successional consequences. However, while some properties, such as plant productivity may be relatively easily measured others, such as ‘stability’ may be very difficult to measure (Walker and Smith 1997).

2.1.7.2. How to measure plant impacts

Four principal techniques can be used to determine invasive plant impacts: (1) multi site comparisons, (2) weed removal, (3) weed addition, and (4) time series studies. These are reviewed by Adair and Groves (1998) and Walker and Smith (1997).

The multi site comparison approach involves comparing sites where the invader species is present with sites where the invader is absent (Adair and Groves 1998). The advantage of this method is that it allows detailed data to be collected within a short time period. However, considerable care needs to be taken in matching invaded and control sites and to explore alternative hypotheses that could explain any observed differences. The method assumes that the invaded and control sites were similar prior to the invasion (Adair and Groves 1998) but very often the relevant pre-invasion data needed to verify this are not available. Invasion often occurs simultaneously with habitat modification (D'Antonio *et al.* 1998), making it difficult to differentiate between effects of the plant and disturbance (Vitousek 1986; Woods 1997; Lambrinos 2000). Invasive species are often so widespread that by the time they are noticed it is impossible to identify comparable control (uninvaded) and invaded sites for study (D'Antonio *et al.* 1998).

Weed removal and addition studies use manipulative techniques to investigate the impacts of invasive plants. Weed removal studies, where the invasive species is totally or partially removed, may provide strong evidence of invasive plant impacts (Adair and Groves 1998). However, the removal process may itself impact on the system, thereby confounding disturbance and invasive plant effects (D'Antonio *et al.* 1998). Plant removal studies have been criticized because of potential problems such as soil disturbance during removal, soil compaction during monitoring and unknown effects of leaving root material in the soil (refer D'Antonio *et al.* 1998). A further limitation of this method is that a long time frame may be required to detect changes due to plant removal. This method is not suitable in situations where the invader has caused irreversible damage such that the ecosystem is unable to return to its uninvaded state (Walker and Smith 1997; Adair and Groves 1998).

Weed addition studies can provide irrefutable evidence of the impacts of invasive plants as pre-invasion conditions can be measured. However, long monitoring times may be required to assess any impacts (Adair and Groves 1998). The greatest disadvantage with this method is the issue of weeds escaping and invading new areas. As noted by Vermeij (1996), "Invaders can have unforeseen and often destructive effects on recipient communities. The field of invasion biology should therefore adopt the standard that work with non-native species or populations be carried out under strictly controlled laboratory conditions from which accidental release of individuals, including gametes and dispersal stages is impossible". Weed addition experiments are commonly conducted under artificial conditions, for example in pots in a glasshouse, and very few attempts have been made to use this technique under field conditions (Adair and Groves 1998).

Time sequence studies involve monitoring the impact of invasive species at a site over time (Adair and Groves 1998). Walker and Smith (1997) stated that the best way to measure the impact of an invader is to have measurements before, during and after invasion has occurred. However, such opportunities are rare and again, this technique may require long monitoring periods to detect invasive plant impacts.

As the limitations of these different techniques indicate, the measurement of invasive plant impacts is hindered by a number of factors. Lack of detailed background information and the coarseness of most ecosystem-level measurements make it difficult to detect small or subtle effects (Vitousek 1990). For example, invasive plant species are likely to alter plant-herbivore interactions but the wide fluctuations in herbivore populations, particularly following a disturbance, make it difficult to determine the effects of an invasive plant (Breytenbach 1986). Most studies documenting changes in species diversity or vigour have used the multi-site comparison technique (Adair and Groves 1998). This is essentially a survey technique and its value in determining invasive plant effects is limited by problems of lack of pre-invasion information and confounding factors as described above. It provides only correlative data and lacks the power of manipulative studies for determining causal relationships (Adair and Groves 1998). Consequently, there is a need for manipulative experiments in invasive plant impact studies (Walker and Smith 1997). However, the more powerful, controlled, replicated methods are the most difficult to conduct (Woods 1997; Parker *et al.* 1999).

2.1.7.3. Impact assessment

The assessment of invasive plant impacts is a critical one for management. If the impact of an invasive plant is not quantitatively assessed, valuable resources may be wasted in control programs (Adair and Groves 1998). In Australia, there are no uniformly recognised national criteria to assess environmental weed effects (Humphries *et al.* 1991). Assessing the impacts of invasive plants is not straight forward. In contrast to invasions on agricultural land where impacts of invasive plants can be assessed in terms of economic losses, impacts of invasive plants on natural and semi-natural systems involve some kind of ‘ecological damage’ that can be hard to define (Eser 1998) and evaluate in economic terms. As noted by Williams and West (2000), problems caused by environmental weeds cannot be simply stated in economic terms because they include issues of ecosystem stability, function and biodiversity.

Central to assessing invasive plant impacts is determining what level of change will be considered an impact and how significant that impact is (Morrison 1997). Parker *et al.* (1999) noted that relatively little attention has been placed on developing generalizations regarding the level of invasive species impact. They pointed out that there can be surprising disagreement over the magnitude of invasive species impacts, due, in part, to lack of baseline data on the original ecosystem structure or function as well as the fact that there is no common framework for quantifying or comparing the total impacts of invaders. They proposed describing the overall impact of an invasive species in terms of the total area occupied, the abundance of the species and some measure of the impact per individual. However, they acknowledged that while measuring area and abundance may be straight forward, quantification of ecological effects is not.

2.1.8. CONCLUSIONS

Invasive plants are of increasing ecological importance world wide (Groves 1991) and exotic grasses in particular have been involved in some of the most destructive and widespread invasions (Parsons 1972; D’Antonio and Vitousek 1992). As superior competitors for light, water and nutrients, invasive, exotic grasses often dominate vegetation and displace native species and grass invasions have been associated with reduced biodiversity and the alteration of successional processes (D’Antonio and Vitousek 1992). As well as directly affecting vegetation composition and structure, exotic grasses may cause major habitat change via effects on ecosystem processes. Their effects on fire regimes are probably the most significant. Exotic grasses often produce more biomass and burn later in the season than the native species they replace (Low 1997). They may promote hotter, more frequent fires and introduce fire into areas where it was previously rare or absent (Smith 1985; Mack and D’Antonio 1998). The resultant changes to fire intensity and timing may have profound implications for ecosystem structure and function (Macdonald *et al.* 1989; Vitousek 1990). Such major, habitat-changing impacts mean that exotic grasses are a serious problem in many different ecosystems worldwide.

Until recently, the ecological impacts of grasses in natural ecosystems in Australia had received little attention (Adair and Groves 1998). However, today there is considerable concern about their negative impacts and particular attention has been drawn to those species deliberately introduced for pasture improvement (Humphries *et al.* 1991; Lonsdale 1994; Low 1997; Whitehead and Wilson 2000). Invasive, introduced grasses are believed to have a profound effect on a broad range of plant and animal communities in Australia at both the habitat and landscape level (Adair and Groves 1998). The problems associated with introduced grasses were highlighted by Humphries *et al.* (1991) in their report on environmental weeds in Australia. Of the 18 species they listed as Australia's worst environmental weeds, five are tropical pasture grasses. One of the most controversial inclusions in this list is *C. ciliaris*.

In a pastoral context *C. ciliaris* has been highly regarded, both for its value as pasture for livestock and for its soil protecting properties (Hall 2001). However, more recently it has received increasing attention because of its apparent effects on biodiversity and fire regimes (Humphries *et al.* 1991; Low 1997). C*enchrus ciliaris* is a strong competitor and its high seed yields and light, fluffy seed allow it to spread readily via wind and water (Hall 2001). It aggressively colonizes moist habitats, such as river levees, and has been reported to form dense monocultures displacing native vegetation (Humphries *et al.* 1991). Its effects on native flora may flow-on to affect native animals (Humphries *et al.* 1991; Ludwig *et al.* 2000) and *C. ciliaris* has been associated with decreased plant (Fairfax and Fensham 2000; Franks 2002), invertebrate (Best 1998) and vertebrate (QPWS 2001) diversity. In addition to directly out-competing native species, *C. ciliaris* invasion may result in major habitat change via its effects on fire regimes. *Cenchrus ciliaris* invasion leads to hotter late-season fires and an increased incidence of fire (Humphries *et al.* 1991; Latz 1991; Butler and Fairfax 2003). Consequently, invasion by *C. ciliaris* is seen as a major threat to key mesic habitats in the arid zones (Humphries *et al.* 1991) and fire sensitive vegetation (Woinarski 2001).

Although *C. ciliaris* is now considered one of Australia's worst environmental weeds (State of the Environment Advisory Council 1996), there are relatively few published studies quantifying its ecological effects. Given the extensive distribution of *C. ciliaris* in Queensland, its potential for further spread, and the controversy regarding its 'value', the ecological impacts associated with this species need to be determined.

2.2. IS THERE A RELATIONSHIP BETWEEN HERBACEOUS SPECIES RICHNESS AND *CENCHRUS CILIARIS* ABUNDANCE?

2.2.1. INTRODUCTION

There are few published studies quantifying relationships between *C. ciliaris* and species richness. *Cenchrus ciliaris* has been associated with reduced plant species richness in central Queensland (Fairfax and Fensham 2000; Franks 2002) whereas in north-eastern Queensland, both increases and decreases in species richness in *C. ciliaris*-dominated vegetation were found at one site, depending on the scale of measurement (McIvor 1998).

In this chapter two studies are described. The overall aim of the studies was to document herbaceous species richness patterns in relation to *C. ciliaris*. In the first study, the relationship between *C. ciliaris* and herbaceous species richness was investigated by comparing species richness of *C. ciliaris*-dominated sites and non-*C. ciliaris* sites in the Dalrymple Shire, north-eastern Queensland. In such site-comparison studies it is often difficult to determine the effects of exotic plants on species richness since other factors, such as soil fertility and grazing regime, may influence species richness and their effects are often confounded with those of the invader. In the second study, the relationship between *C. ciliaris* and species richness was investigated at a single site in the absence of grazing to help minimize some of these confounding factors. Rather than comparing species richness between areas with and without *C. ciliaris*, in this study the relationship between *C. ciliaris* and herbaceous species richness was investigated by comparing areas with varying levels of *C. ciliaris* biomass.

There is a considerable literature dealing with the relationship between plant species richness and community productivity, often measured as biomass (see reviews by Grace 1999; Waide *et al.* 1999; Mittelbach *et al.* 2001). It has been suggested that there is a general relationship, described by the well known ‘humped-back curve’ (Grime 1973; 1979), in which species richness is highest at intermediate biomass levels and lower at high and low biomass, reflecting changes in stress and/or disturbance levels. However positive, negative and no relationship between biomass and species richness have also been reported (Waide *et al.* 1999). The aim of the second study was to determine if there was a relationship between herbaceous species richness and *C. ciliaris* biomass and whether the species richness-biomass relationship for *C. ciliaris* was different from that for a dominant native species. Herbaceous species richness and biomass data were collected from plots varying in composition from dominance by *C. ciliaris* to dominance by *Bothriochloa ewartiana*, a native perennial grass. This enabled comparison of patterns of species richness in relation to *C. ciliaris* and *B. ewartiana* biomass.

2.2.2. METHODS

2.2.2.1. Study area

Sites for both studies were located within the Dalrymple Shire, north-eastern Queensland, Australia. The Dalrymple Shire covers an area of 68,850 km^2, extending from 22^{o}05'S to 18^{o}30'S and is bounded by the Great Dividing Range on the west and a chain of coastal ranges on the east. The climate is dry tropical with an average annual rainfall of between 500 and 700 mm, 80% of which falls between December and April. However, rainfall is extremely variable from year to year (Quirk *et al.* 1997; Ash *et al.* 2002). There are many geological landscapes in the region, which give rise to a complex mixture of land types (Ash *et al.* 2002). Soils vary from sands and massive earths to cracking clays and are generally low in nitrogen and phosphorus. The main vegetation type is eucalypt woodland with a grassy understorey. There are scattered acacia communities throughout the Shire, open grasslands in the south-west and some small areas of rainforest, mainly on the coastal ranges (Quirk *et al.* 1997).

Livestock grazing is the predominant land use in the Shire (Quirk *et al.* 1997). Although native grasses are the main pasture resource supporting the livestock industry, increasing areas have been sown to introduced legumes and grasses (McIvor 1998). The main sown exotic grasses are *C. ciliaris* and *Urochloa mosambicensis* (sabi grass). As well as deliberate sowing, significant areas have been colonized by exotic grasses. *Cenchrus ciliaris* has spread readily in disturbed river frontage country and other exotic grasses, such as *Bothriochloa pertusa* (Indian couch), have become naturalized in the region (Ash *et al.* 2002).

2.2.2.2. Study one: herbaceous species richness with and without *Cenchrus ciliaris*

Study sites

Herbaceous species richness was surveyed at seven *C. ciliaris*-dominated sites and nine non-*C. ciliaris* sites between April and June 2000. Sites were selected on the basis of dominant herbaceous species, being either dominated (in terms of biomass) by *C. ciliaris* or not. It was not possible to find paired sites (neighbouring sites with and without *C. ciliaris*) due to limited resources. The sites used here were selected on the basis that they were accessible given the resources available. Sites included a range of landscape types and grazing regimes that varied from currently ungrazed to grazed by livestock and native marsupials (Table 2.2). At each site, a survey plot (8 m by 8 m) was positioned to avoid trees, shrubs, grazed-out patches and scalds. Where possible, plots without *C. ciliaris* (non-*C. ciliaris* plots) were positioned to avoid large patches of exotic grasses. However, two non-*C. ciliaris* plots were dominated by *B. pertusa*.

Table 2.2. Latitude and longitude, soil type and current grazing regime of *C. ciliaris* and non-*C. ciliaris* plots surveyed in the Dalrymple Shire.

Latitude	Longitude	Soil type*	Current grazing
***Cenchrus ciliaris* plots**			
20°13´S	146°34´E	Chromosol	yes
20°07´S	146°19´E	Chromosol	yes
20°10´S	146°30´E	Chromosol	yes
19°25´S	145°51´E	Tenosol	yes
19°49´S	146°06´E	Tenosol	no
19°53´S	146°11´E	Ferrosol	yes
19°41´S	145°45´E	Ferrosol	no
Non-*C. ciliaris* plots			
20°12´S	146°34´E	Chromosol	no
20°27´S	145°44´E	Kandosol	no
20°21´S	145°48´E	Kandosol	yes
20°10´S	146°28´E	Chromosol	yes
20°14´S	146°40´E	Chromosol	yes
20°33´S	146°08´E	Sodosol	yes
19°53´S	146°11´E	Ferrosol	yes
19°53´S	146°11´E	Ferrosol	yes
19°41´S	145°46´E	Ferrosol	no

*Soil type determined using the Land Resources of the Dalrymple Shire (Rogers *et al.* 1999) data base. Soils were classified to order using the Australian Soil Classification (Isbell 1996).

Vegetation sampling

In each plot, herbaceous species were recorded using a nested plot design (Rosenzweig 1995). Given the importance of scale in assessing patterns of species richness (Bond and van Wilgen 1996), this method was chosen to provide data at a range of scales. Starting at one corner, data were collected from areas doubling in size from 1-64 m^2, providing seven scales. A string grid was laid out over each plot to facilitate data collection. Species were counted by recording the species found at the first scale and then recording any new species found at each successive scale. While successive scales doubled in size, all scales were searched on a 1 m^2 basis using a square metal frame moved over the area to outline contiguous quadrats. When determining species numbers, unidentifiable plants were counted if they were distinct from species already counted. Unknown species were collected for later identification. Plants that could not be assessed as different, such as small seedlings, were excluded from the species counts. Numbers of species of legumes, other forbs (referred to from here on as forbs), sedges, perennial grasses, annual grasses, exotic and 'rare' species were determined. Rare species were defined as those species found in only one plot in the survey. Numbers of species in some plant groups were under-estimated since unidentified plants could not be categorized.

Species-area curves

Species-area curves for *C. ciliaris* and non-*C. ciliaris* plots were derived using the power function in CurveExpert 1.3 (Hyams 2003). Species-area curves relate species number and area, usually by the power function: $S = cA^z$ where S is the number of species found in area A (Williams 1996). C and z are estimable parameters, c being the expected number of species in a unit areas and z being the instantaneous rate by which species richness increases with an incremental increase in area (Pastor *et al.* 1996).

2.2.2.3. Study two: herbaceous species richness with varying *Cenchrus ciliaris* biomass

Study site

The second study was conducted at Hillgrove Station (19°40'S; 145°45'E). The soil is a eutrophic red ferrosol (Isbell 1996) developed on basalt and is of moderate fertility. The vegetation is open woodland with an average tree density of 64 trees/ha and average tree basal area of 5.5 m^2/ha. The upper stratum is comprised mainly of *Eucalyptus crebra* (ironbark) and *Corymbia erythrophloia* (bloodwood) trees (McIvor *et al.* 1991). The herbaceous layer is dominated by perennial grasses including *C. ciliaris* and native species such as *B. ewartiana*, *Heteropogon contortus* and *Chrysopogon fallax*. An experimental site had been established on this property for a different study in 1981 and a detailed site description is given by McIvor *et al.* (1991).

The area used for this study was a spare paddock within the original experimental site. This paddock, of approximately 3 ha, was used to hold cattle from time to time and has been ungrazed or very lightly grazed since 1981. The herbaceous layer was dominated by two perennial grasses, *C. ciliaris* and *B. ewartiana*. *Cenchrus ciliaris* was not originally present at the site (McIvor *et al.* 1991). It was sown in some paddocks along with other exotic species in 1981 and has since spread into unsown areas. Eighteen 8 m by 8 m plots were located in the paddock in March 2000 using a stratified, random sampling procedure. Plots were selected to vary in biomass composition, from dominance by *C. ciliaris* to dominance by *B. ewartiana*. Trees and large patches of other grass species were avoided.

Vegetation sampling

In each plot, herbaceous species numbers were recorded using the nested plot design described above, but in study two data were collected from areas doubling in size from 0.25-64 m^2, providing nine increasing scales/plot. In addition, herbaceous biomass and the percentage *C. ciliaris* and *B. ewartiana* biomass were estimated at each scale. Total herbaceous biomass was estimated using the BOTANAL technique (Tothill *et al.* 1992). This method involves visually ranking quadrats and converting rank scores to biomass using a relationship determined from a set of ranked and weighed standards. For scales 1-8 m^2, biomass was estimated over the whole area using 1 m^2 contiguous quadrats. (Smaller quadrat sizes were used for the 0.25 and 0.50 m^2 scales). Due to time constraints, the whole area of larger scales (16 m^2 and above) could not be surveyed. For these larger scales, the biomass in additional areas was estimated by surveying half the area using randomly selected quadrats. For example for the 16 m^2 scale, 8 m^2 was fully surveyed (as it made up the previous scale). The biomass of the other 8 m^2 was estimated using four randomly positioned 1 m^2 quadrats. In addition to biomass rank, the percentage of *C. ciliaris* and *B. ewartiana* biomass present in each quadrat was estimated to the nearest 5%.

Plots were surveyed in March and April 2000. As it was not possible to rank and cut standards for each sampling day, a series of 12 permanent biomass standards were set up at the start of the data collection period. The standards were 1 m^2 plots ranging from low to high biomass and varying in dominant species. At the end of each sampling day the standards were ranked. After all plots had been surveyed the standards were cut at approximately ground level. Material was considered in the quadrat if it fell within the vertically projected quadrat boundaries. The material was oven dried at 65°C before being weighed. For each sampling day, the linear rank–biomass relationship calculated from the standards was used to convert the biomass ranks of plots surveyed that day.

Data analysis

Relationships between biomass and species richness in study two were investigated using linear regression. Data from each scale were analysed separately. Different methods were used to investigate species richness-*C. ciliaris* biomass relationships at small and large scales because of differences in biomass composition with scale. At the smallest scales (up to 1 m^2), most plots were dominated, in terms of biomass, by either *C. ciliaris* or *B. ewartiana*; that is plot biomass was at least 70% *C. ciliaris* or *B. ewartiana.* Linear relationships between dominant species biomass and species richness for *C. ciliaris*-dominated plots (n = 9) were compared with those for *B. ewartiana*-dominated plots (n = 8). At larger scales, plot biomass composition was more variable and few plots were dominated by one species. Therefore, biomass-species richness relationships were investigated using all 18 plots together. Relationships between *C. ciliaris* biomass and species richness were investigated using multiple linear regression with *C. ciliaris* biomass and total biomass as independent variables (there was little correlation between *C. ciliaris* and total biomass in these data sets). This method allowed investigation of *C. ciliaris* biomass effects on species richness while allowing for total biomass effects (i.e. total biomass was treated as a covariate). Relationships between *C. ciliaris* biomass and the number of grass, forb (here forbs included one sedge species), legume and forb plus legume species as a group were similarly investigated. Where there was no total biomass effect, simple linear regression was used. Relationships between total biomass and species richness and *B. ewartiana* biomass and species richness were also investigated using linear regression. Since *B. ewartiana* biomass and total biomass were highly positively correlated (average r = 0.724) the multiple linear regression model was inappropriate.

Correlations between species-area curve parameters and biomass have been used to investigate species richness-biomass relationships (Pastor *et al.* 1996; Weiher 1999). Species-area curves were derived for each plot using CurveExpert 1.3 (Hyams 2003) as described above. Linear regression was used to test for relationships between the parameters *c* and *z* and *C. ciliaris* biomass and total biomass. All analyses were performed using Genstat (2001).

2.2.3. RESULTS

2.2.3.1. Study one: herbaceous species richness with and without *Cenchrus ciliaris*

Mean species richness was lower in *C. ciliaris* plots than in non-*C. ciliaris* plots at all scales investigated (Figure 2.1a). At the smallest scale (1 m^2), species richness ranged from 1-4 (mean ± SE of 3 ± 0.4) species/m^2 for *C. ciliaris* plots and from 4-14 (mean ± SE of 9 ± 1.2) species/m^2 for non-*C. ciliaris* plots. At the largest scale (64 m^2), species richness ranged from 17-32 (mean ± SE of 21 ± 2.0) species/64 m^2 for *C. ciliaris* plots and from 20-53 (mean ± SE of 40 ± 3.7) species/64 m^2 for non-*C. ciliaris* plots.

New species were found in the last sampling area in all plots. On average, the final doubling of the search area, from 32 m^2 to 64 m^2, resulted in an additional six species being found in *C. ciliaris* plots (a 46% increase in species number) and an additional eight species in non-*C. ciliaris* plots (a 25% increase in species number).

Trends in species richness within individual plant groups generally reflected the pattern found for total species richness. There were fewer forb, legume and perennial grass species at all scales (Figures 2.1b-d) and fewer sedges at the two largest scales in *C. ciliaris* plots compared with non-*C. ciliaris* plots. Numbers of sedge species at smaller scales and annual grasses at all scales were too low to determine distribution patterns. In total 47 forb, 26 legume, 28 perennial grass, 13 annual grass and four sedge species were found in the survey (see appendix 1A).

In terms of species numbers, *C. ciliaris* and non-*C. ciliaris* plots differed at all scales. However, in terms of proportional composition, *C. ciliaris* and non-*C. ciliaris* plots differed at the smallest scales only (Figure 2.2a). At the 1 m^2 scale, most species in *C. ciliaris* plots were perennial grasses. Only one *C. ciliaris* plot contained a forb at this scale and only four legume species were found over all *C. ciliaris* plots. In comparison, although perennial grasses were the largest group in non-*C. ciliaris* plots, forb and legume species were almost as abundant. All non-*C. ciliaris* plots contained one or more legumes at the 1 m^2 scale and all but two plots contained forbs. This difference in proportional composition declined with increasing scale with *C. ciliaris* and non-*C. ciliaris* plots being similar in terms of proportional composition by the 4 m^2 scale. At the largest scale, forbs were the most abundant species group in both *C. ciliaris* and non-*C. ciliaris* plots (Figure 2.2b).

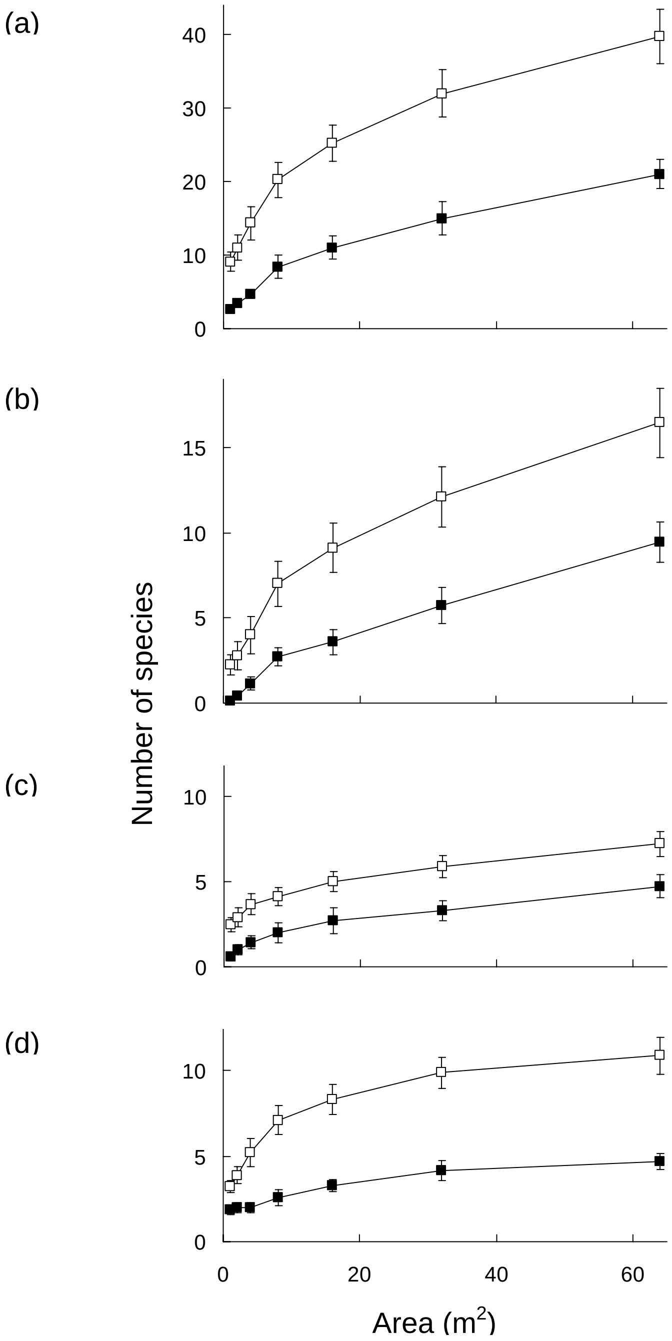

Figure 2.1. Mean (± SE) numbers of species for *C. ciliaris* plots (■) and non-*C. ciliaris* plots (□) at each of seven scales from 1-64 m^2. Figure (a) shows the total number of species. Figures (b-d) show numbers of non-leguminous forb, legume and perennial grass species respectively.

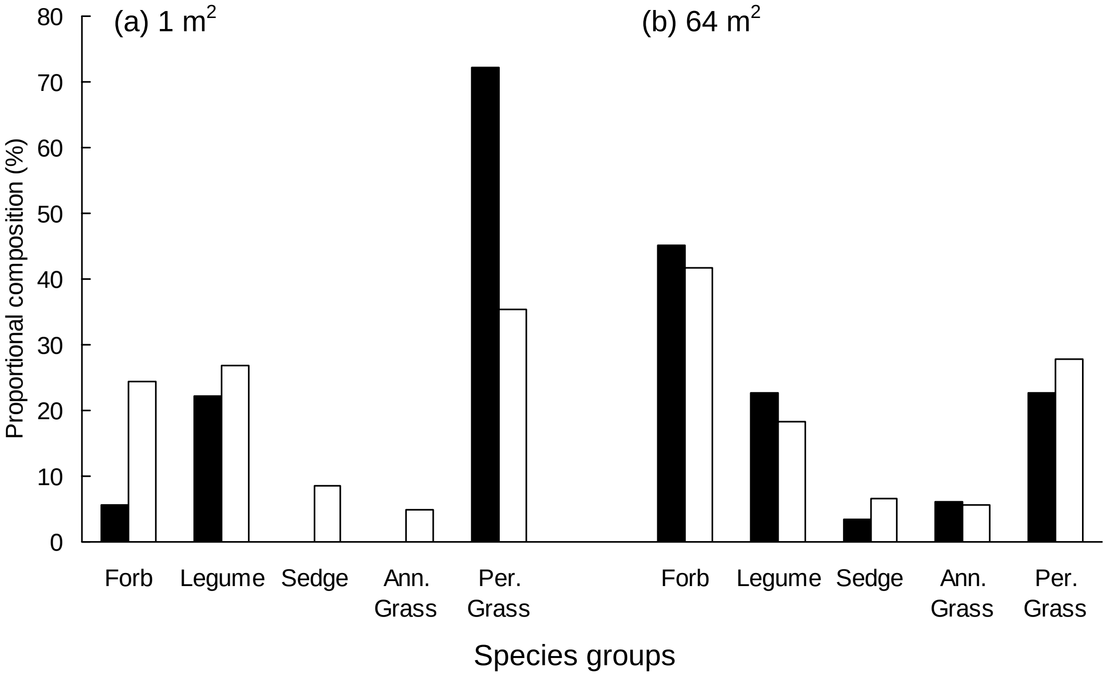

Figure 2.2. Proportional composition, in terms of numbers of non-leguminous forb, legume, sedge, annual grass and perennial grass species, of *C. ciliaris* plots (■) and non-*C. ciliaris* plots (□) at (a) 1 m^2 and (b) 64 m^2 scales.

Exotic species were found in all plots and mean numbers were not very different between *C. ciliaris* plots (mean ± SE of 4.6 ± 0.43 exotics/plot) and non-*C. ciliaris* plots (mean ± SE of 3.7 ± 0.47 exotics/plot). The exotic species identified included four forbs, four legumes, one annual grass and four perennial grasses. *Cenchrus ciliaris* plots had fewer native species (mean ± SE of 9.4 ± 1.39 native species/plot) than non-*C. ciliaris* plots (mean ± SE of 26.2 ± 2.76 native species /plot).

In this study 28 species were classified as 'rare' (occurring in only one plot in the survey). Most plots contained rare species and there was little difference in mean numbers of rare species between *C. ciliaris* plots (mean ± SE of 1.1 ± 0.40 rare species/plot) and non-*C. ciliaris* plots (mean ± SE of 2.2 ± 0.52 rare species/plot). Rare species included 14 forbs, six legumes, one sedge, four annual grasses and three perennial grasses.

The distribution of some individual species/genera differed between plot types. Three forbs, one legume and five grasses occurred in most non-*C. ciliaris* plots but were absent from most or all *C. ciliaris* plots (Figure 2.3).

Taxa	Number of *C. ciliaris* plots							Number of non-*C. ciliaris* plots								
	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9
Evolvulus alsinoides						▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	
Hybanthus enneaspermus								▨	▨	▨	▨	▨	▨	▨	▨	
Phyllanthus spp.						▨	▨	▨	▨	▨	▨	▨	▨			
Zornia spp.								▨	▨	▨	▨	▨	▨	▨	▨	
Aristida spp.								▨	▨	▨	▨	▨	▨			
Bothriochloa ewartiana							▨	▨	▨	▨	▨	▨	▨	▨	▨	
Chrysopogon fallax						▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	
Panicum spp.								▨	▨	▨	▨	▨	▨			
Tripogon loliiformis						▨	▨	▨	▨	▨	▨	▨	▨			

Figure 2.3. Herbaceous taxa showing contrasting distribution between *C. ciliaris* and non-*C. ciliaris* plots. The number of shaded cells indicates the number of plots in which the species was present.

The mean species-area curves for *C. ciliaris* and non-*C. ciliaris* plots differed. While *c* values were lower for *C. ciliaris* plots (mean ± SE of 2.9 ± 0.46) than for non-*C. ciliaris* plots (mean ± SE of 9.3 ±1.41), the reverse was true for *z* values (mean ± SE of 0.51 ± 0.058 and 0.37 ± 0.024 for *C. ciliaris* and non-*C. ciliaris* plots respectively).

2.2.3.2. Study two: herbaceous species richness with varying *Cenchrus ciliaris* biomass

The 1999-2000 wet season experienced higher than average rainfall (866 mm from October 1999 to April 2000), the third consecutive wet season to do so (Ash *et al.* 2002). These good seasons and the absence of grazing resulted in very high biomass levels in the Hillgrove plots. Mean (± SE) estimated biomass at the largest scale (64 m^2) was 768 (± 45.0) g/m^2. Plot biomass composition varied as area increased. At the smallest scales (up to 1 m^2), all but one plot were dominated by either *C. ciliaris* or *B. ewartiana*: nine plots had greater than 70% *C. ciliaris* while eight plots had greater than 70% *B. ewartiana*. At larger scales, plot composition was more variable and fewer plots were dominated by a single species (Figure 2.4). Other species generally made a minor contribution to total biomass (for example between 1 and 29% at the largest scale). At all scales, plots ranged in composition from less than 1% to greater than 95% *C. ciliaris* biomass.

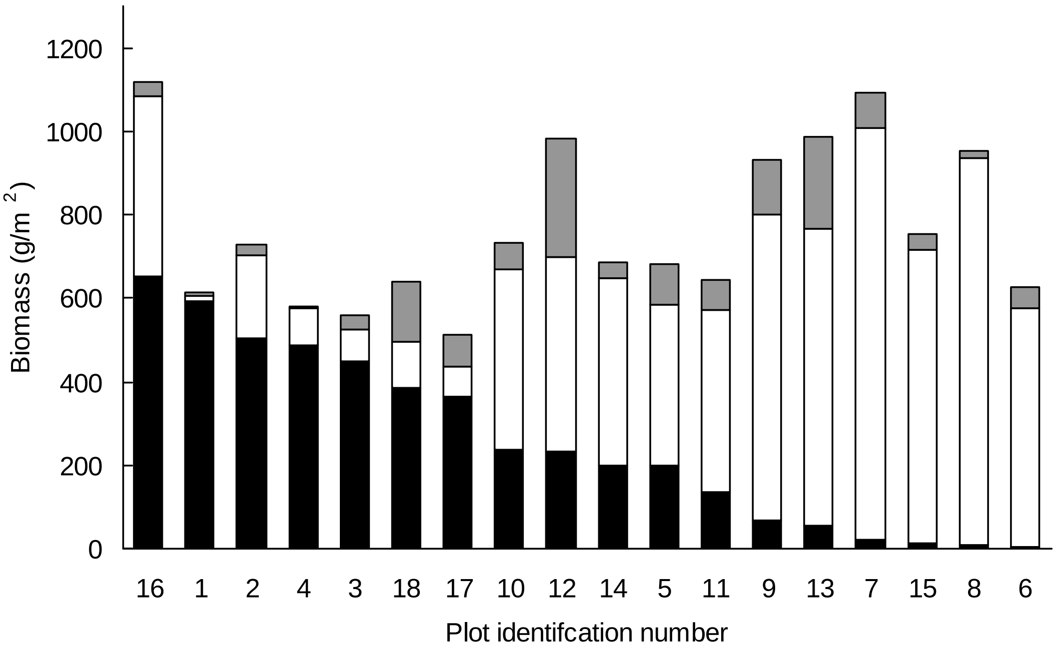

Figure 2.4. Composition of 18 plots in terms of *C. ciliaris* (■), *B. ewartiana* (□), and other herbaceous species (▨) biomass (g/m^2) at the 64 m^2 scale, presented in order of declining *C. ciliaris* biomass.

Species richness ranged from 1-4 (mean ± SE of 2.4 ± 0.2) species/0.25 m^2 at the smallest scale (0.25 m^2) and from 14-30 (mean ± SE of 20 ± 1.0) species/64 m^2 at the largest scale (64 m^2). Over all plots 24 forbs, 20 legumes, 17 perennial grasses, three annual grasses and one sedge were identified (see appendix 1B).

Significant linear trends of declining species richness with increasing *C. ciliaris* biomass were found at some scales. At the smallest scales, species richness declined with increasing *C. ciliaris* biomass in *C. ciliaris*-dominated plots and *C. ciliaris* biomass explained up to 57% of the variation in species number (Figure 2.5). In contrast, no significant linear trends were found between *B. ewartiana* biomass and species richness at these scales ($P > 0.10$) in *B. ewartiana*-dominated plots (Figure 2.5).

At intermediate scales also, species richness tended to decline with increasing *C. ciliaris* biomass. At these scales, the multiple linear regression model with predictor variables total biomass and *C. ciliaris* biomass was significant ($P < 0.05$) (Table 2.3). After accounting for the effects of total biomass, *C. ciliaris* biomass had a significant effect ($P < 0.05$) on species richness at the 2 m^2 and 8 m^2 scales while its effect was not significant at the 0.05 level ($P < 0.08$) at the 4 m^2 and 16 m^2 scales. At the two largest scales, the multiple linear regression model was not significant (P > 0.10) and no relationships between species number and *C. ciliaris* biomass were detected using simple linear regression (P > 0.10). No significant relationships between *B. ewartiana* biomass and herbaceous species richness were found at intermediate or large scales (P > 0.05) (Table 2.3).

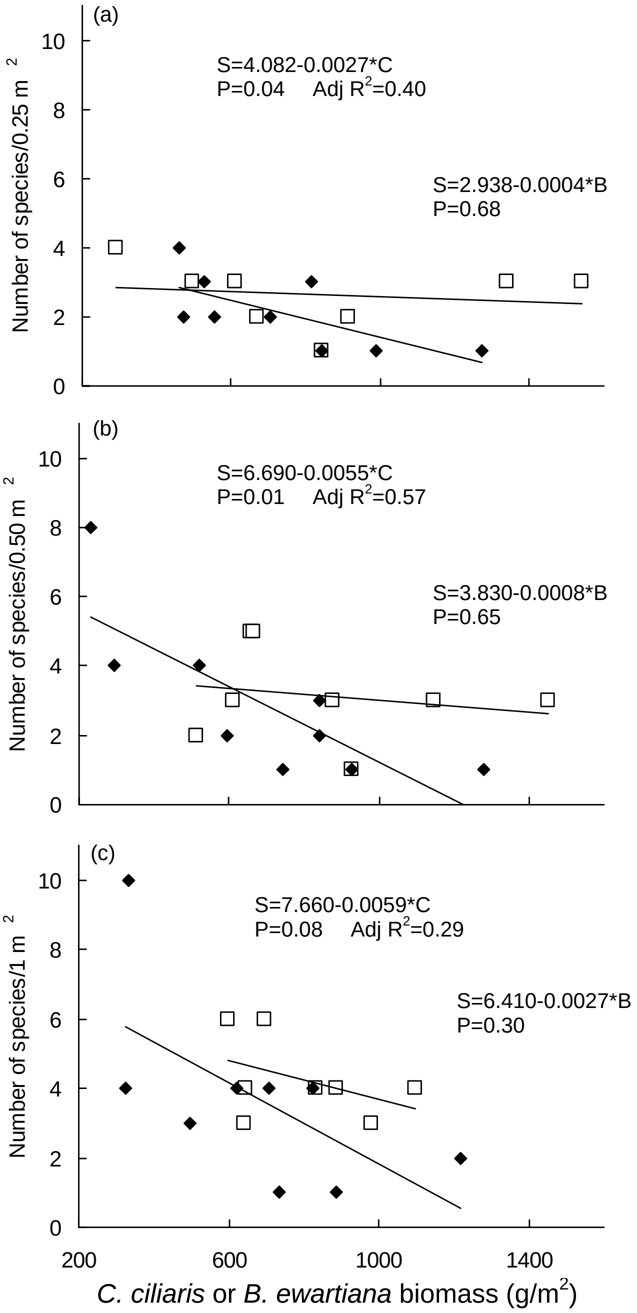

Figure 2.5. Herbaceous species number in relation to dominant species (*C. ciliaris* or *B. ewartiana*) biomass (g/m^2) for *C. ciliaris* (◆) and *B. ewartiana* (□) dominated plots at (a) 0.25 m^2, (b) 0.5 m^2 and (c) 1 m^2 scales. Regression lines and equations are shown. S = species number, C = *C. ciliaris* biomass and B = *B. ewartiana* biomass.

Table 2.3. Summary of regression analyses investigating relationships between biomass and herbaceous species richness at scales 2-64 m^2 for (a) *C. ciliaris* and (b) *B. ewartiana*. Multiple linear regressions were significant for scales 2-16 m^2 where the predictor variables were *C. ciliaris* biomass and total biomass. (The response variable was species number). (Note: correlation between total and *C. ciliaris* biomass ranged from r = -0.164 to -0.359). Simple linear regression was used to investigate *C. ciliaris* biomass-species number relationships at 32 and 64 m^2 scales (since total biomass was not significant) and *B. ewartiana* biomass-species number relationships at 2-64 m^2 scales; multiple linear regression being inappropriate because *B. ewartiana* and total biomass were highly correlated.

Scale		Parameter	Estimate	SE	t prob.	Regression	
						F. prob.	Adj. R^{2*}
2 m^2	(a)	Constant	9.38	1.48	<0.001	0.01	0.41
		C. ciliaris biomass	-0.0038	0.0014	0.014		
		Total biomass	-0.0047	0.0017	0.013		
	(b)	Constant	4.42	0.79	<0.001	0.75	
		B. ewartiana biomass	0.0004	0.0013	0.745		
4 m^2	(a)	Constant	12.47	2.20	<0.001	0.02	0.31
		C. ciliaris biomass	-0.0038	0.0020	0.077		
		Total biomass	-0.0072	0.0027	0.016		
	(b)	Constant	6.32	1.00	<0.001	0.73	
		B. ewartiana biomass	-0.0006	0.0019	0.734		
8 m^2	(a)	Constant	18.30	3.02	<0.001	0.01	0.41
		C. ciliaris biomass	-0.0077	0.0026	0.010		
		Total biomass	-0.0105	0.0036	0.011		
	(b)	Constant	8.14	1.28	<0.001	0.85	
		B. ewartiana biomass	0.0050	0.0025	0.847		
16 m^2	(a)	Constant	22.87	4.00	<0.001	0.03	0.30
		C. ciliaris biomass	-0.0076	0.0037	0.058		
		Total biomass	-0.0131	0.0047	0.013		
	(b)	Constant	11.84	1.52	<0.001	0.55	
		B. ewartiana biomass	-0.0018	0.0029	0.547		
32 m^2	(a)	Constant	14.96	1.54	<0.001	0.54	
		C. ciliaris biomass	0.0029	0.0046	0.537		
	(b)	Constant	17.54	1.62	<0.001	0.19	
		B. ewartiana biomass	-0.0044	0.0032	0.194		
64 m^2	(a)	Constant	19.27	1.65	<0.001	0.44	
		C. ciliaris biomass	0.0040	0.0050	0.440		
	(b)	Constant	22.72	1.76	<0.001	0.11	
		B. ewartiana biomass	-0.0056	0.0034	0.114		

*Adj. R^2 is the difference between residual and total mean squares expressed as a proportion of the total mean square (Lane and Payne 1998).

Herbaceous species richness tended to decline with increasing total biomass, but only at intermediate scales (simple linear regression P = 0.06, 0.04, 0.09 and 0.06 for scales 2, 4, 8 and 16 m^2 respectively). However, the amount of variation in species number explained by total biomass was less than 20%. (Other parameters affecting species number were not investigated). No linear relationships between species number and total biomass were found at the larger scales.

Significant relationships between *C. ciliaris* biomass and numbers of species in individual plant groups were found at some scales ($P < 0.05$) (Table 2.4). However, it is not clear whether any group was more responsive to *C. ciliaris* biomass than others. Trends of decreasing species numbers with increasing *C. ciliaris* biomass were found for grasses, legumes and forbs plus legumes. No relationship between forb species and *C. ciliaris* was detected except at the largest scale at which forb species richness increased with increasing *C. ciliaris* biomass. No relationships between numbers of species in individual plant groups and *B. ewartiana* biomass were found except at the largest scale where the numbers of forb and forb plus legume species declined with increasing *B. ewartiana* biomass ($P < 0.05$).

The species-area curve parameters *z* and *c* were not linearly related ($P > 0.05$) to *C. ciliaris* biomass or to total biomass.

Table 2.4. Summary of regression analyses investigating relationships between *C. ciliaris* biomass and the numbers of species of forbs, legumes, forbs plus legumes and grasses at scales from 2-64 m^2. Values are t probabilities for the estimates of *C. ciliaris* biomass where significant ($P < 0.05$). (Non-significant t probabilities are denoted 'ns'). Multiple linear regression, using *C. ciliaris* and total biomass as predictor variables, was applied when the total biomass effect was significant ($P < 0.05$) (denoted *). Otherwise simple linear regression was used. The direction of statistically significant trends between *C. ciliaris* and species number is given in brackets.

Scale	Forbs	Legumes	Forbs+Legumes	Grasses
2 m^2	ns	ns	0.017 (-)*	ns
4 m^2	ns*	ns	ns*	ns
8 m^2	ns	0.014(-)*	0.023 (-)*	0.017 (-)*
16 m^2	ns	0.019 (-)*	0.050 (-)*	ns
32 m^2	ns	ns	ns	ns
64 m^2	0.023 (+)	ns	ns	ns

2.2.4. DISCUSSION

Cenchrus ciliaris has been associated with decreased plant species richness both in Australia (McIvor 1998; Fairfax and Fensham 2000; Franks 2002) and overseas (Saucedo-Monarque *et al.* 1997; Daehler and Carino 1998). The two studies reported here also provide quantitative data demonstrating a negative association. In study one, species richness of *C. ciliaris* plots was, on average, only 53% that of non-*C. ciliaris* plots. This difference falls within the range found by Fairfax and Fensham (2000) who reported that the species richness of *C. ciliaris* pastures was 29% of that of native pastures in cleared brigalow woodlands and 65% of that of native pastures in cleared eucalypt woodlands in central Queensland. The trend of decreasing herbaceous species richness with increasing *C. ciliaris* biomass found in study two provides further evidence of this negative association.

Species richness was lower in *C. ciliaris* plots than in non-*C. ciliaris* plots at all scales investigated. These findings contrast with those of McIvor (1998) who reported that pastures oversown with *C. ciliaris* had higher species richness compared with native pastures at the quadrat scale (0.25 m^2) but lower species richness at the plot scale (12.5 m^2). Patterns of species richness may vary across spatial scales (Bond and van Wilgen 1996) and, although *C. ciliaris* was found to be associated with reduced species richness at the scales investigated, it is not clear how the species richness of *C. ciliaris*-dominated vegetation compares with that of non-*C. ciliaris* vegetation at much larger scales. The species-area curves predict that *C. ciliaris* plots will have more species than non-*C. ciliaris* plots at large scales since the mean z for *C. ciliaris* species-area curves was greater than that of non-*C. ciliaris* curves. However, caution is required in extrapolating species-area curves. The power function model generally applied to the species-area relationship may not be the best model, or even a valid model, for fitting data at large scales (Kilburn 1966; Williams M. R. 1995). The power function is unbounded and so predicts that as area increases, species increase without limit. However, it is known that species-area curves are asymptotic. In addition, in this study it appears that the plot area was not large enough to adequately sample community species richness. In all plots, a considerable number of additional species were found in the last search area and additional species were frequently observed outside the plot boundaries. Consequently, c and z have been derived from only a portion of the curves and the shapes of these curves, and estimates of c and z, are likely to alter as larger areas are added. Given these constraints, it is not valid to extrapolate these species area curves to predict species richness patterns at much larger scales.

