CHAPTER ONE

General introduction

General introduction

The weedy potential of deliberately introduced plants has been a growing concern in Australia for a number of years. Many perennial grass species that were introduced as potential pasture plants are now declared agricultural and environmental weeds (Cook and Dias 2006). One such species is *Hyparrhenia hirta* (L.) Stapf (Coolatai grass) which is a summer active, C4 perennial grass, native to southern Africa and the Mediterranean region. It was introduced in the 1890s to the Coolatai district of northern New South Wales (NSW), Australia, as a pasture and erosion control plant (Hunt 2006). Faithful (2002) suspected that at least 10 races of *H. hirta* were introduced for pasture trials in the 1960s by the CSIRO, which were sourced from Iraq to Portugal and South Africa. Many different ecotypes have been recognized within Australia (Jackson and Jacobs 1985) making it highly likely that several introductions from various locations have been made and this may contribute to its wide distribution in Australia.

In the early years after introduction into northern NSW, *H. hirta* was observed in relatively small patches. However, in recent years it has been spreading rapidly on the North West Slopes and Northern Tablelands, and now also occurs on the Central West Slopes, South West Slopes, North West Plains and Central and North Coast of NSW (Wheeler *et al.* 2002). It has also spread rapidly throughout south-east Queensland, where it has invaded large areas of grazing country, roadsides and travelling stock routes (McCormick *et al.* 1992, McCormick and Lodge 1998). It has also become naturalized in the south-west of Western Australia and South Australia where it is regarded as a weed with environmental potential (Lloyd and Moore 2002, Warner 2004).

Ecological impacts of *H. hirta* include lower plant community diversity and replacement of native vegetation due to its fast and dominating growth (McArdle *et al.* 2004). Major ecosystems of national significance appear to be threatened by this weed.

There has been very little study of *H. hirta* and thus little is known about its biology and ecology in grassy ecosystems. An understanding of the key aspects of seed ecophysiology, population dynamics and community ecology of *H. hirta* will be of significant value in the planning and implementation of control and management techniques.

1.1 General aims

The broad aims of this study were to:

determine the effect of environmental factors (e.g. light, temperature, moisture, pH) on the germination of *H. hirta* seeds;

study the population dynamics, including density and survival of seeds in the soil seed bank;

investigate the competitive and allelopathic interactions of *H. hirta* with other plant species;

determine the effects of mowing, vegetation cover and herbicide application for the management of *H. hirta* under different climatic conditions; and

model the effect of climate change on the potential geographic distribution of *H. hirta* world-wide.

1.2 Format of thesis

This thesis comprises nine chapters including an introduction, a review of the literature, the experimental chapters and general conclusions. The review of literature

(Chapter 2) covers the available literature specific to the area of study. Each experimental chapter (Chapters 3-8), presented in Journal Article format, is comprised of an abstract, introduction, aims, methods, statistical analysis, results and discussion.

Chapter 3 reports a range of laboratory experiments on factors affecting seed germination of *H. hirta*. This work has been accepted for publication in the *Weed Science* journal. Chapter 4 describes glasshouse and field experiments on vertical distribution and viability of *Hyparrhenia hirta* seeds and seedling emergence in soils of different textures. This work is under review in the *Weed Science* journal.

Chapter 5 reports on field experiments to determine the effects of herbicides and mowing on seed and seedling dynamics of *H. hirta* in northern NSW from December 2005 to December 2007. This paper will be submitted to the *Journal of Ecology*.

Chapter 6 is a summary of a glasshouse study on the competitive interactions of *H. hirta* with the native grass species, *Bothriochloa macra*. This paper is under review with the *Journal of Arid Environments*. Chapter 7 reports laboratory bioassay and glasshouse experiments on the comparative allelopathic potential of *H. hirta* and *Phalaris aquatica* on the native grasses, *B. macra* and *Dichanthium sericeum*. This work is under review with the *Plant Ecology* journal.

Chapter 8 describes the world-wide potential geographic distribution of *H. hirta* under current and future climates. This paper will be submitted to the *Weed Research* journal. Chapter 9 presents a general conclusion that describes the key findings from each chapter, discusses the limitations of the work and highlights future research needs arising from this study.

All the units of measurement within each chapter are in a consistent format, but the unit format differs slightly between chapters according to specific journal requirements.

CHAPTER TWO

Literature review

Literature review

2.1 Introduction

An understanding of the biology, ecology and competitive relationships among species is essential to develop effective weed management strategies (Bhowmik 1997, Booth *et al.* 2003a). A brief review of previous work on the biology and ecology of grassy weeds relevant to the management of *Hyparrhenia hirta* (L.) Stapf is presented in this chapter. Published information regarding the biology, and ecology of *H. hirta* is meager, and so literature on other related grass species has been reviewed to provide insights regarding that species.

2.2 Taxonomy and nomenclature

The genus, *Hyparrhenia*, is made up of about 50 species mostly of African origin, with some species widely distributed throughout the tropics (Wagner *et al.* 1999). The Latin name *Hyparrhenia* is derived from the Greek *hypo* means below and *arrhenos* means male and refers to the lower male floret of the fertile spikelet. *Hirta* means hairy and refers to the hairy florets (Wagner *et al.* 1999). It is commonly known as Coolatai grass (New South Wales), tambookie grass (Australia), South African bluestem (United States), and common thatching grass (southern Africa). A detailed morphological description of *H. hirta* is summarized here from previous publications (Clayton 1969, Watson and Dallwitz 1992).

Hyparrhenia filipendula is regarded as a native species in Australia but is a cosmopolitan species that also occurs in Africa, China, India, Malaysia, etc. *Hyparrhenia rufa* is also a weed in Australia. *Hyparrhenia hirta* is C4, and is a member of the Subfamily Panicoideae and the Tribe Andropogoneae which includes native species to Australia.

Figure 2.1 Large infestation of *Hyparrhenia hirta* at Travelling Stock Reserve, Manilla, NSW.

2.3 Distribution

The current global distribution of *H. hirta* is shown in Figure 2.2. It is cultivated and naturalized in the Mediterranean, extending throughout the middle East to Afghanistan and Pakistan. To the west its southern limit lies in the Cape Verde Islands and Hoggar massif (Algeria), but in the east it extends southwards through Egypt and Arabia to northern Tanzania. It is absent from West Africa, and is uncommon in the Congo and Zambesi regions, but is abundant in South Africa (Clayton 1969). It also occurs in North America, the northeastern states of South America, Madagascar and Australia (Global Biodiversity Information Facility 2007). It is widely distributed in regions with a sub-tropical, warm temperate or Mediterranean climate. It includes areas receiving low to relatively high rainfall, with maximum in summer or winter. It is naturalised in America and some European countries but it is not currently reported as a significant weed there.

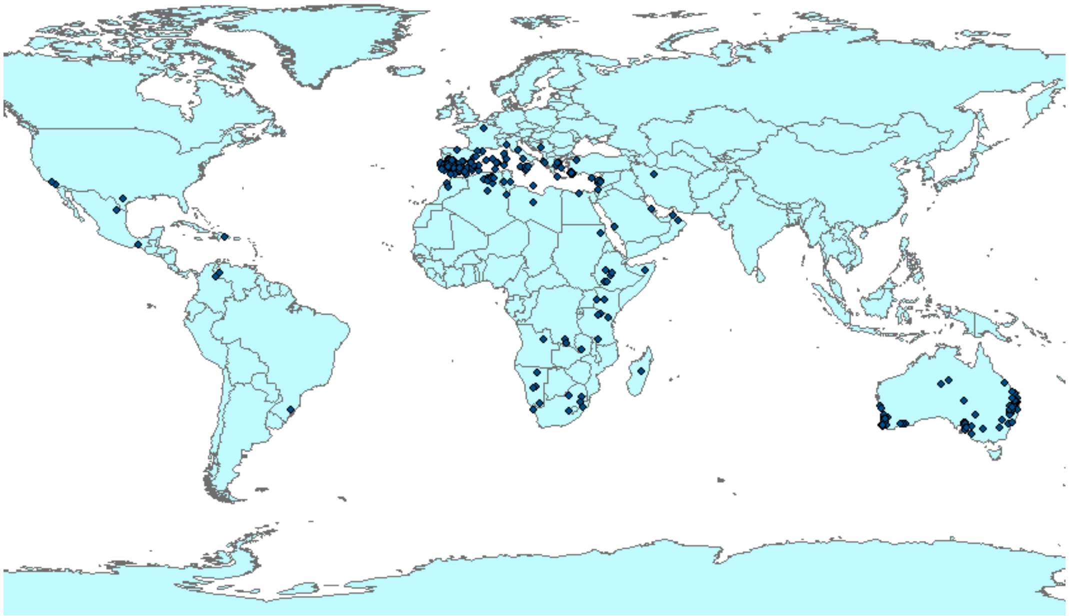

Figure 2.2 The world-wide distribution of *Hyparrhenia hirta* (Australia's Virtual Herbarium 2006, Global Biodiversity Information Facility 2007)

2.3.1 Introduction and distribution in Australia

Hyparrhenia hirta was introduced into Australia in the 1890s to the Coolatai district of northern New South Wales as a pasture plant and was later used for erosion control (Hunt 2006). Faithful (2002) suspected that at least 10 races of *H. hirta* were introduced by the CSIRO in the 1950s and 1960s for pasture trials, which were sourced from Iraq to Portugal and South Africa. There are now populations of *H. hirta* in all states and Territories of Australia (Figure 2.3) except Tasmania (Australia's Virtual Herbarium 2006, Global Biodiversity Information Facility 2007) and it is found in a range of climatic conditions in Australia.

Many different ecotypes have been recognized within Australia (Jackson and Jacobs 1985) making it clear that several different introductions from various locations have occurred which may have contributed to its wide distribution in Australia. Since then, it has been spreading rapidly on the North West Slopes and Northern Tablelands of New South Wales, and now occurs on the Central West Slopes, South West Slopes, North West Plains and Central and North Coast (Wheeler *et al.* 2002). It has spread rapidly throughout New South Wales and south-east Queensland, where it has invaded large areas of grazing country, roadsides and travelling stock routes (McCormick *et al.* 1992, McCormick and Lodge 1998). It is also present in the south-west region of Western Australia (Lloyd and Moore 2002) due to its introduction to control soil erosion in 1943 (Humphries 1959). The circled points shown in Figure 2.3 are unlikely to be sites usually suitable for *H. hirta* invasion, but instead reflect favourable micro-sites (e.g. domestic gardens) in generally unfavorable regions.

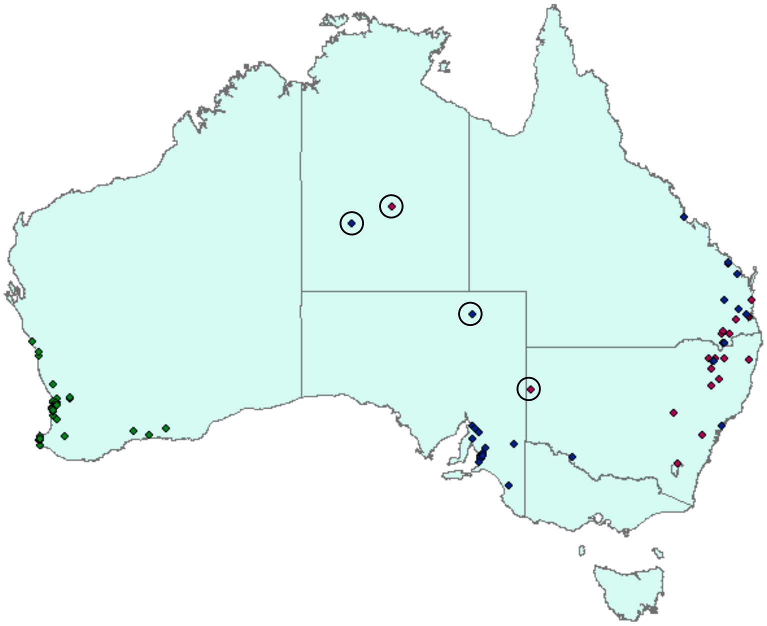

Figure 2.3 The distribution of *Hyparrhenia hirta* in Australia. Records regarded as doubtful or non-current are circled (Australia's Virtual Herbarium 2006, Global Biodiversity Information Facility 2007).

2.4 Factors affecting distribution

The potential distribution of an invasive weed is largely related to the suitability of a region or locality to its physiological requirements although this can be modified by its dispersal and demographic characteristics of the habitat. Different plant species have evolved within distinct ranges of environmental conditions. The success of an invasive species mainly depends on its adaptation in its new environment. Knowledge of the distribution of an introduced plant can be useful for land managers, is required for noxious plant legislation and can be used in assessing the weed potential of new introductions (Panetta 1993).

Figure 2.4 *Hyparrhenia hirta* on travelling stock reserve (foreground) and in paddocks (background), near Manilla, NSW.

2.4.1 Climate

Plant species differ in their tolerance of, and requirements from, the environment so that their distribution or abundance varies along environmental gradients (Swaine 1996). This central concept in ecology has been widely demonstrated in distribution maps of species (Engler *et al.* 2004, Guisan and Thuiller 2005, Kriticos *et al.* 2005) which often show clear associations between species occurrence and known environmental conditions. Climatic factors appear to have a marked influence on the distribution of plant species. Large scale analyses of the distributional patterns of C3 and C4 plants in North America (Teeri and Stowe 1976), Kenya (Tieszen *et al.* 1979) and Australia (Hattersley 1983) have yielded information on the relative importance of climatic factors in determining the distribution of C3 and C4 grasses in these particular areas. The results of these studies have supported hypotheses based on physiological evidence that temperature, light intensity and moisture supply are the most important factors determining C4 species distribution. Hattersley (1983) concluded that C4 grass species in Australia ‘increase in number with increasing rainfall, in their preferred temperature regime’. Faithful (2002) suggested that *H. hirta* is widely distributed in regions with a Mediterranean climate, but its most rapid growth occurs in late spring or midsummer after rain, with a growth pattern typical of a subtropical species. Information about the potential distributions of weeds can play an important role in planning and allocating resources to build community and management support capacity to manage existing infestations, and to prevent further invasions.

The early prediction of biological invasions can often be obtained by using climate based modelling tools that provide information relevant to the decision-maker’s needs (Rastetter 1996, Kriticos *et al.* 2003). Bioclimatic models are widely used tools for assessing potential distribution of a species on the basis of its ecology and climate (Beaumont *et al.* 2005). The commonly used bioclimatic models to predict the potential distribution of species are ANUCLIM, BIOCLIM, DOMAIN, CLIMEX, GARP and HABITAT (Kriticos and Randall 2001). All the models work on the assumptions that climate is the primary determinant of the distribution of plant species (Baker *et al.* 2000, Kriticos *et al.* 2003). However, Panetta and Mitchell (1991) found in a study with *Emex australis* using BIOCLIM (Bioclimatic Prediction System) in New Zealand that the use of climate to predict ultimate limits is no guarantee that a species will act as a major weed within that range or that the expense of a control campaign will be justified. It was also acknowledged that other species of invasive plants may be able to persist beyond their predicted suitable boundaries.

The modelling tool, CLIMEX, uses a combination of climate matching and physiological tolerances of an organism to determine the suitability of environments. It was developed by Sutherst and Maywald (1985) and is based on various growth and stress related indices to assess the potential growth and survival of a population at a given location (Sutherst *et al.* 2004). In a comparative study of different systems to analyse potential weed distribution, Kriticos and Randall (2001) found that CLIMEX (Sutherst *et al.* 2004) was the most suitable climate modelling program for undertaking this analysis because it can support model-fitting to a known global plant distribution, and assesses the climatic suitability of habitat under current and future climate scenarios. The growth and stress indices which describe the distribution of the new organism are determined by adapting the indices of an existing template file to fit the distribution of the new organism. A series of stress indices (cold, wet, hot and dry) also plays an important role in the estimation of the response of the species to adverse climatic conditions. The stress indices play the biggest part in defining the species' range boundaries, whilst the growth indices play a larger role in defining the species' relative abundance within its geographic range. However, some knowledge of the physiological tolerance of the new organism for example tolerance to heat, cold and wet is required to make an accurate description using these stress indices.

The principle assumptions within CLIMEX are that the geographical distribution of a species is primarily determined by climate (Sutherst and Maywald 1985, Sutherst and Maywald 2005), and that the species distribution is in dynamic equilibrium with the climate with which it is being analysed and modelled. This system does not cover other biophysical factors such as soil, land use, vegetation cover, disturbance activities and the ability of a species to disperse in a new area (Sutherst *et al.* 1999, Lawson *et al.* 2004), though these factors can be considered in a stepwise fashion after the climate modelling has been completed.

2.4.2 Impact of climate change on potential distribution

Climate change, in combination with the impacts of land use, is also likely to affect the distribution of plant species, particularly those which have limited ranges (Buckland *et al.* 2001). Biological invasions, habitat disturbance and climate change are three of the greatest environmental challenges that we face with managing invasive weeds (Dukes and Mooney 1999, Mack *et al.* 2000, Kriticos *et al.* 2006). Climate change acts as a potential threat by promoting habitat disturbance, for example, following extreme weather for that site. It is also a great challenge for researchers to quantify and predict the impacts each weed will have on biodiversity and production at global and local levels (Vitousek *et al.* 1996, Norby *et al.* 2001, Gallagher *et al.* 2006, Kriticos *et al.* in prep). According to most climate models, if the pattern of build-up of carbon dioxide (CO_2) and other infrared-absorbing 'greenhouse' trace gases continues, then the surface air temperature is likely to rise by up to 1.5 - 5.5 ºC and induce changes in precipitation patterns over the next 50-75 years (Adams *et al.* 1990, IPCC 2000, Rahmstorf *et al.* 2007). Nicholls and Collins (2006) reported that Australia's mean maximum temperature has already increased by about 0.6 ºC and mean minimum temperature by 1.2 ºC in the last century (1910 – 2004).

Some of the most immediate effects of recent climate change are becoming apparent through impacts on biodiversity, and have the potential to cause significant ecological and economic damage. A rapidly changing climate can favour invasive species that can extend or shift their ranges quickly or species that can tolerate a wide range of climatic conditions and may have greater competitive success than most native species (Dukes 2003). Individual factors that have been investigated include increased concentrations of atmospheric CO_2 and changes in water availability, salinity and temperature. For instance, increased CO_2 can create favorable conditions for species invasion by increasing productivity of species biomass, soil moisture and nitrogen uptake (Weltzin *et al.* 2003).