Although no absolute conclusions can be drawn from the species-area curves, there is some evidence that species richness differences between *C. ciliaris*-dominated vegetation and non-*C. ciliaris* vegetation may diminish at larger scales. The magnitude of the difference between the two vegetation types decreased with increasing scale. The species richness of non-*C. ciliaris* plots was 3.5 times that of *C. ciliaris* plots at the 1 m^2 scale but only 1.9 times higher at the 64 m^2 scale. Also, *C. ciliaris* and non-*C. ciliaris* plots were more similar in terms of proportional composition as scale increased. Further work is required to determine species richness patterns in relation to *C. ciliaris* dominance at larger scales.

Both the spatial and temporal scales at which measurements are made are important considerations in ecological studies (Critchley and Poulton 1998; MacNally and Quinn 1998). Patterns of species richness at small spatial scales may not reflect species richness patterns at larger scales. Temporal changes in species richness patterns are also difficult to predict as the influences of disturbance and competition on species richness change over time. The role of disturbance may be detrimental or beneficial depending on its characteristics and those of the vegetation. For example, increases in *C. ciliaris* biomass may alter local fire regimes (Humphries *et al.* 1991; Latz 1991; Butler and Fairfax 2003) resulting in the loss of some native species. Alternatively, disturbances including fire may prevent the competitive exclusion of other species by *C. ciliaris* by creating gaps in the sward.

The negative association between *C. ciliaris* and species richness found in study one was supported by the results of study two in which negative *C. ciliaris* biomass-species richness relationships were found. Species richness may be influenced by site biomass and many studies report biomass-species richness relationships (e.g. Wheeler and Giller 1982; Moore and Keddy 1989; Wisheu and Keddy 1994). However, the effects observed here were not simply total biomass effects: *C. ciliaris* biomass effects were detected in addition to total biomass effects. Importantly, while total herbaceous species richness responded to *C. ciliaris* biomass, it appeared unaffected by *B. ewartiana* biomass. No relationships between total herbaceous species richness and *B. ewartiana* biomass were detected. The negative association between *C. ciliaris* biomass and species richness is consistent with the view that *C. ciliaris* reduces species richness. The results also support those of Franks (2002) who found a negative correlation between *C. ciliaris* cover and herbaceous species richness at the 1 m^2 and 'site' (30 m^2) scales in central Queensland. However, the results do not provide an explanation for the *C. ciliaris*-species richness association. Explanations for the relationship, such as competitive and/or allelopathic effects (Cheam 1984ab; Nurbin and Fulbright 1990), need to be tested experimentally.

Although relationships between *C. ciliaris* biomass and species richness were statistically significant ($P < 0.05$), the results should be interpreted with caution because of variability in the data and inconsistency in results. Occasionally individual plots had high leverage and their omission alters the outcome of the analyses. In addition, the observed trends were not statistically significant at all scales within the range over which relationships were detected. The relationships detected were generally not strong, with biomass explaining less than 50% of the variation in species richness in most cases.

Determining the role of invasive plants in reducing biodiversity is problematic. Invasion often occurs simultaneously with habitat modification (Ramakrishnam and Vitousek 1989; Vitousek 1990; D'Antonio *et al.* 1998), making it difficult to differentiate between the effects of the exotic species and other disturbance factors (Vitousek 1986; Woods 1997). Many studies make comparisons between invaded and non-invaded sites and then imply a causal relationship between exotic invasion and the differences detected. However, correlative data do not provide evidence of cause and effect (Wheeler and Giller 1982). Plant species richness may be influenced by a range of factors that vary across sites and these may be confounded with exotic plant effects. For example, Fairfax and Fensham (2000) acknowledged that the precise cause of species loss associated with *C. ciliaris* pastures in central Queensland could not be easily identified since grazing and tree clearance could also have affected species richness. Some of these major confounding factors were eliminated in the Hillgrove study by investigating the relationship between *C. ciliaris* biomass and species richness within a single vegetation type in the absence of grazing. However, the cause of species richness decline with increasing *C. ciliaris* biomass remains unclear. Although it is likely that the observed trends reflect the superior competitive ability of *C. ciliaris*, it is possible that species richness is affected by other factor(s) correlated with *C. ciliaris* biomass.

The failure to detect consistent, strong biomass-species richness relationships may reflect the fact that other factors are important in influencing species richness at this site. Although it was selected for its relative uniformity in terms of soil type and overall vegetation structure, the site varies in soil nitrogen%, phosphorus% and rockiness (McIvor *et al.* 1991). These and other unmeasured factors may be influencing species richness. Another explanation for the failure to detect consistent, strong biomass-species richness relationships may be that the range of biomass levels was insufficient. Detecting trends in species numbers is likely to be more difficult over small ranges in biomass. For example, in their study of wetland plant species richness–biomass relationships in eastern Canada, Moore and Keddy (1989) detected species richness trends with biomass only when a wide range of biomass values was included in the analysis. When more restricted ranges were used, no systematic trends were found. Insufficient variation in independent and dependent variables may make detecting biomass-species richness patterns difficult (Grace 1999). In my study the range of biomass levels was greatest at small scales but here the range in species numbers was small. This may have restricted the capacity to detect patterns.

Variability in both biomass and species number may have been depressed in the favourable growing conditions experienced during this study. Biomass levels in all plots were very high compared with average production recorded previously at the site (Ash *et al.* 2002). The high biomass produced by exotic grasses contributes to some of the detrimental changes associated with these plants. For example, *C. ciliaris* is believed to produce more biomass than native grasses (Humphries *et al.* 1991; Butler and Faifax 2003), resulting in changes to fire regimes. Interestingly, in this study it was the native grass, *B. ewartiana*, which was positively correlated with total biomass. Plots dominated by *C. ciliaris* did not have greater biomass than plots dominated by *B. ewartiana*, demonstrating that the presence of *C. ciliaris* does not always signify greater biomass. Species richness appeared lower than that found previously at the site. McIvor (1998) reported means of 4.3 and 3.7 species/0.25 m^2 (estimated over eight years) for oversown and native pastures respectively at this site. I found a mean of 2.4 ± 0.2 species/0.25 m^2. At a larger scale, McIvor (1998) reported means of 28 and 31 species/12.5 m^2 (estimated over eight years) for oversown and native pastures respectively. This compares with only 11 species/12.5 m^2 estimated from the mean species-area curve from my study. It is likely that species richness was depressed in the very high biomass conditions prevailing during the study. However, this large difference in richness between the two studies may be due, in part, to differences in data collection methods. McIvor (1998) collected his data from scattered plots, a method that over-estimates species numbers relative to using contiguous plots as in the nested design (Rosenzweig 1995).

Species richness appeared unaffected by *C. ciliaris* or total biomass at scales greater than 16 m^2. The species richness-biomass relationship may vary with spatial scale and various workers have highlighted the importance of scale in understanding species richness-biomass relationships (Moore and Keddy 1989; Rosenzweig 1995; Waide *et al.* 1999; Mittelbach *et al.* 2001). Moore and Keddy (1989) found a relationship between plant species richness and biomass when comparing among vegetation types (coarse scale) but were unable to detect any trends when comparing different areas within vegetation types (fine scale). They suggested that different patterns and processes are found at different levels of organization. Pastor *et al.* (1996) showed that the scale of measurement could influence the shape of the species richness-biomass relationship and noted that relationships determined at one scale would not necessarily be the same as those found at another. It is unclear whether the lack of association between species richness and *C. ciliaris* biomass at larger scales in this study is a consequence of sampling regime or simply indicates that species richness is unresponsive to *C. ciliaris* at larger scales. Plots greater than 16 m^2 generally became more alike in terms of amount and composition of biomass as they exceeded the size of single-species patches. Sampling larger *C. ciliaris* patches would help clarify the biomass-species richness relationships at larger scales.

Relationships between species richness and scale have been summarized using species-area curves (Rosenzweig 1995) and correlations between biomass and the species-area curve parameters *c* and *z* have been used to demonstrate association between biomass and species richness (Pastor *et al.* 1996; Weiher 1999). I found no relationships between *C. ciliaris* biomass and *c* or *z* estimated from species-area curves derived from data up to 64 m^2. Failure to detect a relationship has been interpreted as evidence that species richness is unresponsive to biomass (Pastor *et al.* 1996). Therefore, the results may indicate that biomass is not a major factor accounting for variation in species richness at this site. Alternatively, the failure to find relationships between biomass and *c* and *z* may be due to the small range of biomass levels sampled, as explained above, and/or to poor estimation of the parameters. As in study one, it is likely that the maximum area surveyed was too small to adequately sample community species richness. Therefore *c* and *z* are derived from only a portion of the curve and are likely to differ from estimates made from more complete curves. Sampling larger *C. ciliaris*-dominated areas may provide more accurate parameter estimates.

Although the results from these studies show that *C. ciliaris* is associated with reduced species richness, no plant groups appeared more affected than others. In study one, the association between *C. ciliaris* and lower species richness was found for all major plant groups (forbs, legumes and perennial grasses) present. In study two there was no strong evidence to suggest that *C. ciliaris* biomass had a greater effect on some groups than others. Legumes as a group may have been more responsive to *C. ciliaris* biomass but the results were not definitive. The increase in forb numbers with increasing *C. ciliaris* biomass at the largest scale is puzzling since it contrasted with all other trends found.

No differences in numbers of exotic or rare species were detected between *C. ciliaris* and non-*C. ciliaris* plots in study one. Exotic species richness has been found to be variously higher or lower in *C. ciliaris*-dominated vegetation than in non-*C. ciliaris* vegetation (Fairfax and Fensham 2000). Relationships between exotic species numbers and *C. ciliaris* dominance are difficult to predict. Exotic species richness might be expected to be high in *C. ciliaris*-dominated vegetation. Exotic species richness has been shown to be positively associated with soil fertility and disturbance (McIntyre and Lavorel 1994; Stohlgren *et al.* 1999). *Cenchrus ciliaris* establishes best on more fertile soils and disturbances promoting *C. ciliaris* establishment may favour the establishment of other exotics. Alternatively, domination by *C. ciliaris* may competitively exclude other species including other exotic species. The influence of disturbance and competition on exotic species will vary between sites and over time. Given the inter-plot variation in fertility, disturbance regimes and time since *C. ciliaris* establishment, it is not surprising that an association between *C. ciliaris* and exotic species richness was not found. In contrast, native species richness was lower in *C. ciliaris*-dominated vegetation as reported elsewhere (McIvor 1998; Fairfax and Fensham 2000). With regard to rare species, these are generally considered to be especially endangered by exotic invasions (Daehler and Strong 1994) and numbers of rare species have been found to be negatively correlated with exotic species abundance (McIntyre and Lavorel 1994). In this study the numbers of rare species tended to be lower in *C. ciliaris* plots and a larger sample size may have yielded a statistically significant pattern.

The implications of *C. ciliaris* dominance for the persistence of individual species are unknown. The abundance of individual species has been found to differ between sites sown with *C. ciliaris* and unsown sites (McIvor 1998). Franks (2002) also found that the presence of *C. ciliaris* affected the frequency of occurrence of some species, including *Aristida* spp. and *Tripogon loliiformis* that declined in frequency with increasing *C. ciliaris,* as found here. In study one, some species showed an uneven distribution, being found in most non-*C. ciliaris* plots but in few or no *C. ciliaris* plots. In contrast, in study two the occurrence of individual species appeared to be evenly distributed between *C. ciliaris* and *B. ewartiana*-dominated plots at the 1 m^2 scale (although there were not enough data to be analysed statistically). From these studies it is unclear whether the persistence of any native species is threatened by *C. ciliaris* invasion. Species richness is often an inadequate indicator of changes in plant species assemblages (Critchley and Poulton 1998) and may therefore be a somewhat insensitive measure of the consequences of *C. ciliaris* invasion. Measures of species abundance (numbers of individuals of species present) rather than richness may be more informative and an understanding of the effects of *C. ciliaris* on species abundance may enable better prediction of the implications of *C. ciliaris* invasion on the long-term persistence of individual species.

Although exotic pasture species are the basis of all virtually sown pastures in Australia and have provided considerable economic benefits (McIvor and McIntrye 1997), the very characteristics that make them successful pasture introductions also make them potential weeds. *Cenchrus ciliaris* is considered one of the most destructive introduced grasses in

Australia (Low 1997) and the findings of these two studies are consistent with the view that invasion by *C. ciliaris* poses a threat to biodiversity. However, further work is required to document the ecological effects of this species. Although *C. ciliaris* has been found to be associated with reduced species richness at the scales investigated, it is not clear whether this pattern holds at larger scales. Are native species able to persist, perhaps at lower abundances, in *C. ciliaris*-dominated communities? Or will *C. ciliaris* invasion lead to considerable loss of species over time? To resolve the issue of *C. ciliaris* effects on species richness the mechanisms behind the species richness-*C. ciliaris* relationships must be fully understood.

CHAPTER 3. MANAGING *CENCHRUS CILIARIS*-DOMINATED VEGETATION WITH FIRE

3.1 INTRODUCTION

Cenchrus ciliaris is recognized as one of Australia's worst environmental weeds (State of the Environment 1996). This vigorous, prolific seeding, drought and grazing-tolerant grass has been widely promoted as a valuable pasture species and now dominates the herbaceous layer of large areas of northern and inland Australia (Griffin 1993;Woinarski 2001). It is believed to be significantly modifying ecosystems via effects on local fire regimes (Humphries *et al.* 1991; Latz 1991; Low 1997; Butler and Fairfax 2003) and has been associated with reduced native species richness (Best 1998; Fairfax and Fensham 2000; QPWS 2001; Franks 2002). Given its perceived negative impacts, its extensive distribution in arid and semi-arid habitats and its potential to spread, strategies for containing or preventing the spread of *C. ciliaris* into non-target areas are now being sought (for example in the Alice Springs Desert Park, see Pitts and Albrecht 2000).

Fire is one of the few tools available for manipulating plant community composition in extensively managed vegetation. It has been used to manage tree-grass dynamics, maintain pasture condition, increase the availability of nutritious herbage to cattle, manage grazing distribution and reduce the hazards of wild fire (Tothill 1971; Dyer 2000). Fire also has a role in the control of invasive species and has been investigated as a tool for controlling invasive woody (Bebawi *et al.* 2000; Campbell and Setter 2002) and herbaceous (Parsons and Stohlgen 1989; DiTomaso *et al.* 1999) species.

Fire has been suggested as a management tool to maintain or restore Hawaiian grasslands invaded by African grasses such as *C. ciliaris* (Daehler and Carino 1998). However, there is little information available regarding the use of fire for managing *C. ciliaris* in Australia. In the past, interest in *C. ciliaris*-fire interactions focused on the development of 'improved' pastures and, generally, fire was not seen as particularly useful for developing or maintaining *C. ciliaris* pastures (McIvor and Gardener 1981; 't Mannetje *et al.* 1983, Pressland and Graham 1989). In contrast, in the more recent literature discussing *C. ciliaris* as an invasive species, fire is reported to favour *C. ciliaris* (Humphries *et al.* 1991; Lazarides *et al*. 1997; Butler and Fairfax 2003). Many invasive grasses are associated with changes in fire regimes (D'Antonio and Vitousek 1992; D'Antonio 2000; Wilson and Mudita 2000; Rossiter 2003) and the fire-promoting properties of *C. ciliaris* are highlighted in the invasive plant literature (Humphries *et al.* 1991; Low 1997).

The use of fire to control fire-adapted species such as *C. ciliaris* (refer section 3.2.4) may initially appear inappropriate. However, even fire-adapted species are affected adversely by fire at particular times and conditions (Vogl 1974). Manipulation of the fire *regime* may offer opportunities to alter competitive interactions and disadvantage *C. ciliaris* relative to the native species. Fires can be implemented at different frequencies, intensities and in different seasons (Bond and van Wilgen 1996) and alteration of the fire regime can result in significant changes in vegetation responses. In addition, species growing together may respond very differently to the same fire (Daubenmire 1968) due to differences in morphology, phenology and regeneration and/or recruitment strategies. Consequently, the strategic use of fire may promote some species over others.

A key factor influencing the effects of fire is the season of burning. Both fire and vegetation characteristics vary seasonally and the effects of fire may be dramatically different, depending on its timing. Fire characteristics such as intensity and patchiness vary seasonally with changes in fuel and weather conditions. Late dry season fires are generally more intense and extensive than early dry season fires (Gill *et al.* 1996; Williams *et al.* 1997) since fuel moisture levels are lower and weather conditions are more favourable for high intensity fires at this time (Gill *et al.* 1996). Vegetation characteristics, such as plant size, moisture content and phenological condition, also vary over time and plants will be more or less susceptible to fire, depending on their life cycle and condition in relation to the timing of fire. Changes in fire characteristics and changes in the relative susceptibility of species to fire mean that the season of burning may have a dramatic effect on the composition and structure of grasslands (Collins and Gibson 1990).

The use of fire to manipulate vegetation composition requires an understanding of fire characteristics and the ecological consequences of particular fire regimes (Hodgkinson *et al.* 1984). Fire has the potential to change vegetation composition by affecting recruitment and establishment patterns. As well as directly killing seedlings, fire affects recruitment and establishment patterns via its effects on the availability of (1) sites suitable for plant establishment and (2) propagules to colonize these sites. In perennial grasslands, the resident plants sequester resources and major disturbances such as fire may be required to eliminate or reduce competition and free resources for the establishment of new individuals (Cheplick 1998). In addition, fire may affect site availability by altering micro-site conditions. After burning, light levels at the soil surface are increased and soil chemistry, biological activity and soil and air temperatures may be altered (Bond and van Wilgen 1996). Fire affects propagule availability by killing seed held in seed heads and in the soil seed bank. It may also affect propagule availability via effects on flowering and seed germinability. The effects of fire on establishment sites and propagules depend, in part, on the timing of fire. Burning in different seasons may result in significant differences in site and propagule availability. For example, late dry season fires may open up more sites for plant establishment than early dry season fires if the higher intensity of these fires results in greater plant mortality and/or more extensive removal of cover. Early dry season fires may destroy more seed than late dry season fires if seed is still be held in seed heads or is on the soil surface at the time of burning.

Can fire be used to reduce the abundance of *C. ciliaris* and promote the recruitment of native species? This chapter describes a series of studies investigating the effects of season of burning on two *C. ciliaris*-dominated communities in northern Queensland. The aim of these studies was to investigate the effects of fire on establishment sites, propagules and on herbaceous community composition to help evaluate fire as a tool to manipulate the composition of *C. ciliaris*-dominated grassland. Experimental plots were established in two communities, a *Eucalyptus* savanna (Dalrymple) and an *Astrebla* (Mitchell grass) grassland (Moorrinya), and three burning treatments were imposed: early dry season burn (June), late dry season burn (November) and no burn (control). Early and late dry season fires in these communities were expected to generate significantly different fire intensities.

Three studies were conducted to investigate effects of season of burning on establishment site availability:

(1). Can fire kill *Cenchrus ciliaris* (section 3.4)?

> In this study the effects of season of burning on perennial plant persistence were investigated by assessing the survival of tagged *C. ciliaris* and *Astrebla* plants after the implementation of burning treatments

(2). Does fire increase plant nutrient availability in *Cenchrus ciliaris* dominated grassland (section 3.5)?

> A bioassay technique was used to investigate season of burning effects on plant nutrient availability.

(3). Litter - a help or hindrance to seedling emergence (section 3.6)?

> The effects of soil surface cover on *C. ciliaris* and *Heteropogon contortus* (a native perennial grass) seedling emergence were investigated to help predict the effects of litter removal by fire on seedling recruitment patterns.

Two studies were conducted to investigate the effects of season of burning on propagule supply:

(1). Effects of season of burning on soil seed banks of *Cenchrus ciliaris*-dominated grassland (section 3.7).

> A germination method was used to investigate the effects of season of burning on the soil seed banks of *C. ciliaris*-dominated vegetation.

(2). Does fire promote flowering in *Cenchrus ciliaris* (section 3.8)?

> The aim of this study was to quantify the effects of season of burning on flowering in *C. ciliaris* and *Astrebla*.

The effects of fire on establishment site and propagule availability may be reflected in seedling emergence patterns and plant community composition. Difficulties in access to field sites due to weather and resource limitations prevented a detailed investigation of seedling emergence patterns in response to season of burning. However, two seedling studies were conducted at the Dalrymple site (section 3.9). In the first study the pattern of forb and grass seedling emergence was assessed early in the growing season after the late dry season fires. In the second study grass seedling emergence was monitored over the course of the following growing season. The aim of these studies was to determine if season of burning altered seedling emergence patterns. The effects of season of burning on plant community composition were investigated at both sites by recording the herbaceous species present and their cover pre and post fire (section 3.10).

Treatment comparisons were made between *C. ciliaris* and *Astrebla* at Moorrinya because *Astrebla* was co-dominant at this site. Treatment comparisons were made between *C. ciliaris* and *H. contortus* because *H. contortus* was a common native at Dalrymple whereas *Astrebla* was not present.

This chapter consists of 11 sections. Following this introduction (section 3.1) there is a brief review of the use of fire as a tool for manipulating vegetation composition (section 3.2). A description of the experimental sites and fire treatments is presented in section 3.3. The individual studies are then reported (sections 3.4-3.10). For each study, the specific methods used are described. However, site and fire treatment details are not given as these have been described in section 3.3 and are common for all studies. In the final section of this chapter (the general discussion, section 3.11), the implications of the findings for the development of strategies using fire as a tool to manipulate *C. ciliaris*-dominated grasslands are discussed.

3.2. LITERATURE REVIEW:
THE ROLE OF FIRE AS A VEGETATION MANAGEMENT TOOL

3.2.1. INTRODUCTION

Fire is of global importance in natural and managed ecosystems, both as a destructive force and as a management tool (Raison 1979). As a management tool, it is one of the few available for managing vegetation on a broad scale and has been used by humans for thousands of years to manipulate communities of plants and animals in many different parts of the world (Christensen and Burrows 1986). In pre-modern times, fire was used in Australia and elsewhere for a wide variety of purposes such as to clear undergrowth, hunt game, engage in warfare and signal presence (Wilson and Mudita 2000). More recently, it has been used to aid the establishment of improved pastures, maintain pasture condition, increase the availability of nutritious herbage to cattle, manipulate grazing patterns/distribution, control diseases and pests such as ticks, and reduce the hazard of uncontrolled wildfires (West 1965; Tothill 1971; Dyer *et al.* 1997; Dyer 2000). Fire has also been used to manipulate tree-grass dynamics as well as herbaceous community composition to reduce the abundance of undesirable, invasive species (e.g. Whisenant 1990b; Bebawi *et al.* 2000). The use of fire in northern Australian communities is reviewed elsewhere (Tothill 1971; Leigh and Noble 1981; Hodgkinson *et al.* 1984; Dyer *et al.* 1997; Grice and Slatter 1997)

“Fire is a powerful and rapidly acting modifier of the environment” (Raison 1979). It directly affects plant growth, survival and reproduction and is one of the few natural disturbances that, alone or in combination with other forces, regularly kills mature plants (Bond and van Wilgen 1996). Fire affects all stages of the plant life cycle (Lunt and Morgan 2002), impacting upon the vigour of individual plants and their regenerative and/or recruitment capacity (Copeland *et al.* 2002). At a community level, it may alter composition and structure via effects on seed banks, establishment site availability, seedling survival and competitive interactions. Fire is an important factor structuring plant communities (Tyler 1995); the establishment sites it creates provide the potential for vegetation change (Bond and van Wilgen 1996).

The effects of fire on vegetation are determined by complex interactions between fire characteristics, plant characteristics, soils, grazing regimes and climate (Walker *et al.* 1981). Fires vary in type and behaviour and differences in fire regime (frequency, intensity and timing) can result in drastically different plant responses. Plants vary in morphology, phenology and life strategy and, consequently, species differ in their tolerance of particular fire regimes. In this section the characteristics of fire, its effects on the biotic and abiotic environment, and plant responses to fire are briefly described with emphasis on grassland/savanna systems. The role of fire in the control of invasive species is reviewed and the relationship between *C. ciliaris* and fire is described.

3.2.2. FIRE: AN ECOLOGICAL PHENOMENON

Fire is a natural environmental phenomenon in many Australian ecosystems (Gill 1975) and most of Australia's 77×10^7 hectares is subject to its influence (McArthur 1972). Fire has long been an important ecological factor in northern Australia, probably contributing to the development of the region's plant and animal communities even before occupation by humans (Hodgkinson *et al.* 1984; Grice and Slatter 1997). The arrival of Aborigines and, more recently, Europeans, has seen changes in fire regimes (Grice and Slatter 1997; Noble and Grice 2002). As well as changes over time, fire regimes vary over the landscape; different regimes occur in different vegetation types and in different management systems (Gill *et al.* 1990). Today fire is widely acknowledged as an important ecological factor in many Australian plant communities (Dyer *et al.* 1997) and fire management is recognized as important for the conservation and management of northern Australian ecosystems (Gill *et al.* 1990).

For fire to occur there must be a source of ignition, sufficient fuel and suitable environmental (weather) conditions (Bond and van Wilgen 1996). Differences in vegetation, topography and climate result in different types of fire and different fire behaviour.

3.2.2.1. Fire type

Cheney and Sullivan (1997) defined three types of fire on the basis of the orientation of the edge of the fire with respect to the wind. Heading fires are fires where the flames are blown towards the fuel, backing fires are those that move into the wind with flames leaning over the burnt ground and flanking fires are those where the fire edge is parallel to the direction of the wind. These fire types differ in the way they burn and different fire types will occur at different positions in the one fire (Cheney and Sullivan 1997). Fires can also be categorized as ground, surface or crown fires, each having different burning characteristics (Bond and van Wilgen 1996). The most common types of fires in savanna areas are surface fires, although crown fires do occur in extreme conditions (Trollope 1997). In northern Australia crown fires are virtually unknown (Stocker and Mott 1981).

3.2.2.2. Fire behaviour

Fire behaviour refers to the physical attributes of individual fires (Williams and Cook 2001) including rate of forward spread, flame zone characteristics (flame height, length and angle, residence and smoulder time) (Cheney and Sullivan 1997), scorch height and intensity, temperature, extent and patchiness (McArthur and Cheney 1966; Dyer *et al.* 1997). The characteristics of grass fires have been described by Daubenmire (1968) and Vogl (1974) and the characteristics of fire in northern Australia have been described by Gill *et al.* (1990) and Williams *et al.* (2002).

Fuel and weather conditions are the major factors influencing fire behaviour. Topographic factors are also important since slope affects the forward rate of spread of surface fires (Trollope 1997). The amount, chemical properties, size and spatial arrangement of plant material greatly influences how it will burn and these fuel characteristics vary considerably between ecosystems (Bond and van Wilgen 1996). Fuel dynamics have been described for Australian vegetation in general (Walker 1981) and for northern Australian vegetation in particular (Williams and Cook 2001). The minimum amount of fuel required to carry a fire depends on fuel distribution and moisture content (Walker *et al.* 1981; Hodgkinson *et al.* 1984). In savannas, grass is a particularly important fuel due to its flammability, particularly in the dry season when the grasses either die out completely (annuals) or die back to the root stock (perennials) (Gill *et al.* 1990). Weather conditions also determine how and when fire will burn. Wind speed and atmospheric conditions directly affect the spread, intensity and behaviour of fire. Rainfall, relative humidity and temperature affect fire behaviour indirectly via effects on fuel moisture content (Bond and van Wilgen 1996). Weather also affects fire by influencing the growth and accumulation of fuel. 'Fire weather' has been described for the wet-dry tropics by Gill *et al.* (1996).

3.2.2.3. Fire regime

The term ‘fire regime’ describes how often fire occurs (frequency), when it occurs (season) and how fiercely it burns (intensity) (Bond and van Wilgen 1996). Natural fire regimes are determined by ignition probability and type (Williams and Cook 2001), by the amount, seasonality and reliability of rainfall, and by the nature of the plant community (Dyer *et al.* 1997).

Generally the term ‘fire frequency’ is used to describe the time interval between successive fires at a particular location (fire return interval), although it may also be used to refer to the number of fires per unit area over a landscape (regional frequency) (Christensen 1985). Potential fire frequency is controlled by fuel load and condition that, in turn, are determined by factors such as vegetation type and rainfall (Walker *et al.* 1981). Fires of different frequency may have different characteristics. For example, annual fires have been found to have lower temperatures and shorter durations of surface heating than less frequent fires. These effects are related to differences in fuel loads (refer Morgan 1999).

Season of burning defines the timing of fire in relation to climatic and vegetation conditions. The timing of fire may greatly influence its behaviour. For example, fires in the early dry season in savanna in the Northern Territory are patchy, of low intensity and tend to go out at night. In contrast, late dry season fires are of higher intensity, remove grassy fuels over extensive areas and persist overnight (Gill *et al.* 1990). The fuel and meteorological conditions that influence seasonal changes in fire behaviour are described by Hoare (1985) and Gill *et al.* (1996). The length of fire season varies between communities (Walker *et al.* 1981) depending on plant community type, climate and management practices. Wild fires in Australia’s savannas generally occur from March to December (dry season fires), although prescribed fires may be imposed in the early wet season (Williams *et al.* 2002).

Fire intensity (I) is the rate of energy release or rate of heat release per unit time per unit length of fire front:

$$I = H\omega r$$

where H is the heat yield of the fuel burnt (kJ/kg), ω is the amount of fuel consumed (kg/m^2) and r is the rate of spread (m/sec) (Cheney and Sullivan 1997). The heat yield is the amount of heat released during a fire and is somewhat less than the heat of combustion because some energy remains in partially burnt products (Cheney and Sullivan 1997) and there are heat losses resulting from radiation, vaporization of moisture and other processes (Byram 1959).

Heat yields of grass fuels range from 11500-18600 kJ/kg (Cheney and Sullivan 1997).

The concept of fire intensity was developed by Byram (1959) (McArthur and Cheney 1966) and is known as ‘fire line intensity’. ‘Fire intensity’ has also been used to refer to peak flame temperature, maximum soil temperature and flame height (Walker *et al.* 1981). Another measure of intensity, ‘Rothermal’s reaction intensity,’ has been defined as the rate of heat released per unit area of the flaming zone (Rothermal 1972).

Fire intensity is strongly affected by fuel moisture as well as fuel load. Fuel moisture affects the ease of ignition and the combustion rate (Trollope 1997) and heat yields are generally lower at higher fuel moisture contents (Cheney and Sullivan 1997). In addition, fuel moisture affects the rate of spread with levels above 40% usually preventing the spread of grassland fires (Walker *et al.* 1981). The rate of spread is also determined by slope (Trollop 1997), wind speed and relative humidity (Williams and Cook 2001). In grasslands, wind speed is critical where grass tussocks are separated and there is little herbage between the discrete plants (Walker *et al.* 1981).

Fires in grasslands are generally less intense than those in forest communities (Williams J. R. 1995). Consequently, the range of fire intensities is less for grasslands and savannas than for woodlands (Bond and van Wilgen 1996). Most fire intensities in Australian’s northern savannas range from 500-10,000 kWm^{-1} with intensities in excess of 20,000 kWm^{-1} being rare (Williams *et al.* 2002). In contrast, fire intensities of up to 100,000 kWm^{-1} have been reported for eucalypt forest fires (Gill and Knight 1991). There is a close link between fire intensity and fire frequency at a site with intensity being inversely related to frequency due to the availability of fuel (Whelan 1995). However, recovery rates influence this relationship. Fire intensity also varies with season of burning (Lonsdale and Braithwaite 1991; Williams *et al.* 1997), being affected by seasonal influences on weather conditions, particularly wind speeds, temperature, humidity, fuel moisture content and fuel load and arrangement (Gill *et al.* 1996; refer Dyer *et al.* 1997). The intensities of fires generally increase over the dry season as daily wind patterns change, maximum temperatures increase, relative humidity decreases and fuel moisture levels decline (Gill *et al.* 1996).

Although the fire regime is usually described in terms of frequency, season and intensity (Gill 1975), other factors such as fire type (Trollope 1997) and extensiveness and patchiness (Whelan 1995; Williams and Cook 2001) have also been listed as components of the fire regime.

3.2.2.4. The effects of fire

Fire is the most ubiquitous, terrestrial disturbance after human urban and agricultural activities (Bond and van Wilgen 1996). It affects a large range of plant communities, has an extremely short period of occurrence at any point, may consume a large portion of the standing vegetation and has a self-propagating tendency (Gill 1975). Most fires have both beneficial and detrimental effects within an ecosystem (Raison 1980).

Fire affects plants directly by consuming or damaging biomass. It kills plants and may destroy seed held in the standing vegetation or in or on the soil. In addition, the effects of heat and smoke may affect flowering and seed germinability (Enright *et al.* 1997; Williams *et al.* 2003a).

Fire affects plants indirectly by altering abiotic and biotic factors that influence plant growth. Light, temperature, water and nutrient conditions are often markedly affected by fire. The removal of living plant shoots and litter, that had previously intercepted much of the direct solar radiation and retarded loss of heat by radiation (Daubenmire 1968), results in increased light levels at the soil surface (D'Antonio *et al.* 2001). Removal of surface cover can also cause major changes to temperatures of the soil surface and the adjacent layer of air (Daubenmire 1968; Hulbert 1988). Post-fire soil and air temperatures are generally increased (Tothill 1969; Hulbert 1988) and there may be greater fluctuations in temperature (refer Christensen 1985; Auld and Bradstock 1996). Soil moisture and surface humidity are also altered by fire (refer Christensen 1985; Whelan 1995). Moisture availability may increase, due to reduced transpiration (Bond and van Wilgen 1996) and reduced loss via absorption by litter (Daubenmire 1968), or decrease (refer Hulbert 1988) due to increased evaporative loss (Daubenmire 1968) and to increased exposure to raindrops, leading to surface sealing and reduced hydraulic conductivity (Bridge *et al.* 1983). Fire has also been found to reduce soil wettability and hence water penetration into soils (Raison 1980). Nutrient availability is generally increased by fire as nutrients are added to the soil surface as ash (Bond and van Wilgen 1996). However, some nutrients are lost through volatilization and as particulates through air and water movement (Kellman *et al.* 1985). Nutrient availability may be altered as increased temperatures and changes in chemical conditions promote increased biological mineralization (Christensen and Muller 1975; Stock and Lewis 1986). It has also been suggested that fire alters the chemical environment via the creation of charred wood products (Keeley *et al.* 1985) and by destroying allelochemicals (refer Bell 1999), although the prevalence of this effect is uncertain (Christensen 1985).

Fire also affects plants indirectly via its effects on microbial and animal communities. Fire-induced changes in temperature, moisture and pH affect microbial populations, altering nutrient cycling (refer Raison 1979) and pathogen activity. Fire also transforms the habitats of animals (Daubenmire 1968). The post fire environment may be hostile for invertebrates and vertebrates including granivorous species such as ants and rats (Bond and van Wilgen 1996), altering levels of seed predation and herbivory (Christensen and Muller 1975; Tyler 1995). For example, seed predation has been found to be lower in burnt than in unburnt grassland in southern Australia (Watson 1995).

3.2.2.5. Plant responses to fire

Fire affects plant growth and phenology. It influences the regenerative and recruitment capacity of plants via effects on sprouting, flowering and seed set, seed viability and germinability, and seedling establishment.

Although fire kills some plants, it may alter or even promote the growth of surviving individuals. Many species are able to sprout after fire and surviving individuals may start growing earlier and faster (Hulbert 1988). Fire has been reported to enhance growth and tillering in grasses (Cheplick and Quinn 1988; refer Collins 1990). It may also affect the size of plant organs and canopy structure (Daubenmire 1968). For example, burning was reported to increase tiller number but reduce tiller weight in *Astrebla* spp. (Scanlan 1980) and increase seed size in *Nassella pulchra* (Dyer 2002). New foliage may be held more erect on burned than on unburned grassland (O'Connor and Powell 1963) and high intensity fires can alter tree architecture, causing a reduction in foliage height (Bond and van Wilgen 1996; refer Anderson *et al.* 1998).

Fire affects plant recruitment by altering propagule supply. It destroys seed held in seed heads as well in the seed bank (Gardener 1980) and seed that is not consumed may be damaged by overheating ('t Mannetje *et al.* 1983). However, although fire may decrease the total amount of seed, it may increase the amount of germinable seed and fire-promoted germination has been reported for many plant groups (Purdie and Slatyer 1976; Shea *et al.* 1979; Bell 1999; Williams 2000). Germination may be promoted by heat. Many hard-seeded Australian species require a heat shock to permit germination (Bell 1999) and the importance of heat in breaking dormancy has been illustrated in several plant families including Fabaceae, Lamiaceae, Rhamnaceae (refer Auld and O'Connell 1991). For example, the 'hard-seededness' of legume species is broken by heat which allows water to enter the seed and germination to begin (Bond and van Wilgen 1996). The degree of heat scarification depends on the amount of seed present at various soil depths, the amount and depth of fine fuel present, and the residence time of the fires (Noble and Grice 2002). Heat-promoted germination may result from the heat generated in the fire itself and/or from raised soil temperatures due to the removal of surface cover (Tothill 1969). Changes in other factors such as light and the chemical micro-environment around the seed may also promote germination (refer Bell 1999; refer Parker and Kelly 1999). For example, smoke has been associated with increased germination (Roche *et al.* 1998; Read *et al.* 2000; Williams *et al.* 2003a). However, its importance in stimulating germination of semi-arid and tropical plant species has yet to be determined on a comprehensive scale (Noble and Grice 2002).

Fire also affects propagule supply via effects on flowering, with both increases and decreases in post-fire flowering being found (refer Daubenmire 1968). The association between flowering and fire ranges from near obligate in some herbaceous species to weakly facultative in sprouting shrubs (Bond and van Wilgen 1996). Fire-stimulated flowering is very common in monocotyledons including Poaceae and Cyperaceae and increased flowering after burning has been reported for grasses including *Astrebla* spp. (Scanlan 1980), *Amphicarpum purshii* (Cheplick and Quinn 1988), *Andropogon* spp. (Hulbert 1988), and tallgrass prairie grasses (Collins 1990). Flowering in other grassland plants, such as some forbs, is also be promoted by fire (Lunt 1994). The stimulus to flower varies and has been attributed to smoke or changes in temperature, light and nutrients (refer Bond and van Wilgen 1996; refer Lunt and Morgan 2002). The effects of burning on flowering are likely to alter seed production and input to the seed bank. Fire has been reported to increase seed production in grasses (refer Orr *et al.* 1991; Scanlan 1980), although decreases in grass seed production due to fire have also been reported (Whisenant 1990b). In some species fire stimulates seed release. Such serotinous species include many woody species found in Australian shrublands (Bond and van Wilgen 1996).

The effects of fire on seed banks and flowering flow on to affect seedling emergence patterns. Burning often results in greater and/or earlier emergence (Daubenmire 1968) and flushes of seedling emergence after fire are commonly reported (Christensen and Muller 1975; Shea *et al.* 1979; Peart 1984; Robertson *et al.* 1999). However, some studies have found no evidence of fire-stimulated germination (Collins and Gibson 1990). For example, in temperate Australian grasslands, mass germination of most perennial species does not occur in response to single fires, probably because of small soil seed banks (Lunt and Morgan 2002). Changes in seedling emergence patterns may result from the direct effects of fire on seed germinability and/or from the environmental changes in the burnt area such as decreased soil cover, reduced competition for resources and reduced herbivory (Tyler 1995). Increased emergence after fire of some shrubs of wet sclerophyll forest in north-eastern Australia is believed to result from the heat generated by fire (Williams 2000). In contrast, *Heteropogon contortus* seedling emergence associated with burning (Shaw 1957) was attributed to post-fire increases in soil temperature (Tothill 1969). Removal of shade by fire was also considered important in influencing seedling emergence patterns in *Themeda triandra* grasslands in south-eastern Australia (Morgan 1998). Fire results in reduced emergence of species whose seeds are killed by fire (Peart 1984) or where fire creates micro-site conditions unfavourable for seedlings.

Seedling establishment patterns are also altered by fire. In the post-fire environment where resources such as light, water and nutrients increase, and seed and seedling predation decline (Bond and van Wilgen 1996), seedling survival may be enhanced. For example, Tyler (1995) concluded that increased seedling survival in burnt chaparral vegetation was associated with reduced herbivory following fire. Given suitable growing conditions, seedling survival is generally enhanced where fire results in reduced competition from established plants.

At the community level, fire can result in changes in vegetation composition and structure (Cheal 1996). Some species are favoured by a particular fire regime, increasing in abundance, while other species are reduced in abundance or are eliminated altogether. Disturbances such as fire may promote coexistence by preventing competitive exclusion (Morgan 1999; Valone and Kelt 1999; Lunt and Morgan 2002) and many studies report increased species richness after fire (Parsons and Stohlgren 1989; DiTomaso *et al.* 1999; Valone and Kelt 1999; Copeland *et al.* 2002; Williams *et al.* 2003b). However, the reverse has also been reported: annual burning of tallgrass prairie increased native grass dominance and depressed native and exotic species richness (Smith and Knapp 1999). Fire also affects site productivity. The reported effects of fire on grassland biomass production vary. Vogl (1974) stated that burning has generally been found to increase the productivity of grassland. In contrast others report that burning generally reduces the biomass and cover of dominant grasses and other species in the post-fire growing season (Tothill 1971; Lunt and Morgan 2002). Post-fire biomass production is strongly dependent on seasonal rainfall (Orr *et al.* 1991) and variations in rainfall and other factors, such as nutrient availability, are important in determining biomass production.

Plant responses to fire are described in detail in Bond and van Wilgen (1996). The responses of grassland plants to fire are reviewed by Daubenmire (1968) and the effects of fire on vegetation of the wet-dry tropics of Australia have been reviewed by Gill *et al.* (1990).

3.2.3. FIRE AS A MANAGEMENT TOOL FOR INVASIVE PLANT CONTROL

Fire is used to manage vegetation on a broad scale to achieve various land management goals. One of its main uses has been to manipulate vegetation composition to control unwanted species and it has been used to control both invasive woody and herbaceous plants.

Fire is an important factor influencing tree-grass dynamics, with regular fires tending to act against woody plants and favour grasses (Wilson and Mudita 2000). The absence of regular fire has enabled woody species to increase in density in many ecosystems (Hodgkinson *et al.* 1984; Dyer *et al.* 1997) and the invasion of exotic and native woody species is now a major problem in Australia's rangelands (Russell-Smith *et al.* 2000; Noble and Grice 2002). Fire can result in high mortality of woody plant seedlings and fire regimes can be designed to increase or decrease the abundance of woody plants once life histories and fire-survival strategies of individual species are understood (Hodgkinson *et al.* 1984). Fire has been used to control invasive shrubs including *Prosopis pallida* (mesquite) (Campbell and Setter 2002), *Cryptostegia grandiflora* (Bebawi *et al.* 2000), *Cytisus scoparius* (Robertson *et al.* 1999), *Acacia sophorae* (McMahon *et al.* 1996) and *Genista monspessulana* (Alexander and D'Antonio 2003). Although most woody species in tropical eucalypt forests and woodlands are vulnerable to fire at the seedling stage (Dyer *et al.* 1997; refer Noble and Grice 2002), many trees in tropical Australia can regenerate after fire (Gill *et al.* 1990). Therefore, high fire intensities may be needed to kill mature individuals (Williams J. R. 1995; Dyer *et al.* 1997).

Fire may also be useful for manipulating the composition of herbaceous communities and has been investigated as a tool to reduce the dominance of undesirable grasses such as *Elymus caput-medusa* (Furbush 1953), *Setaria* (Davidson 1951), exotic annual grasses including *Avena, Bromus* and *Festuca* species in California (Parsons and Stohlgen 1989), *Bromus japonicus* (Whisenant 1990b) and *Aristida* spp. (Orr *et al.* 1991; Dyer *et al.* 1997). It has also been used to manipulate problem forb species, for example *Watsonia* spp. (Groves 1991) and *Centaurea solstitialis* (yellow starthistle) (DiTomaso *et al.* 1999).

The use of fire as a management tool is not simply a matter of deciding whether to burn or not (Bond and van Wilgen 1996). It requires an understanding of fire characteristics and the ecological consequences of particular fire regimes (Hodgkinson *et al.* 1984). Fires can be implemented at different frequencies, intensities and in different seasons and the size of burnt areas and their location relative to unburnt areas can be varied (Bond and van Wilgen 1996). Differences in these characteristics can have a profound effect on the outcome of burning. The use of fire also requires an understanding of the characteristics of vegetation that influence its responses to burning. The effects of fire on plant communities depend on the species present and the stage of their life cycle exposed to fire (Gill *et al.* 1990). Finally, interactions between fire and other factors such as climate, soils and grazing must be considered.

3.2.3.1. The importance of fire regime

"[All] fires are not equal" (Bond and van Wilgen 1996). Fires vary in intensity, frequency, and seasonality and the effects of fire can differ enormously depending on the circumstances of the particular fire (Bond and van Wilgen 1996). Variations in fire regime may result in very different effects on vegetation dynamics and different regimes may be needed to achieve different land management goals (Williams and Cook 2001). The frequency, intensity, duration and seasonality of fire are considered important for assessing effects of fire on plants (refer Auld 1986).

The frequency of burning may significantly affect vegetation composition and structure, particularly where composition is strongly influenced by biomass accumulation (Lunt and Morgan 2002) or where plant life cycles can be severely interrupted (Vogl 1975). For example, fire frequency, rather than other attributes such as intensity, has the most profound influence on the composition of temperate, lowland grasslands in southern Australia (Lunt and Morgan 2002). This is because fire frequency, rather than intensity, has the greatest effect on biomass accumulation and biomass accumulation is a major determinant of composition in these grasslands (Lunt and Morgan 2002). Frequent burning generally favours sprouting perennials over non-sprouting species, disadvantages species that rely solely on on-site storage of seed, promotes herbaceous over woody species, and promotes grasses over dicotyledons (Vogl 1977). Communities, such as mulga shrublands, that rely on regeneration from seed following the mortality of adults are particularly susceptible to changes in fire frequency. In some communities, fires in close succession can totally eliminate particular species (Griffin and Hodgkinson 1986) and cause complete conversion of community type (Vogl 1975). Frequent burning of heathlands has been found to reduce both structural and floristic diversity (Cheal 1996) and in savanna woodlands, the abundance of individual species varies with changes in fire frequency (Williams *et al.* 2003b). Fire frequency may be important in altering the success of colonizing species (Baird 1977; Laterra 1997) and reducing fire frequency may be an effective control method for some weeds, for example the South African grass *Ehrharta calycina* (Groves 1991).

Although fire frequency has a major effect on the composition of some communities, it appears to be less important in others, for example some northern Australian savannas (refer Williams *et al.* 2002) and tallgrass prairies in Oklahoma (Engle *et al.* 2000). Fire frequency (annual versus biennial fires) was found to have little effect on the composition of tropical woodlands in the Northern Territory (Bowman *et al.* 1988).

The effects of fire also depend on the number of burns. For example, exotic forbs were found to increase after a single grassland burn in California but then decrease in cover after repeated burns (Eller 1994). Exotic grasses, also in Californian grasslands, were reported to decrease with burning, but only after three burns, and they quickly regained their pre-treatment dominance if burning was halted (Parsons and Stohlgren 1989).