Invasive species benefit greatly from habitat disturbances because they are generally better dispersers and breeders, and these characteristics are likely to make them benefit from climate change (Hilbert *et al.* 2007). Warm-season (C4) grasses dominate tropical and temperate areas where mean monthly temperature exceed 22 ºC for at least one month of the year (Collatz *et al.* 1998, Clark *et al.* 2001). Therefore, climate change can be expected to favour their invasion if there is an increase in extreme conditions such as droughts alternating with very wet years. The literature linking climate change to geographic distribution of invasive weeds shows a general poleward trend for a range of species under future scenarios (Kriticos *et al.* 2003, 2003a, Kriticos *et al.* 2006).

2.4.3 Soil

Species distributions also show association with soil conditions, more often recognized on relatively small scales because soil data are generally not useful at a regional scale. *Hyparrhenia hirta* can grow on a range of soil types from light textured granite soils to heavy black earths, but it prefers light textured soils (McCormick *et al.* 1992). In a field trial conducted in south-western Australia, *H. hirta* was reported as a moderately salt tolerant pasture species (Rogers and Bailey 1963).

2.5 Habitat

Hyparrhenia hirta is widely distributed in regions with a Mediterranean climate, but its most rapid growth occurs in late spring or mid-summer after rain (Faithful 2002), with a growth pattern typical of a subtropical species. Most recordings of large stands in Australia and overseas occur in the 175-600 mm annual rainfall belt (Van Gils 1988, Rubin and Palmer 1996). Perkins *et al.* (1999) reported that it prefers *Acacia* wooded grasslands, but will grow in a wide range of temperate habitats from full sun to semi-shade. McWilliam *et al.* (1970) suggest that *H. hirta* has found a niche in Australia's Mediterranean environment and has developed special adaptations to survive periods of drought in the summer. *Hyparrhenia hirta* can grow on a range of soil types from light textured granite soils to heavy black earths, but it is more common on light textured soils (McCormick *et al.* 1992). In a field trial conducted in south-western Australia, *H. hirta* was reported as a moderately salt tolerant pasture species (Rogers and Bailey 1963). The root system of *H. hirta* is unusually large and can reach depths of up to 3 m (Humphries 1965). This deep root system gives *H. hirta* the ability to access water available at depth during summer, contributing to its tolerance to drought and competitive advantage through summer growth (McCormick *et al.* 1992).

2.6 Invasiveness

In Australia, *H. hirta* is regarded as a highly invasive weed species (McCormick *et al.* 1992). After the introduction of *H. hirta* to Coolatai, McCormick and Lodge (1991) found that its tough older growth was unpalatable to grazing cattle and that it had invaded a wide range of vegetation communities, such as grassy woodlands and grasslands that represent some of Australia's rarest native plant communities. It often forms monocultures due to its dense growth of leaf and stem material. It has become well established in areas of native flora, particularly roadsides and travelling stock routes, national parks and pastures where it reduces species richness in many regions (Nadolny 1998, Smith *et al.* 2000, McArdle *et al.* 2004, Chejara *et al.* 2006).

Figure 2.5 *Hyparrhenia hirta* can replace diverse native understorey in grassy box woodlands, Travelling Stock Reserve, Manilla, NSW.

2.7 Life cycle and population dynamics

2.7.1 Seeds

Seed germination is one of the most critical events for the success of any weed because it represents the first stage at which the weed can compete for an ecological niche (Forcella *et al.* 2000). Germination is conditioned by intrinsic (dormancy) and extrinsic (environmental) factors (Benech-Arnold *et al.* 2000, Leon *et al.* 2004). Knowledge of the germination biology and ecology of a plant helps to understand its population dynamics (Cousens and Mortimer 1995, Sindel 2000). Long term control of weed populations require a knowledge of seed dormancy, longevity, germination and the impact of environmental factors on germination (Bhowmik 1997, Buhler *et al.* 1997). There is little published information about the seed germination biology and ecology of *H. hirta* apart from the work by McWilliam *et al.* (1970).

2.7.2 Seed dispersal

Knowledge of seed movement and fate is essential for ecosystem restoration and conservation efforts and for the control of alien species in all biomes. Seed dispersal is commonly divided into two phases (Chambers and MacMahon 1994), (a) primary dispersal of seed from its parent plant to the ground and (b) secondary subsequent movement of seed to other sites. The extent of primary dispersal is mainly determined by the morphological characteristics of the seed (Booth *et al.* 2003b). For example, small winged or plumed seeds (e.g. *Conyza spp.*, *Erigeron spp.*) travel further in wind than unadorned and relatively heavy seeds (e.g. *Amaranthus spp.*). Secondary dispersal depends on both biotic and abiotic processes. Biological processes that affect diaspores on the soil surface or in the soil seed bank include dormancy or lack of germination, germination following the proper physiological stimuli, senescence and physiological death, mortality from interactions with predators or pathogens, deep burial by animals or humans, or secondary dispersal (Harper 1977, Chambers *et al.* 1991).

Hyparrhenia hirta is spreading rapidly along roadsides, rail verges, pastures, travelling stock routes, bushland and areas of remnant vegetation (Faithful 2002). Little is known about *H. hirta* seed dispersal and spread to new sites. Anecdotal evidence suggests that *H. hirta* is mainly dispersed by means of hairy seeds with long awned husk that are capable of catching on people, animals and vehicles that move past the plant (Luckens 2002). Human activities such as slashing or vehicular traffic can assist in spreading the weed, particularly along roadsides (Luckens 2002). It spreads along drainage lines, suggesting that water can also help in the seed dispersal.

The vertical movement of seeds in the soil profile also depends on the interactions of seed morphology (size and shape), soil surface characteristics and texture (Peart 1984, Chambers *et al.* 1991, Thompson *et al.* 1993, Chambers 1995). The active and hygroscopic awns in many species of grasses help to drill or to propel dispersal units into cracks or holes in the soil surface (Peart 1979, 1984). However, the seeds of other grasses with awns may readily anchor and quickly germinate at the soil surface without developing a seed bank at greater depth in the soil (Peart 1984).

The dispersal units of *H. hirta* have small, active awns as well as inactive hairs, and the role of these structures in vertical seed movement is unknown. Large seeds and seeds with a large surface/volume ratio are less likely to be incorporated into the soil profile (Bekker *et al.* 1998) and have less chance of finding their way passively down cracks in the soil or being buried by earthworms (Van der Reest and Rogaar 1988, Thompson *et al.* 1994). However, small compact seeds can escape from processes that prevent penetration across the ground surface, such as predation or secondary dispersal, and thus tend to have greater longevity than big seeds. In a study conducted in an alpine ecosystem by Chambers *et al*. (1991), the vertical movement of seeds in the soil depended on the ratio of seed size to soil particle size, with larger seeds moving further in soils with large particle size. Alternating dry/wet periods often develop fine-textured soils that experience pronounced alterations in the key physical properties of the soil throughout the year and tend to develop cracks during the dry season of varying width and depth, which become closed during the wet season thus allowing greater vertical seed movement (Eswaran *et al.* 1999).

The influence of soil texture on vertical movement of seed may be associated with the colloidal component of the soil (Benvenuti 2007). The cohesive forces of smaller soil particles particularly clay soil particles, in the presence of bivalent and trivalent cations helps to attract the particles to one another, possibly forming a barrier to the raindrop-induced gravitational movement of seeds (Marshall *et al.* 1996, Benvenuti 2007). However the tiny awned seeds of *H. hirta* may tend to bury themselves in the soil and form a persistent seed bank. There are no published reports on the effect of different soil types on *H. hirta* seed distribution in the soil profile.

2.7.3 Seed banks

The seed bank has been recognized as a vital component in the perennial grass life-cycle (Cook 2003), as it provides an opportunity for members of the grass family to establish a new population or regenerate an existing one. Regeneration strategies of commonly occurring weed species vary (Buhler *et al.* 1997). Seeds of some species germinate soon after they leave their parent plant (Bazzaz 1990). In other species, seeds may persist in the soil for long periods with intermittent germination of a part of the population (Murdoch and Ellis 1992). Invasive species are vulnerable to control in their early stages of naturalisation and before they have produced a large seed bank.

Once an invasive species has become established it is difficult to eradicate, and effective management may be uneconomic. Knowledge of seed bank dynamics and levels of seed production can assist in understanding weed biology and ecology and in developing successful control or management strategies (Buhler *et al.* 1997, Gardener *et al.* 2003, Lodge 2004, Gallandt 2006). An earlier study conducted on *H. hirta* in South Australia showed there is a viable seed bank that is mainly distributed within two meters from the clump (Warner 2004).

2.7.4 Seed dormancy

Dormancy is a common attribute of many weed seed populations and can hamper the task of predicting timing and extent of emergence of weeds . Weed seeds frequently mature with inherent dormancy mechanisms that prevent germination while the seed is still on the parent plant, ensure temporal dispersal into environments favourable to seedling survival and allow some seeds to persist in the soil for many years before completing germination (Bewley 1997, Murdoch and Ellis 2000). Low germination rates in autumn, from seed produced in the summer of the same year, and a higher germination rate in autumn from seed produced in the summer of the previous year, are mainly caused by the presence of seed dormancy in *N. trichotoma* (Campbell 1998).

Seed covering can act as a physical barrier to germination, in which case the obvious dormancy-breaking mechanism involves damage of the seed covering (Baskin and Baskin 1998). The lemma and palea in some grass species can prevent seed germination by limiting water and oxygen uptake by the embryo (Baskin and Baskin 1998). For example, the removal of the lemma and palea of the grass *Stipa tenacissima* promoted greater and faster germination (Gasque and Garcia-Fayos 2003).

Seed dormancy can be affected by parental environment, seed morphology, day length, temperature, position of the seed in the inflorescence, age of the mother plant, and water stress (Peart 1979, Mousseau and Fox 1998, Gutterman 2000, Murdoch and Ellis 2000, Gasque and Garcia-Fayos 2003). As plants experience variations in the environment among sites and years, seed dormancy may vary among and within populations from year to year in a given location (Mousseau and Fox 1998, Gutterman 2000, Murdoch and Ellis 2000). For example, *N. trichotoma* seeds, collected at the same time and location, germinated at different times over a period of 800 days. Therefore, there is large variation in dormancy of the species Healy (1945) as cited in (Trotter 2006). Asynchronous germination is particularly well developed in certain plant families such as the Poaceae (Gasque and Garcia-Fayos 2003), with only a portion of the total seed population of particular species germinating at one time even under favourable conditions (Gutterman 2000). These species are nonetheless capable of forming at least a transient seed bank. An understanding of the particular seed-dormancy mechanisms involved is also vital when devising control strategies for weedy grasses (Adkins *et al.* 2002).

The effect of characteristics such as asynchronous germination, seed morphology, dormancy mechanisms and post dispersal behaviour is unreported for *H. hirta*, and the implications for seedbank dynamics are unclear.

2.7.5 Seed longevity and viability

In the absence of the re-introduction of seeds to a site, weed infestation depends on the abundance of weed seeds in the soil, and their viability (Omami *et al.* 1999). The survival of seeds in the soil seed bank has important implications for the design of long term weed control strategies (Bourdot and Hurrell 1992). The seeds of many successful pasture weeds such as *N. trichotoma* and *N. neesiana* have prolonged dormancy and viability, which enables them to survive through unfavorable conditions and to persist for long periods in the soil (Altieri and Liebman 1988).

Seeds of some weed species, such as *Phalaris paradoxa*, and *N. trichotoma* persist in the soil seed bank for 1-2 years (Campbell 1998, Taylor *et al.* 2005), whereas seeds of other weed species, for example, *Polygonum convolvulus* and *Chenopodium album* persist in the soil seed bank for decades (Conn *et al.* 2006). Seed persistence of many grassy weeds is relatively short-lived compared to woody weeds (Murdoch and Ellis 2000, Booth *et al.* 2003b).

Seed bank persistence or longevity depends on depth of seed burial (Dawson and Bruns 1975, Alex 1980). The viability of grass seeds tends to decline faster at shallow depths (e.g. 2 cm) than at deeper depths (e.g. 15 cm) (Conn *et al.* 2006). Miller and Nalewaja (1990) also found that *A. fatua* maintained viability longer with increased soil depth. There is little evidence where seed longevity is greater near the soil surface although the viability of *P. paradoxa* seeds in an Australian sub-tropical environment was found to be greater when placed on the soil surface than buried deeper (Taylor *et al.* 2005). It is likely that this response was observed due to rain during the warmer season reducing harshness of climatic conditions at or near the soil surface. There is no published information available on the seed longevity and viability of *H. hirta* in the soil seed bank.

2.7.6 Seed germination

Seed germination is the first stage at which the weed can compete for an ecological niche (Forcella *et al.* 2000). Many weeds are able to germinate at various times during the year. This important trait increases their success in new environments (Booth *et al.* 2003b). Defining the environmental conditions suitable for germination and growth is an essential part of an autoecological study of any species (Harper 1977).

Seed germination is mainly affected by internal and external environmental factors (Booth *et al.* 2003b).

The speed or rate of germination is also an important mechanism which helps invading species in their invasion process. The high rate of germination is likely to provide a competitive advantage to an invading species compared with native species if they have a lower rate. This trait may also confer an advantage in sandy soils that may dry out more rapidly than heavier textured soils. Andrews *et al.* (1997) and Roundy and Biedenbender (1996) also found a more rapid germination rate for the warm-season grasses at higher temperatures. The influence of various environmental variables such as light, temperature, pH and moisture stress on weedy species seed germination has been well documented in many studies (Andrews *et al.* 1997, Chachalis and Reddy 2000, Koger *et al.* 2004, Chauhan *et al.* 2006).

2.7.7 Moisture stress

The effect of soil moisture on germination and emergence varies among plant species, and field conditions may differ significantly both spatially and temporally, depending on rainfall, temperature and soil type. Water available to plants in the soil lies between field capacity (-0.03 MPa) and permanent wilting point (-1.5 MPa) (Miller and Donahue 2004). Low rates of water supply to the seed, or steeper water potential gradients, prevent germination at lower soil water potentials (Watt 1982). As the available soil water potential in the immediate area of the seed is depleted, the absorption of water by becomes more difficult due to the decreased diffusion gradient (Devlin and Witham 1983). *Setaria viridis* emergence was reduced by 80% in semi-arid conditions (-0.65 MPa) with less than 20% emergence occurring at osmotic potentials of -1.03 to -1.53 MPa (Blackshaw *et al.* 1981). Burke *et al.* (2003) found that germination of *B. platyphylla* decreased with more negative water potential, and no germination occurred below -0.8 MPa. Mullahey *et al.* (1996) suggested that germination of *Paspalum notatum* at higher water stress level (-0.35 MPa) increased the opportunity for successful establishment of this species in dry soil conditions of Florida.

Light

Species with small seeds tend to require more light for germination than large-seeded species (Milberg *et al.* 2000). The effect of light on germination of *H. hirta* seed appears to be unreported, although anecdotally, soil disturbance (not necessarily a light trigger) is not needed for germination and seedling recruitment (C. Nadolny, *pers. comm*. 2005). Observations of invasions of travelling stock routes by *H. hirta* indicate that soil disturbance is not necessary for its germination and establishment.

Temperature

Many tropical and temperate grasses have a wide range temperature requirements for optimal germination (Gardener 1998). Seeds of some species require alternating temperature while others simply do better under alternating temperatures. Alternating temperatures requirement for the germination of many grassy weed species, including *N. neesiana*, *N. trichotoma*, *Sporobolus indicus* and *L. rigidum* (Bourdot and Hurrell 1992, Chauhan *et al.* 2006). The germination speed may also depend on the alternating temperature combinations. McWilliam*, et al.* (1970) found that *H. hirta* seeds can germinate over a range of constant temperatures between 5-45 ºC, with a peak at 25 ºC or 30 ºC. However, the effect of diurnally alternating temperatures on *H. hirta* seed germination has not been studied.

Soil pH

The pH of Australian soils varies from as low as 3.6 to as high as 10.6 for a range of different soil textures and parent materials (Slattery *et al.* 2001). In general, plants can tolerate a pH range between 4.0 and 8.0 although many have more specific requirements (Arnon and Johnson 1942). Beyond this range, high concentrations of ions can be directly toxic to some species. In addition to the direct physiological effects of H^+ and OH^-, the substrate pH also affects the availability of nutrients and toxic elements (Redmann and Abouguendia 1979) and it can lead to water stress by disturbing movement of water in to seed.

Burke *et al.* (2003) stated that germination of *Brachiaria platyphylla* decreased as solution pH increased; with maximum germination occurring at pH values of 4 and 5. Seed germination of *L. rigidum* and *C. canadensis* was tolerant to a wide range (4-10) of pH (Chauhan *et al.* 2006, Nandula *et al.* 2006). In a field trial conducted in south-western Australia, *H. hirta* was reported as a moderately salt tolerant pasture species (Rogers and Bailey 1963). *Hyparrhenia hirta* occurs in soils that range from pH 3.6 to 10.6 indicating *H. hirta* can tolerate a wide range of soil pH levels.

2.7.8 Seedling recruitment and survival

The success of an alien species naturalization is determined by the number of introduced propagules and the species intrinsic rate of increase (Warren *et al.* 2006). Once propagules, usually dispersal units (seeds), have arrived at a new site, naturalization depends on the intrinsic rate of increase, which is mainly determined by the recruitment and establishment of seedlings (Van Kleunen and Johnson 2007). The seedling stage is critical in demographical, ecological and evolutionary plant dynamics (Kitajima and Fenner 2000). The timing of seedling emergence of a species is an important consideration in its management because on the basis of that we can determine when it will be able to compete with its neighbors, be subject to herbivory or disease, and the timing of other life history events (Forcella *et al.* 2000).

In a study conducted on the Adelaide plains of South Australia, seedling emergence along the edge of the *H. hirta* infestation was reported between April to August with a peak in early June at 450 seedlings/m^2 (Warner 2004). Lodge (2004) suggests that in some perennial grasses seedling recruitment is an episodic event that is dependent upon favourable seasonable conditions. Andrews *et al.* (1996) found that *Sporobolus indicus* var. *major* had two different germination peaks in November/December and March/April but germination occurred at other times as well when there was sufficient soil moisture and favourable temperature. Once the seedlings established, they can withstand in many unfavourable environmental conditions and live for several years (Campbell 1998, Lodge 2004).