Fire intensity is a major factor determining vegetation responses to burning. Intensity levels influence the proportion of biomass consumed (Williams and Cook 2001), the level of plant mortality (Griffin and Friedel 1984a; Williams J. R. 1995), germination responses (Shea *et al.* 1979), vegetation structure (Williams J. R. 1995) and plant biodiversity (Braithwaite 1995). Species differ in their tolerance of particular fire intensity levels and differences in mortality rates can result in marked changes in relative abundance (Lonsdale and Braithwaite 1991). Generally, high intensity fires favour the regeneration of hard-seeded legumes and limit the growth of obligate-seeding, proteaceous species (Groves 1991). Plant species within tropical eucalypt forests and woodlands are well adapted to frequent, low-intensity fires (Dyer *et al.* 1997) and unusually intense fires following favourable seasonal conditions can increase tree mortality (Lonsdale and Braithwaite 1991) and cause significant changes in forest structure (Williams J. R. 1995). Fire intensity also affects habitat heterogeneity. Fuel consumption tends to be complete for savanna fires greater that 2000 kWm^{-1} while below this intensity some fuel remains, creating a heterogeneous mix of burnt and unburnt patches (Williams and Cook 2001). Patchiness in vegetation created by fire is recognized as important for promoting diversity (Hodgkinson *et al.* 1984) and the patchiness of litter removal by fire can affect community structure (Facelli and Pickett 1991a).

Although fire intensity is considered a key attribute determining the effects of fire, its relevance in determining fire effects at the plant level has been questioned. Fire intensity may be an inadequate indicator of the effects of fire since other factors, such as flame dimensions, temperature profiles, smoke and fine grain patchiness left by fire, may be biologically more important (Gill *et al.* 1990). Raison (1979) considered that fire intensity may not be useful for describing the heat pulse that produces the ecological effect and Noble and Grice (2002) stated that the duration of fire, or fire residence time, is probably more important than fire intensity. The length of time required to kill plant tissue is exponentially and inversely related to temperature (Bond and van Wilgen 1996) and therefore, the length of time fire is adjacent to a plant (residence time) is critical to plant survival (Walker *et al.* 1981). Much of the variation in plant responses to burning can be attributed to the varying sensitivity of different species or tissues to heating (Bond and van Wilgen 1996). Flame height in relation to bud position is also important. Often the height of maximum heat in grass fires is well above the ground surface such that low placed buds and seeds escape damage and head fires may cause less damage than backfires because the maximum temperature is well above the ground (Daubenmire 1968). Whether plants actually respond to 'fire line intensity' or to other related fire characteristics remains unclear (Noble and Grice 2002).

Another key determinant of the effects of fire is the season of burning. As noted by Daubenmire (1968), "the time of year, or even the time of day, when the fire occurs is almost as important at the occurrence of the fire itself. Complete reversals of the type of influence may result simply from differences in timing". Season of burning can affect herbaceous community composition (Tothill 1971; Mott and Andrew 1985a) and structure (Lane and Williams 1997). For example, summer fires in central Australia were found to reduce the yield of palatable grasses whereas winter fires either maintained or increased them (Griffin and Friedel 1984b). Season of burning has also been found to affect tree seedling recruitment, tree sprouting (refer Bond and van Wilgen 1996) and tree mortality. For example, burning mallee eucalypts in autumn causes much greater mortality than spring burning (Noble 1997).

The timing of fire is important since both fire characteristics and the condition of plants and their susceptibility to fire vary seasonally. The effects of season of burning may be attributed to seasonal variation in fire intensity as a result of seasonal variations in fuel and weather conditions (section 3.2.2.2). In Northern Territory savannas, tree mortality may be higher in late dry season fires because they are generally more intense than early dry season fires (Williams *et al.* 1997). Alternatively, season of burning effects may be independent of fire intensity effects, being instead related to the condition of the vegetation. Species adapted to being burnt in one season are likely to be adversely affected by a burn at some other time of the year (Hodgkinson *et al.* 1984).

Whether or not plants are actively growing and the stage of life cycle at the time of fire can have major effects on plant responses to burning. Fires that occur at the beginning or end of the growing season, before plants become physiologically active, should have less effect on recovery than fires in the middle of the growing season (Bond and van Wilgen 1996). The end of the dry season has been reported to be the least injurious time for burning grassland in South Africa (West 1965) and northern Australia (Mott and Andrew 1985ab) since the grasses have seeded and become dormant by this time (Dyer 2000), Consequently, dry season fires may have little effect on biomass production or composition (Mott and Andrew 1985a). In contrast, burning these communities in the wet season can result in changes in species abundance (Smith 1960; refer Trollope 1997). Early wet season burning may kill recently established seedlings (Hodgkinson *et al.* 1984) and eliminate annual grasses because they are burnt before flowering and seed set can occur (refer Stocker and Mott 1981).

The effects of fire are also influenced by its timing in relation to other factors such as soil moisture and cover. Seasonal changes in soil moisture may influence the effects of fire on plant and seed survival since, the drier the soil, the higher its surface temperature when grass burns. However, at the same time the low moisture content reduces downward conduction of heat (Daubenmire 1968). Plants may respond to season of burning effects on nutrient availability. For example, late dry season fires may have greater effects on nutrient stores than early dry season fires (refer Williams *et al.* 2002). The timing of cover removal also influences the outcome of burning. Run-off and erosion may be more severe following late-dry season fires (Townsend and Douglas 2000). In north American tallgrass prairie, the removal of litter by fires in spring may contribute to an increase in productivity and flowering due to increased light and solar warming of the soil while removal of litter by summer fires may result in desiccation and inhibition of regrowth (Copeland *et al.* 2002). The timing of cover removal may also affect competitive interactions between species.

3.2.3.2. The importance of vegetation characteristics

Factors such as plant morphology, chemical composition, phenology and the spatial arrangement of plants influence both fire characteristics and vegetation responses to fire. Plant communities have a significant influence on fire regimes and behaviour. The amount and flammability of the biomass produced by plants controls fire frequency, intensity and seasonality. The spatial arrangement of plants influences how well fire may be carried by the vegetation and morphological and chemical differences between species can affect rates of spread (Walker *et al.* 1981). Fire, in turn, can affect all stages of the plant life cycle (Lunt and Morgan 2002). Although fire may be considered indiscriminate in its removal of above ground vegetation (Alexander and D’Antonio 2003), plant responses to fire can vary considerably between and within vegetation types. Importantly, species growing together may respond very differently to the same fire (Daubenmire 1968).

The survival of individual plants is affected by a number of factors including bark thickness, crown architecture and the location of buds (Bond and van Wilgen 1996). Differences in bark type afford differing degrees of fire protection (Lonsdale and Braithwaite 1991) with bark thickness and its thermal properties being important (Whelan 1995). Differences in growth form may also result in varied responses to fire. For example, it has been suggested that the more loosely packed tussocks of *Heteropogon contortus* make it more susceptible to heat damage from fire than *Themeda triandra*, whose dense, internally damp tussocks effectively insulate the growing apices (Walker *et al.* 1981). Size influences the effects of fire. In theory, the bulk of a seed or organ has a bearing on its susceptibility to heat damage: the smaller the organ the more quickly it is brought to lethal temperature (Byram 1948). Mortality due to fire has been found to be greater for smaller individuals (refer Bond and van Wilgen 1996; Grice 1997). However, smaller diameter plants are sometimes less susceptible to fire, presumably because the smaller volume of fuel results in less heat being released (Wright and Klemmedson 1965). The position of buds at the time of burning is also important. Plants with underground, perennating buds are likely to be less sensitive to fire than those that tiller from above the ground (Daubenmire 1968) and plants whose stems remain compact are likely to be less vulnerable than plants whose stems elongate slowly, exposing the apex over a long period (Tainton 1981). Grasses are among the most fire resilient components of plant communities (Bond and van Wilgen 1996). Although they may form highly flammable fuels, they recover quickly from burning (D'Antonio and Vitousek 1992). Since the growing points of grasses are generally near or beneath the soil surface and protected from all but extreme heat, fire destroys little more than the accumulated growth, most of which is dry and dead when the plant is dormant. Most woody plant species in tropical eucalypt forests and woodlands are able to sprout from protected buds in lignotubers, lateral roots and stem bases at or below ground level and from protected aerial epicormic buds (Dyer *et al.* 1997).

Plant phenology is also important in determining the effects of fire (Hodgkinson *et al.* 1984; Williams *et al.* 2002). Plant moisture content and the location of carbohydrate stores (roots or shoots) significantly influences plant responses to fire. Plants with higher moisture contents are killed at lower temperatures (Bond and van Wilgen 1996). Therefore, actively growing individuals may be highly susceptible to fire while dormant individuals are relatively unaffected (Daubenmire 1968; Bond and van Wilgen 1996). The strong seasonal growth patterns of many grassland species have significant implications for burning in different seasons (Lunt and Morgan 2002). As noted above, burning when grasses are dormant may have little effect on plants. At this time, carbohydrate levels are at a maximum in root storage organs and the regenerative buds of many species are tightly held in tussock bases, effectively insulated from direct fire damage (Lunt and Morgan 2002). Perennial grasses will be most affected by fire when they are actively growing (Bond and van Wilgen 1996) and the major part of the food reserves have been withdrawn from the underground organs (Aldous 1934).

Differences in the phenology of resident plant groups may result in changes in community composition with burning since fire may damage or promote certain species. For example, in tallgrass prairies in Wisconsin, species flowering before mid July are favoured by July burns while late-flowering species are favoured by March (dormant season) fires (Howe 1994). Burning annual grassland in northern Australia at the start of the wet season after the majority of *Sorghum* spp. seeds have germinated but prior to flowering and seed set can reduce sorghum abundance (Stocker and Sturtz 1966). Species also differ in the time taken to recover reproductive capacity after fire (Hodgkinson *et al.* 1984) and such differences can influence vegetation composition since species that are quick to recover gain a competitive advantage over slower species (Daubenmire 1968).

Factors such as fire-promoted seed germination, protected seed embryos (hard seededness), heavy seed production, early reproductive maturity, seed burial and seed longevity improve the recruitment ability of species after fire (Walker *et al.* 1981). The position of seeds at the time of burning is critical (Daubenmire 1968; Cheplick and Quinn 1988). The high temperatures generated by fire may not penetrate deeply into the soil (Cheplick and Quinn 1988) and so, while seed on the soil surface may be killed by heat, seed buried below the surface may be protected. Differences in seed size and shape are important in determining the degree of burial on a particular soil surface (Grubb 1977) and consequently differences in seed morphology will influence the seed's vulnerability to fire (Walker *et al.* 1981; Peart 1984). In monsoon and tallgrass communities in northern Australia, perennial species such as *Themeda triandra* and *Heteropogon contortus*, and annual *Sorghum* spp. have seeds with twisting hydroscopic awns that help bury them into the soil thus protecting them from fire (Dyer *et al.* 1997). The seeds of conifers and some other tree species are protected from the heat of fire by woody fruits (Whelan 1995).

Plant species vary in their susceptibility to fire and in their vegetative and reproductive responses to fire. Researchers have attempted to classify plants into fire life-history categories based on plant survival and reproductive responses to fire (Gill 1981). Characteristics of grassland plants that affect their reactions to fire have been described by

Daubenmire (1968) and traits that adapt plants to fire are reviewed for the Australian biota by Gill (1975, 1981).

3.2.3.3. The importance of other factors

Both fire and plant characteristics are influenced by factors such as climate, topography, soils and grazing. These factors influence fire regimes via their effects on fuel loads and composition. They are also critical in determining post-fire vegetation responses. In fact, interactions between fire, rainfall and grazing and/or browsing are often far more important than the effects of fire alone (Noble and Grice 2002)

Climate has a major effect on fire-vegetation interactions. The frequency and intensity of fires is determined by the build up and condition of fuel. Climate influences fuel loads and type via its influence on species composition, biomass production and plant phenology. Weather conditions directly influence fire behaviour via effects on humidity and wind speed and post-fire weather conditions play a major role in determining vegetation responses after fire (Mott and Andrew 1985a). Rainfall in particular influences recruitment success (Bond and van Wilgen 1996) and post-fire productivity (Orr *et al.* 1991). For example, increased growth in *Astrebla* grassland after fire occurred only at sites that received more than 500 mm of rain during the growing season; below this, no change or a reduction in growth occurred (Scanlan 1980). In some communities, the rainfall regime following fire is the dominant influence on post-fire development (Noble 1989).

Grazing patterns may alter local fire regimes by affecting plant biomass and species composition and changes in grazing regime are accompanied by changes in fire regime (Christensen and Burrows 1986). The presence of livestock and/or concentrations of native herbivores before and particularly after burning can completely alter the responses of vegetation to fire (refer Vogl 1974). Post-fire grazing by domestic, feral and native animals is a critical factor in determining the effects of fire on herbaceous species (Walker *et al.* 1981).

In addition to grazing, management practices such as the development of improved pastures with high yielding species such as *C. ciliaris* can also alter fire regimes (Walker *et al.* 1981).

Soil type is an important determinant of vegetation composition and productivity and plays a role in determining fuel quality and quantity. Soil type is also likely to be important in determining the effects of fire on soil nutrients (Raison 1979) as well as post-fire erosion processes (West 1965; McIvor *et al.* 1995). Topography also affects fire-vegetation interactions. Slope affects fire behaviour directly (refer page 66) while differences in nutrient, water and propagule availability between run on and run off zones influence fuel accumulation and vegetation responses to burning.

3.2.3.4. The efficacy of fire as a tool to manage vegetation composition

Fire is an effective tool for manipulating both woody and herbaceous vegetation. It is the cheapest tool available (Christensen and Burrows 1986) and has the advantage that it can be easily used over large areas (Grice *et al.* 2000). However, it must be tailored to the objectives and circumstances. With regard to managing invasive plants, the efficacy of fire as a management tool depends on the invasive species and the plant community involved.

Many species are actually promoted by particular fire regimes (Grice *et al.* 2000; Wilson and Mudita 2000) and generally fire promotes, rather than limits, invasive plants (see review by D'Antonio 2000). Disturbances such as fire enhance the success of invasive species by altering resource availability and by altering biotic interactions and community structure and productivity (refer Smith and Knapp 1999). The invasion of fire-tolerant, exotic plants often results in positive feedback loops between fire and weed invasion: as the weed becomes more abundant, fire frequency and intensity increases, native species decline, the exotic species increases in abundance, further altering the fire regime (D'Antonio and Vitousek 1992; Wilson and Mudita 2000). This is believed to be the case for various perennial, tussock-forming grasses of mainly African origin that have been introduced into northern Australia, including *C. ciliaris* (Wilson and Mudita 2000; Butler and Faifax 2003), *Andropogon gayanus* (Rossiter *et al.* 2003) and *Pennisetum polystachyon* (Gill *et al.* 1990).

The exotic-promoting effects of fire may occur in ecosystems where fire is naturally uncommon. For example, fire has been reported to promote exotic species in Hawaiin woodlands. The native species in these woodlands, which have not been previously exposed to fire, respond poorly to burning while the exotic grasses respond well (D'Antonio *et al.* 2001). In contrast, fire may be ineffective in promoting exotics in ecosystems where fire has a long evolutionary history, for example Californian chaparral and mixed conifer forest, Australian monsoonal forests and African savanna. Nevertheless, fire has been found to promote exotic species in systems where fire has been important as a long-term ecological force (D'Antonio 2000).

Hitchmough *et al.* (1994) concluded from the literature that “fire has often been seen as the most appropriate means by which to manage grass weeds”. However, although fire is available as a management tool, it is often inappropriate in practice, being ineffective or even promoting invasive species. It may not be useful for promoting native species at the expense of exotics where seed banks are dominated by exotic species (Lunt 1990; D’Antonio *et al.* 2001). D’Antonio (2000) concluded from her review of fire-plant invasion studies that fire was often not effective in controlling invasive species and that, in some cases, it resulted in an increase in the abundance of other non-target exotics (e.g. Parsons and Stohlgren 1989).

The value of fire as a management tool depends on the responsiveness of the plant community to fire. Fire may be highly effective for manipulating community composition where resident plant groups differ significantly in fire tolerance and/or phenology (Howe 1994). Season of burning may be particularly effective in changing vegetation composition in such communities since fire damages plants at different stages in their development, resulting in altered competitive interactions (Copeland *et al.* 2002). Fire may also be effective for manipulating vegetation in communities where fire normally plays a major role in plant dynamics. Dry season fires may have significant effects on communities containing fire-triggered germinators (Williams *et al.* 2003b) but be less effective in communities where other factors, such as edaphic conditions (Bowman *et al.* 1988) or climate, have a large influence on species composition. For example, dry season fires may have little effect on communities in which seeds of the resident species are prompted to germinate at the start of the wet season regardless of fire (Williams *et al.* 2003b).

In savanna systems, the primary determinants of composition and structure are variations in moisture and soil nutrients whereas disturbances such as fire are of secondary importance (refer Williams *et al.* 2002). In these systems the usefulness of fire alone as a tool for manipulating vegetation composition may be limited since other environmental factors are key determinants of vegetation dynamics.

However, fire is often useful in combination with other tools and the use of fire as part of an integrated approach to weed control, or ‘ecological control’ as described by Groves (1991), has been advocated (Vitelli 2000; Noble and Grice 2002). Although individual weed control methods, such as mechanical control, herbicides, burning and biological control, have their advantages and disadvantages, no single method is usually sufficient for effective weed management. A combination of control options implemented at appropriate times will be more effective (Vitelli 2000). Thus burning followed by the application of herbicides has been investigated as a control strategy for woody species in semi arid (Noble *et al.* 2001) and temperate (Robertson *et al.* 1999) woodlands. In relation to invasive grasses, the chances of developing biological control agents are slim (Wapshere 1990) and the scope for using chemical controls limited (Grice pers. comm.). However, the use of grazing combined with fire has been found to be effective. Fire and grazing management may interact to cause large shifts in composition and has been used to reduce the abundance of undesirable *Aristida* spp. and promote *H. contortus* in pastures in southern Queensland (Orr and Paton 1977). Fire and grazing has also been used in Californian grasslands to control unwanted non-native species (refer Dyer 2002).

As well as recognising the advantages of an integrated approach to weed management, it is important to note that single applications of any method are unlikely to achieve control and follow-up action is inevitably necessary (Grice *et al.* 2000). Regular burning may be needed to maintain control (Parsons and Stohlegren 1989).

Determining the efficacy of fire for manipulating vegetation composition is difficult. Climatic effects may complicate the interpretation of burning treatments (Norman 1969) and both weather and grazing factors can make it difficult to predict vegetation changes resulting from fire (Walker *et al.* 1981). On this point, Tothill (1971) stated that the "Often quoted usefulness of fire for vegetation management is largely or wholly due to some other factor such as grazing". Plant community responses to fire are influenced by the many complex interactions between plant species, previous fire regimes, fire intensity, rainfall before and after the fire, soil type and prior or subsequent animal grazing (Walker *et al.* 1981) and combinations of factors are most likely to control responses to burning (Hulbert 1988).

Recent literature on fire and exotic species suggests that fire generally tends to promote rather than discourage invasive species (D'Antonio 2000). Nevertheless, fire may be a useful tool for decreasing the prominence of species that may otherwise dominate the community (Stuwe and Parsons 1977; Whisenant 1990b) and there is evidence that many introduced species can be controlled by fire (D'Antonio 2000). However, if fire is to be used for invasive plant control it must be carefully applied and plant and fire factors must be critically evaluated (D'Antonio 2000). The effectiveness of fire in controlling invasive plants depends on physiological properties of both the native community and the invading organism as well as the fire regime itself (Christensen and Burrows 1986). The invasive species must be susceptible to a particular fire regime and the community to be restored must be resilient to that fire regime (Grice, unpublished). Caution is required since fire may have undesirable side effects such as reducing resource availability (Smith and Knapp 1999) and promoting soil erosion (Shaw 1957). In addition, there may also be costs associated with loss of grazing capacity (Hodgkinson *et al.* 1984). In pastoral lands, the benefits from burning, in terms of livestock production, may not be sufficient to justify the loss of forage from burning to control small infestations of weeds (Vitelli 2000). Also, if fire is to be used as a management tool, the environmental benefits, for example reduction of one invader, must be weighed against the costs, for example, increases in another invader or decline in native species (D'Antonio 2000).

3.2.3.5. Community responses to fire: creating gaps and filling them

Fire is a major factor structuring plant communities (refer Tyler 1995). It may alter community composition, richness, and diversity as well as competitive interactions, succession and patch structure (Collins and Gibson 1990) and its role in changing the relative abundance of plants is broadly recognized (refer D'Antonio *et al.* 2001). Can fire be used to reduce the abundance of *C. ciliaris*?

The aims of management strategies to control invasive plants are to prevent or contain invasion, and where invasion has occurred, to eliminate or reduce the abundance of the invasive species while promoting, or at least not disadvantaging, desirable species. To assess the usefulness of fire as a tool for altering the composition of invaded grassland we need to understand how fire affects (1) the persistence of the invasive species, (2) the availability of sites for plant establishment, via effects on plant competition and other factors that influence resource availability and (3) recruitment processes, via effects on seed availability and seedling establishment patterns. It is also important to understand how the outcomes of fire are influenced by other factors such as climate and grazing.

The role of establishment sites, or 'ecological gaps', in plant community dynamics has long been recognized (Harper 1977; Cook 1979; Cook *et al.* 1993a). Establishment sites are defined by the growth requirements of individual plants since resource availability is a function of both the resources present and the ability of a plant to compete for those resources. This is an important point; individual sites may be suitable for some species but not for others. Establishment sites may be vacant space where a plant has died, freeing up resources which are then available for new individuals. Establishment sites may also exist where plants are present, but the available resources limit their growth, and new species are able to colonize due to lower requirements for the limiting resources or an alternative strategy for overcoming the resource limitation (Cook *et al.* 1993a).

Establishment events are rare in many perennial grasslands (Lunt and Morgan 2002; Lauenroth and Aguilera 1998) where the persistence of the resident perennial plants precludes the establishment of new individuals. In communities where the longevity of individual plants is significant, habitat disturbance plays an important role in creating openings for seed germination and seedling establishment (refer Cheplick 1998). Fire alters the availability of establishment sites directly, by increasing or decreasing nutrient levels, and indirectly, by removing or reducing competition from resident plants, freeing up resources for new individuals (Cook 1984; Cheplick and Quinn 1988). Fire may also affect the availability of establishment sites via effects on factors such as herbivory, allelopathic chemicals and litter. For example, litter removal by fire may have significant consequences for the persistence of some species (Whisenant 1990b). The effects of fire on establishment site availability may result in major shifts in species composition.

The establishment of new individuals also requires a source of propagules. Fire may cause increases or decreases in seed input via its effects on flowering. It may reduce the amount of viable seed held in seed heads or in the soil seed bank while its effects on germinable seed availability may be positive or negative, depending on the species involved and fire characteristics.

Developing fire management strategies requires an understanding of the mechanisms by which fire affects plants (Whisenant 1990b). While the fire-promoting properties of *C. ciliaris* are often highlighted in the invasive plant literature (Humphries *et al.* 1991; Low 1997; Franks *et al.* 2000; Pitts and Albrecht 2000), there is little published information on how fire affects the dynamics of *C. ciliaris*-dominated communities.

3.2.4. *CENCHRUS CILIARIS* AND FIRE

There is a divergence of opinion regarding *C. ciliaris*-fire interactions in Australia depending on the context in which it is discussed. In a pastoral context, fire has not been seen as particularly useful for managing *C. ciliaris* (McIvor and Gardener 1981; ’t Mannetje *et al.* 1983; Pressland and Graham 1989). In contrast, in literature discussing *C. ciliaris* as an invasive species, fire is believed to promote *C. ciliaris* (Lazarides *et al.* 1997; Franks *et al.* 2000; Butler and Fairfax 2003).

Fire has not been considered particularly useful for *C. ciliaris* pasture establishment (McIvor and Gardener 1981, 1985) or maintenance. With regard to using fire to rejuvenate *C. ciliaris* pastures, Pressland and Graham (1989) reported that annual burning failed to improve grass yield over a three year period. ’t Mannetje *et al.* (1983) concluded that, although fire caused an initial reduction in green material, it had no lasting effects on the pastures. However, in the invasive plant literature, *C. ciliaris* is considered to be favoured by fire and to promote it (Humphries *et al.* 1991; Low 1997; Franks *et al.* 2000; Pitts and Albrecht 2000). Lazarides *et al.* (1997) stated that *C. ciliaris* was “encouraged” by fire and Butler and Fairfax (2003) found that burning increased *C. ciliaris* cover. The vegetative growth of *C. ciliaris* has been reported to respond vigorously after fire and seed production has been reported to be prolific, particularly if fire is followed by rain (L. Baker, pers. comm. cited in Humphries *et al.* 1991). In turn, domination of vegetation by *C. ciliaris* is reported to lead to hotter, late season fires and increased incidence of fire (Humphries *et al.* 1991; Latz 1991; Butler and Faifax 2003). These changes to fire regimes are attributed to the higher fuel loads and later curing of *C. ciliaris* biomass compared with that of native species (Humphries *et al.* 1991) in combination with rapid regrowth after fire (Pitt and Albrecht 2000). *Cenchrus ciliaris* has been reported to produce two to three times as much biomass as native species in central Australia (Latz 1991). In *Eucalyptus populnea* lands, clearing of native vegetation and establishment of *C. ciliaris* has been reported to lead to increases in fuel loads of up to 20 times that found in similar intact, native vegetation (Walker *et al.* 1981). From their study of *C. ciliaris*-dominated vegetation in Northern Territory, Pitts and Albrecht (2000) considered fire unsuitable for reducing *C. ciliaris* abundance since it recovered rapidly after fire while the germination of native species was negatively affected.

Cenchrus ciliaris is a fire-adapted species (Butler and Fairfax 2003). Many exotic invasive species, particularly the invasive African grasses, have co-evolved with fire and some of these species are referred to as ‘fire weeds’ since they produce much greater flammable biomass than the native species they replace, promoting positive feedback loops between fire and weed invasion (Wilson and Mudita 2000). However, this does not preclude fire as a useful tool to manage these species. Although many invasive species are promoted by fire, there is evidence that others can be controlled by fire (D’Antonio 2000). Even fire-adapted species are adversely affected by fire at particular times and under certain conditions (Vogl 1974) and the strategic use of a controlled fire regime has been suggested as a way to maintain or restore areas in Hawaii invaded by *C. ciliaris* and other invasive African grasses (Daehler and Carino 1998). In tropical Australia, the native perennial grasses have evolved with fire and survive, although species differ in their responses to burning (McIvor and Orr 1991). The strategic use of fire may alter the competitive interactions between *C. ciliaris* and the resident native species.

The role of fire in either reducing or enhancing biological invasions in native communities depends on the properties of the native community, the invading organism and the fire regime (Christensen and Burrows 1986) and research is required to determine how fire influences competitive interactions between native and exotic species (Daehler and Carino 1998). How might fire work to influence *C. ciliaris* abundance relative to other species? Can fire be used to kill established *C. ciliaris* plants? How does fire affect *C. ciliaris* seed availability and seedling recruitment compared with other species? Little is known about how different fire regimes affect *C. ciliaris* compared with native species. In the following sections a series of studies investigating the effects of early dry season and late dry season burns on *C. ciliaris*-dominated grasslands in two vegetation communities are described.

3.3. SITE AND TREATMENT DESCRIPTIONS

3.3.1. STUDY SITES

Experimental plots were established in two vegetation communities in north Queensland: a eucalypt savanna at Dalrymple National Park and a perennial grassland at Moorrinya National Park.

3.3.1.1. Dalrymple National Park

Dalrymple National Park (19^0 48'30'' S 146^0 15'30'' E) is approximately 46 km north-west of Charters Towers (QDE 1998a), in the Dalrymple Shire, north Queensland (Figure 3.1). Covering 1640 ha, the park conserves part of the upper Burdekin River catchment and lava flows of the Great Basalt Wall in the Einasleigh Uplands biogeographic region (QDE 1998a). The Burdekin River, the longest river on Queensland's east coast, flows through the park. The geology of the area is variable and includes lava flows, limestone, sandstone and sandy deposits. Six vegetation communities containing 198 plant species have been identified. The vegetation is dominated by tall eucalypts (*Eucalyptus tessellaris* and *E. tereticornis*), she-oak (*Casuarina* spp.) woodlands and dry vine thicket. The herbaceous layer is dominated by exotic perennial grasses including *C. ciliaris* and *Panicum maximum.* The diverse vegetation and reliable water provide significant habitat for animals including 183 birds, 47 reptiles and 36 mammals (QDE 1998a). The park lies within the wet-dry tropics and has a warm, subhumid climate (Rogers *et al.* 1999). Average annual rainfall in the Dalrymple Shire ranges between 500 and 700 mm, 80% of which falls between December and April, although rainfall is extremely variable from year to year (Quirk *et al.* 1997).

The park was 'dedicated' in 1990 to conserve a diverse range of plant and animal communities of the Burdekin River catchment (QDE 1998a). The area also has cultural heritage values. Remains of the old Dalrymple township, the first surveyed inland settlement in northern Australia, are surrounded by the park but are privately owned. The park was previously a cattle station and was grazed by stock prior to August 1992 (QDE 1998a). The extensive grazing regime maintained low to moderate fuel levels which largely precluded a systematic prescribed burning regime and reduced the incidence of wild fires. The only major wildfire in recent history occurred in October 1983 when 50% of the northern section of the park was burnt (Paul Williams pers. comm.).

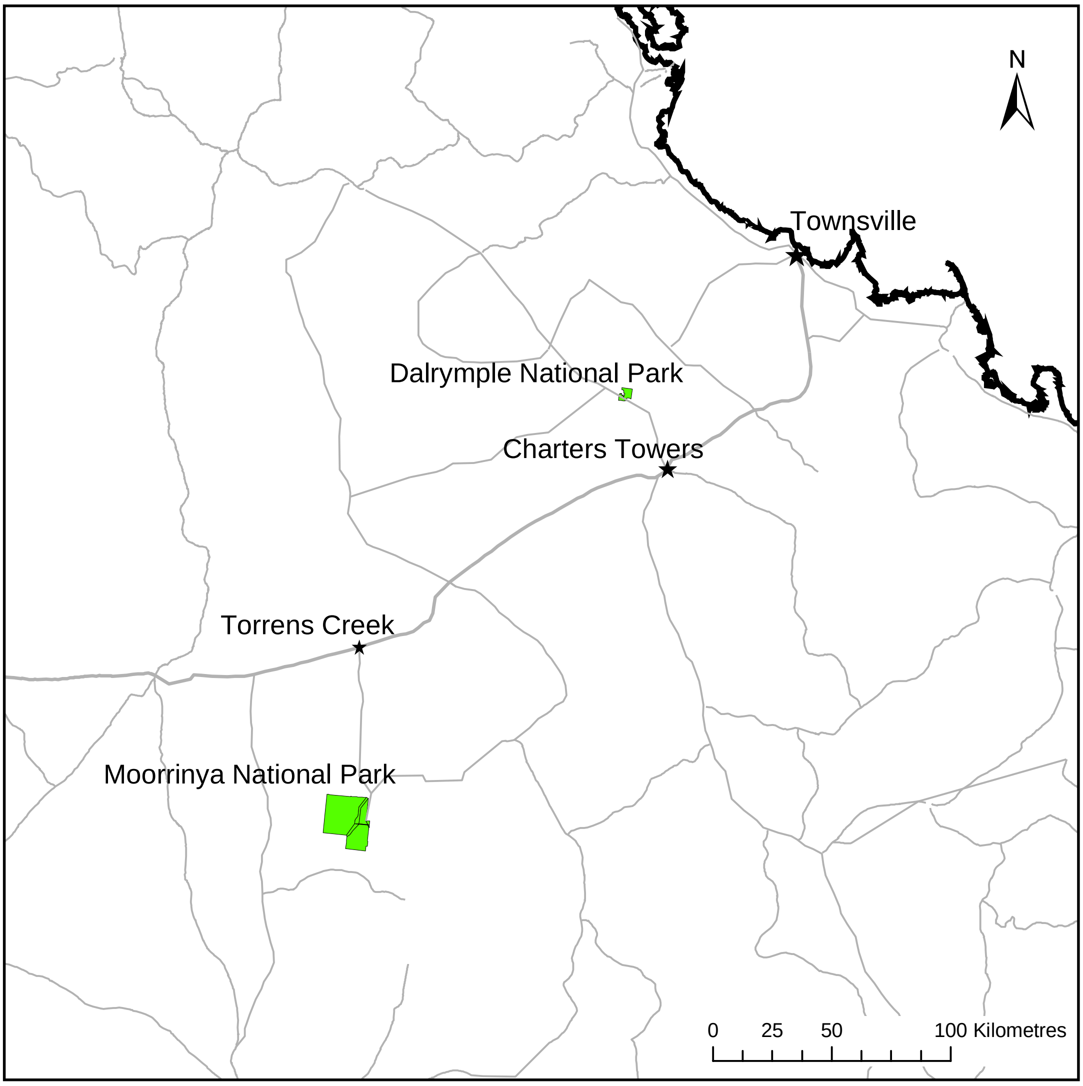

Figure 3.1. Location of Dalrymple and Moorrinya National Parks. Grey lines indicate roads.

The site for this study was located on the western side of the Burdekin River near the site of the old Dalrymple township. This area is a flat to gently undulating alluvial plain bordered by river levees. The soil is an orthic Tenosol (Isbell 1996). It is a dark yellowish-brown, fine sand grading to a brown loam. The vegetation is open eucalypt woodland with an upper stratum dominated by *Eucalyptus tessellaris* and *E. tereticornis*. The herbaceous layer is dominated by *C. ciliaris* with some native grasses present including *Bothriochloa* spp., *Chrysopogon fallax*, *Enneopogon* spp., *Eragrostis* spp. and *Heteropogon contortus.*

3.3.1.2. Moorrinya National Park

Moorrinya National Park ($21^0$30’ S, $145^0$00’ E) is 85 km south of Torrens Creek, north Queensland (Figure 3.1). Covering 32,607 ha, it comprises flat plains crossed by shallow, intermittent watercourses. The geology is mostly Quaternary silt, clay, sand and rubble with rises of Tertiary conglomerate (QDE 1998b). The vegetation includes grassy plains and open eucalypt, acacia and melaleuca woodlands. Over 300 plant species have been identified (QDE 1998b). A diverse fauna has been found in the park including 165 species of birds, 40 reptiles, 17 mammals, nine frogs and seven fish (QDE 1998b). The climate of the area is semi-arid with a highly variable, summer dominant rainfall (DNR 1998). The mean annual rainfall at Hughenden is 491 mm (Bureau of Meteorology, unpublished).

The park was ‘dedicated’ in 1993 and conserves a diverse range of plant and animal communities (12 of the 15 regional ecosystems found in the Prairie-Torrens Creek alluvial Province of the Desert Uplands biogeographic region) (QDE 1998b). Prior to 1993 Shirley Station, as the park was formerly known, was grazed by sheep and cattle. The fire history of the park is not well documented although fire is considered to be the major influence on vegetation patterns (QDE 1998b).

The site used for this study is open grassland north of Bells Outstation near Alice’s creek. The area, which was cleared and sown with *C. ciliaris* in the 1960s (McCallum 1998), is dominated by *C. ciliaris* and *Astrebla* spp. Other grasses present include *Dichanthium* and *Iseilema* species. It is likely that prior to clearing the site was a mixture of gidgee (*Acacia cambagei*) and native grasses including *Astrebla* spp. The site is treeless, although there are scattered shrubs (*Acacia farnesiana*, *A. cambagei* and *A. shirleyi*). The landform is a gently undulating plain of grey cracking clay (grey Vertisol, Isbell 1996) with a gilgai micro-relief.

3.3.2. EXPERIMENTAL DESIGN AND TREATMENTS

Twelve plots (20 m by 20 m) were pegged out at each site in February 1999 at Dalrymple and April 1999 at Moorrinya. At Dalrymple, nine plots were located on a level site and three plots were located about 200 m away, on the side of a levee bank. These three plots were positioned away from the main experimental areas to avoid heavily timbered areas, although trees could not be completely avoided and were present in some plots. At Moorrinya, 12 plots were set up in a three by four grid within an area (approximately 100 m by 150 m) of grassland. Although treeless, some plots contained shrubs such as *A. cambagei*, *A.*

farnesiana and *A. shirleyi*. Fire breaks were slashed around the perimeters of all plots prior to burning.

The treatments imposed were: early dry season burn, late dry season burn and no burn (control). These treatments were chosen to achieve significantly different fire intensities. While an early wet season burn treatment was also of interest, wet season fires are logistically more difficult to achieve and resources were not available to implement them. Early dry season fires were conducted on 10th and 15th of June 1999 at Moorrinya and Dalrymple respectively. Late dry season fires were conducted on the 12th and 17th of November 1999 at Dalrymple and Moorrinya respectively. The wet season in this region is considered to run from November to April (Ash *et al.* 2002), although its duration is highly variable (see Figure 3.2. for mean monthly rainfall).

The experimental design was a randomized complete block with four replicates of each treatment at each site. At Dalrymple, plots located on the levee bank were considered one block. The other plots were blocked on the basis of percentage *C. ciliaris* cover, estimated as described below. At Moorrinya, plots were blocked on the basis of percentage *C. ciliaris* cover although one high *C. ciliaris* cover plot (plot 10) was incorrectly allocated to the low *C. ciliaris* cover block. For most analyses, blocking was not significant and block effects were ignored unless stated otherwise.

3.3.3. PRE-FIRE MEASUREMENTS

Prior to the imposition of burning treatments the plant species composition of plots was recorded. Immediately pre-fire, fuel biomass and moisture content, air temperature and relative humidity were determined for each fire.

3.3.3.1. Plant species composition

Plant species composition and abundance were assessed in April 1999 at Dalrymple and in April and June 1999 at Moorrinya. Each plot was searched for 10-15 minutes and the species found recorded. The height (estimated) and circumference at breast height (measured) of trees and shrubs were also recorded. Twenty quadrats (1 m^2) per plot were assessed in detail. Quadrats were located by throwing a 1 m by 1 m wire frame from five positions along each side of the plot. In each quadrat, the species present and their visually estimated percentage cover (the percentage of the total vegetative cover in the quadrat) were recorded. Plant specimens were collected for identification of unknown species and to produce a herbarium collection.

3.3.3.2. Fuel biomass and moisture content

Fuel biomass and moisture content were estimated immediately prior to burning at each site. Herbaceous biomass was estimated using a ‘standing crop disc’. This apparatus consists of a metal rod marked with a scale and a metal disc with a central hole through which the rod is inserted. The rod is held vertically with one end resting on the ground. The disc is held at the top of the rod at a set position with its flat surface parallel to the ground. It is then allowed to drop and the position on the rod at which the disc comes to rest is recorded. The greater the amount of biomass under the disc, the higher it sits in relation to the rod and the higher the ‘score’. Although this method works best in continuous swards, random sampling ensured a representative measure of biomass (bare ground was also sampled). The method allowed rapid, non-destructive sampling providing a greater sample size than would have been possible with destructive sampling. Eighty standing crop disc scores were randomly collected at Dalrymple (60 within the main experimental area and 20 within the levee bank area). Sixty standing crop disc scores were collected within the experimental area at Moorrinya. An additional 10 disc score measurements were made at each site to calibrate scores with biomass. After each of these 10 scores was recorded, all herbaceous material under the disc (0.5 m^2 quadrat) was cut at ground level. These samples were weighed after being dried at 70^oC. The relationship between score and dry weight of herbaceous material (kg/ha) was determined by regression analysis.

Fuel moisture content was determined by collecting biomass samples around, but not within, the experimental plots. At Dalrymple, 10 and five samples were collected around the main and levee experimental areas respectively. Ten samples were collected at Moorrinya. Each sample of 200-300 g of plant material was cut at ground level and placed in an air-tight plastic bag. Samples were weighed fresh and reweighed after drying at 70^oC.

3.3.3.3. Weather conditions

Temperature and relative humidity were measured with a hygrometer immediately prior to lighting the fires.

3.3.4. FIRE CONDITIONS

Fire management resources dictated that plots allocated to burning treatments were burnt one at a time. One measurement of fire speed was made in each plot using two markers. Markers were placed in the direction of the fire, one about 10 m from the other and the distance and time taken to burn between the markers were recorded. Fire intensity (I) for each plot, defined as the heat released per metre of fire front (kW/m) was calculated using the relationship:

$$I = H\omega r$$

where H is the heat yield of the fuel burnt (the heat yield of herbaceous fuels is approximately 17 kJ/kg (Byram 1959), ω is the amount of fuel consumed (kg/m^2) and r is the rate of spread (m/sec) (Cheney and Sullivan 1997).

The fires were generally slow moving and of low intensity, creating patchy burns with some biomass remaining either unburnt or scorched in most plots. However, the late dry season fires at Moorrinya were more intense, reducing most biomass to ash. A summary of the conditions on the day of the fire and fire characteristics is given in Table 3.1. Fire intensities were probably over-estimated since not all the fuel was burnt.

3.3.4.1. Early dry season fires

At Dalrymple on the 15th June 1999 conditions were cool (23°C at 1 pm) and relative humidity was low (30% at 1 pm). Breezes were light and changed direction often. Plots were burnt by lighting back burns before lighting head fires. The first fire was lit around 1.20 pm and all fires were completed by about 3.30 pm. The fires produced patchy burns leaving some plants scorched or unburnt. Estimated fire speeds ranged from 0.05 m/sec to 0.29 m/sec and estimated fire intensity ranged from 441 kW/m (plot 10) to 3030 kW/m (plot 1) (Table 3.1).

At Moorrinya on the 10th June conditions were cool (23.5°C at 12.30 pm). Relative humidity was 57% at 10 am and had declined to 48% by 12.30 pm. The prevailing breeze was from the south-east. Plots were burnt with head fires lit from the south-east corners. The first fire was lit around 11.15 am and all fires were completed by about 2.00 pm. The fires produced patchy burns because of variability in fuel levels: the plots contained areas with little or no biomass present. Some spot burning was carried out but kept to a minimum to simulate a natural burn. Estimated fire speeds ranged from 0.07 to 0.12 m/sec and estimated fire intensities ranged from 525 to 1125 kW/m (Table 3.1).

3.3.4.2. Late dry season fires

On the 12th November 1999, conditions at Dalrymple were warm and humid. The temperature was 28°C and relative humidity 42% at 1.20 pm. Breezes were light and changed direction often. The first fire was lit around 1.20 pm and all fires were completed by about 3.00 pm. The fires generally produced very patchy burns leaving many plants scorched or unburnt. Estimated fire speeds ranged from 0.07 m/sec to 0.22 m/sec and estimated fire intensities ranged from 326 to 1619 kW/m (Table 3.1).

On the 17th of November 1999, conditions at Moorrinya were dry and gusty. Relative humidity was 35% and the temperature 34°C at 11.00 am. The first fire was lit around 11.00 am and all fires were completed by noon. All fires burnt strongly leaving relatively few patches unburnt and reducing most above ground biomass to ash. Estimated fire speeds ranged from 0.07 m/sec to 0.31 m/sec and estimated fire intensities ranged from 462 to 2047 kW/m (Table 3.1).

Table 3.1. Summary of conditions for early and late dry season fires at Dalrymple and Moorrinya National Parks. Values are means ± SE.

Site	Date	Fuel load[a] (kg/ha)	Fuel moisture (%)	Fire speed (m/sec)	Fire intensity (kW/m)
Dalrymple					
	15/6/99	6150 ± 238[b] 5180 ± 241[c]	33 ± 1.3	0.14 ± 0.075	1400 ± 819
	12/11/99	4330 ± 320[b] 2950 ± 720[c]	26 ± 1.6	0.12±0.036	820 ± 285
Moorrinya					
	10/6/99	4410 ± 245	25 ± 2.1	0.12 ± 0.017	860 ± 125
	17/11/99	3880 ± 272	28 ± 2.1	0.22 ± 0.052	1490 ± 351

a. Mean biomass was estimated from standing crop scores using the following relationships (regression analyses performed using Genstat (2001):

Dalrymple: Early dry season fire biomass = $371+36*1.11^{score}$ (Adj $R^2 = 0.85$)

Dalrymple: Late dry season fire biomass = $59.38*Score^{0.91}$ (Adj $R^2 = 0.88$)

Moorrinya: Early dry season fire biomass = $60.04*Score^{0.76}$ (Adj $R^2 = 0.97$)

Moorrinya: Late dry season fire biomass = $23.55*Score^{1.09}$ (Adj $R^2 = 0.97$)

b. Mean fuel load in main experimental area.

c. Mean fuel load in levee bank area.

3.3.5. LOCAL RAINFALL

Detailed climate data were not available for the experimental sites. Rainfall data for Fletcher View station, 11 km south-east of Dalrymple National Park are given in Figure 3.2a. Rainfall data were available for Moorrinya National Park from January to August 1999 and from October 2000 to June 2001. These data and data from Uanda Station, about 14 km south-west of Moorrinya, for the missing months are given in Figure 3.2b.

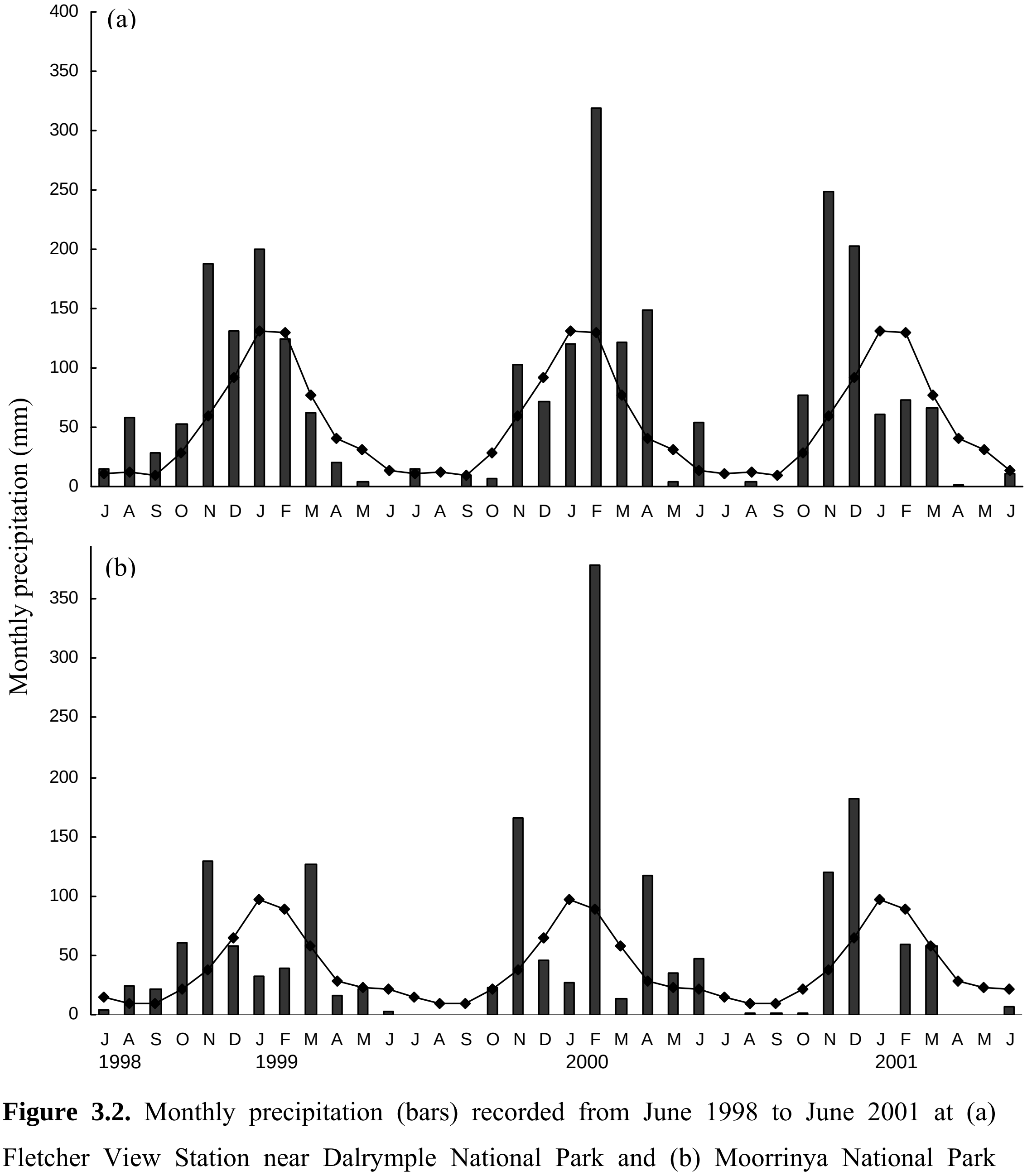

Figure 3.2. Monthly precipitation (bars) recorded from June 1998 to June 2001 at (a) Fletcher View Station near Dalrymple National Park and (b) Moorrinya National Park (except from September 1999 to September 2000 when precipitation for nearby Uanda Station is given). Line graphs show monthly rainfall averages for Fletcher View and Uanda stations respectively (Commonwealth Bureau of Meteorology, unpublished; Queensland Parks and Wildlife Service, unpublished).