The seedling stage is the most vulnerable stage of the plant life cycle (Harper 1977) because seedlings are generally sensitive to environmental stress. Many biotic and abiotic factors affect seedling survival and establishment. Biotic factors include herbivory, pathogen infections, seed dispersal, litter, competition with herbs and disturbance (Fenner 1987, Facelli and Pickett 1991, Ida and Nakagoshi 1996, Russo and Augspurger 2004). Abiotic factors include light, temperature, soil physical and chemical properties and water stress during drought periods (Harradine and Whalley 1980, Lodge 2000, Rey and Alcantara 2000, Lodge 2004). Lee and Hamrick (1983) suggests that even within a single species, the causes of seedling mortality vary from season to season and from place to place.

Effect of disturbance on seedling emergence and survival

Seedling recruitment and survival of many invasive species were studied by many researchers world-wide under several treatments which resemble the conditions which may be experienced in the field (Meyer and Schmid 1999, Guardia *et al.* 2000, Garnier and Dajoz 2001, Lamoureaux and Bourdot 2002, Verrier and Kirkpatrick

2005). The disturbance of invasive plant populations by mowing or slashing and spraying with herbicides of mature tussocks (leaving bare ground) provides more growing opportunity to native and rare or threatened species. The presence and nature of disturbance regimes has proven to be critical in the survival of rare or threatened species of Australian temperate grassy ecosystems (Gilfedder and Kirkpatrick 1994, Verrier and Kirkpatrick 2005). Hansen and Wilson (2006) found that the population growth of an invasive grass *Agropyron cristatum* declined in the clipped and herbicide treated plots in comparison to unmanaged plots and varies in different environmental situations.

2.8 Interference

2.8.1 Introduction

The term interference was proposed by Harper (1977) to describe all changes in the environment, brought about by the proximity of individuals. It includes neighbouring effects due to the consumption of resources in limited supply (competition), the production of toxic chemicals (allelopathy), or changes in conditions such as smothering, shading, protection from wind and influences on the behaviour of predators (Gill and Davidson 2000). Gill and Davidson (2000) suggested that it is difficult to distinguish between competition and allelopathy experimentally and under field situations they simply measure their combined effects.

2.8.2 Competition

Competition is a broad term that is often used loosely outside its ecological context (Tokeshi 1999). Within an ecological context, competition has been described in detail by many authors. Connell (1990) defined competition simply as “a reciprocal negative interaction between two organisms” or as Crawley (1986) put it “a reduction in fitness of one or both of them". Tokeshi (1999) had a broader definition, defining competition as a relationship in which two (or more) species exert a negative influence on each other through resource exploitation or interference. These definitions are simple and describe the phenomenon of competition but do not describe the mechanisms involved (Tilman 1990). If competition is to be used in the development of Integrated Weed Management (IWM) systems, it is important to understand the mechanisms or underlying processes involved. Grime (1979) defined competition as the tendency of neighbouring plants to "utilize the same quantum of light, ion of a mineral, molecule of water, or volume of space". Tilman (1986) stated that changes in the population density of one plant species are likely to affect the availability of various resources, such as light, water, N or P; thereby influencing the growth of other species. Tilman's definition best describes the mechanisms of competition that are being examined here.

When comparing competition between plant species there are two process involved with competitive ability (Goldberg and Landa 1991), competitive effect, which is the ability to suppress other individuals, and competitive response, which is the ability to avoid being suppressed. These two processes are important because they determine the long-term outcome of competition (Goldberg 1990).

Competitive interactions

In determining the inter-specific competition between neighbours there are three basic possible effects that species may have on one another. One species may cause an increase in the survival, growth or fecundity of another species, or it may cause a decrease, or it may have no effect at all (Begon and Mortimer 1986). Inter-specific competition occurs when there is a negative interaction between two species (- -). This is in contrast to amenalism, in which there is a negative impact on one species and no effect on the other (0 -) (Begon and Mortimer 1986, Connell 1990). Many ecologists do not separate amenalism from competition (Crawley 1986, Tokeshi 1999) as many competitive interactions occur in an asymmetric manner and mutually negative cases are rare (Schoener 1983, Connell 1990).

When two species are growing in close proximity their interaction can be classified as either symmetric or asymmetric. Symmetric competition occurs when either (1) both species experience more intense inter-specific interactions than intra-specific interactions or (2) both species experience less intense inter-specific interactions than intra-specific interactions. Asymmetric competition occurs when one species experiences less intense inter-specific interactions than intra-specific while the other species experiences more intense inter-specific interactions than intra-specific interactions (Shipley 1993, Shipley and Keddy 1994).

Plant traits and competitive ability

From plant competition studies varying views have emerged as to what plant traits make a plant a superior competitor, particularly since the interactions between different plant species will vary as the resources available vary. There are two alternative drivers for plant competition proposed by Grime (1979) and Tilman (1990). Grime (1979) proposed that plants that deplete the limiting resources more rapidly have a greater competitive ability, whereas Tilman (1990) proposed that plants with the capacity to continue to grow at depleted resource levels have a greater competitive effect.

To support his proposition of competition, Grime (1979) defined three basic strategies that plants use to deal with interactions with other species. The strategies are: (1) competitors (which exploit conditions of low stress and low disturbance); (2) stress-tolerators (high stress, low disturbance); and (3) ruderals (low stress, high disturbance). Grime stated that no plant could remain dominant in an environment of high stress and high disturbance. These strategies depend on the environment where the individual species evolved.

Depending on local conditions, plant species show different resource capture patterns, which enable it to compete efficiently for limiting resources (Gleeson and Tilman 1994, Schippers and Olff 2000). Although inter-specific competition has been suggested as an important tool to the development of IWM systems (Michalk *et al.* 1999, Badgery *et al.* 2005), there has been little integration of research on the importance of competition mechanisms between native grasses and weedy introduced grasses as a control practice (Fowler 1995, Wedin and Tilman 1996, Navas *et al.* 2002, Groves *et al.* 2003).

Hyparrhenia hirta predominately exhibits the traits of a stress-tolerator species such as fast growth, deep and strong root system, tolerance to drought, unpalatability, accumulation of biomass and a long lifespan (Humphries 1965, Bokhari *et al.* 1987, McCormick *et al.* 1992, Fetene 2003). Fetene (2003) found that *H. hirta* was competitively aggressive towards *Acacia etbaica* and would inhibit the growth of tree seedlings when the latter are planted within the grass community. These characteristics allow *H. hirta* to dominate pastures and various undisturbed ecosystems. *H. hirta* also has some ruderal characteristics evident in its capacity to invade as a weed. The traits include very high seed production, seed dispersal and the requirement of disturbance to provide conditions for its seedlings to establish may also provide competitive ability to *H. hirta* against native grass species.

2.8.3 Allelopathy

Allelopathy has also been suggested as a mechanism for the impressive success of invasive plants, in part because invaders often establish virtual monocultures where diverse communities once flourished (Heirro and Callaway 2003). The term allelopathy generally refers to the detrimental chemical effects of higher plants of one species (the donor) on the germination, growth and development of plants of another (recipient) species (Putnam 1985) and therefore allelopathy is just one form of non-resource interactions among plants (Callaway 2002).

The literature providing evidence on the role of allelopathy in exotic invasion includes some of the best known plant invaders in the world, including *Eltrygia repens* (Weston *et al.* 1987, Korhammer and Haslinger 1994), *Bromus tectorum* (Rice 1964), *Centaurea* species (Stevens 1986, Ridenour and Callaway 2001), *Chenopodium murale* (El-Khatib *et al.* 2003, Inderjit and Bhowmik 2004), *Cyperus rotundus* (Quayyum *et al.* 2000, Agarwal *et al.* 2002), *Lolium arundinaceam* (Orr *et al.* 2005) and *Parthenium hysterophorus* (Kanchan and Jayachandra 1980, Pandy 1994). Although the number of studies suggesting allelopathic effects of exotic plants is impressive, research on allelopathy and exotic invasion is less convincing than the argument for allelopathy in general. The argument for allelopathy in exotic invasion has been criticised primarily by two issues. First, questionable experimental approaches, particularly the use of laboratory bioassays, have been over emphasized as evidence for allelopathy and warrant the skepticism many have expressed the importance of allelopathy in general (Harper 1977, Keeley 1988, Inderjit and Weston 2000). Second, target species used to evaluate the potential allelopathic effects of invaders have been predominantly crop species and other exotic weeds rather than the native species that are actually excluded (Heirro and Callaway 2003). However, in the recent decade, the allelopathic effects of exotic invasive species has been tested on native plant species (Yamamoto 1995, Orr *et al.* 2005).

Allelopathy has been found potentially involved in the invasion process of *Anthoxanthum odoratum* in *Zoysia*-dominated seminatural grasslands of Japan (Yamamoto 1995). He found the extracts of *Anthoxanthum odoratum* inhibited the seedling growth of *Zoysia japonica* in a labotary bioassay experiment. Orr *et al.* (2005) also found that leaf extracts of invasive species *Lolium arundinaceam* inhibited the seedling emergence of *Elaeagnus umbellate*. Boughey *et al.* (1964) and Munro (1966), cited in Clayton (1969), found that some species of *Hyparrhenia* secrete a toxin which suppresses the growth of nitrifying bacteria. Previous work by Warner (2004) on the allelopathic potential of *H. hirta* with low concentrations (< 10%) of shoot extract indicated that higher concentrations of *H. hirta* extracts may have some inhibitory effect on an invasive species *Lolium rigidum* root growth. However, no research has been conducted on whether allelopathic effects have played a role in the *H. hirta* invasion process. Both laboratory and field experiments are required to assess the importance of allelopathy in invasion of *H. hirta*.

2.9 Control of Hyparrhenia hirta

Hyparrhenia hirta has become highly invasive in several parts of the world, including Australia where it has become a serious environmental weed in recent decades. Management of weeds such as *H. hirta* can be grouped into the following five major areas of control: prediction, preventive, eradication, mechanical, cultural and chemical. Although each of these methods provides a certain level of success in control of rangeland and grassy invasive weeds, an integrated approach using multiple methods is ultimately the most effective way to manage invasive grassy weeds such as *H. hirta*.

2.9.1 Prediction

Bioclimatic analysis, involving computer modelling tools such as ANUCLIM, BIOCLIM, DOMAIN, CLIMEX, GARP and HABITAT has been used to predict the potential ranges of invading species (Kriticos 1996, Kriticos and Randall 2001). All the models work on the assumptions that climate is the primary determinant of the distribution of plant species (Baker *et al.* 2000, Kriticos *et al.* 2003). Predictions of the potential ranges of invasive weeds in Australia, include those for *A. nilotica*, *Chromolaena odorata* and *Crytostegia grandiflora* and *Nassella neesiana* (Gardener 1998, Kriticos *et al.* 2003, 2003a, Kriticos *et al.* 2005).

Little attention has been given to predict the range of potential distribution of invasive species, which is the most useful from the context of practical weed management because of the need to focus on containment and minimising the potential impacts of invaders (Grice 2000). It requires the knowledge of the spatial aspects of the process whereby invasive plants colonise new areas. These processes have been used for a few invasive weed species at local and national scales, for example, *N. trichotoma* (Auld and Coote 1981), *A. nilotica*, *Chromolaena odorata* and *Crytostegia grandiflora* (Kriticos *et al.* 2003, 2003a, Kriticos *et al.* 2005). An understanding of the ecology of *H. hirta* would facilitate the prediction of it's potential range of invasion, and developing management strategies.

2.9.2 Prevention

The first priority in weed management is to prevent the weed from entering or establishing within a given area. Limiting dispersal can help contain a weed's spread into new areas (Brown and Carter 1998). Better understanding of a weed's dispersal mechanisms may identify means to minimise range extension, and knowledge of its phenology will indicate the times when action to reduce dispersal to new areas are most critical (Grice 2000). *Hyparrhenia hirta* has been shown to spread by seeds, therefore, measures must target mechanisms of dispersal. The main modes of seed dispersal may be along water courses, on roadwork machinery and slashing or mowing equipment, spreading *H. hirta* between parks and other areas of significance (Luckens 2002).

Knowledge of the seed dispersal mechanism has been successfully used in management of *Acacia nilotica*. *Acacia nilotica* was widely planted as a fodder and shade tree in the Mitchell grasslands (Mackey 1997) but bioclimatic predictions suggest that in Australia *A. nilotica* could expand its range of invasion south and inland (west) where areas are climatically suitable for its growth (Kriticos *et al.* 2003). The national strategy for the management of invasive species aims to raise the public awareness of the invasion threat posed by such species, their identification, suitable control techniques and to eradicate scattered infestations and prevent introduction into new areas (Grice 2000, Kriticos *et al.* 2003).

2.9.3 Eradication

Eradication is the complete elimination of all live weeds, weed parts and weed seed from an area and is chiefly used where recolonisation of the plants is unlikely (Zimdahl 1999). Eradication is the most desirable outcome for weed control but is not feasible in many situations. It is usually easy to eliminate live plants, because they can be seen. It is difficult to eliminate seed and vegetative reproductive parts in soil. To help improve the likelihood of containment and eventual eradication of a weed it is important to have a good understanding of the distribution of the weed and sound detection techniques (Panetta and Timmins 2004). Knowledge of the stage of invasion will help in assessing the achievability of an eradication program for individual weed

(Panetta and Timmins 2004). Early detection and prediction of the potential invasion range of a species are important processes in developing eradication strategies.

The most likely method of practical eradication for weed species such as *H. hirta* requires a combined understanding of the knowledge of the establishment and survival of seedlings, and competitiveness of several species present in areas invaded by *H. hirta*.

2.9.4 Mechanical control

A range of mechanical techniques are used to control weeds including hand-pulling, hand hoeing, tilling and mowing. Hand-pulling pulling is practical and more efficient, especially in gardens, but it is difficult and hard work and mainly effective in loose and moist soil (Sheley *et al.* 1999). It can be effective for annual weeds, but is often not feasible for perennials that are capable of vegetative reproduction, because roots remain in the ground and then produce a new shoot (Zimdahl 1999). These techniques can be effective for the control of small infestations or weeds at the fringe of a major infestation (DiTomaso 2000).

Mowing or slashing is also a useful and commonly used technique for control of annual and perennial weeds (Benefield *et al.* 1999). Defoliation by clipping and mowing was investigated because grazing is integral to grassland management (Milchunas and Noy-Meir 2002, Verrier and Kirkpatrick 2005). Verrier and Kirkpatrick (2005) found that regular mowing resulted in greater cover of rare or threatened species, greater native cover and less exotic grass cover in Tasmania. In another study on *Solidago altissima* and *Agropyron cristatum* mowing removed biomass and prevented seed production and addition of seeds in the soil seed bank (Meyer and Schmid 1999, Hansen and Wilson 2006). On the other hand, it could open up the vegetation cover sufficiently to allow seeds to germinate and seedlings to grow up, therefore new genets might establish (Gross 1980). For example, Trotter (2006) found that slashing encouraged seedling survival of *N. trichotoma* on the northern Tableland region of New South Wales, Australia, and suggested that minimal disturbance created by slashing a pasture is not an adequate method to control this weed. Currently, in New South Wales and South Australia, one established method of control of *H. hirta* is based on a method that integrates slashing and spraying over a nine week of period. This process consists of slashing the tussocks to ground level and then allowing a period of 2-4 weeks for regrowth. The regrowth is then sprayed with a high rate of glyphosate (1080g acid equivalent ha^{-1}), and 2-3 weeks later the regrowth is sprayed again (Luckens 2002).

Tillage practices also can control annual species, but in perennial species rarely provide control and can often lead to the spread of weeds such as *C. maculosa* or *Lepidium latifolium* (Young *et al.* 1998). While tillage can be used in cropping areas, it is not a practical approach or technique for weed control in most rangeland and travelling stock routes.

2.9.5 Cultural control

Proper grazing management can be directly used to remove the weed or to manipulate pasture to become more competitive against invading and already present weeds. Olson (1999) describes three grazing strategies for managing weeds: (1) moderate grazing to minimize the physiological impact on native plants and to reduce soil disturbance, (2) intensive grazing to counteract inherent dietary preferences of cattle, resulting in equal impacts on all forage species including weeds and (3) multispecies grazing that distributed the impact of livestock grazing more uniformly among desirable and desirable species. Weeds where evidence is available that controlled by grazing in Australia are *N. neesiana* (Gardener *et al.* 2005) and *Carthamus lanatus* (Grace *et al.* 2002).

Lodge *et al.* (2005) found that *H. hirta* has the ability to persist under systems of strategic grazing, involving intermittent grazing at both high and low rates of stocking. Therefore, it appeared unlikely that grazing could be used as a management strategy for this species.

Burning has also been used successfully to control weeds in many ecosystems. Controlled burning has been a common management technique to reduce competition from woody species and competition for water (Zimdahl 1999). Prescribed burning in rangeland also can stimulate germination and growth of annual and perennial grasses (Sheley *et al.* 1999) and enhance native forb diversity (DiTomaso *et al.* 1999). Williams (2005) suggested that burning every 3 years maintains species diversity in a temperate native grass ecosystem in Australia. If grasses are not burnt regularly, *Themeda triandra* can become excessively dominant and the growth of other plant species such as perennial herbs can be inhibited. However, *T. triandra* has been seen to limit the establishment of more invasive weeds such as *N. neesiana* and *N. trichotoma* (Badgery *et al.* 2002). On the other hand, it is important to note that burning may promote colonization by weeds or allow rapid recovery of noxious perennial species such as *L. latifolium*, *Tamarix* spp., and *Euphorbia esula* (Lacey *et al.* 1992). *Hyparrhenia hirta* has been found to be fire responsive, when it is usually burnt to destroy old growth and makes a good and quick recovery after a burn (Fynn *et al.* 2005a). Therefore, burning is unlikely to control *H. hirta*, but it may improve the efficiency of follow up herbicidal control.