3.4. CAN FIRE KILL *CENCHRUS CILIARIS*?

3.4.1. INTRODUCTION

The aim of weed management is to limit or reduce the abundance of invasive species with minimum negative impacts of the weed or the treatment on the establishment and vigour of desirable species. A key factor determining the efficacy of fire as a tool for manipulating the composition of *C. ciliaris*-dominated grassland is the effect of fire on *C. ciliaris* plant persistence.

Competition from established plants is a major factor preventing plant establishment in perennial grasslands (Cook 1980). Consequently, the longevity of existing plants is a significant factor influencing community dynamics. *Astrebla* plants may live for 23 years (Orr and Holmes 1984) and *C. ciliaris* plants are also considered to be long-lived (Brown 1985). Habitat disturbances that reduce or remove established plant competition are important since they create gaps that could provide ‘safe sites’ (Harper 1977) for germination and seedling establishment (Cheplick 1998) (section 3.2.3.5). Fire is an important agent in structuring communities since the openings it creates provide the potential for vegetation change (Bond and van Wilgen 1996). By removing perennial vegetation, fire may free up resources and create conditions more conducive to germination (Cheplick and Quinn 1988) and establishment and many studies report increased seedling emergence and/or establishment in grasslands after fire (Shaw 1957; Christensen and Muller 1975; Williams *et al.* 2003b) (section 3.2.2.5). In *C. ciliaris*-dominated grasslands, the effects of fire on other ecosystem components and processes, such as seed banks and flowering, are likely be irrelevant in promoting compositional change unless *C. ciliaris* plants can be removed and resources made available to support the establishment of new individuals.

Can fire be used to kill *C. ciliaris* plants? In this study the effects of season of burning on the survival of *C. ciliaris* were investigated. At Moorrinya the effects of season of burning on the survival of the dominant native *Astrebla* spp. were also investigated. At Dalrymple, native species such as *Heteropogon contortus* were not abundant enough to include in the study. Season of burning is important in determining the extent of fire-induced plant mortality (Trollope 1997) due to seasonal differences in fire and plant characteristics (section 3.2.3.1). Late dry season fires are generally more intense than early dry season fires (Williams *et al.* 1997) and, since the level of plant mortality is positively related to fire intensity (Williams J.R. 1995), late dry season fires may result in higher plant mortality

(Lonsdale and Braithwaite 1991; Williams *et al.* 1997). The timing of fire in relation to plant phenology also influences the degree of damage caused by fire (West 1965; Tainton 1981). Tissue moisture content and the location of carbohydrate stores (roots or shoots) varies seasonally and affects both plant susceptibility to fire and recovery after fire (Bond and van Wilgen 1996). Actively growing species may be highly susceptible to fire while dormant species are relatively unaffected (Daubenmire 1968; Bond and van Wilgen 1996). Consequently, although late dry season fires may be more intense than early dry season fires, early dry season fires may cause more injury if plants are still actively growing.

3.4.2. METHODS

3.4.2.1. Field set-up

Cenchrus ciliaris plants in the experimental plots at Dalrymple and *C. ciliaris* and *Astrebla* spp. plants in the experimental plots at Moorrinya were tagged in April 1999 using numbered metal pegs pushed into the soil beside each plant. At Dalrymple, 10 large and 10 small *C. ciliaris* plants were tagged per plot. Plants were considered small if their basal area was less than 50 cm^2. Plots were searched to provide 10 pairs of plants where possible (each pair being a large and small tussock within 1 m of each other). The growth habit of *C. ciliaris* was such that it was often difficult to determine the origin of tillers and thus identify individual tussocks. Plants difficult to distinguish as individual tussocks were avoided. At Moorrinya, 20 *C. ciliaris* and 20 *Astrebla* plants were tagged per plot. Most *Astrebla* plants were *A. squarrosa* although some individuals of *A. pectinata* were included. Plants were chosen to include a range of sizes. The difficulty in determining individual tussocks was even greater at this site. Clearly identifiable *C. ciliaris* and *Astrebla* tussocks were selected where possible but in some cases the extent of individual tussocks was uncertain.

The basal area of each tagged plant was estimated as:

$$\text{Basal area (cm)} = \pi * \text{diameter 1(cm)} * \text{diameter 2 (cm)}/4$$

where the diameters were the longest and shortest lengths of the tussock base. Tussock base measurements were made prior to the imposition of burning treatments.

The post-fire status (dead or alive) of tagged plants was recorded in January and June 2000 at Dalrymple and in February and August 2000 at Moorrinya. The results were similar between sampling times and only the latter results are reported.

3.4.2.2. Statistical analyses

Burning treatment effects on the percentage of dead small plants at Dalrymple were investigated using one-way ANOVA. Data on large plants were not analysed since only one large plant died. The percentages of dead plants at Moorrinya were analysed using a split-plot design with burning treatments as main plots and species as subplots after checking for homogeneity of error variances. Data were arcsin transformed prior to analysis to normalize the distribution of residuals where necessary. In these cases, the reported means have been back-transformed. Means were compared using the protected LSD test at the 5% significance level. Basal areas were compared between small and large plants at Dalrymple and between *C. ciliaris* and *Astrebla* plants at Moorrinya using t-tests assuming unequal variances. Regression analysis was used to investigate relationships between plot fire intensity and the percentage of dead plants per plot. All analyses were conducted using Genstat (2001).

3.4.3. RESULTS

Plant mortality was low at both sites with less than 6% of tagged plants dying over the monitoring period. Despite this, burning treatment effects were detected.

At Dalrymple, the mortality of small plants was greatest in the early dry season burn treatment ($P < 0.05$) where 24% of plants died compared with less than 3% in other treatments (Table 3.2). In contrast only one large tagged plant died at the site. At Moorrinya, *C. ciliaris* and *Astrebla* mortalities were greatest in the late dry season burn treatment (Table 3.2). No differences in mortality between *C. ciliaris* and *Astrebla* plants were detected ($P>0.05$).

Generally, the plants that died had smaller basal areas than average. Of the dead small plants at Dalrymple, all but one had smaller basal areas than the average for that size class. The basal area of small plants ranged from 0.1-44.0 cm^2 (mean ± SE = 12.6 ± 1.03) while the basal area of killed small plants ranged from 0.1-15.7 cm^2 (mean ± SE = 3.4 ± 1.39 cm^2). The large plant that died was also smaller than average (77.8 cm^2) (Table 3.2). At Moorrinya, the average size of dead plants (72 ± 37.9 cm^2 and 72 ± 30.2 cm^2 for *C. ciliaris* and *Astrebla* plants respectively) was less than the average for these species (Table 3.2). Only two of the 15 dead *C. ciliaris* plants and two of the 10 dead *Astrebla* plants were larger than average.

At both sites over 50% of tagged plants had basal areas of 100 cm^2 or less. The size class frequency distribution of tagged plants is given in Figure 3.3. At Moorrinya, a few very large *C. ciliaris* plants were tagged and mean basal area of *C. ciliaris* plants was significantly greater ($P < 0.05$) than that of *Astrebla* plants.

Table 3.2. Mean basal area (cm^2) and mortality (%) of tagged plants at Dalrymple and Moorrinya. Different lower case letters denote significantly different ($P < 0.05$) percentage mortality within plant size classes (Dalrymple) and within species (Moorrinya).

Site	Plant type	basal area (mean ± SE) (cm^2)	Plant mortality (% of tagged plants that died)		
			Control	Early burn	Late burn
Dalrymple					
	Small	13 ± 1.0	$^*3^a$	$^*24^b$	$^*1^a$
	Large	180 ± 13.1	0	3	0
Moorrinya					
	C. ciliaris	244 ± 22.6	3^a	3^a	14^b
	Astrebla	137 ± 10.0	0^a	0^a	14^b

* Back-transformed means

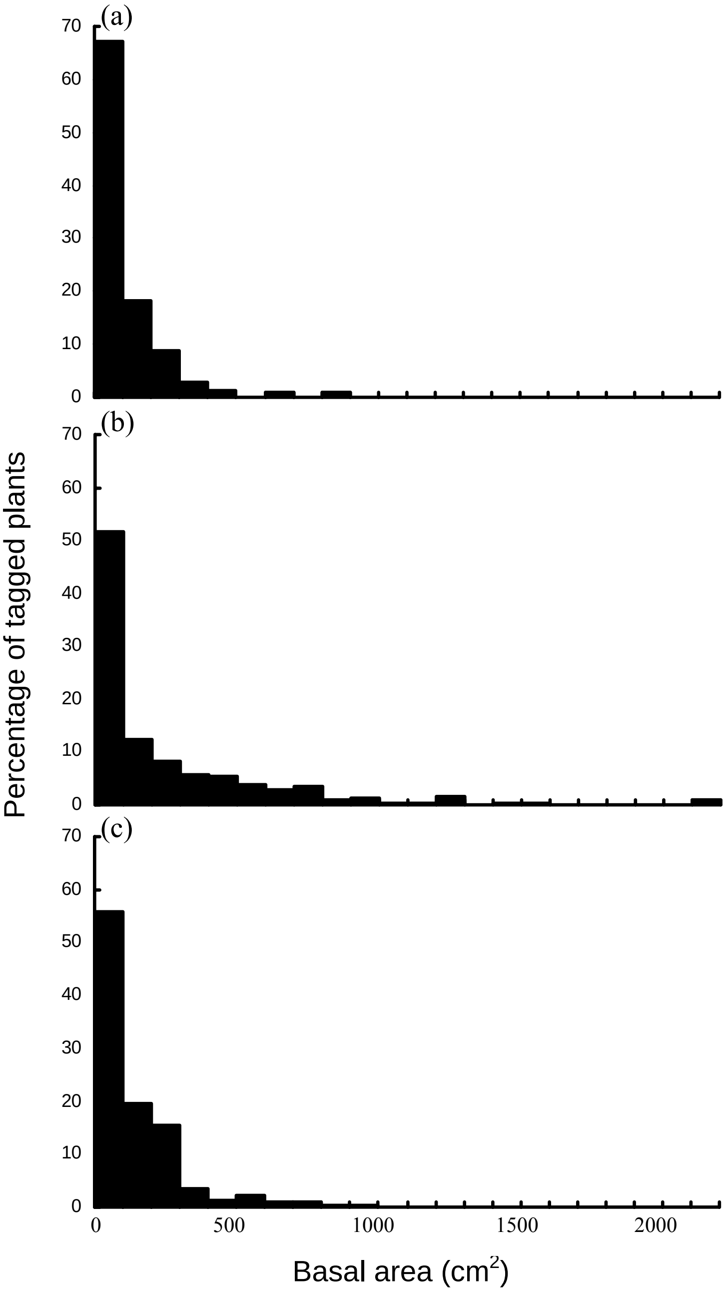

Figure 3.3. Percentage of tagged plants in basal area size classes (increments of 100 cm^2). (a) *C. ciliaris* plants at Dalrymple, (b) *C. ciliaris* plants at Moorrinya and (c) *Astrebla* plants at Moorrinya.

Linear relationships between plot fire intensity and the percentage of dead tagged plants were significant ($P < 0.05$) for both sites. However, individual plots had high leverage and distribution of the data prevented valid assessment of these relationships (Figure 3.4).

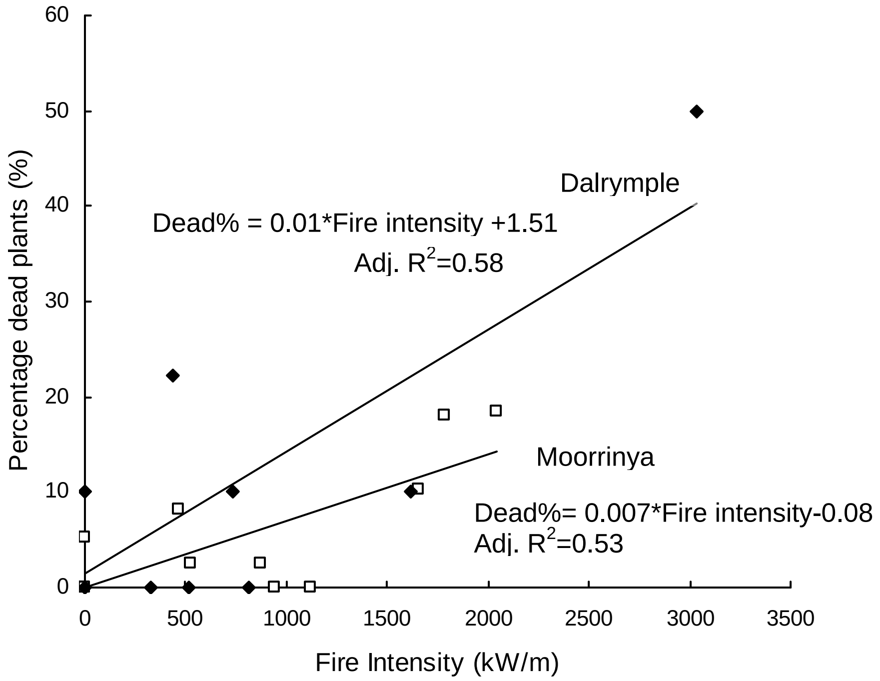

Figure 3.4. Relationships between plot fire intensity and percentage of tagged plants that died/plot at (♦) Dalrymple and (□) Moorrinya. Regression lines are shown.

3.4.4. DISCUSSION

Fire-induced plant mortality is related to fire intensity and many studies report greater plant mortality with higher intensity fires (Williams J.R. 1995; Lippicott 2000; D'Antonio *et al.* 2001). In this study also, more plants were killed in the higher intensity fires. However, the relationship between fire intensity and season of burning differed between the two sites. At Moorrinya, the mean intensity of late dry season fires was higher than that of early dry season fires while at Dalrymple, the reverse was found. The unexpectedly low intensities of late dry season fires at Dalrymple were due to lower fuel loads and the weather conditions at the time of burning.

Although greater plant mortality was associated with higher mean fire intensity, regardless of season of burning, it was not possible to determine a clear relationship between fire intensity and mortality using the individual plot data. A more even distribution of plot fire intensities is needed to validly assess fire intensity-plant mortality relationships. It is also important to recognize that plot-level fire intensities may not adequately describe the fine scale fire conditions that are critical in determining the fate of individual plants. An average site fuel load and only one fire speed estimate per plot were used to calculate plot fire intensity.

However, the fire intensities experienced by individual tussocks clearly varied widely. Due to the patchy nature of the fires some plants were reduced to ash while others remained unburnt. In addition, fire residence time may be more biologically important than fire intensity (Walker *et al.* 1981; Noble and Grice 2002) (section 3.2.3.1).

Fire intensity probably explains the reversal of season of burning effects between the two sites. However, differences in the growing season and phenological condition of plants between sites may offer an alternative explanation for the increased early dry season mortality at Dalrymple. Since plants with higher moisture contents are killed at lower temperatures (Bond and van Wilgen 1996), actively growing plants are more vulnerable to fire (Daubenmire 1968; Bond and van Wilgen 1996). If *C. ciliaris* plants at Dalrymple were still growing at the time of the early dry season fires, they may have been more vulnerable to fire than dormant plants. It is likely that plants were dormant by the time of the late dry season fires. A shorter growing season at Moorrinya may have resulted in plants being dormant at this site at the time of the early dry season fires. Although it is not possible to estimate the duration of the growing seasons, at the time of the early dry season fires at Dalrymple, fuel moisture contents were higher (33 ± 1.3%) than those at the late dry season fires (26 ± 1.6%) at this site and higher than those at any fires at Moorrinya (25 ± 2.1 and 28 ± 2.1% moisture for early and late dry season fires respectively) (section 3.3.4). This may indicate that the vegetation at Dalrymple had not senesced to the degree it had at Moorrinya.

It is unlikely that the amount of biomass removed in these fires had much effect on establishment site availability. Although burning resulted in *C. ciliaris* and *Astrebla* mortality, the numbers of plants killed were low and those killed tended to be smaller than average. The greater susceptibility of small plants was not surprising since smaller plants are brought to lethal temperatures more quickly than larger plants (Bryam 1948) and other studies have found fire-induced mortality is greater for smaller individuals (refer Bond and van Wilgen 1996; Grice 1997) (section 3.2.3.2). The death of the few small plants in this study would have been insignificant in opening up establishment sites in these grasslands.

Although the removal of large individuals is more effective in creating establishment sites, the susceptibility of small plants to fire is important since it is likely that a large proportion of individuals in these populations are small. Although the size distribution of tagged plants may not accurately represent the plant size distributions of these populations (since tagged plants were not selected randomly), the actual size class distributions are probably skewed, as found for the tagged plants. If so, and if plant size is an important determinant of susceptibility to fire, it appears that many individuals in these populations are susceptible to relatively low intensity fires. Ninety percent of tagged *Astrebla* plants and 60% of tagged *C. ciliaris* plants were of the same size or smaller than the largest killed plants. The small numbers of plants actually killed probably reflects the patchy nature of the burns in which some plants were reduced to ash while others were barely singed. A more uniform burn is likely to cause more deaths and create more significant gaps. Higher intensity fires are likely to be even more effective if larger individuals are also killed.

Co-occurring species may respond very differently to the same fire (Daubenmire 1968). For example, in burning experiments in Hawaiian woodland, *Schizachyrium condensatum* tolerated fire with 94% and 40% plant survival after low and high intensity fires while *Melinis minutiflora* was greatly affected with 30% and 0% plant survival after the same fires (D'Antonio *et al.* 2001). Such responses may occur where species differ in condition (size and vigour), morphology, and/or life strategy (section 3.2.3.2). For example, differences in plant responses to fire may be related to plant architecture and the degree to which meristematic sites are protected from heat injury (Tainton 1981; Walker *et al.* 1983). The more loosely packed tillers of *Heteropogon contortus* may make it more susceptible to heat damage from fire than the dense internally damp tussocks of *Themeda triandra* which effectively insulate the apices against heat damage (Walker *et al.* 1981). However, the relative responses of species to fire may change over time and it appears that *T. triandra* may be more susceptible to fire later in the dry season since its tussocks produce significantly higher temperatures than *H. contortus* tussocks (refer Walker *et al.* 1983).

Different responses to fire by *C. ciliaris* and local native species are of particular interest. However, in this study it was not possible to monitor fire effects on native species other than *Astrebla* at Moorrinya. Further work is required to investigate fire-induced mortality of *C. ciliaris* compared with that of native species. Are *C. ciliaris* plants susceptible to the strategic use of fire? The removal of above ground biomass by fire is likely to have less impact on *C. ciliaris* than on some native species. Defoliation experiments have found that, while defoliation reduces root biomass, *C. ciliaris* maintains a relatively high root:shoot ratio compared with some native species (Brown 1985) and its persistence under heavy grazing is testimony to its ability to recover after defoliation. However, high intensity fires may kill *C. ciliaris* plants. Fatal fire intensities may be easier to achieve in *C. ciliaris* patches since *C. ciliaris* is associated with greater biomass production than native species (Humphries *et al.* 1991; Latz 1991), although this is not always the case (section 2.2.3). Differences in plant phenology may be exploited. *Cenchrus ciliaris* has been reported to remain green and cure later than native species (Cavaya 1988; Humphries *et al.* 1991). This may make it more susceptible to early dry season burns than native species which senesce earlier.

3.5. DOES FIRE INCREASE PLANT NUTRIENT AVAILABILITY IN *CENCHRUS CILIARIS*-DOMINATED GRASSLAND?

3.5.1. INTRODUCTION

Fire alters plant community productivity, composition and structure via direct effects on plant growth, survival and reproduction. However, fire-induced changes in the environmental conditions experienced by plants may also result in significant vegetation change. Fire alters the availability of light, water and nutrients and causes changes in microbial and animal populations (section 3.2.2.4). Although plants respond to the combined influence of these and other post-fire conditions, changes in one factor can be a significant determinant of vegetation change. Fire can rapidly alter the amount, distribution and form of plant nutrients (Raison 1979) and fire-altered nutrient status may have major impacts on plant communities. Enhanced plant growth (Christensen and Muller 1975; Scanlan and O'Rourke 1982; Hulbert 1988) and changes in species composition (Daubenmire 1968; D'Antonio *et al.* 2001) have been attributed to post-fire increases in nutrient resources.

Fire directly affects plant nutrient availability by incinerating organic matter and by heating the soil (Raison 1979). It indirectly affects nutrient availability via effects on the activity of soil biota (Christensen and Muller 1975), water movement and erosion processes (Kellman *et al.* 1985). Changes to soil properties may also result from fire effects on plant community composition, structure and productivity (Raison 1979).

Nutrients are released from burnt organic matter and nutrient availability is commonly, though not universally, increased by fire due to ash added to the soil surface (Bond and van Wilgen 1996). Ash contains large quantities of various nutrients in mineral form as well as a readily available soluble, organic reservoir of these materials (Christensen and Muller 1975). Fire also alters soil chemistry via heating effects (Raison 1979). For example, soil phosphorus and nitrogen fractions may be altered by heat (refer Humphries and Craig 1981). As well as changes in the amount and form of nutrients, nutrient concentrations may be considerably more variable after fire due to variations in fire intensity and the uneven distribution of ash (Christensen 1985). The effects of ash and heat on soil chemistry and plant responses to these effects are reviewed by Raison (1979).

Not all the nutrients from burnt biomass are retained in the soil. Some nutrients, particularly nitrogen and sulphur, may by lost through volatilisation and nutrients may be removed as particulates via air and water movement (Kellman *et al.* 1985). Although it is often considered that most of the N and S in biomass is volatilized during fires and most of the phosphorus, potassium, calcium and magnesium is deposited in ash, P, K and Mg can be volatilized during fires and all elements can be transferred to the atmosphere as particulates (Cook 1992). The magnitude of nutrient losses due to fire depends on fire intensity, flame dimensions and temperature profiles, the spatial pattern of these properties across the landscape as well as fire frequency (Cook 1992). The proportion of nutrients in volatile versus particulate states depends on the vapourization temperature of the elements involved and the fire intensity (Raison *et al.* 1985). The more intense the fire, the greater the volatilization losses (Bond and van Wilgen 1996; Mack *et al.* 2001). Volatilization losses from soil organic matter are likely to be low in savannas because soil temperatures and intensities of savanna fires are relatively low and the build up of organic matter between fires is also relative low (Cook 1992). However, volatilization losses from aboveground biomass can be significant. Nitrogen losses due to volatilisation have been found in north American tallgrass prairies (Knapp and Seastedt 1986; Turner *et al.* 1997) and savannas in the Northern Territory, Australia (Cook 1992; 1994).

Nutrients may also be lost via air and water movement. Nutrients transported into the air as particulates may be re-deposited. Since the movement and redistribution of ash by wind is patchy (Cook 1994) and material can settle out at the site or many kilometres away, the assessment of whether such material is lost or re-distributed depends on the scale considered. Fire converts nutrients to readily soluble forms, increasing the potential for losses via leaching. However, leaching losses may be insignificant where there is rapid uptake by plants (Cook 1992) or where nutrients are rapidly immobilized in the soil after fire (Kellman *et al.* 1985). Removal of nutrients in runoff can be a major cause of nutrient loss (Kellman *et al.* 1985). The nature and season of the burn, the interval between burning, topography, soil type and the timing and intensity of rainfall influence fire effects on run-off and erosion (West 1965). Post-fire nutrient losses via runoff have been reported in Australian savannas (Douglas *et al.* 1996). However, while runoff and soil loss is related to soil cover, soil structure also has a significant influence and soil losses after fire may be less than expected if infiltration rates are high (McIvor *et al.* 1995).

In the longer term, nutrient availability after fire may be affected by increased soil temperatures and altered soil moisture and pH. The removal of surface cover by fire results in increased air and soil temperatures and greater temperature variability (refer Christensen 1985; Whelan 1995) whereas moisture conditions may increase or decrease after fire (section 3.2.2.4). Soil pH generally increases after fire due to the addition of ash (Daubenmire 1968; Christensen and Muller 1975). These changes may directly affect nutrient availability. They may also effect nutrient availability indirectly via effects on microbial activity, and consequently, nutrient transformations. Rates of mineralization may be increased due to changes in pH, reductions in C:N ratios (refer Van de Vijver *et al.* 1999) and increased temperatures (Daubenmire 1968). Nutrient cycling may also be affected by fire-induced changes in plant species composition and both increases (refer Daubenmire 1968) and decreases (Mack *et al.* 2001) in nitrogen fixation have been attributed to species changes. Nutrient availability is influenced by the degree of uptake by plants and the nutrients available to individual plants may be affected by the altered competitive relationships that exist after fire.

Soil fertility is fundamental in controlling the functioning of plant communities and an understanding of the effects of various fire regimes on soils is needed to properly evaluate fire-management options (Raison 1980). Plant competitive interactions are influenced by nutrient conditions (Howden 1988) and exotic species such as *C. ciliaris* may be favoured by post-fire flushes of nutrients. The aim of this study was to investigate the effects of season of burning on plant nutrient availability in *C. ciliaris*-dominated grassland. I expected that, in general, fire would enhance nutrient availability. However, season of burning effects were more difficult to predict. Season of burning effects on soil nutrients depend on the timing of fire in relation to vegetation condition and on fire characteristics, such as extent and intensity. Late dry season, high intensity fires may convert more biomass to ash than milder, early dry season fires, increasing the supply of readily available nutrients. However, volatilization losses will be greater in more intense fires. In addition, nutrient concentrations may be lower in late dry season fuel, and consequently late dry season ash, since plants have relocated nutrients to roots by this time (Norman 1963).

3.5.2. METHODS

3.5.2.1. Soil collection and processing

A bioassay technique was used to determine the surface soil nutrient availability of all experimental plots at the start of the growing season. Soil samples were collected from unburnt (control) plots and from plots burnt in the early or late dry at Dalrymple and Moorrinya after the late dry season fires (section 3.3.1). Samples were collected on the day of the fires at Moorrinya. Due to time constraints only block one was sampled immediately after the fires at Dalrymple and the other blocks were sampled 20 days later. Six surface soil samples, approximately 20 cm by 20 cm by 5 cm deep, were dug from random positions within the central 18 m by 18 m zone of each plot. Samples were collected beside plant bases when the random sampling position fell on a plant base. Where present, surface ash was included in the samples. The six samples were bulked, providing one sample per plot.

Samples were air-dried before being processed with a concrete roller to crush soil aggregates. Samples were then sieved (to pass a 6.7 mm mesh) and mixed thoroughly. While in storage some samples were accidentally wet. To insure samples received similar processing, all soils were wet, re-dried and re-sieved.

3.5.2.2. Pot set up

The experiment was set up in a glasshouse at Davies Laboratory, Townsville (19°15’S, 146°45’E) in September 2000. Three pots (approximately 13 cm diameter, 14 cm high) of each sample were prepared using either 1600 g Dalrymple soil/pot or 1500 g Moorrinya soil/pot. Since the soils from the two sites differed in bulk density, different weights of soil were used to achieve a similar volume. Pots were free draining but were lined with gauze to prevent any soil loss with watering. Pots were arranged in four blocks, the allocation of pots to blocks corresponding to the blocking of the field plots. The pots were re-randomized within blocks at frequent intervals and kept well watered.

Twelve forage sorghum (*Sorghum bicolor* (L.) Moench, variety ‘Sudenensis’) seeds were sown in each pot. This species was chosen because it is highly responsive to soil nutrients and re-shoots readily after decapitation (A. Noble pers. comm.). During the first week additional pre-germinated seed was added to achieve uniform emergence. Seven days after sowing emerging seedlings were thinned to three plants per pot and a layer of black plastic beads (1 cm deep) was added to the soil surface to prevent algal growth.

The experiment was run for 31 weeks, from September 2000 to April 2001. Over this period above ground biomass was harvested five times at approximately six week intervals. For each pot, all plants were cut at the soil surface, placed in a paper bag and dried at 65°C before being weighed. After the fourth harvest, plants failed to re-shoot in some pots and no plants re-shot after the fifth harvest. The cumulative biomass produced from each pot was calculated for the five harvest periods.

3.5.2.3. Statistical analysis

Total cumulative biomass data for each harvest period were analysed separately using one-way ANOVA procedures in Genstat (2001). Data from each site were analysed separately and since block effects were not significant ANOVA without blocking results are reported. Results for each harvest were similar and only the final (total) biomass data are reported. Relationships between plot fire intensity and sorghum biomass were investigated using linear regression, also in Genstat (2001). While the biomass produced from pots containing Dalrymple soil could not be directly compared with that from pots containing Moorrinya soil because different weights of soil were used, the amount of biomass produced per gram of these soils was calculated.

3.5.3. RESULTS

No burning treatment effects on above-ground sorghum biomass were detected for either site (P > 0.05) (Figure 3.5). Plants grown in Dalrymple soil produced more biomass per gram of soil (3.2 ± 0.13 mg biomass/g soil) than plants grown in Moorrinya soil (2.2 ± 0.06 mg biomass/g soil).

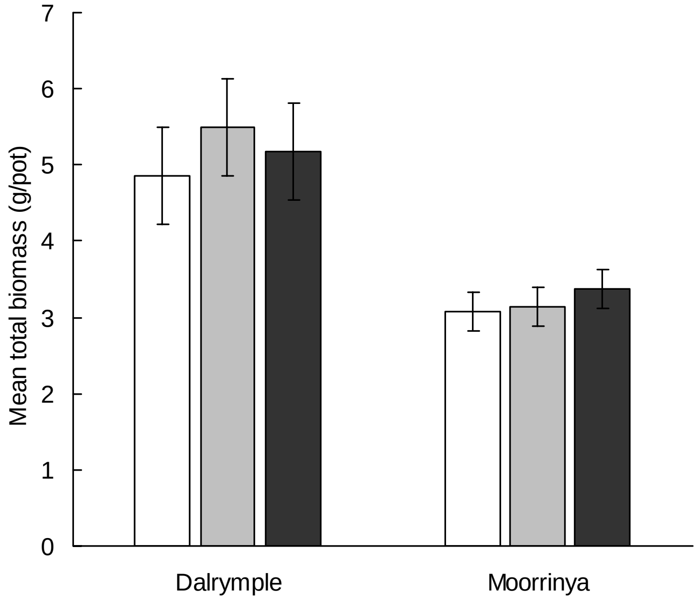

Figure 3.5. Mean (± SE) total above-ground biomass (g/pot) of sorghum plants grown in soil from (□) control (no burn), (▨) early dry season burn and (■) late dry season burn plots at Dalrymple and Moorrinya.

There was a significant linear relationship between plot fire intensity and sorghum biomass for Dalrymple ($P < 0.05$; adjusted $R^2 = 0.57$) (Figure 3.6). However, no relationship was detected when the high intensity plot, which had high leverage, was omitted from the analysis. No relationship between plot fire intensity and sorghum biomass was found for Moorrinya ($P > 0.05$) (Figure 3.6).

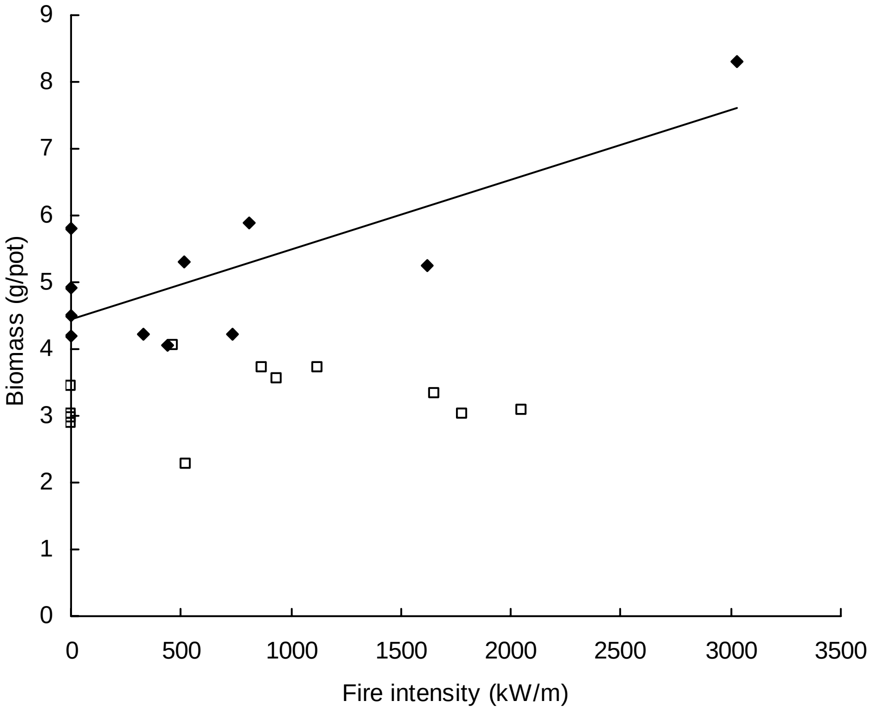

Figure 3.6. Relationship between plot fire intensity (kW/m) and mean total above ground sorghum biomass (g/pot) for (◆) Dalrymple and (□) Moorrinya. Regression line for Dalrymple shown (Biomass = Plot fire intensity*0.001 + 4.4).

3.5.4. DISCUSSION

Development of fire management regimes requires a consideration of nutrient dynamics if conservation and productivity values are to be maintained (Cook 1992). The single fires reported in this study appeared to have little effect on soil nutrient availability. Other studies have also failed to detect significant differences in nutrient availability in grasslands/savannas due to fire (Shaw 1957; Harrington and Ross 1974).

Fire effects on nutrient availability may vary between early and late dry season fires since the season of burning is associated with differences in fire intensity (Lonsdale and Braithwaite 1991; Williams *et al.* 1997) and differences in fire intensity may result in different effects on nutrient status (refer Christensen and Abbott 1989). However, in this study fire intensity was not related to season of burning in the usual way since the mean intensity of late dry season fires was lower than that for early dry season fires at Dalrymple. In addition, nutrient availability appeared to be unaffected by fire intensity: although the higher intensity fires converted more biomass to ash, there was no convincing evidence that nutrient availability was related to fire intensity.

Nutrient conversion and loss processes due to burning in these grasslands remain unclear. Although burning may enhance nutrient availability, some nutrients may be lost via volatilisation or removal from the site by leaching, run-off and the erosive action of wind (Raison 1980). Volatilisation losses of N have been reported from savanna fires (Cook 1992;1994). Also, while about three-quarters of the ash stays on the ground, the remainder is carried up in the smoke plume to be deposited many kilometres away (Cook 2001) and losses of ash by water erosion may be important in certain landscapes after late dry season fires (Cook 1992). The generally patchy, low intensity fires in this study did not convert all the standing biomass to ash and volatilization losses were probably minimal. Grassland fires are generally of lower intensity than forest fires (Williams J. R. 1995) and the quantity of nutrients released by burning savannas is only a fraction of that released in forest situations (Nye 1959). Daubenmire (1968) concluded that the ash produced by grass fires was so scanty compared to that produced by forest fires that it seemed negligible. It is likely that the fires in this study produced insufficient ash to cause detectable changes in nutrient availability. Alternatively, given the patchy distribution of ash, it is possible that insufficient soil samples were taken to adequately sample the burnt plots.

It is unclear how much of the ash produced remained on site. Air and water-borne particulates may be re-deposited within a site, representing spatial re-distribution rather than loss. Generally the smoke plumes of these fires were small and did not travel far. Although there was considerable time (about 20 weeks) for ash to be blown from the early dry season burnt plots, there were plenty of obstructions to trap and retain wind blown material. Rainfall prior to soil sampling may have promoted nutrient uptake by plants or microbes or resulted in loss in runoff water. There was significant rainfall at Moorrinya (85mm) two weeks prior to the late dry season fires. However, rainfall details for the experimental sites are not available and it is not possible to estimate pre-sampling nutrient losses.

Bioassay techniques have been used by other investigators to determine the effects of fire on plant nutrients (Christensen and Muller 1975). This method has cost advantages over chemical determination of soil nutrients plus it provides a clear demonstration of how plants will respond to the total nutrient profile. However, the method used here does not permit investigation of the fate of specific nutrients. Fire may have differential effects on nutrients. However, since plant growth is determined by the most limiting factor, increases in one nutrient may not be detected if growth is limited by another. In addition, while ash is a supply of readily available nutrients, high nutrient concentrations in ash may be deleterious to plant growth (Facelli and Kerrigan 1996). Therefore it is possible that the fires did affect nutrients but that these effects were not detected. Difficulties in studying fire-nutrient interactions are reviewed by Raison (1980).

The results of this study suggest that burning has little effect on soil nutrient availability in these *C. ciliaris*-dominated grasslands. Compared with vegetation communities that experience severe fires, the effects of grassland fires on nutrient availability may be relatively small (refer Raison 1980). Also, the amounts of nutrients lost in any one fire are generally small compared with the reserve in the soil and biomass (Raison 1980). In this study, the effects of single, generally low intensity, patchy fires were investigated. However, one-off fires are unlikely to be effective in achieving management goals and, in the context of manipulating species composition, the effects of repeated burning on the nutrient dynamics of these grasslands need to be determined. The cumulative effect of small but persistent losses of nutrients from infertile soils may decrease site productivity and cause degradation in the long term (Kellman *et al.* 1985; Cook 1994). *Cenchrus ciliaris* is favoured by moderate to high fertility conditions (Humphries 1967; McIvor 1984). If burning increases nutrient availability, *C. ciliaris* establishment may be favoured over that of native species while a decline in nutrient availability may favour native species establishment. This study has not shown any effect of single fires on nutrient availability.

3.6. LITTER: A HELP OR HINDRANCE TO SEEDLING EMERGENCE?

3.6.1. INTRODUCTION

Fire may promote changes in plant community composition by altering the availability of sites suitable for the germination and establishment of new plants. The availability of such ‘safe sites’ (Harper 1977) depends on the germination and growth requirements of seeds and seedlings and on the micro-site conditions they experience (section 3.2.3.5). The nature and effects of the environment immediately surrounding seeds and seedlings are of critical importance in determining the dynamics of plant populations and the composition of plant communities (Fowler 1988). Litter influences the condition of seed/seedling micro-sites and many studies report the effects of litter on germination and establishment patterns (Scanlan and O’Rourke 1982; Enright and Lamont 1989; Facelli and Pickett 1991a; O’Connor 1991). By altering the distribution and abundance of litter, fire may have significant impacts on establishment patterns (Lane and Williams 1997). An understanding of the effects of litter on germination and emergence may help predict the effects of fire on plant community composition.

Litter affects plant communities by altering the chemical and physical conditions experienced by plants. Litter alters the chemical environment by modifying the levels and distribution of nutrients (Facelli and Pickett 1991a). Nutrient dynamics are influenced by the composition of litter. For example, differences in nitrogen cycling associated with five perennial grass species were attributed, in part, to differences in the nitrogen and lignin content of their litter (Wedin and Tilman 1990). Nutrient dynamics are also influenced by litter’s effects on environmental variables, such as temperature and pH, that regulate soil biota and mineralization (Knapp and Seastedt 1986; Facelli and Pickett 1991a). Although litter releases nutrients as it decomposes, it may result in reduced nutrient availability. For example, *Bromus tectorum* litter was found to decrease inorganic nitrogen availability because its low nitrogen content resulted in reduced nitrogen mineralization (Evans *et al.* 2001). In grasslands, accumulated litter may alter the chemical composition of rainfall reaching the soil surface, decreasing nitrogen deposition (Knapp and Seastedt 1986). The removal of litter and subsequent increases in soil temperature may promote organic matter decomposition, increasing nutrient availability (refer Facelli and Pickett 1991a). The leaching or decomposition of litter may also alter the chemical environment via phytotoxic effects (see Rice 1979). However, the ecological role of such effects is debated (Barritt and Facelli 2001) since there is little understanding of allelopathic processes in the field (Facelli and Pickett 1991a).

Litter affects the physical environment by intercepting light and rain and by affecting the transfer of heat and water, and probably gases, between the soil and atmosphere (Facelli and Pickett 1991a). Litter reduces light levels (Facelli and Picket 1991b; Facelli and Kerrigan 1996) and can alter light quality (Facelli and Pickett 1991a). By intercepting solar radiation and insulating the soil, litter also modifies soil temperatures (Evans and Young 1970) and smaller diurnal ranges of surface and sub-surface temperatures have been found under litter compared with bare soil (Evans and Young 1970). This moderation of temperatures may affect plants directly, by promoting or inhibiting germination and/or protecting plants from frost, and indirectly, via effects on nutrient dynamics (see Facelli and Pickett 1991a). While soil temperatures may be reduced under litter (Facelli *et al.* 1999), leaf and air temperatures may be increased due to reduced convective cooling (Knapp and Seastedt 1986). Litter affects water dynamics by altering the exchange of water between the soil and atmosphere (Facelli and Pickett 1991a). Moisture conditions under litter are generally more stable than on bare soil since moisture depletion is less rapid (Evans and Young 1970). In grasslands, litter is associated with increased water availability as it reduces rain drop impact (Bridge *et al.* 1983), increases infiltration and reduces evaporation and run-off (see Facelli and Pickett 1991). However, in some circumstances litter reduces moisture availability by retaining rainfall which is then lost by evaporation (Knapp and Seastedt 1986), and by increasing runoff (Walsh and Voigt 1977). Litter may act as a physical barrier (Facelli and Pickett 1991a), impeding the movement of seeds and/or seedlings to or from the soil surface.

The effects of litter on plant development are complex. The environmental changes caused by litter may affect plants directly, by influencing germination and establishment processes, and indirectly, via effects on plant interactions (Facelli and Pickett 1991a; Facelli 1994), herbivory (Facelli 1994) and disease (Facelli *et al.* 1999). The environmental changes associated with litter depend on characteristics of the litter. Plant responses to litter-altered conditions depend on characteristics of the plant species involved (Facelli and Kerrigan 1996). For example, characteristics such as the shape and size of seeds (Evans and Young 1970; Facelli and Pickett 1991a) and the shape of seedlings (Gross and Werner 1982) influence their movement through litter. Plant physiological responses to light and temperature also influence the effects of litter on germination and establishment (refer Facelli and Kerrigan 1996). In addition, plant responses to litter depend very much on prevailing environmental conditions. For example, moisture conditions influence plant responses to litter. In mesic environments litter usually reduces seedling establishment, probably through light limitation (Facelli and Kerrigan 1996). As precipitation decreases, reduced desiccation associated with litter becomes more important and, when water is limiting, the more mesic conditions associated with litter may result in enhanced seedling establishment (Fowler 1986; Whisenant 1990b). Xiong and Nilsson (1999) concluded from their meta-analysis of litter studies that litter generally had a negative effect on vegetation. However, the reported effects of litter on seedling germination and emergence vary considerably depending on the species involved, litter characteristics, environmental conditions, and study methods (see reviews by Facelli and Picket 1991a and Xiong and Nilsson 1999).

The amount and distribution of litter can be manipulated by fire. Generally fire reduces litter, although some fires increase litter where they do not consume the canopy but are hot enough to kill the leaves (Facelli and Kerrigan 1996). Litter may be important in determining seedling emergence patterns (Young *et al.* 1981) and by altering litter cover, fire may significantly affect establishment patterns and species composition. To help evaluate fire as a tool for manipulating the composition of *C. ciliaris*-dominated grassland, I investigated the effects of litter on grass seed germination and seedling emergence. Of specific interest were the litter-grass species interactions at the *C. ciliaris* dominated site at Dalrymple (section 3.3). At this site, soil cover was variable in terms of quantity as well as type, with conditions ranging from no cover (bare soil) to complete litter cover. Litter consisted of dead herbaceous material as well as leaf and other matter from trees and shrubs (predominantly eucalypts) and these litter types were patchily distributed over the site. In some areas, a thick litter mat formed between *C. ciliaris* tussocks. This litter consisted of *C. ciliaris* stem and leaf material, some still attached to the plant, which formed a consolidated mat (Figure 3.7). It contrasted with herbaceous litter in other patches that consisted of individual pieces of stem and leaf material that had not become fused. Matted litter, which is held together by fungal hyphae, is a greater impediment than loose litter (Facelli and Pickett 1991a). Thick layers of litter have been found to hinder germination and/or emergence (Scanlan and O'Rourke 1982; Fowler 1986; Hamrick and Lee 1987; López-Barrera and González-Espinosa 2001) and have been associated with reduced plant productivity (Harrington and Ross 1974; Knapp and Seastedt 1986). I expected that the matted *C. ciliaris* litter would hinder or inhibit seedling emergence by preventing seedlings from emerging from beneath it and/or by preventing the roots of surface-germinated seedlings from reaching the soil surface.

The aims of this study were to determine (1) if soil surface cover affected the germination and emergence of two grass species and (2) whether these effects differed between the two species. The effects of four soil surface cover types on the germination and emergence of two perennial grasses, *C. ciliaris* and *Heteropogon contortus*, were investigated. These are key herbaceous species in this habitat. The exotic *C. ciliaris* is dominant in terms of biomass. The native *H. contortus* is common at Dalrymple and is a desirable replacement for *C. ciliaris*. Therefore, the interactions of these species with soil surface condition were of interest. The diaspores, or dispersal units, of these two species are very different. *Cenchrus ciliaris* has a burr type diaspore which initially prevents direct seed-soil contact. In contrast, the diaspore of *H. contortus* has a hydroscopically active awn and sharply pointed base that facilitate seed burial (Tothill 1969). The ability of *H. contortus* to bury into soil appeared likely to give this species advantages in coping with litter. Seed material of both species were sown under and on top of the different litter types to investigate how litter effects seed dispersed prior to and after litter deposition. Sowing position was expected to have less effect on *H. contortus* than on *C. ciliaris*. However, the observed litter effects and species–sowing position interactions were contrary to expectations. Enhanced emergence from matted litter, species differences in sowing position effects, and the potential effects of fire on establishment patterns are discussed.

Figure 3.7. Litter mat between *C. ciliaris* tussocks at Dalrymple.

3.6.2. METHODS

3.6.2.1. Treatments

Seeds of two perennial grasses were sown on bare soil and under or on top of one of three litter types. The treatments were: two species (*C. ciliaris* and *H. contortus*), four soil surface cover types (eucalypt litter, open *C. ciliaris* litter, matted *C. ciliaris* litter and bare (no litter)) which represented the main surface cover types at the Dalrymple experimental site, and two sowing positions (under and on top of litter).

3.6.2.2. Experimental details

The experiment was conducted on outdoor benches at Davies Laboratory, Townsville ($19^{o}15$'S, $146^{o}45$'E) in January and February 2001. Thirty-two free-draining trays (43 cm by 28 cm by 13 cm deep) were partly filled to a depth of about 7 cm with a loam-organic matter mixture: three parts loam and one part "Aussie peat" (see appendix 2A). Trays were arranged eight to a bench with each bench considered a block. Trays were watered to germinate any pre-existing seed in the potting mix.

Litter was collected from areas beside the experimental plots at Dalrymple (section 3.3) in December 2000. Three types of litter were collected: (1) eucalypt litter consisting of leaves and twigs, (2) open grass litter consisting of *C. ciliaris* leaf and stem material and (3) matted grass litter, consisting of consolidated *C. ciliaris* leaf and stem material forming litter mats. The eucalypt litter was bagged while the matted litter was carefully removed from the soil surface in 'sheets' and stored to ensure its structure remained intact. Stem and leaf material was cut from *C. ciliaris* plants to make the open litter. The litter was wetted and then heated in plastic bags at 60 ^{o}C for five days to kill any resident seed.

Cover types were randomly allocated to trays within benches (blocks), with two trays/bench receiving each cover type. Eucalypt and open litter were spread evenly over the soil surface and the matted litter sheets were cut to fit the trays (Figure 3.8). Litter in each tray was allowed to dry before being adjusted to equal weight. (The mean weight of litter per tray was 1137 ± 29.7 g/m^2. This fell within the range found for matted litter in the field (310-1385 g/m^2 matted litter for 30 20 cm by 20 cm samples collected in January 2001 from the site).

Diaspores of *H. contortus* and *C. ciliaris* were sown in the trays on 31 January 2001. The *H.*

contortus seed had been collected from near the Dalrymple site in June 2000 while the *C. ciliaris* was commercial seed ('USA' variety). Diaspores, rather than clean seed, were sown to imitate field conditions. The diaspore of *C. ciliaris* is a fascicle comprising clusters of spikelets (usually 1-3) surrounded by an involucre of two rows of wavy bristles (Loch 1993). This burr type diaspore may contain one to five caryopses (Humphries 1981). The diaspore of *H. contortus* is a fertile spikelet with a sharply pointed, callused base. Each fertile spikelet contains two florets: a lower sterile floret (reduced to an empty lemma) and an upper fertile floret, the lemma of which bears a stout, twisted and bent awn covered with short bristles in the lower part (Tothill and Hacker 1983). The awned spikelets form tangled clumps of seed. Seed material was sown, one species per tray of each cover type per bench. In the litter treatments, material was sown on top of the litter at one end and under the litter at the other, leaving an unsown buffer of 2.5 cm around the edge of the tray and a 6 cm buffer between the two sowing positions. In bare soil trays, material was sown leaving the same buffer areas, forming two sown plots per tray as in the other treatments. Species were allocated randomly to trays within cover types. Sowing position was randomly allocated within trays. The amounts of seed material sown (2.3 g of *H. contortus* 'clumps' or 0.71 g of *C. ciliaris* fascicles) was estimated to provide about 40 germinable seeds per sowing position (see appendix 2B), although these estimates are imprecise, particularly in the case of *H. contortus*, because of the nature of the seed material. Trays were watered immediately after the addition of seed material and were watered over the experimental period (rainfall and hand watering with 'rose' head sprinkler).

Numbers of emerging seedlings were monitored for three weeks after sowing. Emerged seedlings were counted every day for the first 10 days after sowing and then again 21 days after sowing. Once seedling numbers exceeded about 30 it became difficult to make accurate counts without disrupting the litter or seedlings. Therefore 30 or more seedlings were recorded as 75% emergence. Germination and emergence were not investigated independently and the observed responses are referred to as emergence responses for brevity.

In addition to the soil cover experiment, a survey of soil surface cover types at the Dalrymple experimental site was conducted in January 2001. Thirty 20 cm by 20 cm quadrats were surveyed in each control (unburnt) plot in the main experimental area. Quadrats were positioned about every 3 m along five 14 m long transects spaced 4 m apart within each plot. The percentage of each of the main cover types (bare soil, open, matted, and eucalypt litter) in each quadrat was estimated to the nearest 25%.

Figure 3.8. Soil surface cover types with *H. contortus* seed. From left to right: eucalypt litter, matted litter, bare soil and open litter.

3.6.2.3. Statistical analyses

Seedling emergence data were analysed using the repeated measures ANOVA procedure in Genstat (2001). The time main effect and interactions were significant and more detailed analyses were conducted on data for each sampling day separately. Data for each sampling day were analysed using a modified split plot design, also using Genstat (2001). Species and cover types were main plots. The cover type effect was partitioned to allow comparisons between litter cover and no litter cover (the litter effect) as well as comparisons between cover types. Sowing position was the subplot factor. However, there was no sowing position effect for the bare soil treatment. This was accommodated in the analysis by partitioning variances using litter (present/absent) by subplot interactions. Seedling counts were converted to percentage emergence and arcsin transformed prior to analysis. Means were compared using the protected LSD test at the 5% significance level. Reported results are back-transformed means.

3.6.3. RESULTS

Litter had a significant effect on seedling emergence. Overall, emergence was greater from bare soil than from litter ($P < 0.001$). However, there were significant differences between cover types (Figure 3.9). Generally, emergence from bare soil was similar to that from matted litter and emergence from these two cover types was greater than that from open and eucalypt litter ($P < 0.05$). Initially emergence was greater from open litter than from eucalypt litter but after day eight emergence from these two litter types was similar.

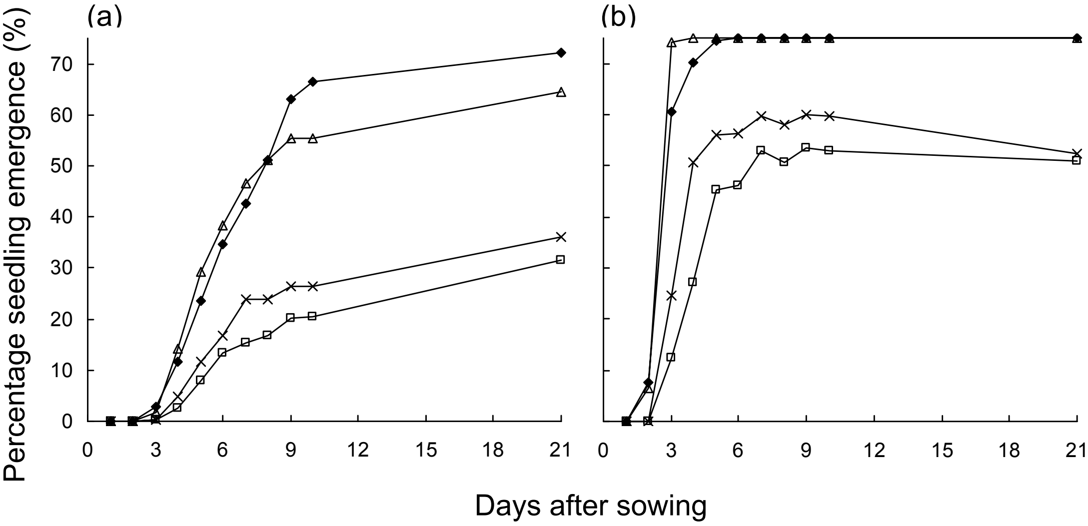

Figure 3.9. Mean percentage emergence of (a) *C. ciliaris* seedlings and (b) *H. contortus* seedlings from four cover types (bare soil (♦), matted litter (Δ), open litter (x) and eucalypt litter (□)) over 21 days.

The effect of sowing position differed between cover types ($P < 0.05$) (Figure 3.10). Emergence from seed sown on top of eucalypt litter was consistently lower than from seed sown under eucalypt litter. The reverse was found for matted litter: top sowing enhanced emergence compared with under-litter sowing, although initially (days three and four) and at day 21 there was no sowing position effect for matted litter. Sowing position had no effect on seedling emergence from open litter over the experiment ($P > 0.05$).

The ranking of sowing treatments for seedling emergence was generally constant over the experimental period (Figure 3.10). Emergence was greatest from seed sown on top of matted litter followed by seed sown on bare soil, under matted litter, under eucalypt litter, under open litter, on top of open litter and on top of eucalypt litter. Emergence from seed sown on top of matted litter was consistently greater than that from seed sown on top of or under open and eucalypt litter (P < 0.05). Emergence was similar from seed sown under eucalypt litter, under open litter and on top of open litter while emergence from seed sown on top of eucalypt litter was lower than from other treatments (P < 0.05) except on day 21 where it was similar to that for seed sown on top of open litter.

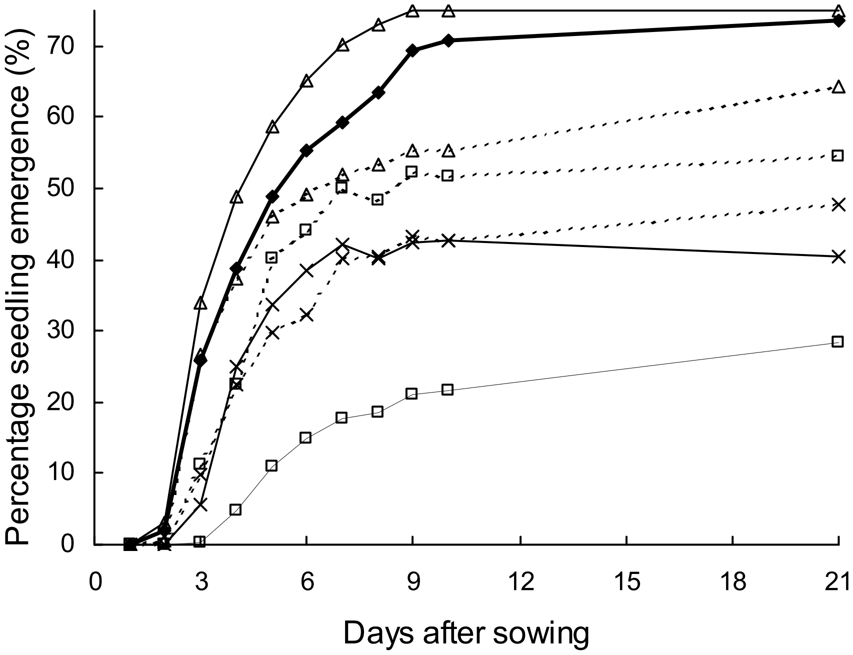

Figure 3.10. Mean percentage emergence of *C. ciliaris* plus *H. contortus* seedlings from four cover types (bare soil (♦), matted litter (Δ), open litter (X) and eucalypt litter (□)) from seed sown top of litter (solid line) and under litter (dashed line) over 21 days.

There were differences in emergence patterns between species. More *H. contortus* than *C. ciliaris* seedlings were found on all sampling days (P < 0.05). While litter depressed the emergence of both species it appeared to have a greater effect on *C. ciliaris*. Significant species by litter interactions were detected initially (day three) and later (days nine and 10) (P < 0.05) where emergence from litter compared with bare soil was about 66% for *C. ciliaris* and 88% for *H. contortus*. Species responded differently to sowing position with significant species by sowing position interactions found on all survey days (P < 0.05) (Figure 3.11). Initially sowing position had no effect on *C. ciliaris* emergence but after day five more *C. ciliaris* seedlings emerged from seed sown on top of litter than from seed sown under litter. By day 21 there was no difference in *C. ciliaris* emergence between sowing positions. *Heteropogon contortus* emergence was affected by sowing position throughout the experiment but, in contrast to *C. ciliaris*, emergence was greater from seed sown under litter.

Although species by litter type by sowing position effects were not significant (P > 0.05), *C. ciliaris* tended to be more responsive than *H. contortus* to sowing position with matted litter. The reverse trend was found for eucalypt litter, that is *H. contortus* tended to be more responsive than *C. ciliaris* to sowing position with eucalypt litter.

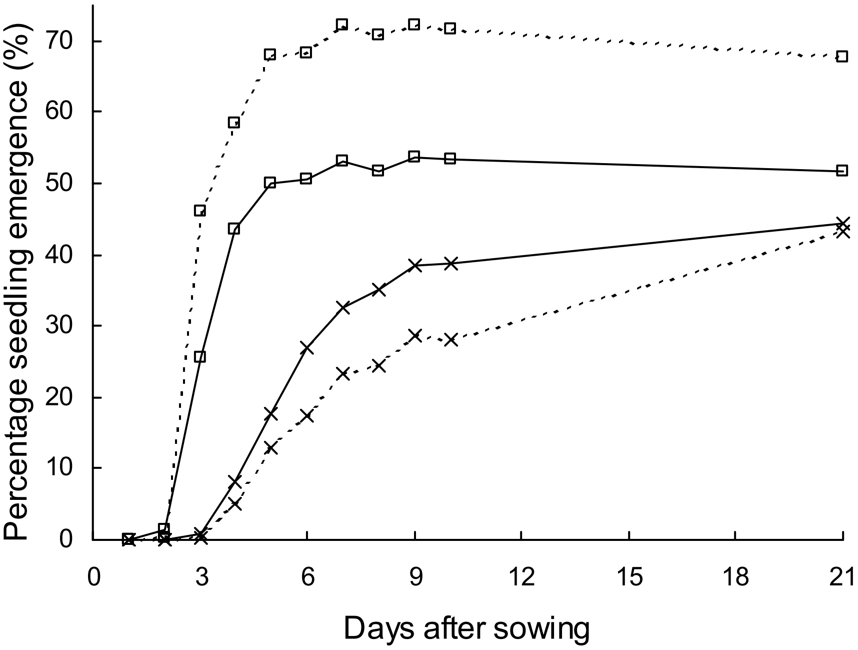

Figure 3.11. Mean percentage emergence of *C. ciliaris* seedlings (x), and *H. contortus* seedlings (□) from seed sown on top of litter (solid line) and under litter (dashed line) over 21 days.

Emergence rates differed between treatments (Figure 3.12). Emergence was faster from bare soil than from litter, taking on average 5.6 days for 50% of seeds to emerge. In comparison emergence from some litter treatments did not reach 50% over the experimental period. *H. contortus* emerged earlier that *C. ciliaris*. Two days after sowing, seedlings were found in 40% of *H. contortus* plots while no *C. ciliaris* seedlings had emerged. In the bare soil treatment 50% seedling emergence took 3 days for *H. contortus* and 8 days for *C. ciliaris*. *Heteropogon contortus* achieved 50% emergence in all treatment plots except where seed was sown on top of eucalypt and open litter. In contrast *C. ciliaris* achieved 50% emergence in only two treatments: bare soil and from seed sown on top of matted litter.

Although the estimated number of germinable seeds added to each plot was imprecise due to the nature of the seed material, emergence from treatment replicates was generally very similar. This may indicate that plots received a similar number of germinable seeds.

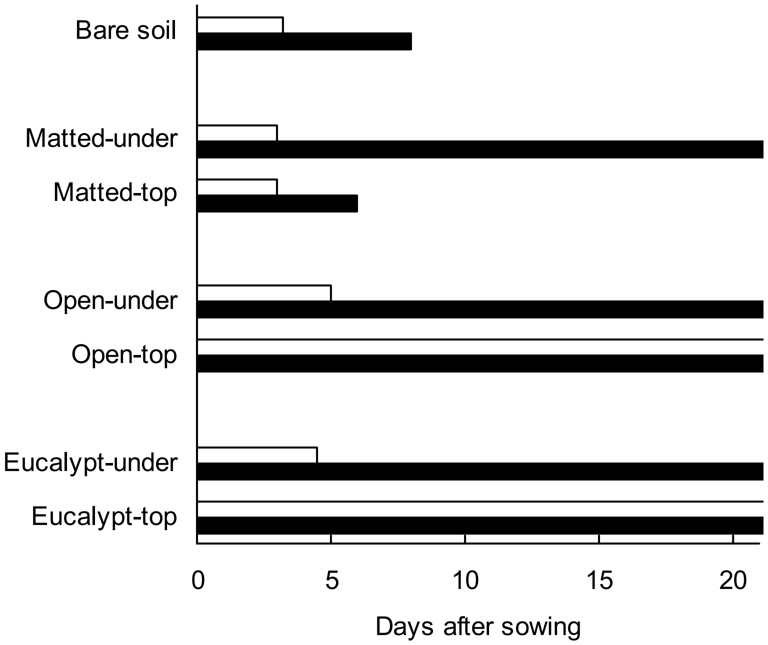

Figure 3.12. Mean days taken for 50% emergence of *C. ciliaris* seedlings (lower solid bars) and *H. contortus* seedlings (upper unfilled bars) from seed sown on bare soil and under and on top of three litter types. Bars running the length of the graph indicate that 50% emergence was not achieved in all replicates by day 21.

The distribution of litter cover types in the field was variable (Figure 3.13). For example, in one plot no bare ground was recorded while in another, bare ground made up 33% of the surveyed area.

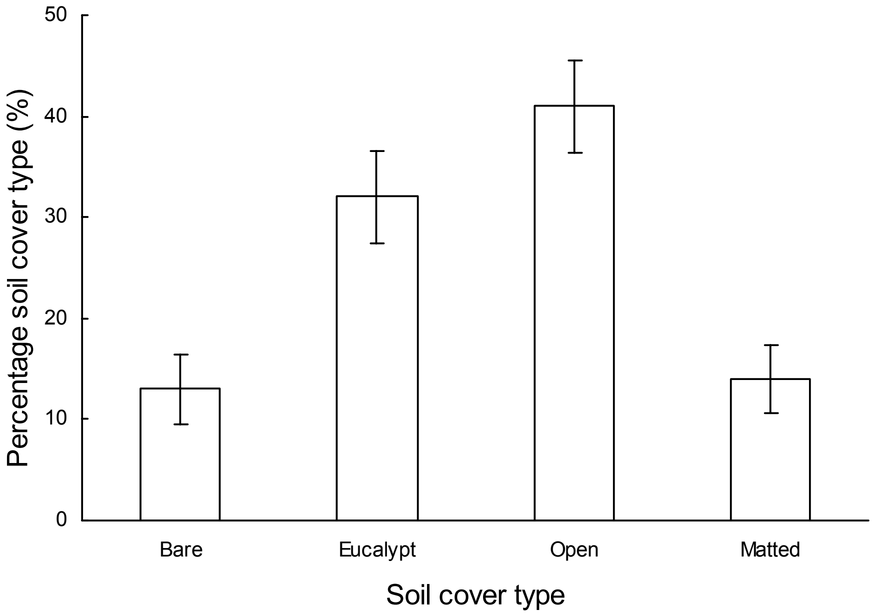

Figure 3.13. Mean (± SE) percentage of soil cover types at Dalrymple in January 2001.

3.6.4. DISCUSSION

Litter type is important in determining the effects of plant litter (Xiong and Nilsson 1999) and differences in litter structure have been shown to differentially affect seed germination and/or emergence patterns (Hamrick and Lee 1987; Facelli and Pickett 1991b; Facelli and Kerrigan 1996; López-Barrera and González-Espinosa 2001). Although the overall effect of litter on emergence in this study was negative, as found by many others (Fowler 1988; Bergelson 1990; Facelli and Pickett 1991b; Barritt and Facelli 2001), emergence of both *C. ciliaris* and *H. contortus* was affected by litter type.

The enhanced emergence from matted litter compared with the other litter types was contrary to expectations. Litter may form a physical barrier hindering seed movement and seedling growth. This may be particularly so in the case of matted litter since it appears to present a greater impediment than open litter (Facelli and Pickett 1991a). Seeds retained in litter may have delayed or unsuccessful germination (Facelli and Pickett 1991a) and thick litter layers have been reported to hinder the germination and/or emergence of *C. ciliaris* (McIvor and Gardener 1981) and *H. contortus* (Kennard and Walker 1973) as well as other species (Scanlan and O'Rourke 1982; Hamrick and Lee 1987). Dense litter slowed the downward movement of *Bouteloua rigidiseta* and *Aristida longiseta* seeds to the soil surface, delaying germination, and in the case of *A. longiseta*, reducing survival since some seed germinated in the litter and died (Fowler 1986). However, it appears that the matted *C. ciliaris* litter used in this study provided favourable conditions for germination and/or emergence and effects on seeds and/or seedlings were less important. In contrast, the open and eucalypt litter appeared to hinder seed movement and/or seedling growth, resulting in reduced emergence.

Seed-soil contact is often cited as a factor influencing germination (Cook *et al.* 1993b) but it is actually the moisture conditions around the seed that are important. As noted by Harper *et al.* (1965), differences in micro-topography exert effects on germination through modifying seed-water relationships. It is likely that differences in seed-moisture conditions between litter types explain the emergence patterns found in this study. The matted litter provided suitable moisture conditions for germination. Its uneven but continuous surface enabled good seed-litter contact and maintained moist conditions around the seeds. In addition, it dried out more slowly than did bare soil or the other litter types, thereby maintaining moist conditions for longer. Seed on the surface of matted litter germinated readily without needing contact with the soil surface. In contrast, it appears that open and eucalypt litter surfaces did not provide such conditions and most seed sown on top of these litter types had to reach the soil surface for successful germination. While not forming a continuous layer, open and eucalypt litter were deeper than the matted litter. Seeds sown on top of open and eucalypt litter had less contact with litter surfaces, were exposed to less humid conditions and were hindered in their movement to the soil surface. Constraints to seed movement and seedling growth are the most likely cause of depressed seedling emergence from open and eucalypt litter. However, since chemical and physical effects of litter were not differentiated in this study, the possibility of chemical differences associated with the different litter types cannot be dismissed. Some eucalypts, for example *Eucalyptus globulus*, have been shown to have allelopathic effects (Babu and Kandasamy 1997).

Whereas emergence from seed sown under matted litter was generally greater than that from other litter types it was less than that from top-sown seed, particularly for *C. ciliaris*. It is unlikely that this was caused by light conditions under matted litter since neither *C. ciliaris* (Chaudhry *et al.* 1999; Sharif-Zaden and Murdoch 2000) nor *H. contortus* (Orr 1998) have a light requirement for germination. Conditions under matted litter would have been at least as moist as conditions on top. Therefore desiccation would have been even less likely for seeds sown under matted litter. The humid conditions associated with litter may promote disease (Facelli *et al.* 1999) and emergence from under matted litter may have been reduced by increased pathogen activity. An alternative or additional explanation is that matted litter physically impeded seedling emergence.

Emergence from seed sown on top of eucalypt litter was lower than that from other treatments. Litter from trees is believed to have a stronger effect on plants than grass litter, although whether this relates to differences in chemical and/or physical properties is unclear (Xiong and Nilsson 1999). Facelli and Kerrigan (1996), who also reported poor emergence from seed sown on top of eucalypt litter, pointed out that eucalypt litter presents many extended flat surfaces that retain seed. Seed falling on eucalypt litter may be trapped in conditions unsuitable for germination while seed germinating in such litter may die if the radicle is prevented from reaching the soil surface.

Open and eucalypt litter may also hinder seedling emergence from the soil surface. Emergence was generally lower from seed sown under eucalypt or open litter than on bare soil. Seed under litter was probably exposed to less desiccation than seed on bare soil so it is unlikely that germination and/or emergence were constrained by moisture. While both litter types were loose in structure, seedlings were forced to bend around obstacles before emerging. Such energy-consuming emergence may weaken seedlings, resulting in increased mortality (Hamrick and Lee 1987; Facelli and Kerrigan 1996). There may have been greater mortality of seedlings emerging from under eucalypt and open litter. Since the fate of individual seedlings was not followed in this study, it is not possible to accurately determine mortality levels. Dead seedlings were observed and cumulative emergence decreased in some plots. However, there were no obvious treatment effects on mortality as far as it could be assessed. Facelli *et al.* (1999) reported that eucalypt litter did not impede the emergence of eucalypt seedlings and an alternative or additional explanation for poor emergence from under litter is that seeds under litter were exposed to greater disease.

Differences in litter structure have been found to affect germination rate (López-Barrera and González-Espinosa 2001). In this study, seedling emergence was faster from bare soil and matted litter than from open and eucalypt litter. Differences in germination rate may have important consequences for plant establishment and the timing of germination is recognized as an important factor influencing seedling survival and community composition (Fowler 1986; 1988). Early germination is usually considered to give an individual a competitive advantage, although too early germination can be fatal in semi-arid and unpredictable environments (Fowler 1986).

In addition to litter type, seed and seedling characteristics also influence plant responses to litter. The size and shape of seeds influence seed movement through litter while seedling morphology may be important in determining the ability of seedlings to penetrate litter (Gross and Werner 1982; Facelli and Pickett 1991a). Although differences in emergence due to *C. ciliaris* and *H. contortus* seedling morphology were not expected to be significant in this study, differences in emergence due to diaspore type were. I expected sowing position to have less effect on *H. contortus* than on *C. ciliaris* since *H. contortus* seed sown on top of litter would work its way through to the soil surface, its movement being assisted by its hydroscopically active awn and pointed seed base. In contrast, the burr type *C. ciliaris* diaspore appeared more likely to be caught in litter and prevented from reaching the soil surface. However, the observed sowing position effects were not as anticipated. *Heteropogon contortus* emergence was affected by sowing position, emergence being greater for seed sown under litter than on top. It appears that litter hindered the movement of *H. contortus* seed, preventing at least some from reaching the soil surface. This result is interesting given that *H. contortus* is believed to have an efficient seed burial mechanism (Tothill 1969; Peart 1979; Dyer *et al.* 1997) which has been cited as giving it an advantage over other species whose seed remain caught in litter (Tothill 1969). While *H. contortus* may be able to penetrate litter more effectively than some other species, the results from this study suggest that litter can have a negative impact on its emergence. *Cenchrus ciliaris* emergence was also affected by sowing position, but its emergence was greater for seed sown on top of litter. This effect tended to be strongest for matted litter, although species by litter type by sowing position effects were not statistically significant. Poor seed-soil contact has been considered a problem in *C. ciliaris* establishment (Cook 1975) and emergence was expected to be greater for seed sown under litter. Good germination and establishment of *C. ciliaris* requires seed to be moist for about five days and a rough surface is considered advantageous for *C. ciliaris* establishment since it maintains moisture for longer (Paull and Lee 1978). The surface of the matted litter provided favourable germination conditions and seedlings were able to penetrate the litter to reach the soil. In contrast, reduced emergence of *C. ciliaris* from seed sown under litter may reflect greater exposure to disease and/or impeded seedling emergence. Hacker (1989) suggested that greater levels of insect and microbial activity associated with litter could lead to deterioration of *C. ciliaris* seed in the field.

The markedly faster emergence of *H. contortus* compared with. *C. ciliaris* may have important implications for plant establishment patterns. Whereas *C. ciliaris* is considered a highly competitive species, it is less so at the seedling stage when seedling survival is strongly affected by competition from established plants (Cook 1984; McIvor, 2003). The slower emergence of *C. ciliaris* compared with *H. contortus* suggests that *C. ciliaris* may also be at a competitive disadvantage against other seedlings. The faster emergence of *H. contortus* may give it a head start in sequestering resources and enable it to out-compete *C. ciliaris* for the occupancy of new sites.

This study was conducted to help predict the effects of fire on seedling emergence patterns. Although the results demonstrate that the removal of litter by fire is likely to effect emergence patterns in this *C. ciliaris*-dominated grassland, it is difficult to predict the outcome of litter removal. Extrapolation to the field of seedling emergence-litter interactions determined under glasshouse conditions is complicated by the fact that environmental conditions can greatly influence plant responses to litter. Glasshouse studies in which moisture conditions are maintained may under-estimate the benefits of litter in arid and semi-arid field conditions (Fowler 1986). As moisture becomes limiting the importance of litter for reducing desiccation increases (Facelli and Kerrigan 1996) and litter has generally been found to have positive effects on emergence in arid and semi-arid environments (Facelli and Kerrigan 1996). McIvor and Gardener (1985) reported higher *C. ciliaris* emergence in unburnt compared with burnt pastures. This was associated with the beneficial effects of cover in the vegetated plots that resulted in longer germination periods. When moisture is limiting to growth, matted-litter sites may become significantly more favourable for seedling emergence than bare ground. The deep layers of open and eucalypt litter used in this study inhibited seedling emergence. However, litter distribution in the field varies greatly and it is possible that lighter levels of these litter types may also have positive effects on emergence in the field. Plant responses to litter have been found to vary with changes in the amount of litter (Scanlan and O'Rourke 1982). Therefore, while overall, litter was found to depress seedling emergence, suggesting that removal of litter by fire will result in increased emergence, the effects of litter removal depend on nature and distribution of litter as well as the prevailing conditions. An additional factor to consider is the direct effect fire has on seed availability. Emergence may be greater from litter microsites because litter traps seed, increasing its availability in these sites (Scanlan and O'Rourke 1982). Both *C. ciliaris* (Hacker and Ratcliff 1989) and *H. contortus* (Tothill 1977) have dormancy mechanisms preventing the germination of freshly fallen seed so much seed is likely to be caught in and under litter by the time it is ready to germinate. Therefore, fire is likely to affect emergence patterns by reducing seed availability (McIvor *et al.* 1993).

Litter, via its effects on establishment patterns, may play an important role in population dynamics (Bergelson 1990), inter-specific interactions (Al-Mufti *et al.* 1977, Facelli 1994) and community structure and composition (Knapp and Seastedt 1986; Hobbs and Aitkins 1988; Facelli and Pickett 1991ab). By altering the distribution and abundance of litter, fire has been attributed with affecting grassland productivity and species richness (Knapp and Seastedt 1986; Xiong and Nilsson 1999). The prevailing fire regime may favour some species over others via litter effects on plant establishment. For example, *Bromus* spp. establishment in American prairies has been found to be enhanced by litter (Evans and Young 1970; Whisenant 1990b) and increases in *Bromus* abundance have been associated with low fire frequency which maintains a favourable litter status. In contrast, emergence of *H. contortus* in southern Queensland is believed to be promoted by the removal of litter and consequent rise in soil temperatures (Tothill 1969). Of particular interest in this study was whether *C. ciliaris* and *H. contortus* emergence would be differentially affected by litter removal. This remains unclear. By removing litter fire may increase *C. ciliaris* emergence since overall litter had a greater negative effect on *C. ciliaris* than on *H. contortus*. However, this effect was not marked or consistent and other observed emergence patterns suggest that *C. ciliaris* may be disadvantaged by litter removal. *Cenchrus ciliaris* seeds are likely to be present in matted-litter sites since this litter type forms around established *C. ciliaris* plants. Consequently, the removal of matted litter is likely to have a greater negative effect on *C. ciliaris* emergence than on *H. contortus* emergence. The consumption by fire of seed in litter may affect both species. While such loss was expected in the case of *C. ciliaris*, the finding that *H. contortus* seed may be trapped in litter suggests that this species may be more vulnerable to seed loss via fire than previously thought.

Understanding how species, litter, precipitation and fire interact is necessary for developing fire management strategies (Whisenant 1990b). Although it is likely that litter affects the early establishment of *C. ciliaris* and *H. contortus*, the responses to litter removal by fire depend on the nature and distribution of litter as well as the prevailing conditions. From this study it is difficult to identify any major, differential effects of litter removal on the emergence of *C. ciliaris* and *H. contortus*. In the field, litter may improve seedling emergence due to the combination of improved moisture conditions, lower soil temperatures and the greater quantity of germinable seed where there is more litter (Scanlan and O'Rourke 1982). However, sites favourable for seedling emergence may not necessarily be favourable for plant establishment (Schupp 1995) since, once established, other factors become important (Gross and Werner 1982). Whereas matted litter may favour seedling emergence, seedling survival and establishment in matted litter sites may be highly unlikely given the competition from surrounding, established plants. In perennial grasslands, the opportunity for new individuals to establish is greatly influenced by competition from established plants (Cook 1980; Lauenroth and Aguilera 1998). Therefore, while fire may affect emergence patterns via its effects on litter, fire effects on established plant survival are likely to play a more significant part in determining vegetation composition.

3.7. EFFECTS OF SEASON OF BURNING ON SOIL SEED BANKS OF *CENCHRUS CILIARIS*-DOMINATED GRASSLAND

3.7.1. INTRODUCTION

The soil seed bank is the reserve of viable seed in the soil and on the soil surface (Roberts 1981). The study of soil seed banks has become an integral part of plant ecology (Grime 1989) and a knowledge of seed bank dynamics is imperative for predicting ecosystem responses to management and natural perturbations (Roberts 1981). Fire may alter both the size and composition of soil seed banks and these effects may result in changes in vegetation composition since the seed bank determines the potential size and composition of the seedling population (McIvor and Gardener 1991). In the context of using fire as a tool to manipulate vegetation composition, an understanding of both the nature of seed banks and their responses to fire is important for predicting vegetation change.

Fire affects soil seed banks directly, by killing seed and altering seed germinability (section 3.2.2.5). Although it may consume or damage seed, and many studies report reductions in seed banks after fire ('t Mannetje *et al.* 1983; DiTomaso *et al.* 1999; Ferrandis *et al.* 1999; Holl *et al.* 2000; Main *et al.* 2000; Alexander and D'Antonio 2003), it may increase the amount of germinable seed (Purdie and Slatyer 1976). Many species require a heat shock to permit germination (Bell 1999) and other factors, such as smoke, may also stimulate germination (Enright *et al.* 1997; Roche *et al.* 1998; Read *et al.* 2000). Fire affects seed banks indirectly, by affecting flowering and seed inputs (sections 3.2.2.5 and 3.8). Fire-stimulated flowering is very common in grasses (Bond and van Wilgen 1996) and increases in post-fire grass seed production have been reported (Orr 1998). The effects of fire on the activity of microbes and animals may also have consequences for seed banks. For example, litter has been associated with greater levels of microbial and insect activity (Hacker 1989; Watson 1995) and its removal by fire may reduce seed losses due to disease and predation. Since fire may affect both the quantity and quality of seed, it may simultaneously decrease the total amount of seed but increase the amount of germinable seed present.

As well as affecting seed bank size, fire may alter seed bank composition where species differ in their response to fire (Auld and Bradstock 1996). Characteristics such as seed morphology (Peart 1984), heat tolerance, germination requirements and the location of seed in the soil profile (refer Tyler 1995; Noble and Grice 2002) will influence how species are affected by fire. For example, differences in seed burial capacity make species more or less susceptible to fire. Since the lethal temperatures generated by grassland fires are generally confined to the upper soil layer and the soil surface (Morgan 1999), species whose seed remain on the soil surface will be more vulnerable than species whose seed is buried. Burning is expected to reduce the abundance of *C. ciliaris* seed since it appears to remain close to or on the soil surface (Hacker 1989), making it more vulnerable to fire than species such as *Heteropogon contortus* that have effective seed burial mechanisms such as hygroscopically active awns (Walker *et al.* 1981), although awned diaspores may not always achieve sufficient burial (Peart 1984). Heat tolerance also varies between species. Many Australian legume species are extremely tolerant of high-intensity or long-duration thermal stress (Bell 1999) enabling them to survive fires that destroy less tolerant species. Therefore, in a single fire, seeds of some species are destroyed while the germination of others is promoted (Purdie and Slater 1976).

Interactions between fire characteristics and seed bank characteristics determine the effects of fire on soil seed banks. For example, Auld (1986) described how the fate of *Acacia suaveolens* seed depended on the interactions between seed depth in the soil and fire intensity and duration. Fire characteristics such as temperature and duration are major factors determining the outcome of burning on soil seed banks. Morgan (1999) concluded that fires in temperate Australian grasslands probably killed most seed on the soil surface since lethal surface temperatures were achieved. In contrast, fires in Mitchell grasslands in north-western Queensland were unlikely to be detrimental to buried seed or seed on the soil surface that were not directly consumed by fire since these fires exhibited low peak temperatures of short duration (Scanlan and O'Rourke 1982). Season of burning may also significantly affect seed banks. For example, in open woodland in New South Wales, soil temperatures are higher after summer fires than after winter fires, influencing the numbers of germinable seeds in the seed bank (Auld and Bradstock 1996).

The aim of this study was to investigate the effects of season of burning on the germinable soil seed banks of *C. ciliaris*-dominated grassland in two vegetation communities in north Queensland. Seed banks may play a significant role in determining vegetation composition, especially following disturbance (Warr *et al.* 1993) and an understanding of the nature of these seed banks and their responses to fire will help predict how the composition of these communities may be affected by fire.

Methods used to determine the numbers and identity of seeds in seed banks can be divided into two groups, germination methods and physical extraction methods, each with their strengths and limitations (Roberts 1981; Simpson *et al.* 1989). The identification of species is generally easier using the germination method. However, it is only effective for determining the germinable seed bank. In contrast, physical extraction methods enable determination of viable seeds. A further limitation of the germination method is it may under-estimate seed numbers of some species since the specific germination requirements of all species present are unlikely to be met by a particular germination technique (Roberts 1981). Despite these limitations, the germination method is suitable for this study and was the method used since, as pointed out by Clifford *et al.* (1995), it is the immediately germinable flora that determines the response to disturbance.

3.7.2. METHODS

3.7.2.1. Soil collection and processing

Soil was collected from the experimental plots at Dalrymple and Moorrinya after the late dry season fires in November 1999 (section 3.3). Samples were collected at this time to determine the seed banks present at the start of the growing season. At Dalrymple, four soil cores (2.8 cm diameter, 5 cm depth) were collected at the corners of a 40 cm by 40 cm quadrat at each of 12 randomly located sampling positions within each plot. A different soil collection method was used at Moorrinya since the soil corer used at Dalrymple was not suitable for sampling the Moorrinya clay. At Moorrinya one soil sample (7.2 cm diameter, 5 cm depth) was collected from each of eight randomly located sampling positions by hammering an open-ended metal cylinder into the soil until it was flush with the soil surface. The cylinder was dug up and the soil removed. While every care was taken, it was difficult to collect consistently sized samples because of the aggregated nature of the cracking clay. Samples collected within a plot were bulked. The bulked plot samples represented 296 cm^2 soil surface per plot for Dalrymple and 326 cm^2 soil surface per plot for Moorrinya.

Each soil sample was sieved through a 6.7 mm sieve before further processing.

3.7.2.2. Glasshouse set up

The composition of the soil seed banks was determined using a germination method. Eight plastic pots (approximately 13 cm diameter, 13.5 cm high) per soil sample were set up in a shade house at Davies Laboratory, Townsville (19°15’ S, 146°45’ E), in November 1999.

Pots were lined with shade cloth to prevent soil loss from the drainage holes and partially filled with sterilized fine sand (autoclaved at 121°C for 20 minutes). For each soil sample, the soil was spread over the sand of eight pots to form a layer about 2.5 cm thick per pot. Pots were randomly allocated to water-tight trays to which water was added to maintain moist conditions in the pots by capillary action over the experimental period. Trays were kept in ambient light conditions and pots were re-randomized during the experiment.

3.7.2.3. Measurements

The identity and number of seedlings that emerged from each pot were recorded over an eleven month period. Most seedlings were identified to species level. Seedlings were removed once they could be identified and were dried to produce a herbarium collection and assist with identification of unknown specimens. Self-sowing occurred in some plots since seedlings were generally grown until they flowered to aid identification. Self-sown plants, which emerged later than original individuals and generally in high densities, were excluded from the analyses.

3.7.2.4. Statistical analyses

Burning treatment effects on total numbers of seedlings and numbers of annual grass, perennial grass, legume, forb (referring to non-leguminous forbs) and sedge seedlings as well as numbers of seedlings of some individual species (those for which sufficient data were available) were compared using one-way ANOVA. Seedling counts per plot were square-root transformed prior to analysis and the reported means have been back-transformed and converted to counts/m^2. Burning treatment effects on species richness (number of species/400 m^2 plot) and diversity (as measured by Simpson's index) were also compared using ANOVA. Simpson's index is calculated as:

$$D = \frac{1}{\sum_{i=1}^{s} P_i^2}$$

Where s is the total number of species in the community and *Pi* is the proportion of individuals of species *i* of the total in the sample (Begon *et al.* 1990). Relationships between plot fire intensity and species richness and between plot fire intensity and seed bank seedling number were investigated using linear regression. All analyses were performed using

Genstat (2001).

The proportional composition of the seed banks was compared graphically to the proportional cover in the standing vegetation. Collection and analysis of the standing vegetation data are described in section 3.10.

3.7.3. RESULTS

Burning appeared to have little effect on the germinable seed banks of either site. No burning treatment effects on numbers of perennial grass, annual grass, forb, legume or sedge seedlings (Figure 3.14) or total seedling numbers were detected ($P > 0.05$). Total seedling numbers ranged from 271-846 (mean 480) seedlings/m^2 for Dalrymple seed banks and 276-1351 (mean 606) seedlings/m^2 for Moorrinya seed banks.

Few *C. ciliaris* grass seedlings emerged (five and four seedlings from the Dalrymple and Moorrinya seed banks respectively). Perennial grasses were a minor component of the seed banks, making up 22% and 12% of the Dalrymple and Moorrinya seed banks respectively. Interestingly, despite its dominance in the standing vegetation, no *Astrebla* seedlings emerged from the Moorrinya seed banks. The seed banks of both sites were dominated by forb seedlings which made up 53% and 41% of the Dalrymple and Moorrinya seed banks respectively (Figure 3.15). This contrasts with the composition of the standing vegetation which was dominated, in terms of cover, by perennial grasses (Figure 3.15). The 175 seedlings that germinated from the Dalrymple seed banks included three annual grass, nine perennial grass, 25 forb, three legume and five sedge species. The 253 seedlings that germinated from the Moorrinya seed banks included four annual grass, seven perennial grass, 21 forb, two legume and four sedge species. (Identified species are listed in appendices 3A and 3B).

Burning treatment effects could not be investigated for most species individually because of low seedling numbers. About three quarters of the species identified were represented by less than five individuals. Eleven species had 10 or more individuals and of these *Iseilema* spp. were by far the most abundant with 66 seedlings, the next most abundant species having less than 20 seedlings. Seedling emergence of these ‘abundant’ species was generally highly clumped with a high proportion of seedlings emerging from single plots. For example, more than half of the Iseilema seedlings that emerged from the Moorrinya seed banks were from

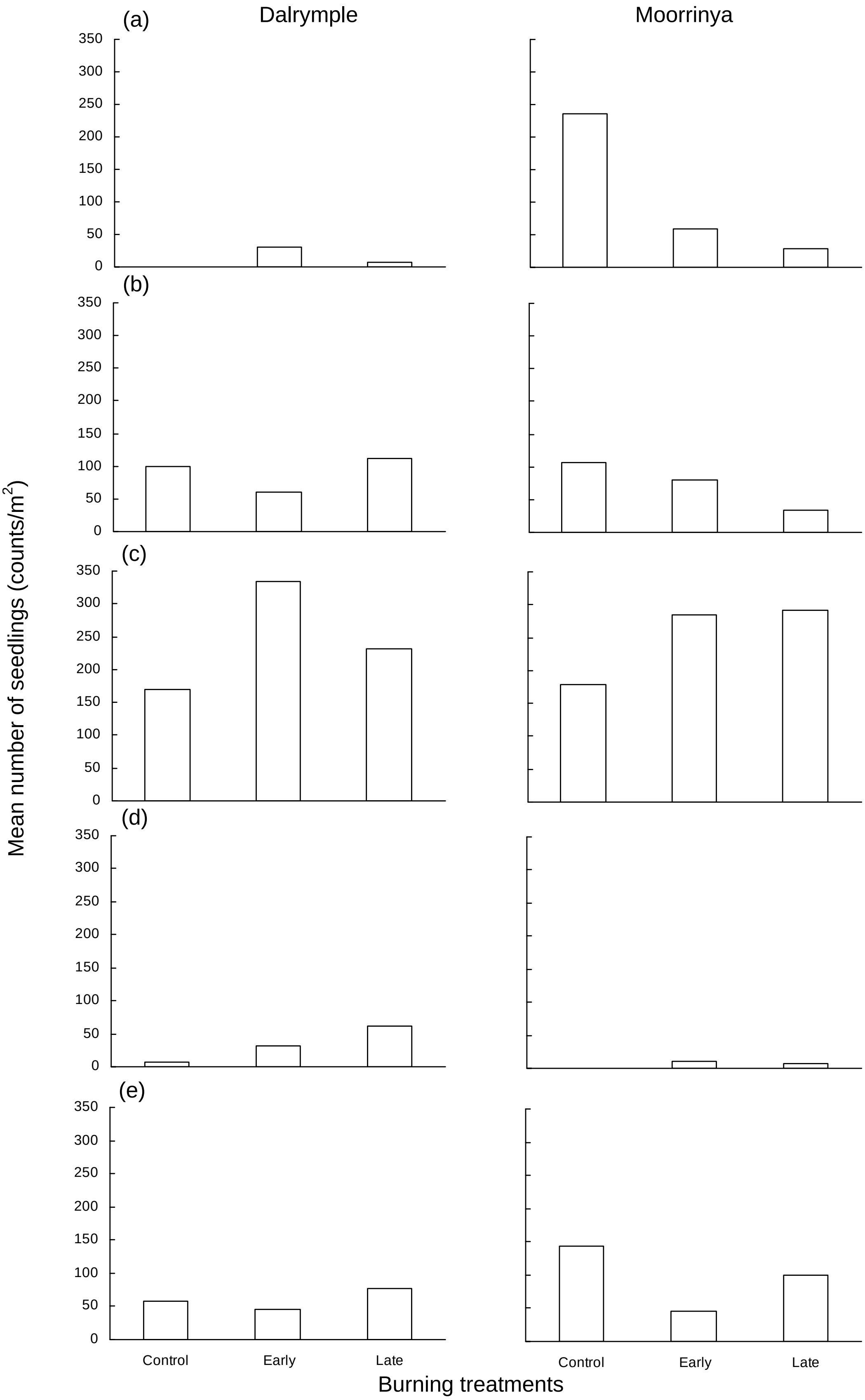

Figure 3.14. Mean number (counts/m^2) of (a) annual grass, (b) perennial grass, (c) forb, (d) legume and (e) sedge seedlings from unburnt (control), early dry season and late dry season burnt seed banks from Dalrymple (1st column) and Moorrinya (2nd column).

one plot. Eight of the 14 *Indigofera colutea* seedlings, eight of the 17 *Corcorus tridens* seedlings and nine of the 14 *Eragrostis brownii* seedlings also emerged from a single plot. Only three of these abundant species occurred in more than half the plots from a site. The highly clumped pattern of emergence made detecting treatment effects difficult and no burning treatment effects on seedling counts were found for the species investigated ($P > 0.05$).