2.9.6 Chemical control

Herbicides are the primary method of weed control in many ecosystems, including grassland ecosystems. Herbicides commonly used to control perennial grasses in pastures and roadside situations of the central and southern NSW are glyphosate, flupropanate and 2,2-DPA. The effectiveness of these chemicals in controlling the perennial grassy weeds *Eragrostis curvula* and *N. trichotoma* has been reported in central and southern NSW (Campbell and Gilmour 1979, Campbell *et al.* 1985). Similarly, Lodge *et al.* (1994) in NSW, tested the efficacy of these herbicides (glyphosate, flupropanate and 2,2-DPA) and their mixtures, and found that after 20 months of treatment application, none of the herbicide treatment gave 100% control of *H. hirta*. Lodge *et al.* (1994) suggested that glyphosate applied at 2.16 and 4.32 kg a.i./ha in autumn and flupropanate applied at 4.4 kg a.i./ha in autumn or spring were the most effective in the long-term control of *H. hirta*. However, in South Australia, it has been observed that the best control takes place during spring (Luckens 2002). While no satisfactory method of control is yet available, research should be focused on the development of mechanical, chemical, and biological control of *H. hirta*.

Long-term control methods should aim to eliminate the weed seed bank, where the plant is not yet well established and eradication is warranted. However, where a weed is already well established it is likely the species will only ever be lowered to a controllable level (Kemp *et al.* 1999). *Hyparrhenia hirta* is so widespread throughout much of the New England region and central, north-west slopes of NSW, that eradication is impossible and thus control needs to focus on reducing its spread into new areas and manages its abundance where it is present. In contrast, eradication may be warranted on the southern slopes where populations are currently small and very localized. Reducing movement of seed and the establishment of new infestations will be important to reduce spread and enable control to focus on pre-existing infestations. By understanding the biology, ecology and population dynamics of this species and the environmental influences in this area, new strategies for control and prevention of spread can be planned and implemented more effectively.

2.10 Conclusion

Hyparrhenia hirta is becoming of increasing importance as a weed of natural and agricultural environments throughout the NSW and other Australian states, due to its dominating, invasive nature. There has been little study carried out on *H. hirta* and thus little is known about its biology and ecology in these ecosystems. The aim of this study was to increase our understanding of the key aspects of seed ecophysiology, population dynamics and community ecology of *H. hirta* to assist in the planning and implementation of control and management techniques, the study included investigations into the:

- effects of environmental factors (e.g. light, temperature, moisture, pH) on the germination of *H. hirta* seeds;
- population dynamics, including density and survival of seeds in the soil seed bank;
- competitive and allelopathic interactions with other plant species;
- effects of mowing, vegetation cover and herbicide application for the management of *H. hirta* under different climatic conditions; and
- modelling the effect of climate change on the potential distribution of *H. hirta* world-wide.

CHAPTER THREE

Factors affecting seed germination of *Hyparrhenia hirta*

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Factors affecting seed germination of *Hyparrhenia hirta*

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Abstract

Hyparrhenia hirta is an invasive, perennial grass from Africa and the Middle East that has infested large areas of northern New South Wales, Australia, and also occurs in other Australian states. An understanding of the seed germination ecology of *H. hirta* can assist in predicting its potential distribution and developing effective management strategies. The effects of various environmental factors on *H. hirta* seed germination were investigated in a series of laboratory experiments. The effect of diurnal alternating temperatures (5-45 C) with a 12 h photoperiod were examined on a thermo-gradient plate. Seed germination occurred at almost all temperature combinations from 5-45 C. At moderate temperatures, the speed of seed germination was very high; at 30/20 C more than 80% of seeds were germinated within 12 hours. Germination was slightly enhanced by the presence of light, but length of photoperiod did not affect germination. Germination at neutral pH was over 90%, and declined to 65% at acidic (pH 4) and alkaline (pH 10) solution pH levels. Germination was completely inhibited at an osmotic stress of -0.55 MPa or greater and was reduced by 50% at -0.37 MPa. Greater germination in relatively dry soil conditions compared to native species may contribute to the establishment of this species in the field. Results indicate that *H. hirta* seeds can germinate over a wide range of diurnal temperatures, light regimes, pH levels, and under marginal water stress. These characteristics help explain the successful invasion of *H. hirta* and provide evidence that this species is capable of establishing in many parts of Australia.

Nomenclature: Coolatai grass, thatching grass, *Hyparrhenia hirta* (L.) Stapf.

Key words: seed biology, germination, light, pH, temperature, osmotic stress, management implications.

3.1 Introduction

Hyparrhenia hirta (L.) Stapf (Coolatai grass) is a summer-active, C4 perennial grass, native to southern Africa and the Mediterranean region. It grows in open savannas, extending into the dry tropics, particularly in highland regions (Clayton 1969). It was introduced in the 1890s to the Coolatai district of northern New South Wales, Australia, as a pasture and erosion control plant (Hunt 2006), but now invades areas of native flora, particularly roadsides, travelling stock reserves and native pastures (Nadolny 1998, McArdle *et al.* 2004).

Hyparrhenia hirta can grow on a range of soil types from light textured granite soils to heavy black earths, but prefers light textured soils (McCormick *et al.* 1992). The root system of *H. hirta* is described as unusually large and can reach depths of up to 3 m (Humphries 1965). This deep root system gives *H. hirta* the ability to explore water available at depth during summer, contributing to its tolerance to drought and competitive advantage during summer growth (McCormick *et al.* 1992).

Once introduced, seed germination is the first stage at which the weed can compete for an ecological niche (Forcella *et al.* 2000) and it is mediated by various environmental variables such as temperature, light, pH, and soil moisture (Chachalis and Reddy 2000, Koger *et al.* 2004, Chauhan *et al.* 2006). Information about the effect of these factors provides a biological basis for the spread and establishment of *H. hirta*. This knowledge is useful in modelling the invasion potential of a species (Kriticos *et al.* 2003) and can improve the ability of farmers and land managers to control weeds such as *H. hirta*.

Although McWilliam *et al.* (1970) tested the effect of constant temperature on *H. hirta* germination, the effect of diurnally alternating temperatures on *H. hirta* has not been studied.

Many plants require light for germination, while some are insensitive to light, and others are inhibited by light (Bewley and Black 1994). The effect of light on *H. hirta* germination appears to be unreported. The pH of Australian soils varies from as low as 3.6 to as high as 10.6 for a range of different soil textures and parent materials (Slattery *et al.* 2001). In general, plants can tolerate a pH range in their environment between 4.0 and 8.0 (Arnon and Johnson 1942), but beyond this range, high concentration of ions can be directly toxic to plants.

The impact of soil moisture on germination varies among weed species, and field conditions may differ spatially and temporally, depending on rainfall, temperature and soil type. Plant-available water in the soil lies between field capacity (-0.03 MPa) and permanent wilting point (-1.5 MPa) (Miller and Donahue 2004), and it is assumed that the water potentials of available water in wet, moist, semi-arid and arid soils are 0, 0 to -0.03, -0.03 to -0.75 and -0.75 to -1.5 MPa, respectively.

There is little published information about the effect of environmental factors on the germination of *H. hirta* apart from the work by McWilliam *et al.* (1970). An understanding of seed germination ecology of *H. hirta* will help to understand current distribution, predict potential spread into new areas and be useful in developing effective control strategies (Chapter 8). The aim of this study was to determine the effect of temperature, light, pH, and osmotic stress on the germination of *H. hirta*.

3.2 Materials and Methods

General Germination Test Protocol. *Hyparrhenia hirta* seeds were harvested from glasshouse grown plants at the University of New England (UNE), Armidale, Australia (30º 29′ S, 151º 38′ E) on 5 October 2006. The plants had been transplanted from a roadside *H. hirta* infestation near the University campus. The panicle dispersal units were harvested by running a thumb and forefinger along the length of mature inflorescences prior to shedding. Only fully developed caryopses, were used in these germination experiments and these were selected by squeezing dispersal units with forceps. Selected dispersal units (seeds) were then stored at room temperature until used in all experiments. Initial viability of this seed sample was tested in a growth cabinet (12 h light at 30 C, and 12 h dark at 20 C). The numbers of seeds germinated (radicle visibly protruding from the seed coat) were counted daily for 15 days. Any seeds that did not germinate were cut transversely slightly above the embryo and then tested with a 0.1% tetrazolium solution for viability, as described in Leist and Kramer (2003). The total viability of this seed sample was 80 ± 5%. The total germination achieved from the viable seed sample was 90 ± 5%.

Except for the temperature experiments, *H. hirta* germination was evaluated by evenly placing 25 seeds on a single layer of Whatman filter paper No. 1 in a 9 cm plastic Petri dish. Each treatment was replicated four times. The filter paper was moistened with 5 ml of deionized water or treatment solution. This ensured uniform contact of treatment solutions with *H. hirta* seeds. Petri dishes were sealed with Parafilm and placed in an incubator at fluctuating day/night temperatures of 30/20 C, unless otherwise specified. The photoperiod was set at 12 h to coincide with the higher temperature period. Fluorescent lamps were used to produce a light intensity of 85 µmol m^{-2} s^{-1}. Percentage of seed germination was calculated by multiplying the ratio of germinated seeds to total number of viable seeds in a single Petri dish by 100.