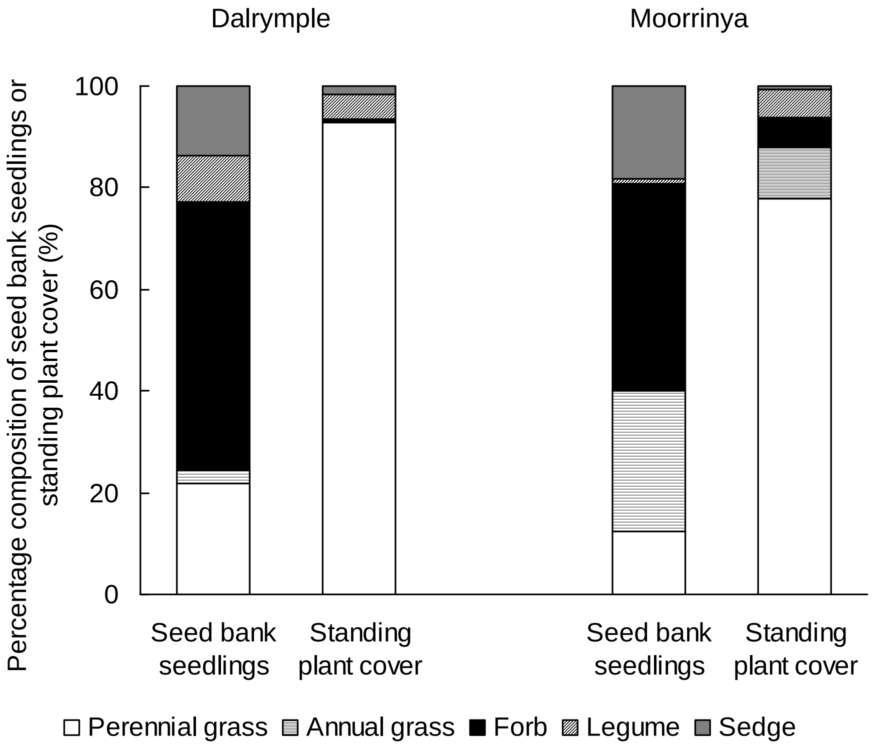

Figure 3.15. Percentages of perennial grass, annual grass, forb, legume and sedge plant groups making up the seed bank seedlings (1st bar) and post-fire standing herbaceous plant cover (2nd bar) at Dalrymple (left) and Moorrinya (right).

Species richness and diversity (Simpson's index) tended to be higher in the burnt treatments compared with the unburnt treatment for the Dalrymple seed banks, although this effect was not statistically significant ($P = 0.053$ and 0.08 for species richness and diversity respectively) (Figure 3.16). Burning treatment effects on the seedling species richness and diversity were not significant for the Moorrinya seed banks ($P > 0.05$) (Figure 3.16).

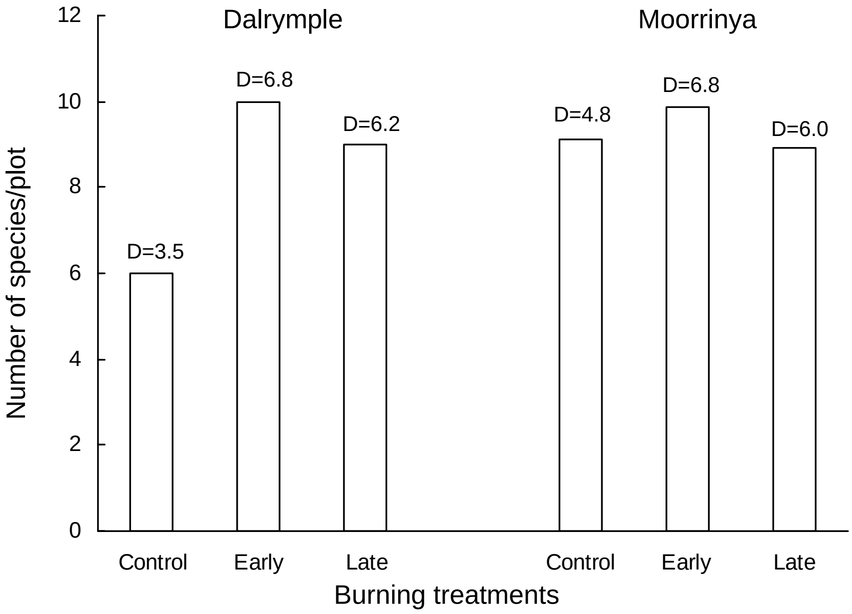

Figure 3.16. Mean species richness (number of species/plot) of seedlings emerging from unburnt (control), early dry season and late dry season burnt seed banks from Dalrymple and Moorrinya. Mean Simpson's diversity index values (D) are also presented (SE = 0.95 and 1.22 for Dalrymple and Moorrinya diversity index values respectively).

There was a significant linear relationship ($P < 0.05$) between plot fire intensity and plant species richness at Dalrymple (Figure 3.17). However, intensity explained only 36% of the variation in species richness and the relationship was not significant when the high intensity plot, which had high leverage, was omitted from the analysis. The intensity-species richness relationship was not significant for the Moorrinya plots ($P = 0.06$) (Figure 3.17). No relationships between fire intensity and number of seedlings were detected ($P > 0.05$).

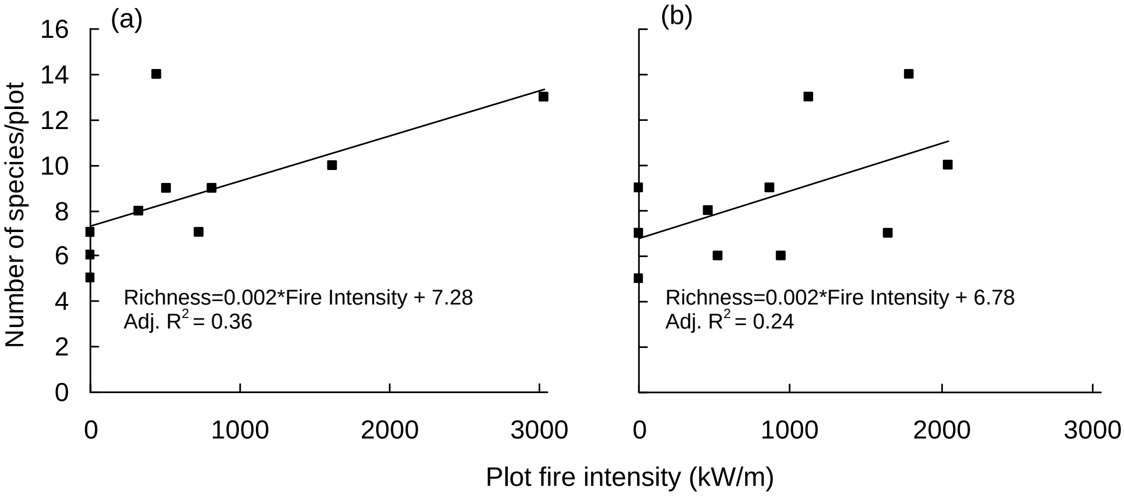

Figure 3.17. Relationships between plot fire intensity (kW/m) and plot species richness (number of species/plot) for (a) Dalrymple and (b) Moorrinya seed banks.

3.7.4. DISCUSSION

The germinable seed banks of many communities are affected by fire (Shea *et al.* 1979; Mott and Andrew 1985b; Ferrandis *et al.* 1999; Holl *et al.* 2000). However, the fires imposed in this study appeared to have had little effect on the germinable seed banks of these *C. ciliaris*-dominated communities. No burning treatment effects on total emergence or the emergence of any plant group were detected. The seed bank densities found here fall within the range reported for other communities in north-eastern Queensland (McIvor and Gardener 1991). However, different methods of seed bank assessment make comparisons between studies difficult (Warr *et al.* 1993).

Both increases (Calvo *et al.* 1999) and decreases (Morgan 1998; Holl *et al.* 2000) in seed bank species richness with burning have been reported. In this study, burning may have increased species richness at Dalrymple, although the results were inconclusive. Trends of increasing species richness with increasing fire intensity were also inconclusive.

Fire reduces seed abundance by consuming or damaging seed. The apparent lack of response to burning found here may indicate that much of the seed in these communities is protected from fire. However, this seems unlikely for early dry season fires at least. Many herbaceous species in northern Australia do not form persistent seed banks and much of the germinable seed bank is produced over the previous growing season (McIvor and Gardener 1994). Consequently, some loss of seed with early dry season burning is expected since the seed has had relatively little time to become incorporated into the soil. For example, early dry season fires are likely to burn *H. contortus* seed whilst in the seed heads or on the soil surface (Walker *et al.* 1983). In contrast, late dry season fires will have less effect since 90% of *H. contortus* seed becomes buried below the soil surface by spring (Campbell 1995). The germinable seed banks of these *C. ciliaris*-dominated communities appeared unaffected by season of burning. These results suggest that the fires did not reduce germinable seed abundance. However, since thick litter, when present, was removed from the edges of samples to enable soil coring, seed trapped in litter may have been under-represented in the sampling procedure, and consequently, reductions in seed abundance were not detected.

Species differ in their response to fire and changes in seed bank composition with burning were expected. *Cenchrus ciliaris* appears vulnerable to fire. Its diaspores have no effective seed burial mechanism and seem to remain on or close to the soil surface (Hacker 1989). Ernst (1991) concluded that *C. ciliaris* on the soil surface would be destroyed by fire due to the high flammability of its glumes and appendices, whilst below the surface it is susceptible to damage by dry heat. This contrasts with other species, such as *Heteropogon contortus,* that have effective seed burial mechanisms (Walker *et al.* 1981) and may be stimulated to germinate by dry heat (Zacharias *et al.* 1988). However, since few seedlings of these species emerged, treatment effects could not be tested. There were fewer *Iseilema* seedlings in burnt seed banks from Moorrinya, suggesting that *Iseilema* seed was killed by fire. However, the highly clumped pattern of emergence may have prevented any statistical differences being detected.

Fire also alters seed germinability, promoting the emergence of particular species and groups, and many studies report that seeds of certain species germinate in greater quantities after fire (Auld 1986; Shea *et al.* 1979; Purdie and Slater 1976). For example, Williams *et al.* (2003b) reported increased emergence of the legumes *Galactia tenuiflora* and *Indigofera hirsuta* and grasses as a group in coastal woodlands in north-eastern Queensland. No plant group or species in the seed banks of these *C. ciliaris*-dominated grasslands appeared responsive to burning. The number of legumes emerging from these seed banks was surprisingly low given the expectation of fire-promoted legume germination. Although there was a trend of more legume seedlings in burnt compared with unburnt seed banks from Dalrymple, this was due to high emergence of *Indigofera colutea* in one plot and statistical differences were not detected. Numbers of legume seeds have been found to be low compared with those of other plant groups in a number of studies (refer Roberts 1981; McIvor and Gardener 1994). However, others have reported that legumes may build up large seed banks (refer Roberts 1981; Young *et al.* 1981). Reasons for the low numbers of legumes found in these seed banks are unclear.

Although no major burning effects were detected, it is not possible to conclude that burning had no effect on the germinable seed banks of these communities. There are sampling and methodological issues that significantly hinder seed bank determination and these issues were relevant for this study. Firstly, the variability in emergence patterns displayed by the more abundant species greatly limited the power of the statistical tests. This clumped distribution is typical of seed banks (Kemp 1989; Morgan 1998). Seeds are unevenly distributed and this is recognized as a major problem for sampling (Bigwood and Inouye 1988; Warr *et al.* 1993). Large numbers of samples may be required to adequately describe soil seed banks (Warr *et al.* 1993). Clearly, the sampling regime used here was inadequate to account for the variability in these tropical grassland seed banks. However, it was not feasible to increase the number of replicates (plots) in this study and it is unclear whether more intensive within-plot sampling, which was precluded by time constraints, would have increased the likelihood of detecting treatment effects. Secondly, seed numbers were probably under-estimated by the germination method used since it is unlikely that optimal conditions for the germination of all species present were achieved (Warr *et al.* 1993). Comparison of seed bank determination methods have shown that different methods give different results (Gross 1990). Emergence from pots watered by capillary action, as in this study, has been found to be lower than from overhead-watered pots in some circumstances (Orr *et al.* 1996), probably because overhead watering simulates field conditions more closely by allowing fluctuations in moisture potential. Other studies have used multiple germination runs with cycles of wetting and drying (e.g. McIvor and Gardener 1994). The use of capillary watering and a single germination cycle may have resulted in under-estimation of the germinable seed banks in this study.

An additional limitation of the germination technique is that it does not distinguish between fire effects on seed abundance and seed germinability. Fire may simultaneously decrease seed abundance but increase seed germinability resulting in similar numbers of seedlings from burnt and unburnt seed banks (Mott 1982). Although it is unclear whether this happened in this study, it would appear unlikely since significant differences in species composition between burnt and unburnt seed banks would be expected if this had occurred.

Seed banks may be important in determining the potential vegetation composition following disturbances such as fire. However, seed bank studies may be of limited value for predicting vegetation change. A major problem with most seed bank studies is that estimates of seed numbers are very imprecise (Bigwood and Inouye 1988). In addition to the problems posed by spatial variability, seed banks may also vary considerably over time (McIvor and Gardener 1994; Kemp 1989), particularly if they are strongly influenced by climate variability and its effects on seed production and loss (Morgan 1998). Consequently, seed banks are difficult to study from a sampling perspective and, as mentioned above, there are also difficulties in species determination with different methods giving different results (Roberts 1981; Gross 1990). Various recommendations proposed to better describe soil seed banks include sampling over time rather than once only, collecting many small samples rather than a few large samples and measuring seed production and/or seed rain (Roberts 1981; Thompson 1992). However, these suggestions are often impractical to implement. It is also important to recognise that although seed bank studies may provide useful information regarding the potential composition of seedling cohorts, the results may not reflect emergence patterns observed in the field. For example, Shaw (1957) found that while fire promoted *H. contortus* emergence in the field, more seedlings came up in the unburnt treatment when the same soil was investigated in a glass house study. (The field effect was probably due to increased soil temperatures after fire, see section 3.2.2.5). Despite the fact that sampling and methodological issues limit the conclusions that can be made regarding the effects of fire on these seed banks, it is likely that the patchiness and relatively low intensities of the fires minimized any burning effects. The fires probably resulted in relatively little destruction or damage to seed and had only minor stimulatory effects on germination.

Although this study is inconclusive regarding the effects of season of burning on the germinable seed banks of these two communities, it does provide useful data regarding the soil seed banks themselves. Of particular interest is the apparent poor representation of perennial grasses in the soil seed bank despite their abundance in the standing vegetation. The composition of these seed banks reflects the commonly reported phenomenon of germinable seed bank composition differing significantly from that of the standing vegetation (McIvor and Gardener 1994; McIvor 1987; Morgan 1998; Roberts 1981; Rice 1989; refer Thompson 1992) and perennial grasses have been found to be poorly represented in the seed banks of other perennial grass-dominated communities (eg McIvor and Gardener 1991, 1994; Lunt 1990; Everson 1999). Another consistent feature of grassland seed banks is the presence of appreciable numbers of viable seeds of dicotyledonous plants (Roberts 1981; Rice 1989). The seed banks of these *C. ciliaris*-dominated communities were also dominated by forbs.

Differences in composition and richness of seed banks compared with the standing vegetation could not be investigated in detail due to inconsistencies in plant identification between this study and the study of vegetation composition (section 3.10). However, species in the standing vegetation were not represented in the seed bank and vice versa. Species richness was lower in the seed banks compared with the standing vegetation, as has been reported elsewhere, for example, temperate Australian grasslands (Morgan 1998). The lack of correspondence between the composition of the germinable seed bank and the standing vegetation may be due to many factors including different levels of seed production, seed mortality and predation, seed dissemination, dormancy characteristics and germination requirements (McIvor 1987; McIvor and Gardener 1994). Differences in seed abundance may reflect regeneration strategies in that species with high turnover in the vegetation are more frequent in the seed bank than species with lower turnover. Most native perennial species can sprout after fire and may offset the need for a large seed bank by long vegetative persistence (refer Morgan 1998). In contrast, annual forbs and grasses which must regenerate from seed each year are reliant on a soil seed bank for regeneration and generally have large seed banks.

Despite the expectation of relatively low numbers of perennial species, the small numbers of *C. ciliaris* seedlings to emerge from both communities and the absence of any *Astrebla* seedlings from the Moorrinya seed banks was surprising and raises an important question: why did so few perennial grass seedlings emerge? Either they are absent from the seed bank or the sampling methodology failed to detect them. With regard to sampling methodology, two issues are important. Firstly, assuming that the seed banks are spatially heterogeneous and contain relatively few seeds of perennial species, it is likely that more perennials would have been found with greater sampling effort. Secondly, it is possible that the germination method used was unfavourable for the perennial species present. Samples were kept wet continuously whereas cycles of wetting and drying may have been more favourable for emergence of perennial grasses. For example, *C. ciliaris* is not tolerant of water-logging (Anderson 1972) and the soils may have been kept too wet for *C. ciliaris* emergence.

Alternatively, the low numbers of perennial grass seedlings found may reflect actual low abundance of germinable, perennial grass seed in these seed banks. Many of the dominant grass species in northern (Mott and Andrew 1985b; McIvor and Gardener 1994) and southern (Morgan 1998) Australian grasslands fail to form long-term persistent seed banks. *Cenchrus ciliaris* seed loses most of its viability within two years under field conditions (Silcock and Smith 1990), although one study reported seed remaining viable for up to four years (Winkworth 1971). *Astrebla* also forms a transient seed bank because it lacks any long-term dormancy mechanisms (refer Orr 1998). Since these species have no long-term storage, seed numbers at the start of the wet season reflect the seed set the previous year and survival over the dry season (McIvor and Gardener 1994). Consequently, the size of their seed banks is largely dependent on the previous season's growing conditions; low seed abundance may reflect poorer than average growing conditions the previous season (Morgan 1998). Seed banks have been found to be very variable from year to year (McIvor 1987). Seed input was not measured in this study and its role in determining perennial grass seed banks cannot be determined. However, rainfall was probably above average at both sites (nearby sites experiences above average wet-season rainfall, section 3.3.) and many *C. ciliaris* and *Astrebla* plants were in flower in 1999 (section 3.8). In addition to low seed input, low numbers of perennial grass seed in the seed banks may reflect seed loss and reductions in seed numbers from seed rain to the seed bank have been reported elsewhere (Schott and Hamburg 1997; Rabinowitz and Rapp 1980). Such losses may be due to various factors such as senescence and loss to deep soil, germination as well as to the activity of granivores and disease (Kemp 1989). Insect and microbial attack have been suggested as a cause of reduced *C. ciliaris* seed in the seed bank (Hacker 1989).

Low seed densities of perennial grasses and high densities of other species groups have important implications for perennial grass establishment. Low numbers of perennial grass seed suggest that these species may not be present to germinate and establish when sites become available (McIvor 1987; refer McIvor and Gardener 1994). Some perennial grass species may be ‘extinction-prone’ due to variable seed inputs and transient seed banks (O’Connor 1991). Clearly, the dominance of *C. ciliaris* in the standing vegetation of both communities and *Astrebla* at Moorrinya indicate that, despite low abundance in the seed bank, these species have successfully recruited in the past. However, their colonizing ability in the present environment remains unknown. The relevance of low seed numbers for the establishment of other perennial grasses in these communities is also unclear.

An additional consequence of the composition of these seed banks is that perennial grass establishment may be suppressed by competition from annual species. In these communities most seeds germinate on the first rainfall event of the wet season and there is intense competition within the seedling stand (McIvor and Gardener 1991). While perennial grasses are good competitors once established, evidence from many studies indicates that perennial grasses have difficulty competing with annual grasses as seedlings (refer Brown and Rice 2000). The outcome of competitive interactions depends on the species and densities involved and environmental conditions. McIvor and Gardener (1991) stated that, while few perennial grass seedlings would be able to survive in very competitive situations since they do not have superior growth rates or other advantages during their early growth phase, they could out-compete other plant groups such as legumes if competition is for light and not water. Studies of competitive interactions between *Astrebla lappacea* and the annual grass *Iseilema* led Orr and Evenson (1993) to conclude that *Astrebla* could be out-competed by *Iseilema* at high densities but that forbs were unlikely to achieve densities high enough to prevent *Astrebla* recruitment. *Cenchrus ciliaris* seedlings are believed to be poor competitors against established plants (Hacker 1989; McIvor 2003). However, I am unaware of any work investigating the competitive ability of *C. ciliaris* seedlings compared with other seedlings.

The importance of seed banks in the colonization of gaps varies between communities (Thompson 1992). In some situations, for example where adult plants are capable of sprouting after fire, seedling recruitment from the seed bank may be unimportant for determining vegetation composition (Auld and O’Connell 1991). In grasslands, small gaps tend to be filled by vegetative growth of surrounding plants, although seeds seem to be crucial for the colonization of large gaps (Thompson 1992). The effects of fire on seed banks may be very important where perennial grasses senesce or suffer mortality and have to be replaced by juveniles (Ernst 1991). In terms of fire-induced changes in perennial grassland composition, the effects of fire on soil seed banks may be less important than fire effects on established plant competition and establishment site availability: unless sites become available for establishment, fire impacts on the soil seed bank will be irrelevant. In addition, seed banks may be strongly influenced by climate, particularly rainfall variability, and its effects on seed production inputs and losses (refer Morgan 1998; Orr 1998). Consequently, in these communities, climate rather that fire, may be the dominant influence on soil seed banks and fire will play a more important role in influencing vegetation composition via its effects on establishment site availability.

3.8. DOES FIRE PROMOTE FLOWERING IN *CENCHRUS CILIARIS*?

3.8.1. INTRODUCTION

Fire may result in shifts in the composition of plant communities via effects on flowering and seed inputs. For example, the abundance of *Bromus japonicus,* an invasive grass in North American mixed-prairie communities, may be altered by changes in the fire regime since seed production in this species is reduced by fire (Whisenant 1990b). Species differ in their flowering responses to fire (Glenn-Lewin *et al.* 1990), varying from being unaffected by burning to near obligate associations (Bond and van Wilgen 1996) (section 3.2.2.5). Fire-stimulated flowering is very common in grasses (Bond and van Wilgen 1996), although both increased and decreased flowering in grasses have been associated with fire in overseas studies (Daubenmire 1968; Glenn-Lwein *et al.* 1990). Fire has been reported to promote flowering in grasses (Scanlan 1980) and forbs (Lunt 1994) in Australian grasslands.

Season of burning may have a significant influence on flowering responses (Glenn-Lewin *et al.* 1990). For example, flowering of grasses of wet prairies in South Florida is promoted by burning in the growing season but not by burning in the dormant season (Main and Barry 2002). The objective of this study was to investigate the effects of season of burning on *C. ciliaris* flowering in two *C. ciliaris*-dominated grasslands. While flowering in *C. ciliaris* has been reported to be enhanced by fire (L. Baker, pers. comm., cited in Humphries *et al.* 1991), little is known about how the timing of burning may affect this response. The flowering response of a native perennial grass, *Astrebla* spp., to season of burning was also investigated at one site where this species was co-dominant.

3.8.2. METHODS

3.8.2.1. Measurements

Flowering of *C. ciliaris* at Dalrymple and *C. ciliaris* and *Astrebla* spp. at Moorrinya was monitored after the implementation of burning treatments at the two sites (section 3.3). The tagged plants used to monitor season of burning effects on plant survival were used for this study (section 3.4). The presence of inflorescences was recorded as plants were tagged in

April and June 1999. The number of inflorescences per tagged plant was counted after the fires, in January and June 2000 at Dalrymple and in February 2000 at Moorrinya. These sampling times were chosen for logistic rather than ecological reasons.

3.8.2.2. Statistical analyses

The effects of season of burning on the numbers of inflorescences per tagged plant and the percentage of tagged plants in flower at Dalrymple were analysed using a repeated measures ANOVA. Inflorescence counts were log transformed and percentage flowering data arcsin transformed prior to analysis. Means were compared using the protected LSD test at the 5% significance level and back-transformed means are presented. Data for small and large plants were also analysed separately using the same methods. Season of burning effects on the numbers of inflorescences per tagged plant and the percentage of tagged plants in flower at Moorrinya were investigated using one-way ANOVA for each species separately. Data were transformed and reported as above. Relationships between plot fire intensity and numbers of inflorescences and between fire intensity and percentage of flowering plants were investigated using linear regression. All analyses were performed using Genstat (2001).

3.8.3. RESULTS

No effects of season of burning on *C. ciliaris* flowering were found at Dalrymple for either small or large plants ($P > 0.05$). Numbers of inflorescences per plant and the percentage of plants in flower were similar between the two sampling times and only the January data are presented for the two size classes combined (Figures 3.18. and 3.19). More large plants flowered (53%) than small plants (14%) and large plants had more inflorescences (5.1 ± 1.05 inflorescences/plant) than small plants (0.3 ± 0.10 inflorescences/plant). There was little difference in the percentage of plants in flower when the plants were tagged in 1999 (30%) and when they were re-surveyed in January (32%) and August (29%) 2000.

At Moorrinya, *C. ciliaris* plants in the late dry season burn treatment had more inflorescences than plants in the early burn treatment ($P < 0.05$) but plants in both burning treatments had similar numbers of inflorescences as unburnt (control) plants (Figure 3.18). There were no burning treatment effects on numbers of *Astrebla* inflorescences per plant (P

> 0.05) (Figure 3.18) or on the numbers of *C. ciliaris* or *Astrebla* plants in flower (P > 0.05) (Figure 3.19). Flowering was similar in the two species. In February, 30% of *C. ciliaris* plants were in flower and plants averaged 2.1 ± 0.39 inflorescences/plant while 44% of *Astrebla* plants were in flower and plants averaged 2.4 ± 0.31 inflorescences/plant. The percentage of plants in flower in February 2000 was lower than in April/June 1999 when the plants were tagged. At this time 54% of *C. ciliaris* plants and 98% of *Astrebla* plants were in flower.

No relationships between plot fire intensity and number of inflorescences/plant or percentage of flowering plants were found for *C. ciliaris* or *Astrebla* plants (P > 0.05).

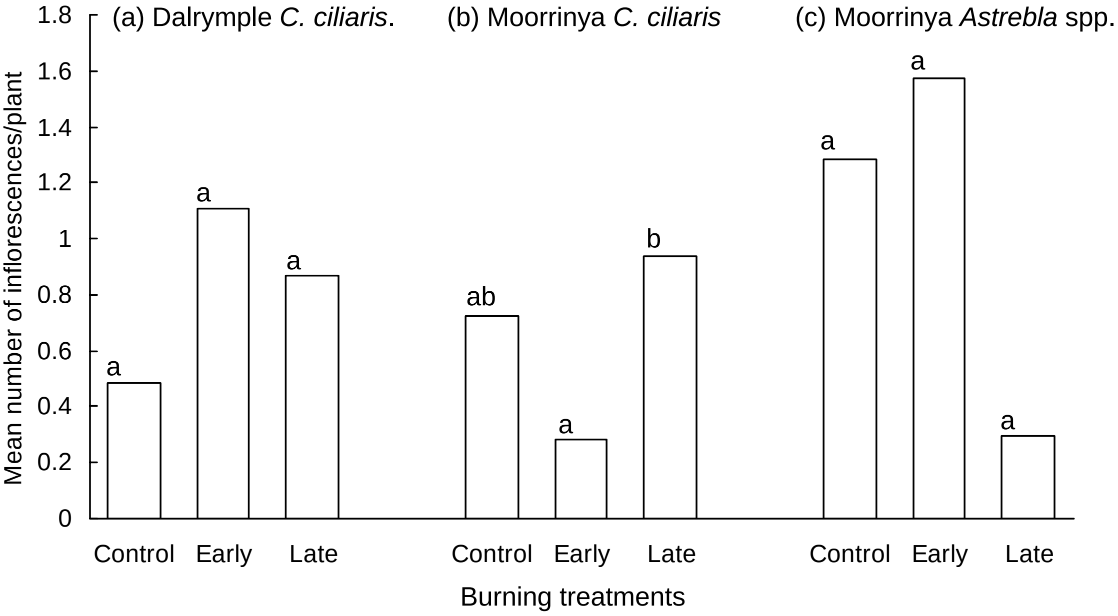

Figure 3.18. Mean number of inflorescences per tagged plant at (a) Dalrymple (all plants in January 2000) and (b and c) Moorrinya (*C. ciliaris* and *Astrebla* spp. plants respectively in February 2000) in control (no burn), early dry season fire and late dry season fire treatments. Different lower case letters denote significantly different means within graphs (P < 0.05).

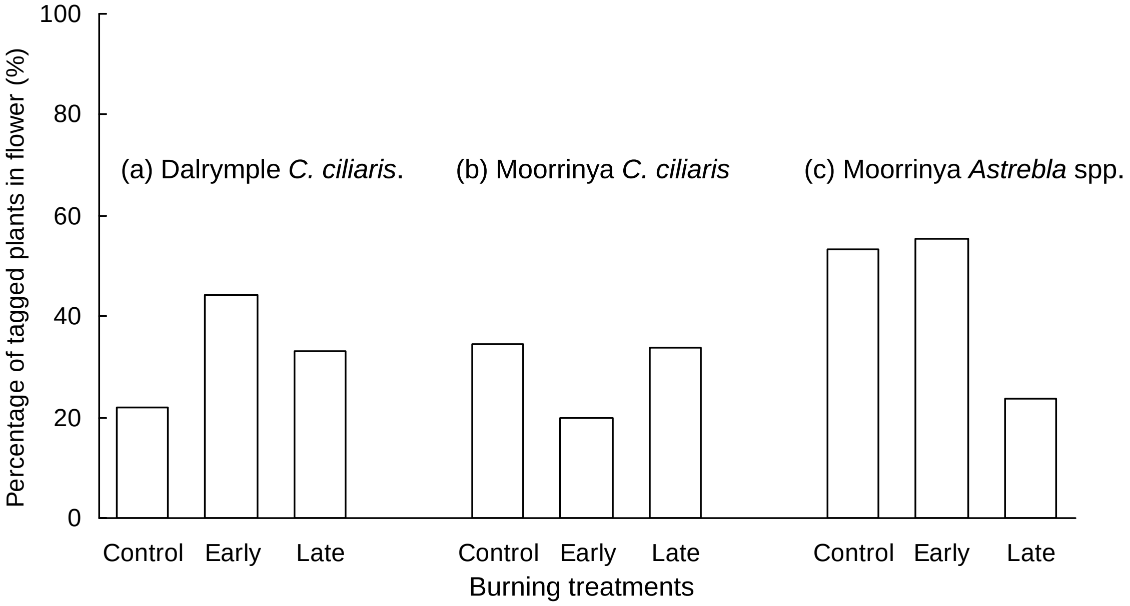

Figure 3.19. Mean percentage of tagged plants in flower at (a) Dalrymple (all plants in January 2000) and (b and c) Moorrinya (*C. ciliaris* and *Astrebla* spp. plants respectively in February 2000) in control (no burn), early dry season fire and late dry season fire treatments.

3.8.4. DISCUSSION

Cenchrus ciliaris is considered to be favoured by fire (Humphries *et al.* 1991; Lazarides *et al.* 1997; Butler and fairfax 2003). However, the fires in this study appeared to have little effect on flowering in *C. ciliaris*. The lack of flowering response to fire in *Astrebla* was also surprising given that fire-stimulated flowering in this species has been reported (Scanlan 1980). This lack of response may be due to the low intensity of the fires. Alternatively, or in addition, sample variability may have limited the power of statistical tests. Inflorescence number per plant was highly variable with many plants producing no flowers while a few produced many. Although flowering in *C. ciliaris* at Moorrinya was greater with the higher intensity, late dry season fires than with the early dry season fires, the treatment effects at this site do not appear to be related to fire intensity and are difficult to explain. No relationships between plot fire intensity and flowering were detected and the greater flowering of *C. ciliaris* in the late dry season fires may simply be a consequence of the variability in flowering and the small sample size.

The interactions between fire, flowering and rainfall are important in seasonally dry ecosystems where rainfall patterns are a major factor influencing plant growth (Orr *et al.* 1991). It is likely that rainfall plays a major role in determining flowering in the *C. ciliaris* grasslands investigated here and that the effects of fire are of secondary importance. It had been reported that fire promotes seed production in *C. ciliaris*, particularly when fire was followed by rain (L. Baker cited in Humphries *et al.* 1991) and Bosch and Dudzinski (1984) noted that seed head production in *C. ciliaris* in central Australia was determined by rainfall. The responses of *Astrebla* to burning have been found to differ depending on rainfall, with increased seed head density on burnt plants at sites experiencing above average rainfall (Scanlan 1980). Although overall wet-season rainfall was above average (section 3.3.5), the soil moisture status over the growing season at the experimental sites is unknown. Consequently, any moisture limitations to flowering are also unknown. Flowering in both *C. ciliaris* and *Astrebla* was lower in 2000 than in 1999. However, the factors influencing flowering responses are not clear. The effects of fire on flowering in grasses in North American tallgrass prairies have been found to vary between years and between habitats (Glenn-Lewin *et al.* 1990). More detailed studies are required to determine the effects of growing season rainfall and other site differences on flowering responses to fire in these *C. ciliaris*-dominated grasslands.

The timing of fire may have a significant influence on the degree of subsequent flowering in grasses (Glenn-Lewin *et al.* 1990). The effects of season of burning on flowering and seed inputs are critical in determining potential recruitment patterns in these grasslands. Unfortunately, in this study it was not possible to monitor season of burning effects of the flowering of native species in detail due to lack of resources. Studies are needed to determine season of burning effects on flowering of *C. ciliaris* and local native grasses in these communities.

It is also important to determine the effects of fire on viable seed inputs. Although inflorescence production may be a good indication of seed production (e.g. as for *Astrebla*, Orr 1998), relationships between flowering and seed inputs are not always positive. For example, Bosch and Dudzinski (1983) reported that whereas severely defoliated *C. ciliaris* plants produced more seed heads than non-defoliated plants, non-defoliated plants produced more seeds per seed head, more than compensating for their lower seed head numbers. Consequently, burning treatment effects on flowering may not be reflected in viable seed production. Again, post-fire rainfall is likely to be a dominant factor determining viable seed inputs since rainfall conditions during seed set influence seed viability (Orr 1998). Further work is required to determine how season of burning affects viable seed inputs by *C. ciliaris* and native species in these grasslands.

3.9. EFFECTS OF SEASON OF BURNING ON SEEDLING EMERGENCE PATTERNS IN *CENCHRUS CILIARIS*-DOMINATED GRASSLAND

3.9.1. INTRODUCTION

Fire may play a major role in shaping vegetation composition via its effects on seedling recruitment patterns. Flushes of seedling emergence after fire are commonly reported for both herbaceous (Shaw 1957; Tothill 1969; refer Tyler 1995) and woody (Purdie and Slayter 1976; Williams 2000) species, although decreases in seedling emergence after fire have also been found (Mott and Andrew 1985b; Glenn-Lewin 1990; Tyler 1994) (section 3.2.2.5).

The importance of seedling dynamics for vegetation composition varies, from being fundamental in annual plant communities, to being relatively unimportant much of the time in many perennial plant communities where the persistence of resident plants means that recruitment events are rare (Lauenroth and Aguilera 1998). However, the composition and establishment success of seedling cohorts may become very significant in determining vegetation composition in perennial systems when disturbances free up resources creating opportunities for recruitment of new individuals.

Seedling recruitment requires a source of viable propagules as well as microsites with specific features that permit seed germination and seedling growth (Harper *et al.* 1965). Fire may result in significant shifts in vegetation composition by altering both these factors. Fire alters germinable seed availability directly, by killing seed and affecting dormancy mechanisms, and indirectly, via effects on flowering (section 3.2.2.5). Fire also alters establishment site availability. The environmental changes produced by fire may stimulate seedling recruitment as competition from established plants is reduced, resources such as light, water and nutrients are increased, allelopathic influences are decreased and seed and seedling predation is reduced (Tyler 1995; Bond and van Wilgen 1996) (section 3.2.2.4). Alternatively, burning may result in fewer establishment sites. For example, moisture conditions may be less favourable for seedlings in burnt compared with unburnt sites (Christensen and Muller 1975).

The importance of fire in promoting seedling emergence varies between communities. In some communities, for example chaparral shrublands in North America (Tyler 1995), significant seedling establishment occurs only following fire (Noble 1989). In other communities, fire is less important since seedling emergence and survival are primarily controlled by climate, particularly rainfall (Lauenroth *et al.* 1994). The importance of seedling recruitment for post-fire recovery also varies, depending on both the fire regime and vegetation characteristics. For example, seedling recruitment is often of little importance in temperate Australian perennial grasslands after single fires. Single fires in these grasslands do not promote mass seed germination of most perennial species, probably because of small soil seed banks (Lunt and Morgan 2002) and also because the perennial grasses generally recover vegetatively from fire (Morgan 1999). In contrast, where fire regimes result in major plant mortality, seedling recruitment may be the only means of re-colonization.

The season of burning may influence seedling recruitment patterns since both the intensity and timing of fire influence the availability of germinable seed and establishment sites. Variations in fire intensity and soil heating can affect recruitment since seeds of different species have different tolerances to heating and different germination requirements (Tyler 1995). For example, high intensity fires may result in flushes of legume germination since these fires are more effective than low intensity fires in breaking down hard-seededness (Mott 1982). High intensity fires are important in legume germination in dry sclerophyll jarrah forests in Western Australia where native legume species rarely germinate after low intensity fires (Shea *et al.* 1979). In addition, fire intensity influences micro-site conditions. The degree of litter removal and mortality of established plants will influence establishment site availability and seedling recruitment success. The timing of fire in relation to vegetation condition also influences the effects of fire on seedling recruitment patterns. Burning annual *Sorghum* grassland at the commencement of the wet season after the majority of seeds have germinated but prior to flowering and seed set may drastically reduce future S*orghum* abundance by eliminating the source of seed (Stocker and Sturtz 1966). Conversely, *Sorghum* abundance may be unaffected by dry season fires (Andrew and Mott 1983). In perennial grasslands, early dry season fires may result in reduced seedling emergence by destroying seed still held in seed heads or on the soil surface (Walker *et al.* 1983) while late dry season fires may have little impact since seed will be buried and protected from fire by this time.

The objective of the two studies reported here was to investigate the effects of season of burning on seedling emergence patterns in *C. ciliaris*-dominated grassland. In the first study, the numbers of grass and forb seedlings emerging early in the growing season after the implementation of burning treatments was assessed. In the second study, the emergence of grass seedlings was surveyed over the duration of the second growing season after the fires.

3.9.2. METHODS

3.9.2.1. Seedling monitoring sites

The effects of different season of burning on seedling recruitment in a *C. ciliaris*-dominated grassland were investigated using plots within the main experimental area at Dalrymple (plots one to nine, section 3.3). Eight metal quadrats were randomly positioned within the inner 18 m by 18 m zone of each plot in December 1999. Each quadrat, measuring 50 cm by 50 cm, was made of 10 cm by 10 cm metal mesh such that each quadrat formed a five by five grid of 10 cm by 10 cm 'cells'. Quadrats were pegged to the ground and marked with 1 m high bamboo stakes to aid relocation.

3.9.2.2. Study 1: Seedling recruitment survey

The numbers of grass and forb (legume and other forb) seedlings in each cell were recorded in December 1999, five weeks after the late dry season fires. Seedlings were identified to species level where possible.

Grass and forb seedling data were analysed using one-way ANOVA. Sub-sample (quadrat) seedling totals were square root transformed prior to analysis. Means were compared using the protected LSD test at the 5% significance level. The reported treatment means have been back-transformed and converted to seedling numbers/m^2. Correlations between forb and grass seedlings were investigated at the cell and quadrat level. Linear regression was used to investigate relationships between plot fire intensity and plot seedling numbers. All analyses were performed using Genstat (2001).

3.9.2.3. Study 2: Grass seedling recruitment and survival

To monitor grass seedling recruitment in more detail, four cohorts of grass seedlings were tagged over the 2000-2001 growing season (in December 2000 and January, February and March 2001) and their survival assessed at the end of the growing season in June 2001. The metal mesh quadrats used in the previous study were used. Grass seedlings found in the nine central cells of each quadrat were individually tagged by pushing a partly unwound paper clip in beside the seedling. Different coloured clips were used to identify each cohort. It was impractical to tag all seedlings when they occurred at high density. Therefore, on each survey day only one seedling was tagged in a cell when it contained more than four untagged seedlings. However, all seedlings were counted. Unfortunately, it was not possible to determine the genus of many seedlings due to their small size and attempts at identification were abandoned.

Cumulative seedling emergence was estimated for each survey date. In cells in which not all seedlings were tagged, new individuals could not be distinguished from those previously counted. In these cases, only seedlings in excess of the number that had been reported for the previous sampling were added to the count. Seedling numbers were underestimated in this study since emergence and death of seedlings may have occurred between sampling dates.

At the end of the growing season the quadrats were re-surveyed to assess the fate of the seedlings. The presence or absence of all tags and seedlings was recorded. The status of seedlings (dead or alive) could not be accurately assessed, since most herbaceous vegetation had begun to brown off, and seedlings were counted as surviving if they were present. Consequently, survival reported here is ‘apparent’ survival. In addition to the total number of surviving seedlings, the numbers of surviving seedlings from each cohort were assessed. Seedlings that could not be assigned to a cohort (untagged seedlings and seedlings with missing tags) were excluded from these counts.

Burning treatment effects on cumulative seedling emergence counts were analysed using a repeated measures ANOVA procedure. The cumulative seedling emergence counts were also analysed for each sampling day separately to check homogeneity of variances. Burning treatment effects on the total numbers of emerged, dead and surviving seedlings were determined using one-way ANOVA. Prior to the analyses, sub-sample (quadrat) totals were log transformed. Means were compared using the protected LSD test at the 5% significance level and back-transformed means converted to counts/m^2 are presented. Seedling survival data were also expressed as percentages of emerged seedlings. Burning treatment effects on the percentage seedling survival per plot were determined using one-way ANOVA with percentages being arcsin transformed prior to analysis. Means were compared using the protected LSD test at the 5% significance level and back-transformed means converted to counts/m^2 are presented. Burning treatment effects on the emergence and survival of seedlings in individual cohorts could only be assessed for the December cohort because seedling numbers in the other cohorts were too small. Data from the December cohort were analysed using one-way ANOVA as above.

Relationships between forb and grass seedling emergence in 1999 and relationships between grass seedling emergence in 1999 and 2000-2001 were investigated using linear correlation. Relationships between estimated plot fire intensity (kW/m) and plot seedling emergence were investigated using linear regression. Relationships between flowering of tagged *C. ciliaris* plants (section 3.8) and grass seedling emergence were also investigated using linear regression. All analyses were performed using Genstat (2001).

3.9.3. RESULTS

Season of burning had a significant effect on forb seedling emergence. Five weeks after the late dry season fires, mean forb seedling number was higher in the early dry season burn treatment than in the other treatments (P < 0.05) (Figure 3.20). The same trends were found for grass seedlings, although treatment means were not significantly different (P > 0.05) (Figure 3.20).

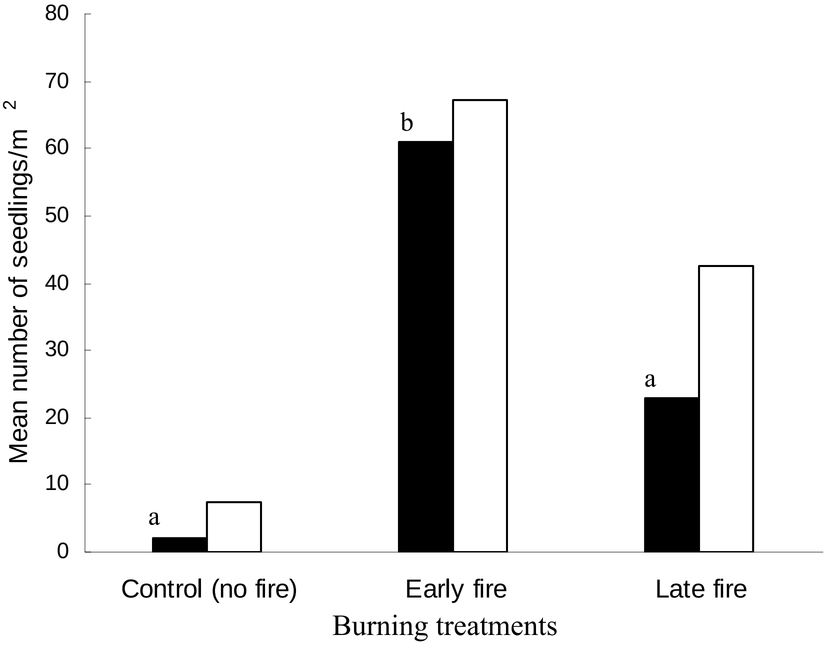

Figure 3.20. Mean number of forb seedlings (solid bars) and grass seedlings (unfilled bars) in control, early dry season and late dry season fire plots at Dalrymple in December 1999. Different lower case letters denote significantly different forb seedling numbers.

Relationships between fire intensity and seedling emergence are unclear since the uneven spread of fire intensity values prevents valid assessment of any relationship (Figure 3.21).

While there was a significant linear relationship between plot fire intensity and forb seedling numbers ($P < 0.05$), no relationship was found when the high fire intensity plot, which had high leverage, was excluded from the analysis. No relationship between fire intensity and grass seedling numbers was detected ($P > 0.05$).

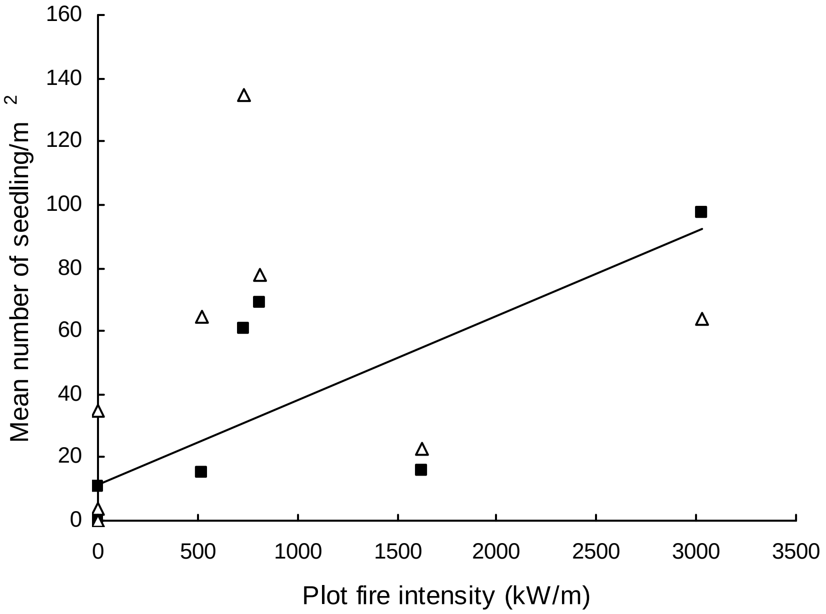

Figure 3.21. Relationships between estimated plot fire intensity and mean number of grass (Δ) and forb (■) seedlings/m^2. Significant linear regression shown for forb seedling numbers (Forb seedling number = 11.2 +0.027*Fire intensity, adjusted $R^2 = 0.50$, $P < 0.05$).

Overall, seedling emergence was patchy with 19% of quadrats containing no seedlings. On a quadrat basis grass seedling densities ranged from 0 to 216 seedlings/m^2 (mean of 49 ± 7.0 seedlings/m^2) while forb seedling densities ranged from 0 to 212 seedlings/m^2 (mean of 36 ± 6.0 seedlings/m^2). There was little correlation between the occurrence of forb and grass seedlings in 1999 ($r = 0.20$ and 0.42 at the cell and quadrat levels respectively).

Almost half of the forb seedlings appeared to be species of *Indigofera*. These legumes appeared to be favoured by early dry season fires with means of 1, 31 and 9 seedling/m^2 in unburnt, early dry season and late dry season fire treatments respectively. However, these treatment means were not significantly different ($P > 0.05$). Seedlings of *Boerhavia*, *Portulaca* and *Sida* species were also identified. Most grass seedlings could not be identified to genus level.

No burning treatment effects on total grass seedling emergence over the 2000–2001 growing season were detected ($P > 0.05$) (Figure 3.22). However, numbers of surviving seedlings were higher for seedlings that emerged in the late dry season fire treatment than in the control or early dry season fire treatments ($P < 0.05$) (Figure 3.22). No treatment effects on the proportion of surviving seedlings were found ($P > 0.05$).

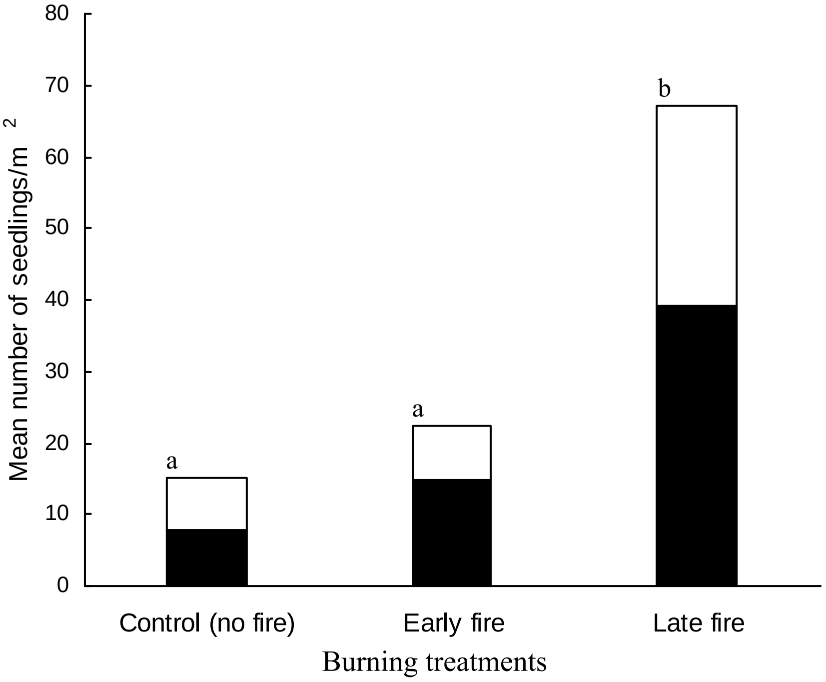

Figure 3.22. Mean number of grass seedlings (seedlings/m^2) found in control (no burn), early dry season and late dry season fire treatments showing seedling status (dead ■ and surviving □) at the end of the 2000-2001 growing season (June 2001). Different lower case letters denote significantly different ($P < 0.05$) means for surviving seedlings.

There was a significant time effect on emergence with most seedlings (85%) emerging by the December survey date. By January and February a further 8% and 4% of seedlings had emerged respectively. The small numbers of seedlings emerging after December meant that trends in cumulative emergence with fire treatments remained constant over time.

Season of burning effects on cohort seedling survival were investigated only for the December cohort because of low seedling numbers in other cohorts. Treatment effects on December cohort seedlings reflected the overall results with greater numbers surviving in the late dry season fire treatment ($P < 0.05$). The percentage of seedlings surviving to June 2001 increased with cohort age: surviving seedlings made up 45%, 30%, 21% and 20% of seedlings in the December, January, February and March cohorts respectively.

There was no relationship between numbers of grass seedlings emerging in the 2000-2001 growing season per plot and mean number of inflorescences of *C. ciliaris* tagged plants earlier in the year ($P > 0.05$). No relationship between plot fire intensity and 2000-2001 grass seedling numbers was detected ($P > 0.05$).

As in the previous growing season, grass seedling emergence was patchy with 26% of quadrats containing no seedlings. On a quadrat basis seedling density ranged from 0 to 1711 seedlings/m^2 (mean of 89 ± 26.7 seedlings/m^2). There was no relationship between grass seedling emergence in 1999 and 2001 ($r = 0.06$ and 0.31 at the cell and quadrat levels respectively).

The tagging method was moderately successful with 79% of tags still in place at the end of the study. About 60% of the lost tags were from cells in which no seedlings survived so their loss did not affect seedling assessment.

3.9.4. DISCUSSION

Fire may alter seedling recruitment patterns and faster and greater seedling emergence after fire is often reported (Tothill 1969; Tyler 1995; Williams 2000). In this study, seedling emergence tended to be higher in burnt than in unburnt plots. However, treatment differences were statistically significant for forbs only. Given the patchy distribution of seedlings, the sampling regime used may have been insufficient to adequately describe seedling emergence patterns. A much greater sampling effort may have detected more treatment effects. However, it is also likely that the lack of major burning treatment effects on seedling emergence reflects the relatively low intensities of the fires.

It is not surprising that forb emergence was promoted by burning since about half the forb seedlings were legumes. Fire is known to promote legume germination via heat effects on the seed coat that break seed dormancy (refer Auld and O'Connell 1991) and flushes of legume germination after burning have been reported ('t Mannetje *et al.* 1983; Robertson *et al.* 1999) (section 3.2.2.5). The effect of season of burning was probably related to differences in fire intensity, with more forb seedlings emerging in the more intense, early dry season burn treatment. While high intensity fires can kill seed (Auld and O'Connoll 1991), they may be more effective than low intensity fires in breaking down hard-seededness (Mott

1982). However, no convincing relationship between plot fire intensity and forb seedling emergence was found. A more even spread of plot fire intensity values is needed to investigate fire intensity-emergence relationships. Although the increase in forb emergence with early dry season burning may have been due, in part, to the increased germinability of legume seeds, fire may also alter emergence patterns via effects on micro-site conditions. It is not known how much of the forb responses to burning were due to direct effects on seed germinability versus the creation of favourable micro-sites.

Burning had no detectable effects on grass seedling emergence. Trends in grass seedling emergence with season of burning were not statistically significant or consistent between years. The greater numbers of surviving grass seedlings in the late dry season burn treatment in June 2001 was simply due to greater emergence in this treatment rather than to fire effects on seedling survival since there was no treatment effects on the proportion of grass seedlings surviving.

Seedling emergence patterns following fire may reflect burning effects on seed and establishment site availability. The trend of greater grass seedling emergence with burning than without burning in the first growing season after the fires perhaps indicates that positive fire effects on establishment sites out-weighed any negative effects on sites or seed availability. Species variations in seed burial mechanisms may result in significant shifts in the relative abundance of species among seedling cohorts emerging after fire (Peart 1984). However, since grass seedlings could not be identified, it was not possible to investigate burning effects on seed of individual species. Grass seedling emergence patterns in the second growing season may reflect burning effects on flowering. Since perennial grasses in these communities do not form persistent seed banks (see Silcock and Smith 1990 for *C. ciliaris* seed banks), most seedlings in the second season would have emerged from seed produced after the fires. Relationships between flowering and seedling emergence could not be investigated in detail since the flowering data was for *C. ciliaris* plants only (section 3.8) whereas grass seedling counts included other species. Although no relationship between plot means of inflorescences per *C. ciliaris* plant and seedling numbers was found, trends in treatment means support the hypothesis that inflorescences per *C. ciliaris* plant (section 3.8.3) and grass seedling numbers tended to be higher in burnt than in unburnt plots. However, differences in treatment means were not statistically significant and it is not possible to identify factors influencing grass seedling emergence patterns.

There was no correlation between forb and grass emergence sites. This may reflect the patchy distribution of seed (Bigwood and Inouye 1988; Kemp 1989). It may also indicate that sites favourable for forb emergence were not necessarily favourable for grass emergence. The effects of particular microsites on germination and emergence vary depending on the species involved since seeds often possess highly specific germination requirements (Harper *et al.* 1965). Differences in seed size and shape can affect seed-soil contact (Evans and Young 1970; Winkel *et al.* 1991) and therefore the same micro-site may present different moisture conditions for seeds of different species. Differences in seedling morphology can also influence the suitability of a particular micro-site for emergence (Gross and Werner 1982). There was also no relationship between grass emergence sites in the first and second growing seasons after the fires. This may reflect differences in patterns of seed availability and/or micro-site conditions between the two seasons. In addition, there may be inter-year variations in the degree to which particular sites are favourable for seedling establishment (Fowler 1988).

Seedling survival is influenced, in part, by both the spatial and temporal patterns of seedling emergence. Where seedlings emerge in high densities there may be high mortality and McIvor and Gardener (1991) concluded that few perennial grass seedlings would survive such competitive situations. However, the reverse situation has also been observed, where seedling survival is greater when there are other seedlings nearby (Fowler 1988), the likely explanation being that the presence of neighbours reflected the favourableness of the site (Fowler 1988).

Temporal patterns of seedling emergence may also influence seedling survival. Earlier germinating seedlings often have a higher probability of survival (Hamrick and Lee 1987; McIvor 1987; Fowler 1988). However, this is not always the case. Rapid germinators may have a competitive advantage if conditions remain favourable and these seedlings have time to grow deeper roots, and hence, are more drought tolerant than later germinating individuals (refer Fowler 1988). However, slow germinators, which may fail to germinate during short favourable periods, could benefit in the long run if they are able to germinate after a catastrophe has killed the rapid germinators (Grubb 1977).

Interactions between competing seedlings are of particular interest where a change in dominance is desired. The results from this study suggest that forb competition is unlikely to affect grass seedling emergence and earlier emerging seedlings have a better chance of survival than later emerging seedlings. However, the outcome of inter-species competition between grass seedlings is unknown. Although *C. ciliaris* seedlings are believed to be poor competitors against established plants (Hacker 1989; McIvor 2003), little is known about competitive interactions between *C. ciliaris* seedlings and seedlings of other species. This is a key issue that requires investigation.

The results from these studies provide little information regarding how fire may affect community composition since it was not possible to identify seedlings and follow the fate of individual species. An understanding of fire-induced emergence patterns is useful for predicting potential vegetation change. However, it is important to recognise that micro-sites favourable for germination and emergence may not necessarily be conducive to seedling establishment (Schupp 1995). For example, surface cover may be important in determining germination and emergence success (section 3.6), whereas other factors, such as distance from nearest neighbours may be more important in determining growth and reproductive output (Gross and Werner 1982). Although the fate of the surviving seedlings is unclear, it is likely that few will persist and become established. In perennial grasslands, the survival and establishment of seedlings is greatly influenced by competition from established plants for water and nutrients (Cook 1980) and removal of this competition is a key factor in promoting seedling survival (Cheplick 1998). The low intensity fires in this study had little effect on the competitiveness of established plants since few plants were killed (section 3.4), although there was a decline in perennial grass cover with burning (section 3.10). McIvor and Gardener (1981) concluded that considerable disturbance was required for *C. ciliaris* establishment and that it was likely that the temporary reduction in above ground competition by burning had no beneficial effect. However, *C. ciliaris* seedling establishment after fire has been observed (Back 2001) and Cook (1984) reported that, although emergence of *C. ciliaris* was lower on burnt than on unburnt plots, seedling survival was higher. In the context of using fire to reduce the abundance of *C. ciliaris*, an understanding of season of burning effects on *C. ciliaris* and native species recruitment is essential.

Seedling establishment patterns are difficult to predict since they are a function of interacting abiotic factors, such as rainfall distribution and soil type, and biotic factors, such as competition and herbivory (Cheplick 1998). Seedling recruitment is sensitive to soil water availability and seedling recruitment patterns are influenced by soil texture and rainfall (Lauenroth *et al.* 1994). Climate will have an over-riding effect on seedling establishment in these *C. ciliaris*-dominated communities with the timing of the opening rains and the adequacy of subsequent rainfall being a major influence on seedling recruitment (McIvor and Gardener 1991). Further work is required to investigate the influence of fire on the establishment of *C. ciliaris* relative to native species in relation to rainfall regimes.

3.10. EFFECTS OF SEASON OF BURNING ON HERBACEOUS COMMUNITY COMPOSITION OF *CENCHRUS CILIARIS*-DOMINATED GRASSLAND

3.10.1. INTRODUCTION

Fire is an important tool for eliminating or reducing the abundance of unwanted species. It is one of the few tools available that can be used economically and effectively over large areas and the strategic application of fire regimes has been employed to manage invasive woody and herbaceous species (section 3.2.3).

The efficacy of fire in controlling invasive plants depends on the fire regime and on the physiological and morphological properties of both the native community and the invading organism (Christensen and Burrows 1986). Fires can be imposed at different frequencies, intensities and in different seasons and the responses of vegetation to fire vary with fire regime (section 3.2.3). In addition, the ecological consequences of particular fire regimes depend on the species present and stage of life cycle when exposed to fire (Gill *et al.* 1990). Fire may result in compositional changes where the resident plants differ in size, vigour, morphology and/or life strategy. Post-fire conditions such as the distribution of rainfall and grazing also influence the responses of vegetation to burning. For example, fire effects on species richness may be dependent on the prevailing moisture conditions (Walker and Peet 1983).

The season of burning can have a marked effect on the structure and composition of grassland vegetation (Tothill 1971; Hodgkinson *et al.* 1984; Collins and Gibson 1990; Howe 1994) since the effects of fire vary with seasonal changes in fire characteristics and vegetation condition. Fire intensities vary seasonally. Generally, late dry season fires are more intense than early dry season fires since fuel moistures are normally lower at the end of the dry season and weather conditions at this time of year promote more intense fires (Gill *et al.* 1996). Fire intensity influences the amount of biomass consumed (Williams and Cook 2001), plant mortality (Williams J. R. 1995), and germination responses (Shea *et al.* 1979) and seasonal changes in intensity may result in fires in different seasons having very different effects (section 3.2.3.1). The effects of fire also depend on the condition of the vegetation at the time of burning (section 3.2.3.2). In tropical savannas, perennial grass plants become dormant at the end of the growing season, translocating resources to their roots. Consequently, individuals are likely to be more susceptible to burning at the start of the dry season, before they have fully senesced, than at the end of the dry season when loss of above ground dry matter is of little consequence. The timing of fire in relation to flowering and the location of seed can also be critical to the response of vegetation to fire (section 3.2.3.2). In addition, other seasonal factors may influence vegetation responses to burning. For example, differences in the timing of soil cover removal by fire may have significant consequences: by removing cover immediately prior to wet season rains, late dry season fires may result in greater soil erosion and nutrient loss than early dry season fires (section 3.2.3.1).

The aim of this study was to investigate the effects of season of burning on the herbaceous species composition of *C. ciliaris*-dominated grassland. Of particular interest was whether fire could be used to reduce the abundance of *C. ciliaris*. While *C. ciliaris* is a fire-adapted species, changes in fire regime may alter plant competitive interactions and the strategic use of fire has been suggested as a method for maintaining or restoring grasslands invaded by *C. ciliaris* (Daehler and Carino 1998). The effect of *C. ciliaris* on fire regimes is frequently highlighted in literature discussing it as an invasive species (e.g. Humphries *et al.* 1991; Low 1997). However less is known about fire regime effects on *C. ciliaris* dynamics. In a pastoral context, fire has not been seen as particularly useful for maintaining *C. ciliaris* pastures (McIvor and Gardener 1981; ’t Mannetje *et al.* 1983; Pressland and Graham 1989). In contrast, in literature discussing *C. ciliaris* as an invasive species, fire is believed to promote it (Lazarides *et al.* 1997; Butler and Fairfax 2003) (section 3.2.4). In this study, the effects of single fires and season of burning on *C. ciliaris* cover as well as herbaceous species composition were investigated in two *C. ciliaris*-dominated grasslands.

3.10.2. METHODS

3.10.2.1. Plant surveys

Plant species composition and abundance in experimental plots were assessed in April 1999 at Dalrymple and in April and June 1999 at Moorrinya, prior to implementing the burning treatments, and again at the end of the post-fire growing season, in June and July 2000 at Dalrymple and in August 2000 at Moorrinya (section 3.3). Each plot was searched for 10-15 minutes to identify the species present. In addition, 20 1 m^2 quadrats per plot were assessed in detail. The quadrats were located by throwing a 1 m by 1 m wire frame from five approximately equally spaced positions along each side of the plot. For each quadrat, the species present and their visually estimated percentage cover were recorded. Percentage cover was the percentage of the quadrat covered by a species. Consequently, where species overlapped, total cover could exceed 100%. Plants were identified to species level where possible and specimens were collected to assist with plant identification.

Total herbaceous species richness as well as species richness within plant groups (perennial grasses, annual grasses, sedges, legumes and other forbs (referred to as forbs) were calculated for each plot at the quadrat (1 m^2) and the plot (400 m^2) scale. Not all plants could be identified to species level. Therefore species richness includes some taxa identified only to genus level. Consequently, actual species richness is underestimated in the reported results. The abundance of individual species was assessed in terms of percentage cover and relative cover (percentage cover/total cover) as well as frequency of occurrence (proportion of 20 quadrats containing the species). Burning treatment effects on percentage cover were assessed for those species that contributed at least 1% to total cover, averaged over all plots. Burning treatment effects on the frequency of individual species was assessed for those species occurring in at least eight plots. The percentage cover and relative cover of plant groups were also calculated.

3.10.2.2. Statistical analyses

Burning treatment effects on herbaceous species richness and plant cover and frequency measures were investigated using analysis of covariance (ANCOVA) of the 2000 data using the 1999 data as a covariate where the covariate was effective. The covariate was considered effective if significant at the $P < 0.10$ level. Where the covariate was not significant, the 2000 data were analysed using one-way ANOVA. (Burning treatment effects were considered significant at the $P < 0.05$ level). Species frequency data were arcsin transformed prior to analysis and the reported results are back-transformed means. Relationships between fire intensity and plant cover and fire intensity and species richness were investigated using linear regression. Data from the two sites were analysed separately and all analyses were performed using Genstat (2001).

3.10.3. RESULTS

Burning increased species richness at the 1 m^2 scale at both sites. At Dalrymple, total species richness differed between treatments ($P < 0.05$) with greatest richness in the early burn treatment (5.7 ± 0.18 species/m^2), followed by the late burn treatment (4.3 ± 0.18 species/m^2) and the unburnt control (3.1 ± 0.18 species/m^2). Similar trends in species richness with burning treatments were found for the major plant groups (Figure 3.23). Perennial grass and legume species richness were higher in the early burn treatment compared with the unburnt treatment ($P < 0.05$) while a comparable trend was not statistically significant ($P > 0.05$) for forb species richness. At Moorrinya, mean total species richness in early and late dry season burn treatments (5.5 ± 0.25 and 5.3 ± 0.25 species/m^2 respectively) were greater than in the unburnt control (4.4 ± 0.25 species/m^2) ($P < 0.05$). Forb and annual grass species richness was also higher with burning at Moorrinya ($P < 0.05$) (Figure 3.23).

Species richness at the 400 m^2 scale appeared unaffected by burning treatments at both sites ($P > 0.05$). At Dalrymple, species richness ranged from 18-33 (mean of 25 ± 1.0) species/400 m^2. Overall 72 taxa were found at this site including three annual grasses, 17 perennial grasses, one sedge, 36 forbs and 15 legumes. At Moorrinya species richness ranged from 19-43 (mean of 36 ± 1.4) species/400 m^2. Overall 75 taxa were found including six annual grasses, 16 perennial grasses, two unidentified grasses, four sedges, thirty nine forbs and eight legumes. Lists of identified species for both sites are given in appendices 4A and 4B. No relationships between plot fire intensity and species richness at the 1 m^2 or 400 m^2 scales were detected ($P > 0.05$).

Burning reduced perennial grass cover and increased legume cover ($P < 0.05$) (Figures 3.24 and 3.25). At Dalrymple, the relative cover of perennial grasses was 97±1.6% with no burning and decreased to 88 ± 1.6% and 93±1.6 % in the early and late dry season burn treatments respectively ($P < 0.05$). At Moorrinya, the relative cover of perennial grasses was lower in the late dry season burn treatment (71 ± 2.4%) than in the unburnt treatment (85 ± 2.4%) ($P < 0.05$). Relative perennial grass cover in the early dry season burn treatment (78 ± 2.4%) was not significantly different from the other treatments ($P > 0.05$). At Moorrinya, legume cover was higher in the late dry season burn treatment compared with other treatments ($P < 0.05$) (Figure 3.25). Relative legume cover was also higher in the late burn treatment (9 ± 0.8 % relative cover) compared with the early burn and unburnt treatments (3 ± 0.8% and 5 ± 0.8% relative cover respectively) ($P < 0.05$). At Dalrymple burning treatment effects on legume cover were not significant ($P = 0.09$) (Figure 3.25). However, treatment

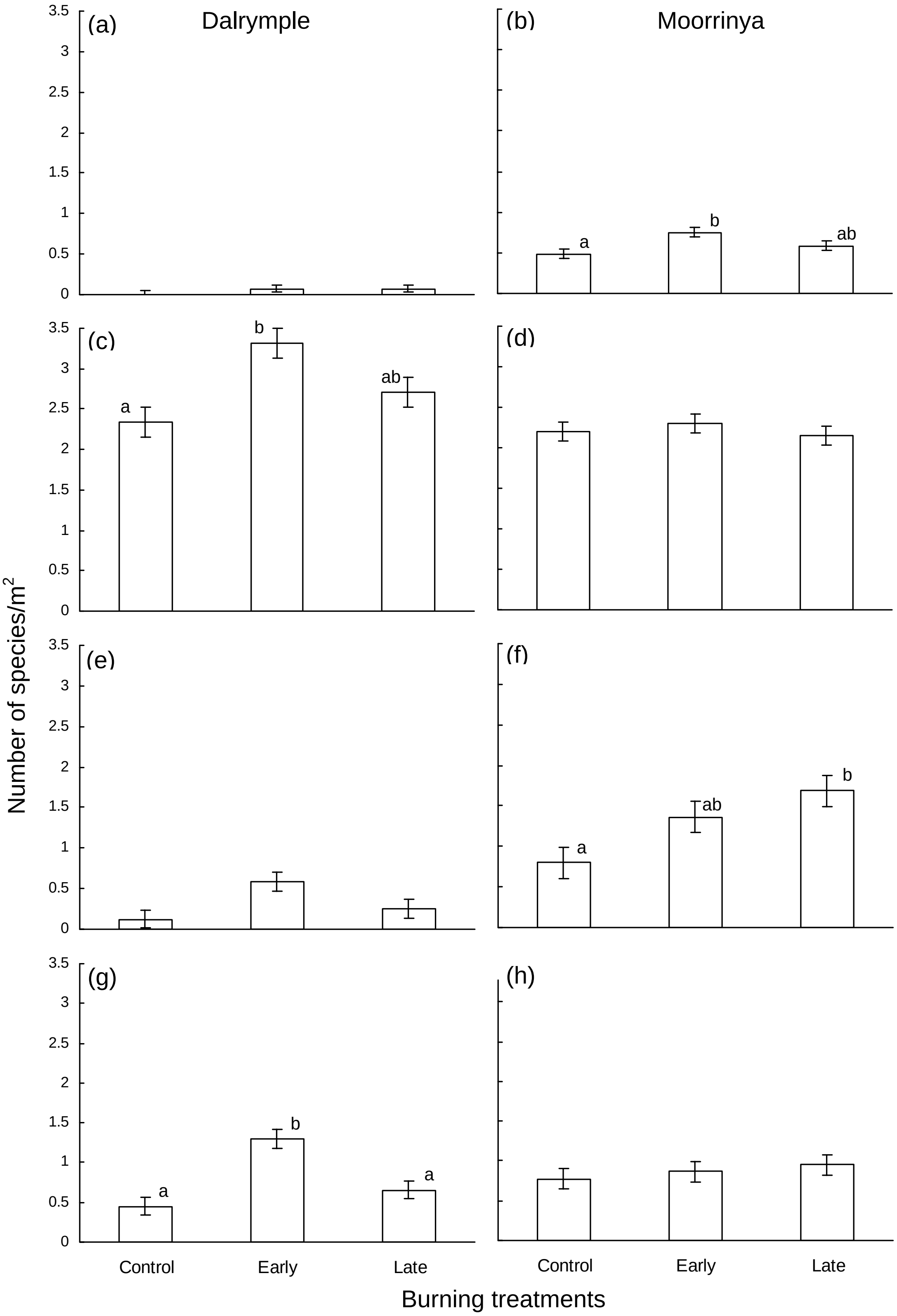

Figure 3.23. Mean (± SE) species richness (number of species/m^2) in control, early and late dry season burn treatments for (a,b) annual grasses, (c,d) perennial grasses, (e,f) non-leguminous forbs and (g,h) legumes at Dalrymple (1st column) and Moorrinya (2nd column). Different lower case letters denote significantly different means within graphs ($P < 0.05$).

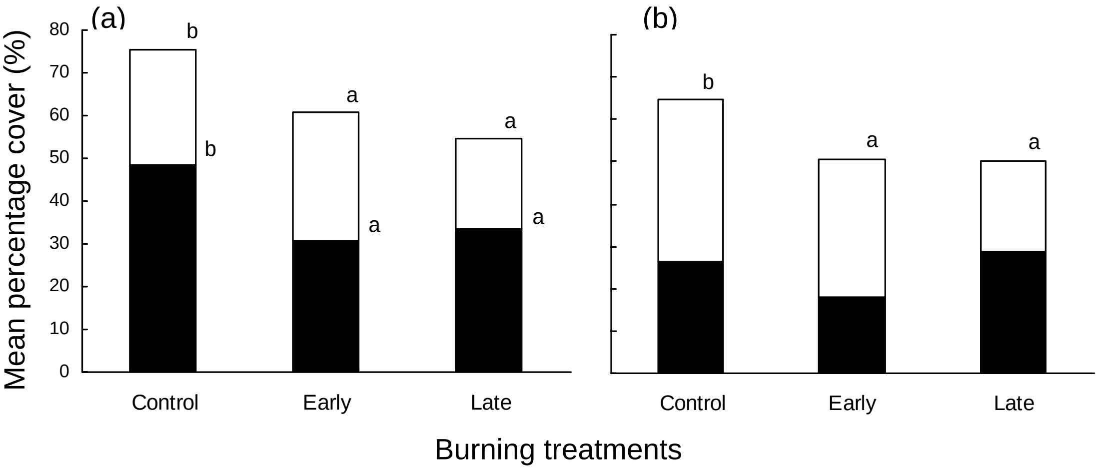

Figure 3.24. Mean *C. ciliaris* percentage cover (shaded portion) and total perennial grass percentage cover (bar) cover at (a) Dalrymple and (b) Moorrinya. Different lower case letters denote significantly different means within graphs ($P < 0.05$).

effects on relative legume cover were significant: relative legume cover was greater in the early dry season burn treatment (10 ± 1.6%) than in the unburnt and late dry season burn treatments (0.3 ± 1.6% and 4 ± 1.6% relative cover respectively) ($P < 0.05$). Annual grass, forb and sedge cover is also presented in Figure 3.25.

Perennial grass cover declined with increasing fire intensity. At Moorrinya, fire intensity explained 49% of the variation in cover ($P < 0.05$) (Figure 3.26). At Dalrymple, there was a significant linear relationship between perennial grass cover and fire intensity ($P < 0.05$, Adj $R^2 = 0.34$) when the high intensity plot was omitted from the analysis (Figure 3.26). No relationships between fire intensity and legume cover were found ($P < 0.05$).

Perennial grasses dominated plots in terms of cover at both sites. At the end of the 2000 growing season, perennial grasses contributed 93 ± 1.5% cover and legumes were next in abundance (5 ± 1.5% relative cover) while annual grasses, sedges and forbs each made up less than 2% of total cover at Dalrymple. This composition was similar to that found in 1999. At Moorrinya, overall plot composition differed between the two years. The perennial grass contribution to cover decreased from 92 ± 1.7% to 78 ± 2.4% while the annual grass contribution increased from 3 ± 1.4% to 10 ± 1.4%. Changes in the relative cover of other groups were less marked and in 2000 forbs contributed 6 ± 1.0%, legumes 5 ± 0.7% and sedges 1 ± 0.4% to total cover.

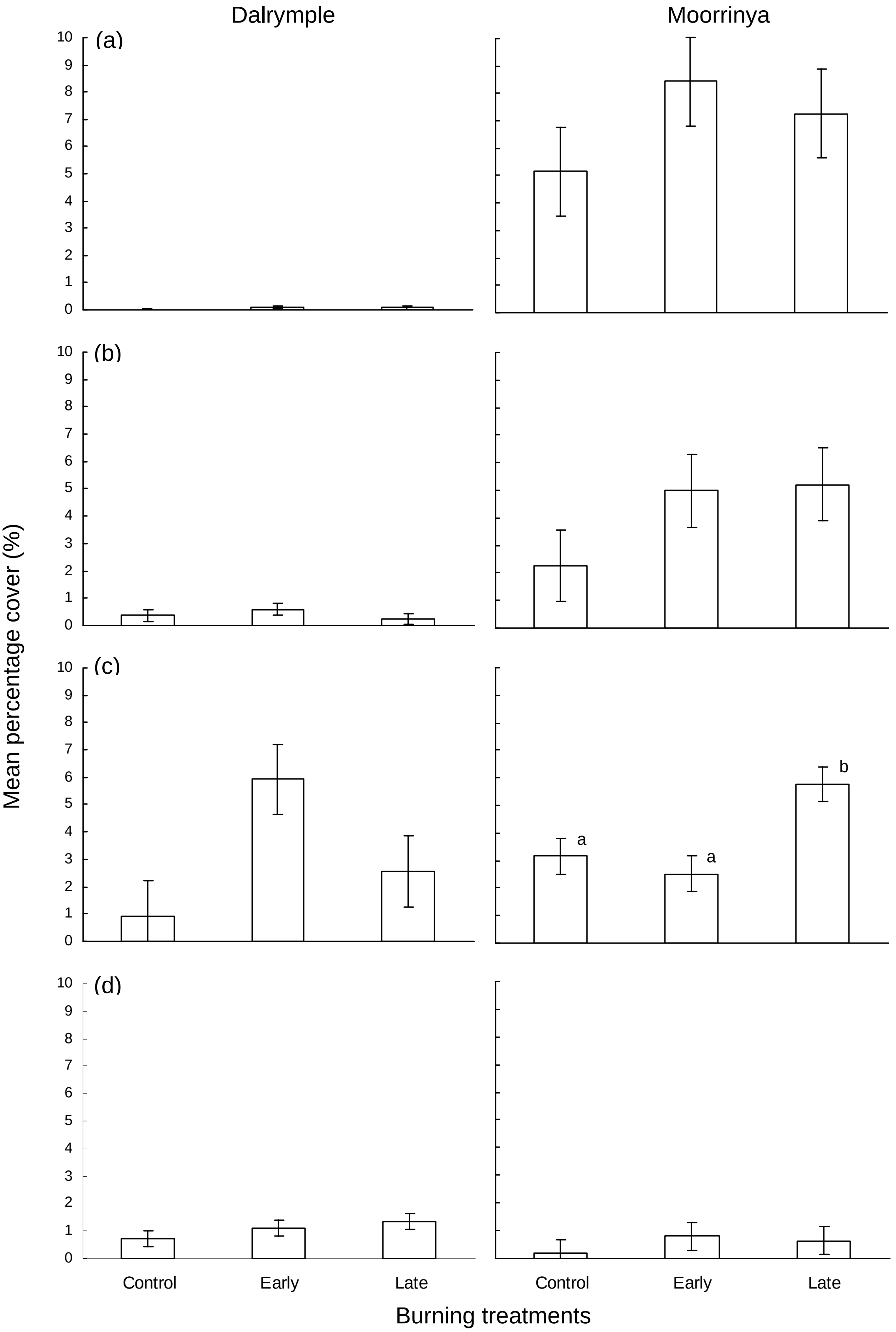

Figure 3.25. Mean (± SE) percentage cover of (a) annual grasses, (b) forbs, (c) legumes and (d) sedges at Dalrymple (1st column) and Moorrinya (2nd column). Different lower case letters denote significantly different means within graphs ($P < 0.05$).

On an individual species basis, only *C. ciliaris* cover was affected by burning. At Dalrymple, its cover was significantly lower in the burnt treatments compared with the unburnt control ($P < 0.05$) (Figure 3.24). Relative *C. ciliaris* cover was significantly lower in the early burn treatment (44 ± 2.8%) compared with the late burn and unburnt treatments (57 ± 2.8% and 66 ± 2.8% relative cover respectively) ($P < 0.05$). At Moorrinya, *C. ciliaris* cover tended to be lower in the early burn treatment compared with the late burn and unburnt treatments ($P = 0.05$) (Figure 3.24). Treatment effects on relative *C. ciliaris* cover were not detected at this site ($P > 0.05$). *Cenchrus ciliaris* cover declined with increasing fire intensity at Dalrymple ($P < 0.05$, Adj $R^2 = 0.41$) while no relationship between *C. ciliaris* cover and fire intensity was found at Moorrinya ($P > 0.05$). No burning treatment effects on the cover of other species investigated were detected ($P > 0.05$). These species included the exotic perennial grasses *Bothriochloa pertusa, Melinis repens* and *Urochloa mosambicensis,* native grasses *Bothriochloa ewartiana*, *Chrysopogon fallax, Heteropogon contortus* and *Enneapogon* spp., the legume *Indigofera colutea* and *Fimbristylis* spp. at Dalrymple and the perennial grasses *Astrebla squarrosa, Dichanthium sericeum, Dichanthium setosum, Enneapogon polyphyllus,* and the annual grasses *Iseilema* spp. at Moorrinya.

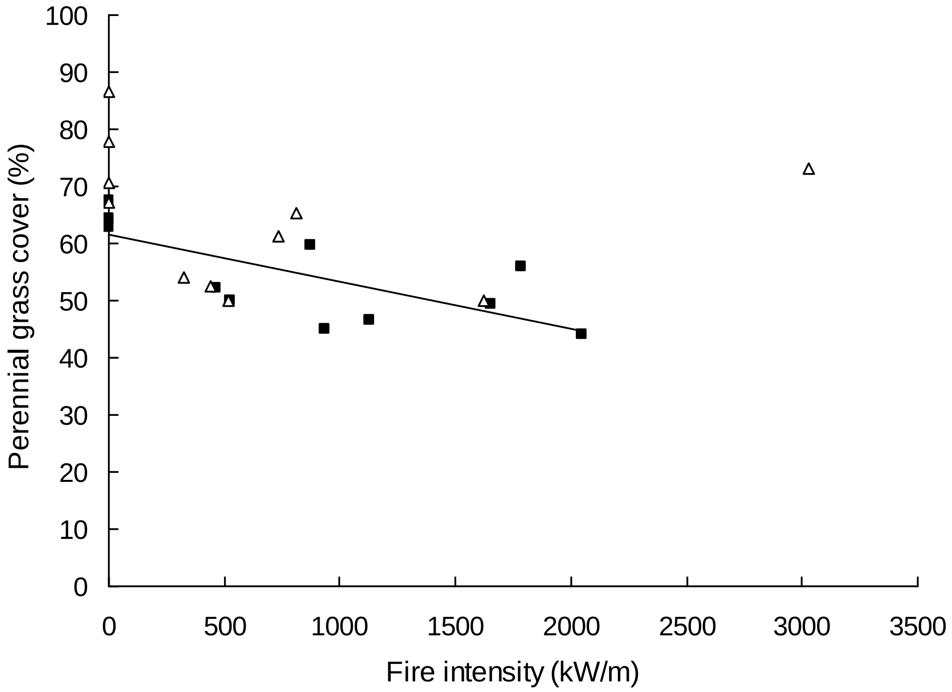

Figure 3.26. Relationship between fire intensity and perennial grass cover at (Δ) Dalrymple and (■) Moorrinya. The regression line (perennial grass cover = 61.51-0.00815*fire intensity) is shown for Moorrinya.

The frequencies of occurrence of most species investigated (13 species at Dalrymple and 14 species at Moorrinya) were unaffected by burning. However, at Dalrymple *Indigofera colutea* was more abundant in the early dry season burn treatment (61% of quadrats) compared with the late dry season burn and unburnt treatments (20 and 7 % of quadrats respectively) ($P < 0.05$). At Moorrinya, *Iseilema* spp. were also more abundant in the early dry season burn treatment, being found in 62% of quadrats compared with 41% and 40% of quadrats in the late dry season burn and unburnt treatments respectively ($P < 0.05$). A forb, *Abutilon malvifolium,* also occurred more frequently with burning at Moorrinya, being found in 22% and 12% of quadrats in early and late dry season burn treatments respectively compared with 2% of quadrats in the unburnt treatment ($P < 0.05$).

The species present at the two sites varied between growing seasons. At Dalrymple, 14 species were found in 1999 but not in 2000 and 12 species were found in 2000 but not in 1999. At Moorrinya, six species were found in 1999 but not in 2000 and 22 species were found in 2000 but not in 1999. Although more species were found at Moorrinya in the post-fire growing season, just under half of those found only in 2000 occurred in unburnt plots, and, at both sites, many species were found in less than three plots, preventing the investigation of any season of burning effects on their abundance.

3.10.4. DISCUSSION

Burning had minor effects on the composition of these *C. ciliaris*-dominated communities. Although there was a reduction in perennial grass cover and an increase in species richness at the 1 m^2 scale at both sites, there were no major changes in composition with burning. Other studies have also reported that fire results in little change to vegetation composition (Gill *et al.* 1990; Lunt 1990; Tolhurst 1996). Generally, fire regimes in Australian tropical savannas affect species abundance rather than cause significant changes in the species present (Bowman *et al.* 1988; Lonsdale and Braithwaite 1991; Williams *et al.* 2003b), although significant changes in structure with burning have been reported for tropical woodlands (Bowman *et al.* 1988; Gill *et al.* 1990). The abundance of four species was affected by burning. However, most species occurred too infrequently for fire effects on their abundance to be determined. Fire plays a critical role in structuring many plant communities (refer Tyler 1995), particularly where critical ecosystem processes such as seed germination are controlled by fire, as in heathlands and wet sclerophyll forests (Lunt and Morgan 2002).

In contrast, fire may be relatively unimportant in effecting vegetation change in communities where edaphic (Bowman 1988) or climatic factors (Williams *et al.* 2003b) have a large influence on vegetation dynamics. In these savanna communities, the primary determinants of composition and structure are variations in moisture and nutrients while fire and other disturbances are secondary determinants (refer Williams *et al.* 2002).

The season of burning has been found to affect grassland composition. For example, wet season fires resulted in significantly different forb species composition compared with dry season fires in sorghum-dominated savannas in northern Australia (Lane and Williams 1997). Early dry season fires promoted *Themeda triandra* while late dry season fires promoted *H. contortus* in *Themeda-Heteropogon* grasslands in central Queensland (Walker *et al.* 1983). Overall, season of burning had only minor effects on these *C. ciliaris*-dominated grasslands. In particular, legumes appeared to be responsive to season of burning. At Dalrymple, *I. colutea* cover and legume species richness were higher with early dry season burning while at Moorrinya, legume cover was higher with late dry season fires. These results probably reflect fire intensity effects (the mean intensity of late dry season fires was higher than that for early dry season fires at Moorrinya but the reverse occurred at Dalrymple), although direct relationships between fire intensity and legume cover or species richness were not detected. Legume germination is promoted by heat (Bond and van Wilgen 1996). Increases in legume emergence after fire have been reported (Williams *et al.* 2003b) and germination responses have been found to be positively associated with fire intensity (Shea *et al.* 1979). Legume abundance was found to be greater with early rather than late dry season fires in a coastal eucalypt savanna in north Queensland (Williams *et al.* 2003b), although no explanation for this was given. The annual grass *Iseilema* spp. was also affected by season of burning, increasing in frequency of occurrence in early dry season burnt plots at Moorrinya. Burning has been found to reduce *Iseilema* seedling emergence but increase seedling tillering (Scanlan and O'Rourke 1982). It is not clear whether the higher frequency of this species in early dry season burnt plots reflects greater seedling numbers or larger plant size or why the effect occurred with early but not late dry season burning. This result conflicts with the trend of lower *Iseilema* seedling emergence from burnt treatments in the seed bank study (section 3.7.3). However, the seed bank result is likely to be an artefact of seed bank determination procedures (section 3.7.4).

In addition to affecting community composition, fire may affect productivity. The reported effects of fire on biomass production vary and both increases and decreases in post-fire production have been reported (section 3.2.2.5). Post-fire production may be reduced, in part because fire kills weaker plants (Tothill 1971). However, in this study the reduced cover with burning is likely to be a reflection of post-fire growing conditions rather than a consequence of plant death as few plants were killed (section 3.4). It is not clear what limited growth at the two sites in my study. Post-fire biomass production is strongly dependent on seasonal rainfall (Orr *et al.* 1991). Unfortunately, detailed weather data are not available for the sites, although rainfall summaries for nearby locations indicate above average rainfall over the 1999-2000 growing season (section 3.3.4.3). At Dalrymple, *C. ciliaris* in the experimental area appeared ‘run down’ (see Pressland and Graham 1989) in that plants were smaller and not as green as plants in other areas nearby, possibly reflecting nutrient limitations to growth. At Moorrinya, moisture may have been limiting during parts of the growing season, despite the likelihood of above average wet season rainfall (section 3.3.4.3). Rainfall for a nearby site was above average but highly variable over time. An uneven distribution of rainfall over time can lessen rainfall effectiveness. An alternative or additional explanation for the reduced cover in burnt plots is that fire reduced the vigour of the surviving plants.

Post-fire productivity may be affected by the season of burning. Burning at the end of the dry season is considered the least injurious time since plants are dormant (West 1965) and in northern Australia the smallest reductions in biomass after burning have been found for end of dry season fires (Smith 1960). However, with the exception of legume cover, no differences in plant cover between early and late dry season burning were found in this study. Rather, reductions in perennial grass cover appeared to be related to fire intensity. Generally the higher the intensity, the lower the following season’s perennial grass cover, although a more even distribution of intensities is needed to clearly determine trends in plant cover in relation to fire intensity. High intensity fires are likely to kill more perennial plants and may reduce the growth of those remaining (Smith 1960). However, fire intensity-cover relationships may reflect fire effects on the cover produced before the fire rather than fire effects on plant growth. Since cover measured in the post-fire growing season includes cover produced in the previous season, the greater carry-over of cover in less intensely burnt plots may have contributed to their greater post-fire cover.

The issue of whether fire can be used to reduce *C. ciliaris* abundance was not resolved by this study. Although burning reduced *C. ciliaris* cover at Dalrymple, it had no such effect at Moorrinya. Importantly however, fire did not promote *C. ciliaris* cover. There is considerable conjecture in the invasive plant literature regarding fire and *C. ciliaris*. The results of this study do not support the positive fire loop model proposed (Butler and Fairfax 2003). This is not to say that fire never promotes *C. ciliaris* biomass. Rather, the results show that *C. ciliaris*-fire interactions are complex and other factors such as site productivity and rainfall may have significant effects. For example, patterns of production in burnt compared with unburnt *C. ciliaris* grassland is greatly influenced by rainfall (Hamilton and Scifres 1982).

The reduction in *C. ciliaris* cover at Dalrymple with burning appeared to be related to fire intensity. Although there is some evidence to suggest that higher intensity fires killed more *C. ciliaris* plants (section 3.4), it is not clear how much of this effect is due to removal or reduced vigour of burnt plants versus the reduction in carry-over cover from the previous season. It is not clear why *C. ciliaris* cover was unresponsive to burning at Moorrinya. Site productivity may affect the accumulation of biomass after fire (Lunt and Morgan 2002). The growth of plants at Dalrymple may have been compromised by nutrient limitations, making these plants here more susceptible to fire than plants at Moorrinya. However, while *C. ciliaris* grassland at Dalrymple appeared to be nutrient limited, results from the bioassay study (section 3.5) suggest that nutrient availability was higher at Dalrymple than at Moorrinya.

No burning treatment effects on the cover of the other perennial grasses in these communities were found. Seedling emergence and growth of some grasses such as *H. contortus* are known to be promoted by fire (Shaw 1957). Although no evidence of increased *H. contortus* abundance with burning was found, an increase in *H. contortus* seedlings may have been difficult to detect since the seedlings may not have been large enough to be identified and/or may have contributed little to cover. It is possible that changes in vegetation composition due to burning may become evident in later seasons if new individuals established after fire.

Although burning did not result in major compositional change in these grasslands, it did result in increased abundance of three species, in terms of frequency of occurrence, as well as an increase in species richness at the small scale (1 m^2). This contrasts with results from a trial in central Australia in which the germination of native species was suppressed in burnt *C. ciliaris*-dominated vegetation (Pitts and Albrecht 2000). Reduced perennial grass cover in burnt plots may have resulted in reduced competition for resources, providing an opportunity for the establishment and growth of other species. Temporary reductions in cover, rather than permanent removal, affect species richness. For example, in tallgrass prairie a surge in herbaceous species richness and frequency was attributed to the removal of shading by the dominant grasses, rather than plant death since numbers of dominant plants were not reduced (Copeland *et al.* 2002). In addition, burning may have directly promoted the germination of some species, for example legumes. Fire-enhanced pulses of forb abundance have also been reported (Williams *et al.* 2003b). Measured changes in species richness, percentage cover and frequency of occurrence may be due to changes in germination patterns and/or changes in individual plant size (larger plants have a greater chance of being included in a quadrat). However, the cause of greater abundance of individual species found here remains unclear since fire effects on germination versus plant growth were not differentiated in this study.

Species richness may be increased by fire if species already in the standing vegetation are not eliminated and the opening up of the stand and removal of litter allows for the recruitment of additional species (Daubenmire 1968). Gill (1975) reported that studies had generally found that species richness either declined or remained unchanged after fire in Australian communities. However, the effects of fire differ between communities and more recent work has reported increases in species richness with burning. In wet eucalypt forests (Bond and van Wilgen 1996), heathlands (refer Cheal 1996) and eucalypt savanna (Williams *et al.* 2003b) species richness has been found to increase after fire but decline over time. Fire has been reported to increase species richness in grasslands in Australia (Morgan 1999). It is also considered to have a strong effect on species richness in overseas grasslands with both increases (Walker and Peet 1983; DiTomaso *et al.* 1999) and decreases in richness being reported (refer Collins and Gibson 1990). The effects of fire on species richness may vary depending on the season of burning (Parsons and Stohlgren 1989; Copeland *et al.* 2002). In this study grass, forb and legume species richness were increased by burning. However, season of burning effects were only found for legume species richness at Dalrymple. While it is likely that this resulted from fire-promoted germination of legumes, it is also possible that greater legume richness reflects the greater reductions in relative *C. ciliaris* cover in the early dry season burn treatment relative to the other treatments.

Measures of species richness are strongly scale-dependent with richness in small plots (1 m^2) often poorly correlated with richness in larger plots within which they are nested (Bond and van Wilgen 1996). Burning increased species richness at the 1 m^2 scale but had no effect on species richness at the plot scale (400 m^2). Others have also reported differences in fire effects on species richness at different scales. Williams *et al.* (2003b) found that the species richness of eucalypt savanna in northern Queensland was unaffected by fire at the 100 m^2 scale but increased at the 1 m^2 scale. The increase in species richness at the small scale but not at the large scale suggests an increase in plant density and/or size rather than an increase in the number of species at the site. This appears to be the case at Dalrymple where fewer species were found after the fires than before. After the fires at Moorrinya, there was a 41% increase in the number of species found. However, only about half of these additional species occurred exclusively in burnt plots. Given that there was no effect on species richness at the plot scale, fire effects on species richness appear to be due more to increases in plant density and/or size than to the addition of new species at this site also.

The seasonality of fire can influence grassland species composition and biomass (Parsons and Stohlgren 1989). However, in these *C. ciliaris*-dominated communities the timing of fire had relatively minor effects on vegetation responses to burning. Season of burning may be a major influence on species composition in communities where there are significant differences in the phenology of plant groups (Howe 1994) since fire will alter the competitive abilities of plants by causing damage at different stages in their development (Copeland *et al.* 2002). However, species in these grasslands generally exhibit similar, strong seasonal growth patterns. Seed dormancy is broken by heat during the dry season (Mott and Andrew 1985a; McIvor and Gardener 1994) and most seed germination occurs at the start of the wet season (McIvor 1987). Above-ground vegetative growth also commences after the first significant rains of the wet season and perennial plants die back at the end of the wet season. In these communities, rainfall has an over-riding influence on vegetation dynamics. The accumulation of biomass after fire is dependent on post-fire moisture availability (Lunt and Morgan 2002). Post-fire rainfall also has a major effect on the recruitment success of newly emerged plants (Bond and van Wilgen 1996). Consequently, the amount and timing of rainfall events may be more significant than the timing of fire in controlling post-fire development (Morgan 1999).

Given that climate and nutrients, rather than fire, are the key determinants of vegetation composition and structure in these savannas (Williams *et al.* 2002) and that there are relatively minor differences in phenology between the key species, fire-induced changes in these grasslands will be more subtle than in some other communities. In addition, single fires are unlikely to cause significant changes in herbaceous community composition. Further studies are required to determine if *C. ciliaris* abundance can be decreased by manipulating the frequency of fire and its timing to exploit differences in *C. ciliaris* and native species phenology and/or other attributes.

3.11. GENERAL DISCUSSION: MANAGING *CENCHRUS CILIARIS* WITH FIRE

3.11.1. THE EFFECTS OF SEASON OF BURNING ON *CENCHRUS CILIARIS*-DOMINATED GRASSLAND

In perennial grasslands, one of the major constraints to vegetation change is the persistence of the established plants. Established plants greatly influence the survival and establishment of seedlings via competition for light (Copeland *et al.* 2002), water and nutrients (Cook 1980). Even where resources are made available by the mortality of an individual, they are often sequestered by the remaining plants (Lauenroth and Aguilera 1998). The removal of plant competition is a key factor in promoting seedling survival (Cheplick 1998; Cheplick and Quinn 1988) and is critical to altering the composition of *C. ciliaris*-dominated vegetation.

Fire is an important agent in structuring communities since, by removing perennial plant competition, it creates the potential for vegetation change (Bond and van Wilgen 1996). Effects of fire on ecosystem components and processes, such as seed banks and flowering, will be irrelevant in promoting change unless resources are made available to support the establishment of new individuals. Although the relatively low intensity fires reported here appeared to have only minor effects on these *C. ciliaris*-dominated communities, it was shown that fire could kill *C. ciliaris* plants and reduce its cover. Fires of higher intensity can be expected to have greater effects on *C. ciliaris* abundance and strategic use of fire may offer opportunities to disadvantage *C. ciliaris* and promote native species. However, the long-term responses of these communities to particular fire regimes are difficult to predict from current knowledge.

The studies reported in the previous sections were conducted to help evaluate fire as a tool to manipulate the composition of *C. ciliaris*-dominated vegetation. Overall, the fires had little impact on herbaceous species composition of these grasslands. Although short-term studies of single fires are unlikely to offer a definitive recommendation regarding the use of fire to manage invasive species, the results from these studies provide information that will aid the development of future work aimed at developing strategies for managing *C. ciliaris*. The management implications of the results of these studies and the use of fire as a tool for managing *C. ciliaris*-dominated vegetation are discussed below.

3.11.1.1. Effects of fire on establishment sites

The fires achieved in these studies probably had little effect on establishment sites. Few *C. ciliaris* plants were killed and nutrient levels appeared unaltered. Burning did reduce perennial grass cover. However, it is unclear how much of this reduction represents permanent effects on the growth of the existing plants. Temporary reductions in cover are unlikely to facilitate the establishment of new perennial plants. Importantly, I found that *C. ciliaris* is not always promoted by fire, in contrast to the general perception in the invasive plant literature (Low 1997; Franks *et al.* 2000; Butler and Fairfax 2003). The positive fire loop model used to describe *C. ciliaris*-fire interactions (Butler and Fairfax 2003) was not supported by the results of this study. Clearly, the *C. ciliaris* abundance-fire relationship is complex and a better understanding of the interactions of nutrient and moisture conditions on this relationship is needed.

Burning effects on establishment sites can be expected to be more significant with higher intensity fires since plant mortality is often greater (Williams J.R. 1995) and cover removal more complete (Williams and Cook 2001) with higher intensity fires. The estimated intensities achieved in my fires (330-3030 kWm^{-1}) were relatively low (section 2.3). Williams and Cook (2001) reported that early dry season fires in Kadadu National Park averaged about 2000 kWm^{-1} while late dry season fires averaged about 8000 kWm^{-1}. Grice (1997) reported an average intensity of about 7000 kWm^{-1} for August fires in shrub-invaded grassland near Townsville and Williams *et al.* (2003b) reported intensities of around 1500 kWm^{-1} for early dry season fires and 5500 kWm^{-1} for late dry season fires in coastal savanna near Townsville, northern Queensland.

Although there was some evidence that burning effects were related to fire intensity, I was unable to unequivocally demonstrate vegetation responses to fire intensity. The range of plot fire intensities achieved was relatively small and the uneven spread of intensities of Dalrymple plots prevented valid assessment of any relationships. It is also important to point out that the estimates, which are based on fuel loads and fire speeds, were approximate. An average site fuel load was used. However, biomass levels varied within the plots. Only one fire speed was recorded per plot, although fire speeds clearly changed across each plot. As pointed out by Gill and Knight (1991), moving fires present difficulties in measurement because they pulsate and surge. More important perhaps is the fact that fire intensity may or may not be related to the intensity of disturbance (Christensen 1985). That is, average plot fire intensities may not adequately describe the local fire conditions that are critical in affecting individual plants (section 3.2.3.1). Difficulties associated with measuring fire are well recognized and Lonsdale and Braithwaite (1991) noted that it was not possible to measure the most important variables at the precise time of ignition.

Although clear relationships between fire intensity and vegetation response were not found, it is likely that relatively high intensity fires will be needed to eliminate or reduce *C. ciliaris* competition. Fires producing higher temperatures are likely to result in higher plant mortality. Alexander and D'Antonio (2003) noted that the success of fire as a control treatment for any exotic species is likely to be strongly dependent on fire temperature. An important point demonstrated by my study is that season of burning may not be a good predictor of fire intensity. Although late dry season fires are generally more intense than early dry season fires (Williams *et al.* 1997), others have also noted that season of burning is not necessarily a good predictor of fire intensity, and, in some years relatively intense fires can occur in the early dry season (Williams J. R. 1995). Consequently, prevailing weather conditions, rather than time of year, may be more important in determining the magnitude of the fire effect in these grasslands. It is also important to appreciate that opportunities for achieving high intensity, high mortality fires may be relatively rare since the use of fire is limited by fuel availability (Hitchmough *et al.* 1994). The imposition of high intensity fires will be constrained by seasonal and grazing conditions with opportunities for effective fires being limited to good seasons when fuel levels are high.

It may be easier to achieve fatal temperatures in *C. ciliaris* patches than in patches of native species. The amount of biomass produced by individual species influences the fire intensities they experience. For example, it has been suggested that *Chrysopogon fallax* is relatively unaffected by fire because it grows in relatively small clumps and does not accumulate large quantities of litter around it, so that immediate heat loads are low (Smith 1960). Compared with native species, *C. ciliaris* may be more susceptible to medium intensity fires since it produces more biomass than native species (Humphries *et al.* 1991; Latz 1991), creating its own higher fuel loads. The thick litter accumulation observed in some *C. ciliaris* patches (section 3.6) would enhance fuel levels. However, *C. ciliaris* biomass is not always greater than that of native species (section 2.2).

The implications of high intensity fires on plant mortality in these systems remain to be investigated. In this study it was not possible to monitor the effects of fire on native species in any detail. Although the resident perennial grasses share a similar morphology and phenology and all have evolved with exposure to fire and survive burning (McIvor and Orr 1991), subtle differences can influence responses to fire. For example, the relatively exposed growing points of *Themeda triandra* and shallow roots of *Sarga* (*Sorghum) plumosum* are believed to make these species more vulnerable to fire than deep rooted species such as *C. fallax* (Smith 1960). In contrast to work by Pitt and Albrecht (2000), the increase in small-scale species richness found with burning (section 3.10) indicates that at least some native species respond positively to burning *C. ciliaris*-dominated vegetation. It is unclear how the resident perennial species in these grasslands will respond, relative to each other, to high intensity fires.

As well as removing established plants, fire may affect establishment site availability via effects on soil nutrients and surface cover. Although no changes in nutrient levels with burning were detected, more intense fires may affect nutrient availability. Changes in nutrient availability have the potential to alter competitive interactions (Howden 1988). *Cenchrus ciliaris* is favoured by moderate to high nutrient conditions (Humphries 1967; McIvor 1984) and post-fire flushes of nutrients may give it an advantage over less nutrient-demanding native species. Litter can also be very important in determining species composition (Lane and Williams 1997). My hypothesis that the thick litter mats that sometimes form in between *C. ciliaris* plants would inhibit seedling emergence was not supported. Matted litter was found to benefit *C. ciliaris* emergence (section 3.6.3). Overall, litter cover reduced *C. ciliaris* and *Heteropogon contortus* emergence compared with bare soil under 'controlled' conditions. However, in the field the effects of litter are likely to be more favourable for seedling emergence. It is not known how the extensive removal of litter by high intensity fires will affect the seedling recruitment patterns of key species.

3.11.1.2. Effects of fire on propagule supply

Burning appears to have little effect on propagule supply in these grasslands, although the low numbers of perennial grasses detected in the soil seed banks prevented any determination of fire effects on perennial grass seed bank composition (section 3.7). The low numbers of *C. ciliaris* and native perennial grass seed found in the seed banks suggest that these species may not be present to establish when sites become available (McIvor 1987; refer McIvor and Gardener 1994). This may present an opportunity to manipulate post-fire seedling recruitment. Sowing desirable native species may be effective in promoting species change since there may be little competition from naturally sown seedlings. However, the seed bank study results should be interpreted with caution. It is possible that the seed bank composition determined by the germination method (section 3.7.2) does not accurately reflect the actual composition and it was not possible to identify the different species of grass seedlings that emerged in the field (section 3.9). Longer-term studies are required to investigate seedling recruitment dynamics in these grasslands.

Some changes in relative abundance of species in seedling populations following fire may be explained in terms of variations in diaspore morphology (Peart 1984). Differences in diaspore morphology were expected to result in differences in abundance in the post-fire seed banks and seedling populations. The diaspore of *C. ciliaris* appears vulnerable to fire since it has no effective seed burial mechanism, remains on or close to the soil surface (Hacker 1989) and is readily destroyed or damaged by fire (Ernst 1991). In contrast, some native species such as *T. triandra* and *H. contortus,* have seeds with twisting hydroscopic awns that help bury them into the soil, thus protecting them from destruction by fire (Dyer *et al.* 1997). In my study, too few perennial grass plants emerged from the soil seed banks to determine any patterns relating to season of burning and I was unable to identify grass seedlings to species level in the field. The results from the litter study (section 3.6.) showed that *H. contortus* may be more vulnerable to fire than expected if seed falls on litter. However, the importance of diaspore type in relation to vulnerability to fire in these grasslands is unclear from this work.

Flowering patterns, rather than diaspore type, may be more important in influencing fire effects in these grasslands. *Cenchrus ciliaris* flowering did not appear to be promoted by burning, contrary to what was expected from other accounts (refer Humphries *et al.* 1991). Seed head production in *C. ciliaris* in central Australia is determined by rainfall (Bosch and Dudzinski 1984) and it is likely that rainfall, rather than fire, is the major influence on flowering in *C. ciliaris* in the communities studied here.

The timing of fire in relation to flowering can have significant effects on grassland composition (Howe 1994). The perennial grasses present in these *C. ciliaris*-dominated grasslands vary in the details of their flowering responses. For example, in its northerly range *Heteropogon contortus* flowering is controlled by day length and plants flower at the end of summer (Orr 1998). In contrast, flowering in *Astrebla* spp. can occur throughout the year and seed production is promoted by rainfall and fire (Scanlan 1980). *Cenchrus ciliaris* also produces flower heads throughout the year (Hacker 1989). By adding seed slowly over the season, the seed inputs of species such as *C. ciliaris* may be less affected by fire. Fires at specific times may significantly affect seed inputs of species such as *H. contortus* that produce all their seed at one time. A year's *H. contortus* seed may be drastically reduced by early dry season burning since the seed may still be held in seed heads or be on the soil surface (Walker *et al.* 1983). Further work is required to determine how season of burning affects the inputs of viable seed of *C. ciliaris* and native species in these grasslands.

3.11.2. FIRE AS A MANAGEMENT TOOL – ARE THERE OPPORTUNITIES TO REDUCE *CENCHRUS CILIARIS* ABUNDANCE?

Fire is an effective tool for managing both woody and herbaceous invasive species. In natural and semi-natural systems it is the cheapest tool available (Christensen and Burrows 1986) and has the advantage that it can be easily used over large areas (Grice *et al.* 2000). However, fire may be ineffective in some communities and may be inappropriate for certain species. It may be highly effective for manipulating vegetation composition in communities where there are significant differences in fire tolerance and/or phenology between plant groups (Howe 1994) or where fire plays a major role in ecosystem processes (Williams *et al.* 2002). Communities vary in these characteristics and, consequently, in their responsiveness to fire. In the *C. ciliaris*-dominated grasslands studied here, the effects of fire may be limited since differences in phenology and morphology between *C. ciliaris* and the native species are relatively subtle and climate, rather than fire, is a dominant force influencing vegetation dynamics (refer Williams *et al.* 2002). The value of fire as a management tool also depends on the invasive species involved. Recent literature on fire and exotic species suggests that fire generally tends to promote rather than discourage introduced species (D'Antonio 2000; Grice *et al.* 2000; Wilson and Mudita 2000)). Nevertheless, there is evidence that many species can be controlled by fire (D'Antonio 2000) and despite its limitations, it is a useful tool for decreasing the vigour of species that may otherwise dominate and exclude other species (Stuwe and Parsons 1977).

Fire may result in compositional changes where there are differences in plant condition (size and health), morphology and/or differences in life strategy. Although differences between *C. ciliaris* and associated native perennial grass species are relatively subtle compared with those found between co-occurring species in some other habitats, there are differences that can perhaps be exploited. Differences in phenology may provide opportunities to reduce *C. ciliaris* abundance using fire while having less effect on the native species. *Cenchrus ciliaris* is reported to remain green longer and cure later than native species (Cavaya 1988; Humphries *et al.* 1991). This may make it more susceptible to early dry season burns than native species that have senesced earlier. The higher *C. ciliaris* mortality with early dry season burns at Dalrymple may reflect this vulnerability (section 3.4.4). *Cenchrus ciliaris* is also noted for its ability to respond quickly to rainfall (Latz 1991). Therefore, opportunistic fires following out-of-season rainfall events when the native vegetation is dormant may also result in increased *C. ciliaris* mortality.

Although season of burning had only minor effects in this study, strategic timing of fire may be vital in manipulating *C. ciliaris* abundance. Dry season fires were investigated here. However, it has been noted elsewhere that burning in the dry season when grasses have seeded and become dormant generally does not affect the composition of perennial grasslands (Mott and Andrew 1985a). In contrast, wet season burning can result in changes in yield and composition (Smith 1960). The fast response of *C. ciliaris* to rainfall, noted above, may result in significant season of burning effects. Early wet season burning may kill *C. ciliaris* plants while slower responding native species may be unaffected. Burning after substantial rainfall in the dry season may also selectively kill *C. ciliaris*. However, the application of opportunistic burning requires considerable resources. Also, as was the case in this work, sites may not be accessible at times during the wet season.

The apparent lack of *C. ciliaris* and perennial grass seed in the soil seed banks presents opportunities to manipulate post-fire recruitment. Since so little perennial grass seed appears available for establishment in fire-created micro-sites, sowing of native perennial seed may be an effective means of shifting vegetation composition. Apart from low numbers of *C. ciliaris* seedlings, due to low seed availability, it also appears that *C. ciliaris* seedlings may be competitively inferior to some native species. Although it is considered a highly competitive species, the slower emergence of *C. ciliaris* seedlings compared with *H. contortus* seedlings observed in the litter cover study (section 3.6) suggests that *C. ciliaris* may be at a competitive disadvantage at the seedling stage. The order of arrival of species can be important in determining which species dominate particular sites (refer D’Antonio *et al.* 2001). Seedlings that germinate first may gain a competitive advantage (section 3.9.4) and the faster emergence of *H. contortus* may give it a head start in sequestering resources, enabling it to out-compete *C. ciliaris* for the occupancy of new sites. Seedling interactions in these grasslands are of considerable interest and I am unaware of any studies investigating competitive interactions between *C. ciliaris* and native seedlings.

Determining the effects of fire on these systems is problematic and the work reported here does not allow a comprehensive assessment of the efficacy of fire as a tool for manipulating *C. ciliaris*-dominated grasslands. The studies were limited by a number of constraints not uncommon to ecological studies. Low levels of replication limit the statistical power to detect treatment effects in these innately variable systems. The time frame of experimentation and monitoring was short and access to field sites was hindered by weather and lack of resources. Added to these logistic constraints is the complexity of the systems being studied. The dynamics of savanna systems, where vegetation change is contingent upon interactions between fire, weather conditions, soil conditions, competition, herbivores and other disturbances are notoriously complex (Walker *et al.* 1981; refer Bond and van

Wilgen 1996). No two fires or the conditions in which they occur are alike and both pre- and post-fire conditions are unique and tend to produce differences in results (Vogl 1974; D'Antonio 2000). Noble and Grice (2002) noted that, due to the unpredictability of rainfall, there was rarely any ordered succession in plant communities following fire in semi arid and tropical grasslands. In addition, the effects of fire may be less important in these grasslands than in other ecosystems where critical ecosystem processes such as seed germination are controlled by fire (Lunt and Morgan 2002). Consequently, fire-induced changes may be more subtle than in other communities. The dynamics of these *C. ciliaris*-dominated communities are chiefly climate driven. Responses to burning are largely determined by pre- and post-fire weather conditions making both predictions (Walker *et al.* 1981) and interpretation (Norman 1969) of experimental results difficult.

3.11.3. CONCLUSIONS

There is an urgent need for management strategies that reduce, prevent or contain invasive plant invasions (Adair and Groves 1998; Wilson and Mudita 2000). While there is a large literature on biological invasions and invasion processes, there appears to be less published information specifically relating to the control of environmental weeds (Barrow 1995). In the case of *C. ciliaris*, there is a vast literature dealing with this species in an agricultural context as a desirable pasture species. More recently, the negative effects of *C. ciliaris* have been highlighted. However, there is little published information specifically relating to the management of *C. ciliaris* in situations where it is not wanted (see Pitts and Albrecht 2000).

Fire plays a critical role in structuring many plant communities (refer Tyler 1995) and is widely used for managing ecosystems worldwide (Bond and van Wilgen 1996). However, its usefulness in managing invasive grasses is limited. Fire may promote invasive grasses (Friday *et al.* 1999; Rossiter *et al.* 2003) and where fire has been found to reduce exotic grass abundance, increases in non-target exotics may occur (Parsons and Stohlgren 1989). Consequently, the use of fire for invasive plant control requires caution and plant and fire factors must be critically evaluated (D'Antonio 2000).

At the beginning of this chapter I asked if fire could be used to reduce the abundance of *C. ciliaris* and promote the recruitment of native species? The removal of established *C. ciliaris* plants is key to promoting change in these grasslands and fire may be useful in promoting compositional change if it removes plants and reduces *C. ciliaris* competition. In this study, *C. ciliaris* abundance was unaffected or reduced by fire, at least temporarily, and burning resulted in increased abundance of some native species. The intensity of fire is likely to be a major factor determining its effectiveness in removing *C. ciliaris*. However, the timing of fire may also be important. Relatively subtle differences in growth and phenology between *C. ciliaris* and the native species in these grasslands may be opportunistically exploited to disadvantage *C. ciliaris*. However opportunities to achieve effective fires will be limited by fuel availability and fires alone are unlikely to result in significant shifts in composition.

Fire is a secondary determinant of vegetation composition in these systems and its effects are greatly modified by climatic conditions. However, since there are few cost-effective management options available for managing vegetation at large scales (Noble and Grice 2002) it is necessary to explore any possibilities that fire may offer. The fires reported here had no major effects on the composition of *C. ciliaris*-dominated grassland. It is important to distinguish between shorter-term changes occurring after a single fire event and the longer-term effects resulting from a particular fire regime (Raison 1979). As pointed out by Lunt and Morgan (2002), short-term impacts of single fires provide little insight into the effects of consecutive fires. Longer-term studies are required to more fully understand fire-vegetation-climate interactions in these grasslands. The effects of high intensity fires on these grasslands also need to be determined if strategies for containing or reducing the spread of *C. ciliaris* are to be developed.

CHAPTER 4. *CENCHRUS CILIARIS* AS AN INVASIVE SPECIES – FUTURE RESEARCH QUESTIONS

Cenchrus ciliaris is perhaps one of Australia's most controversial imports. From a pastoral point of view, this now extensively distributed grass is highly valued for its perseverance and productivity under harsh conditions (Paull and Lee 1978). The success of *C. ciliaris* as a pasture species in Australia's arid and semi-arid zones is due to traits such as its ease of establishment, rapid growth, adaptation to a range of soils and its tolerance of drought and grazing (Franks 2002). However, these traits have led to its spread into non-target areas with reported negative impacts on native species and fire regimes (Humphries *et al.* 1991; Low 1997). From a conservation/sustainable land management point of view, *C. ciliaris* is considered to be one of Australia's worst environmental weeds (Humphries *et al.* 1991; State of the Environment 1996).

Despite these conflicting perceptions, there are relatively few published data quantifying the environmental effects of *C. ciliaris*. Studies investigating this species in an environmental conservation context have been conducted in central Australia, where this species is considered to be a major threat (Pitts and Albrecht 2000; Best 1998), and in central Queensland (Fairfax and Fensham 2000; Franks 2002; Butler and Fairfax 2003). The study reported here is, to my knowledge, the first specifically investigating *C. ciliaris* from an environmental perspective in north Queensland. I addressed two issues: (1) the impacts of *C. ciliaris* on herbaceous species richness and (2) the use of fire to manage *C. ciliaris*.

Quantitative data describing the effects of *C. ciliaris* on biodiversity are critical to achieving rational debate about the values and risks associated with this species. My study and others (Fairfax and Fensham 2000; Franks 2002) provide correlative data showing that *C. ciliaris* is associated with reduced herbaceous species richness. However, these studies fall short of demonstrating a cause and effect relationship. It is difficult to determine the role of invasive plants in reducing biodiversity since plant invasion often occurs simultaneously with other disturbances (Vitousek 1990). Species richness is influenced by factors such as drought and grazing, the impacts of which are confounded with those of the invading species. Consequently, obtaining evidence of a causal relationship between *C. ciliaris* and species richness is a considerable challenge. In the Hillgrove study (section 2.2), I was able to demonstrate a relationship between *C. ciliaris* biomass and herbaceous species richness. However, the cause of this association was not determined. Manipulative studies are required to identify the mechanisms underlying *C. ciliaris*-species richness relationships. *Cenchrus ciliaris* is considered to be a successful competitor (McIvor 2003) and it is also suggested that it has allelopathic effects (Cheam 1984ab; Nurdin and Fulbright 1990). These traits need to be investigated to help understand *C. ciliaris*-biodiversity relationships.

Both spatial and temporal scales have important implications for *C. ciliaris*-biodiversity relationships. Although *C. ciliaris* has been associated with reduced herbaceous species richness at small scales, it is not clear how dominance over large areas affects the survival of native species. Relationships between *C. ciliaris* and native species may also change over time as *C. ciliaris* invasion alters ecosystem processes, such as fire regimes, and changes in ecosystem processes affect *C. ciliaris* dominance. Studies investigating individual species abundance patterns in relation to *C. ciliaris* abundance are needed to determine whether native species can persist in *C. ciliaris*-dominated communities, or whether *C. ciliaris* invasion leads to loss of species over time.

There is an urgent need for effective control strategies for *C. ciliaris* that have minimal negative environmental impacts (Pitts and Albrecht 2000). Fire is one of the few tools available for managing vegetation on an extensive scale, and, despite its limitations (D'Antonio 2000), manipulation of the fire regime has been suggested as a method to maintain or restore *C. ciliaris*-invaded grasslands overseas (Daehler and Carino 1998). In Australia, some workers have discounted fire as a useful, long-term solution to *C. ciliaris* invasion since they found that *C. ciliaris* recovered rapidly and completely after fire (Pitts and Albrecht 2000). However, the results from my short-term fire study demonstrate that *C. ciliaris*-fire interactions are more complex than is suggested from the positive fire loop model proposed (Butler and Fairfax 2003). I found that fire killed *C. ciliaris* plants and reduced its cover and that this was associated with an increase in native species abundance. Post-fire growing conditions, particularly rainfall, influence vegetation responses to burning and responses will differ across sites, depending on factors such as soil nutrient status, soil seed bank composition and grazing regime. The fires in this study were generally patchy and of low intensity. Of interest is how these grasslands respond to more extensive, higher intensity fires and the implications of site conditions on these responses.

Although season of burning had relatively minor effects on these grasslands, the timing of fire can be critical in determining outcomes (Daubemire 1968). More intense fires are likely to be more effective in reducing *C. ciliaris* biomass. However, as shown here, weather conditions, rather than season, may be more important for determining fire intensity in these systems. Studies are also required to investigate the effects of wet season fires. Burning at the start of the wet season or after rainfall in the dry season may selectively kill *C. ciliaris*, given its fast initiation of growth following rainfall.

Manipulation of the fire regime may offer opportunities to disadvantage *C. ciliaris* relative to native species. However, it is unlikely that fire alone will result in significant shifts in composition. Additional strategies are required. The slow emergence of *C. ciliaris* seedlings compared with *H. contortus* seedlings observed in the litter study (section 3.6), together with the probability of relatively low numbers of perennial grass seed in the seed banks of these communities (section 3.7), suggests that over-sowing with native species may be beneficial.

In summary, a number of research questions have been raised in this thesis. Future studies are required to:

- identify the mechanism (s) responsible for negative associations between *C. ciliaris* and herbaceous species richness;
- determine the impacts of *C. ciliaris* invasion on the survival of native species;
- further investigate season of burning effects to determine strategies for reducing *C. ciliaris* abundance (can physiological differences be exploited?);
- determine the impacts of high intensity fires in these communities (how do native species respond to high intensity fires? What are the implications for nutrient/soil stability?);
- develop a better understanding of plant community-fire-moisture regime (rainfall) interactions, particularly in relation to the effects of burning on perennial grass seed inputs and recruitment patterns; and
- investigate the competitive ability of *C. ciliaris* seedlings. Is over-sowing with native species an option?

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APPENDICES

Appendix 1A. Herbaceous species found in *C. ciliaris* and non-*C. ciliaris* plots in the Dalrymple Shire survey. Species classified as rare, that is found in only one plot in the survey, are denoted by *.

FORBS	**Status**
Acanthospermum hispidum DC.	exotic *
Achyranthes aspera L.	exotic *
Alternanthera sp.	unknown
Blumea sp.	unknown
Boerhavia schomburgkiana Oliv.	native
Brunoniella acaulis (R.Br.) Bremek.	native
Camptacra barbata N.T.Burb.	native
Chamaesyce hirta (L.) Millsp.	exotic
Chamaesyce mitchelliana (Boiss.) D.C.Hassall	native
Chenopodium carinatum R.Br.	native *
Commelina cyanea R.Br.	native *
Corchorus sp.	native
Cucumus sp.	native
Drosera sp.	native *
Epaltes australis Less.	native *
Evolvulus alsinoides L.	native
Goodenia glabra R.Br.	native
Goodenia sp.	native
Grewia retusifolia Kurz	native
Heliotropium pauciflorum R.Br.	native
Hibiscus sp.	native *
Hybanthus enneaspermus (L.) F.Muell.	native
Ipomoea coptica (L.) Roth ex Roem. & Schult.	native
Ipomoea eriocarpa R.Br.	native
Ipomoea polymorpha Roem. & Schult.	native
Marsdenia viridiflora R.Br.	native
Melhania oblongifolia F.Muell.	native
Mitrasacme pygmaea R.Br.	native *
Ocimum sp.	unknown
Oldenlandia mitrasacmoides (F.Muell.) F.Muell.	exotic
Peripleura hispidula (F.Muell. ex A.Gray) G.L.Nesom	native *
Phyllanthus virgatus G.Forst.	native
Polycarpaea corymbosa (L.) Lam.	native *
Polygala linariifolia Willd.	native
Polymeria calycina R.Br.	native
Portulaca oleracea L.	native
Pterocaulon redolens (Willd.) Fern.-Vill.	native *
Rostellularia adscendens (R.Br.) R.M.Barker	native
Sida fibulifera Lindl.	native
Sida subspicata F.Muell. ex Benth.	native
Sida trichopoda F.Muell.	native
Solanum sp.	unknown
Spermacoce brachystema R.Br. ex Benth.	native
Thysanotus sp.	native *

Trianthema triquetra Rottb. Ex Willd.	native *
Wahlenbergia sp.	native *
Waltheria indica L.	native

LEGUMES

Alysicarpus sp.	unknown *
Cajanus scarabeoides (L.) Thouars	native
Chamaecrista absus (L.) H.S.Irwin & Barneby var. absus	native
Crotalaria medicaginea Lam.	native
Crotalaria montana Roth	native
Crotalaria verrucosa L.	native *
Desmodium sp.	native
Galactia tenuiflora (Spreng.) Willd. ex Wight & Arn.	native
Glycine tomentella Hayata	native *
Indigastrum parviflorum (B.Heyne ex Wight & Arn.) Schrire	native *
Indigofera colutea (Burm.f.) Merr.	native
Indigofera haplophylla F. Muell.	native *
Indigofera linifolia (L.f.) Retz.	native
Indigofera linnaei Ali	native
Macroptilium atropurpureum (DC.) Urb.	exotic *
Neptunia sp.	native
Rhynchosia minima (L.) DC.	native
Stylosanthes hamata (L.) Taub.	exotic
Stylosanthes humilis Kunth	exotic
Stylosanthes scabra Vogel	exotic
Tephrosia filipes Benth.	native
Tephrosia leptoclada Benth.	native
Tephrosia rosea F.Muell. ex Benth.	native
Vigna lanceolata Benth.	native
Zornia muellerana Mohlenbr.	native
Zornia muriculata Mohlenbr.	native

PERENNIAL GRASSES

Alloteropsis cimicina (Retz.) Stapf	native
Aristida benthamii Henrard	native
Aristida calycina R.Br.	native
Aristida holathera Domin	native
Aristida ingrate Domin	native
Aristida jerichoensis (Domin) Henrard	native
Aristida perniciosa Domin	native
Bothriochloa decipiens (Hack.) C.E.Hubb.	native *
Bothriochloa ewartiana (Domin) C.E.Hubb.	native
Bothriochloa pertusa (L.) A.Camus	exotic
Cenchrus ciliaris L.	exotic
Chloris pectinata Benth.	native
Chloris virgata Sw.	native
Chrysopogon fallax S.T.Blake	native
Dichanthium sericeum (R.Br.) A.Camus	native
Digitaria ammophila (F.Muell.) Hughes	native
Enneapogon polyphyllus (Domin) N.T.Burb.	native
Eriachne sp.	native
Eriochloa sp.	native
Heteropogon contortus (L.) P.Beauv. ex Roem. & Schult.	native
Melinis repens (Willd.) Zizka	exotic

Panicum effusum R.Br.	native
Paspalidium sp.	native *
Sehima nervosum (Rottler) Stapf	native *
Sarga (Sorghum) plumosum (R.Br.) P.Beauv.	native
Themeda triandra Forssk.	native
Tripogon loliiformis (F.Muell.) C.E.Hubb.	native
Urochloa mosambicensis (Hack.) Dandy	exotic

ANNUAL GRASSES

Brachiaria windersii C.E.Hubb.	native *
Brachyachne convergens (F.Muell.) Stapf	native
Dactyloctenium radulans (R.Br.) P.Beauv.	native
Digitaria ciliaris (Retz.) Koeler	exotic
Echinochloa sp.	unknown
Eragrostis brownii (Kunth) Nees ex Steud.	native
Iseilema sp.	native *
Mnesithea formosa (R.Br.) de Koning & Sosef	native
Perotis rara R.Br.	native *
Schizachyrium fragile (R.Br.) A.Camus	native
Sporobolus australasicus Domin	native
Thaumastochloa pubescens (Benth.) C.E.Hubb.	native *
Tragus australianus S.T.Blake	native

SEDGES

Cyperus bifax C.B.Clarke	native
Cyperus gilesii Benth.	native
Fimbristylis sp.	native
Scleria sp.	native *

Appendix 1B. Herbaceous species found in surveyed plots at Hillgrove.

FORBS
Acanthospermum hispidum DC.
Alternanthera sp.
Boerhavia schomburgkiana Oliv.
Camptacra barbata N.T.Burb.
Chamaesyce mitchelliana Boiss D.C.Hassall
Corchorus trilocularis L.
Euphorbia hirta L.
Evolvulus alsinoides L.
Grewia retusifolia Kurz
Hybanthus enneaspermus (L.) F.Muell.
Ipomoea eriocarpa R.Br.
Ipomoea gracilis R.Br.
Jacquemontia paniculata
Marsdenia viridiflora R.Br.
Melhania oblongifolia F.Muell.
Oxalis corniculata L.
Phyllanthus maderspatensis L.
Polymeria sp.
Portulaca filifolia F.Muell.
Pterocaulon redolens (Willd.) Fern.-Vill.
Rostellularia adscendens R.M.Barker
Sida acuta/rohlenae
Sida fibulifera Lindl.
Sida spinosa L.

LEGUMES
Chamaecrista absus (L.) H.S.Irwin & Barneby
Crotalaria goreensis Guill. & Perr.
Crotalaria juncea L.
Crotalaria medicaginea Lam.
Crotalaria montana Roth
Crotalaria verrucosa L.
Desmodium sp.
Galactia Muelleri Benth.
Glycine tabacina (Labill.) Benth.
Glycine tomentella Hayata
Indigofera colutea (Burm.f) Merr.
Indigofera hirsuta L.
Indigofera linifolia (L.f.) Retz.
Indigofera linnaei Ali
Rhynchosia minima (L.) DC.
Stylosanthes hamata (L.) Taub.
Stylosanthes scabra Vogel
Vigna lanceolata Benth.
Zornia dyctiocarpa DC.
Zornia muriculata Mohlenbr.

ANNUAL GRASSES
Brachyachne convergens (F.Muell.) Stapf
Digitaria ciliaris (Retz.) Koeler
Eragrostis sororia Domin

PERENNIAL GRASSES
Aristida calycina R.Br.
Aristida holathera Domin
Aristida leptopoda Benth.
Bothriochloa decipiens (Hack.) C.E.Hubb.
Bothriochloa ewartiana (Domin) C.E.Hubb.
Bothriochloa pertusa (L.) A.Camus
Cenchrus ciliaris L.
Chrysopogon fallax S.T.Blake
Dichanthium fecundum S.T.Blake
Dichanthium sericeum (R.Br.) A.Camus
Enneapogon polyphyllus (Domin) N.T.Burb.
Eriochloa procera (Retz.) C.E.Hubb.
Heteropogon contortus (L.)
Melinis repens (Willd.) Zizka
Panicum decompositum R.Br.
Tripogon loliiformis (F.Muell.) C.E.Hubb.
Urochloa mosambicensis (Hack.) Dandy

SEDGES
Cyperus sp.

Appendix 2A. Aussie peat components.

Aussie peat is an organic product made from boiling and milling pine bark and wood chip, producing a product with texture identical to peat moss.

Chemical analyses:

Air filled porosity (%)	12
Water holding capacity (%)	72
pH approx	6.4
Conductivity (dS/m)	0.11

Appendix 2B. Germinable seed content of *Cenchrus ciliaris* and *Heteropogon contortus* seed material.

To determine the amount of germinable seed in *C. ciliaris* and *H. contortus* seed material, four samples of the diaspores of both species were weighed (0.34 g mean weight) and the seeds from each sample were then separated from their appendages. Germination tests were conducted using all the seed from each *H. contortus* sample (mean of 55 seeds/sample). For each *C. ciliaris* sample, only 50 seeds/sample were used because of the high numbers of seed found in each sample (mean of 117 seeds/sample). Germination was determined for each sample by placing the seed on filter paper in covered petri dishes, one dish per sample. Seed was kept moist and germination was monitored in ambient laboratory conditions over nine days. The average germinability of seed was 10% and 19% for *H. contortus* and *C ciliaris* respectively.

Appendix 3A. Herbaceous species found in the Dalrymple seed banks**.**

FORBS

Abutilon calliphyllum Domin
Amaranthus cochleitepalus Domin
Ammania multiflora Roxb.
Blumea saxitilis Zoll. & Moritzi
Corchorus tridens L.
Dysphania glomulifera (Nees) Paul G.Wilson
Epaltes australis Less.
Glinus oppositifolius (L.) A.DC.*
Heliotropium ovalifolium Forssk.
Hybanthus enneaspermus (L.) F.Muell.*
Ipomoea polymorpha Roem. & Schult.
Melhania oblongifolia F.Muell.*
Mitrasacme pygmaea R.Br.
Ocimum sp.
Oldenlandia coerulescens (F.Muell.) F.Muell.
Phyllanthus sp.
Portulaca filifolia F.Muell.
Portulaca oleracea L.
Pterocaulon redolens (Willd.) Fern.-Vill.
Salsola kali L.
Scoparia dulcis L.
Sida spinosa L.
Tribulus sp.
Wahlenbergia caryophylloides P.J.Sm.

LEGUMES

Chamaecrista absus (L.) H.S.Irwin & Barneby*
Indigofera colutea (Burm.f.) Merr.*
Zornia muellerana Mohlenbr.

ANNUAL GRASSES

Dactyloctenium radulans (R.Br.) P.Beauv.*
Perotis rara R.Br.*
Tragus australianus S.T.Blake

PERENNIAL GRASSES

Bothriochloa pertusa (L.) A.Camus*
Brachiaria subquadripara (Trin.) Hitchc.
Cenchrus ciliaris L.*
Enneapogon polyphyllus (Domin) N.T.Burb.
Eragrostis brownii (Kunth) Nees ex Steud.
Eragrostis tenellula (Kunth) Steud.
Heteropogon contortus (L.) P.Beauv. ex Roem. & Schlt.*
Melinis repens (Willd.) Zizka*
Sporobolus australasicus Domin

SEDGES

Bulbostylus barbata (Rottb.) C.B.Clarke
Cyperus difformis L.
Cyperus squarrosus L.
Fimbristylis bisumbellata (Forssk.) Bubani

* indicates species also found (and identified to species level) in the standing vegetation.

Appendix 3B. Herbaceous species found in the Moorrinya seed banks.

FORBS
Abutilon malvifolium (Benth.) J.M.Black*
Alternanthera nodiflora R.Br.
Ammania multiflora Roxb.
Bergia trimera Fisch. & C.A.Mey.
Blumea diffusa R.Br. ex Benth.*
Centipeda minima (L.) A.Braun & Asch.
Chamaesyce hirta (Kunth) Steud.
Dysphania glomulifera (Nees) Paul G.Wilson
Epaltes australis Less.
Ipomoea lonchophylla J.M.Black
Murdannia graminea (R.Br.) G.Brueckn.
Oldenlandia coerulescens (F.Muell.) F.Muell.
Oldenlandia mitrasacmoides (F.Muell.) F.Muell.
Phyllanthus sp.
Portulaca oleracea L.
Sclerolaena ramulosa (C.T.White) A.J.Scott
Sclerolaena bicornis Lindl.*
Sida fibulifera Lindl.*
Sida spinosa L.
Streptoglossa adscendens (Benth.) Dunlop
Trianthema triquetra Rottb. ex Willd.*

LEGUMES
Aeschynomene indica L.

ANNUAL GRASSES
Brachyachne sp.
Dactyloctenium radulans (R.Br.) P.Beauv.*
Iseilema vaginiflorum Domin

PERENNIAL GRASSES
Cenchrus ciliaris L.*
Dichanthium sericeum (R.Br.) A.Camus*
Enneapogon avenaceus (Lindl.) C.E.Hubb.
Eragrostis kennedyae F.Turner
Eragrostis tenellula (Kunth) Steud.
Sporobolus australasicus Domin

SEDGES
Cyperus difformis L.*
Cyperus gilesii Benth.*
Cyperus squarrosus L.
Fimbristylis subartistata Benth.

* indicates species also found (and identified to species level) in the standing vegetation.

Appendix 4A. Herbaceous species found in burning treatment plots at Dalrymple.

FORBS
Abutilon sp.
Ageratum sp.
Alternanthera sp.
Boerhavia sp.
Brunoniella acaulis (R.Br.) Bremek.
Commelina cyanea R.Br.
Corchorus sp.
Crinum sp.
Emilia sonchifolia (L.) DC.
Euphorbia sp.
Evolvulus alsinoides L.
Glinus oppositifolius (L.) A.DC.*
Hibiscus meraukensis Hochr.
Hybanthus enneaspermus (L.) F.Muell.*
Ipomoea sp.
Malvastrum americanum (L.) Torr.
Melhania oblongifolia F.Muell.*
Ocimum sp.
Parsonsia sp.
Passiflora foetida L.
Phyllanthus sp.
Polygala sp.
Portulaca sp.
Pseuderanthemum sp.
Pterocaulon sp.
Rostellularia adscendens (R.Br.) R.M.Barker
Sida sp.
Spermacoce brachystema R.Br. ex Benth.
Tricoryne anceps R.Br.
Vernonia sp.
Wahlenbergia sp.
Waltheria indica L.

LEGUMES
Chamaecrista absus (L.) H.S.Irwin & Barneby*
Crotalaria medicaginea Lam.
Crotalaria montana Roth
Crotalaria novae-hollandiae DC.
Crotalaria verrucosa L.
Glycine tomentella Hayata
Indigofera colutea (Burm.f.) Merr.*
Indigofera hirsuta L.
Indigofera linifolia (L.f.) Retz.
Indigofera linnaei Ali
Rhynchosia minima (L.) DC.
Senna occidentalis (L.) Link
Stylosanthes sp.
Vigna sp.
Zornia sp.

ANNUAL GRASSES
Dactyloctenium radulans (R.Br.) P.Beauv.*
Perotis rara R.Br.*
Sporobolus sp.

PERENNIAL GRASSES
Aristida sp.
Bothriochloa decipiens (Hack.) C.E.Hubb.
Bothriochloa ewartiana (Domin) C.E.Hubb.
Bothriochloa pertusa (L.) A.Camus*
Cenchrus ciliaris L.*
Chloris sp.
Chrysopogon fallax S.T.Blake
Cymbopogon bombycinus (R.Br.) Domin
Dichanthium sericeum (R.Br.) A.Camus
Digitaria sp.
Enneapogon sp.
Eragrostis sp.
Heteropogon contortus (L.) P.Beauv. ex Roem. & Schlt.*
Melinis repens (Willd.) Zizka*
Panicum sp.
Tripogon loliiformis (F.Muell.) C.E.Hubb.
Urochloa mosambicensis (Hack.) Dandy

SEDGES
Fimbristylis sp.

* indicates species also found (and identified to species level) in the soil seed bank.

Appendix 4B. Herbaceous species found in burning treatment plots at Moorrinya.

FORBS
Abutilon malvifolium (Benth.) J.M.Black*
Abutilon sp.
Alternanthera sp.
Blumea diffusa R.Br. ex Benth.*
Boerhavia sp.
Commelina sp.
Corchorus sp.
Epaltes sp.
Euphorbia sp.
Evolvulus alsinoides L.
Gomphrena celosioides Mart.
Hibiscus trionum L.
Ipomoea sp.
Malvastrum americanum (L.) Torr.
Marsilea sp.
Melhania oblongifolia F.Muell.
Minuria integerrima (DC.) Benth.
Ocimum sp.
Oldenlandia sp.
Peplidium foecundum W.R.Barker
Phyllanthus sp.
Polymeria sp.
Portulaca sp.
Pterocaulon sp.
Ptilotus obovatus (Gaudich.) F.Muell.
Salsola kali L.
Sclerolaena anisacanthoides (F.Muell.) Domin
Sclerolaena bicornis Lindl.*
Sclerolaena muricata (Moq.) Domin
Sida acuta Burm.f.
Sida fibulifera Lindl.*
Sida trichopoda F.Muell.
Solanum sp.
Spermacoce sp.
Streptoglossa sp.
Trianthema triquetra Rottb. ex Willd.*

LEGUMES
Aeschynomene sp.
Crotalaria brevis Domin
Crotalaria montana Roth
Indigofera sp.
Neptunia sp.
Rhynchosia minima (L.) DC.

ANNUAL GRASSES
Brachiaria sp.
Dactyloctenium radulans (R.Br.) P.Beauv.*
Echinochloa sp.
Elytrophorus spicatus (Willd.) A.Camus
Iseilema sp.
Sporobolus australasicus Domin

PERENNIAL GRASSES
Aristida sp.
Astrebla lappacea (Lindl.) Domin
Astrebla squarrosa C.E.Hubb.
Bothriochloa ewartiana (Domin) C.E.Hubb.
Cenchrus ciliaris L.*
Chloris sp.
Dichanthium sericeum (R.Br.) A.Camus
Dichanthium setosum S.T.Blake*
Digitaria sp.
Enneapogon polyphyllus (Domin) N.T.Burb.
Eragrostis sp.
Heteropogon contortus (L.) P.Beauv. ex Roem. & Schlt.
Panicum sp.
Sporobolus actinocladus (F.Muell.) F.Muell.
Sporobolus caroli Mez
Tripogon lolliformis (F.Muell.) C.E.Hubb.

SEDGES
Cyperus difformis L.*
Cyperus gilesii Benth.*
Fimbristylis sp.

* indicates species also found (and identified to species level) in the soil seed bank.