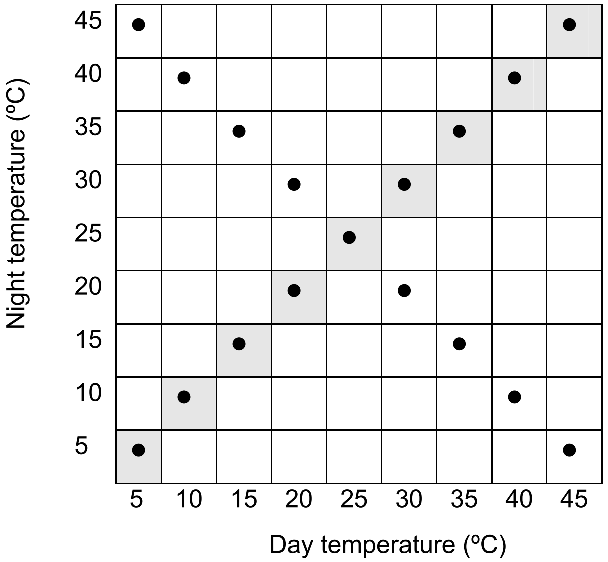

Figure 3.1 Two-way thermo-gradient plate layout, showing 81 diurnal temperature combinations with constant temperature cells shaded, and the location of 17 thermocouples (●).

Effect of Temperature on Germination. The response to temperature of germination of *H. hirta* was studied using a two-way thermo-gradient plate similar to that described by Larsen (1971). This plate provides a surface on which the responses to 81 combinations of diurnally alternating and constant temperature can be simultaneously tested (Figure 3.1). Temperatures in each direction on the gradient plate ranged from 5 to 45 C and trays were at 5 C intervals to give a total of 81 temperature locations (Figure 3.1). Constant temperature occurred along one diagonal as represented by shaded cells, with temperatures alternating between 5 C and 45 C in the corners of the plate. A data logger was attached to the thermo-gradient plate to monitor the temperature of all (17) thermocouples at one hour intervals. The thermocouples were about the same size as a seed and were placed on the surface of the germination pads in the centre of each cell on the two diagonals of the plate (Figure 3.1). The temperature changes were set at 12 h periods from 6 am to 6 pm (day temperatures) and 6 pm to 6 am (night temperatures), and temperatures generally stabilised within an hour of these alteration times. Once stabilized, actual temperatures were within 1.0 C of the expected treatment values. Light was provided by fluorescent tubes above the plate during the day temperatures giving a light intensity of 45 μmol m^{-2} s^{-1} measured with "LI-COR" model LI-250 light meter.

Eighty-one square aluminium trays (5 x 5 cm x 1.5 cm deep) each containing 25 seeds placed on moistened blue germination pads over absorbent cotton pads (Kimpak®) were used for the temperature treatment and the seeds in each treatment were covered with a semicircular-shaped transparent Perspex lid. The aluminium trays with seed lots were placed on the face of the thermo-gradient plate and surrounded by moist sand. The gradient plate was covered with a partially sealed, transparent Perspex lid. Pads were watered by the addition of distilled water when necessary to keep them moist. The surrounding sandy surface of the plate was also kept moist. The number of germinated seeds was counted daily for 13 days. Seeds not germinated on the plate were placed in Petri dishes in an incubator at alternating temperatures of 30/20 C day/night with a 12 h photoperiod and germinated seeds were counted daily for an additional 15 days. Any seeds that did not germinate were dissected and then tested with tetrazolium for viability. The total number of germinated seeds for each temperature combination was expressed as a percentage of the total viable seeds.

Effect of Light on Germination. To determine the effect of contrasting light regimes on the germination of *H. hirta* seeds, the general germination test protocol described above was conducted under varying day/night photoperiod. A growth cabinet was set to alternate temperatures at 30/20 C day/night with light regimes of 0/24, 8/16, 12/12, and 16/8 h light/dark. For the complete darkness treatment, dishes were wrapped in two layers of aluminum foil immediately after adding water. Germination was counted daily until eight days after the start of the experiment, except in the dark treatment which was only counted once after eight days.

Effect of pH on Germination. The effect of pH on germination was studied using buffer solutions of pH 4 to 10 to simulate the pH ranges of Australian soils where *H. hirta* has been naturalised (NLWRA 2001). The general germination test protocol described above was used. Buffer solutions were prepared as per the method described in Burke *et al.* (2003) or Chauhan *et al.* (2006). A potassium hydrogen phthalate (KHP) buffer solution was used to adjust the pH 4 and 5 by adding 0.1 N hydrogen chloride (HCl) or 0.1 N sodium hydroxide (NaOH). A pH 7 or 9 buffer was prepared with 25-mM KHP buffer solution and adjusted with 0.1 N of HCl or 0.1 N of NaOH. A 2-mM tris (hydroxymethyl) aminomethane buffer solution with 1 N NaOH was used to obtain solution pH levels 10. Unbuffered deionized water (pH 6.45) was used as a control. Germination was counted daily until eight days after the start of the experiment.

Effect of Osmotic Stress on Germination. The effect of osmotic stress on germination was tested using solutions with osmotic potentials of 0, -0.09, -0.18, -0.37, -0.55, -0.73 and -0.92 MPa to simulate variations in available soil moisture, and were prepared by dissolving 0, 91.2, 128.7, 182.4, 223.4, 256.7, and 288.2 g, respectively, of polyethylene glycol (PEG) 8000 in 1 L of deionized water (Michel 1983). The general germination test protocol described above was used. Germination was counted daily until eight days after the start of the experiment.

Statistical Analysis. One way analysis of variance (ANOVA) was used to determine the significance of germination response to temperature, light, pH and osmotic potential levels using the statistical package R 2.2.0 (R Development Core Team 2006). An ANOVA was carried out individually for each variable tested. Variances were checked by plotting residual vs. fitted values to confirm the homogeneity of the data. No transformations were necessary. Significantly different treatments were separated using orthogonal contrast. The temperature trials were repeated four times, while the other experiments were repeated twice each. There were no significant differences between repeat experiments or the interaction of repeat experiments and treatment, so the data were pooled in the individual analyses. The thermo-gradient plate data (5 C) were interpolated onto a 0.5 C grid using the `loess` smoothing function and plotted (Figure 3.2) using the contour plot function in R (R Development Core Team 2006).

To determine the speed of germination, a logistic model was fitted to germination as a function of time (x) using $Y = a/(1 + exp((b - x)/c))$, where Y is the total germination (%) at temperature combination x, a is the maximum germination (%), and b is the time taken to obtain 50% germination of the maximum. Regression parameters were estimated by fitting the equation to germination data within each dish on the temperature plate using non-linear regression (`nls`) in R.

3.3 Results and Discussion

Effect of Temperature on Germination. Seeds of *H. hirta* germinated over a wide range of diurnally alternating temperatures from 5 to 45 C (Figure 3.2) and there were no differences between the day and night responses for given temperature combinations ($P > 0.05$). Maximum (100%) germination occurred over a broad diurnal alternating temperature range (20/30, 20/35, 25/30, 25/5, 30/5-30/20, and 35/25 C) and germination percentage decreased at constant day/night temperatures below 25/25 C. Lower numbers of seeds germinated at temperatures above 40 C, especially when the alternate temperature was very low or very high.

The logistic function was fitted to determine the speed of germination at different diurnally alternating temperature combinations from 5 to 45 C (Figure 3.3). Germination rate, indicated by the relative time from the start of imbibition to 50% maximum germination (b), was slow when the alternating temperature was 5 and 45 C, with an average rate of germination 4.82 and 5.34 days, respectively. The germination rate increased with increasing temperature to a maximum in the 20 – 30 C range, and showed a relative decline at temperatures above 40 C. The fastest germination rate was achieved at 30/20 C, where b was 1.09 days. At the alternating temperature 30 C, the germination rate (*b* = 1.62 days) was 47% faster than the germination rate (*b* = 3.14 days) at alternating temperature 20 C.

Seeds of *H. hirta* germinated over a wide range of diurnally alternating temperature combinations from 5-45 C. This ability of *H. hirta* seeds to germinate over a wide range of temperatures may allow it to germinate throughout the year, as these lower (5-10 C) and upper (> 40 C) threshold for temperature often occur throughout the year in wide areas of Australia. Greatest germination was recorded at moderate temperature ranges (20-40 C). These temperature conditions occur between late spring and early autumn in large areas of Australia where *H. hirta* has not yet invaded. The results support the findings of Lodge (1981), that the most favourable period for the establishment of warm-season grasses is from mid-summer to early autumn and are also consistent with the findings of McWilliam *et al.* (1970), that seeds of *H. hirta* can germinate over a wide range of constant temperatures between 5-45 C.

The high rate of germination of *H. hirta* (1.0 – 2 days after sowing) provides a competitive advantage in rapidly imbibing soil moisture from summer rainfall, especially in sandy soils where *H. hirta* has been very successful. Andrews *et al.* (1997) and Roundy and Biedenbender (1996) also found a rapid germination rate for the warm-season grasses at higher temperatures. The ability of *H. hirta* seed to rapidly germinate over a wide range of temperatures provides a partial explanation for the establishment of this species throughout much of Australia. The slow spread of *H. hirta* in the cooler southern Tableland region of New South Wales, Australia, is possibly due to low germination in the lower temperatures from late summer to early autumn.

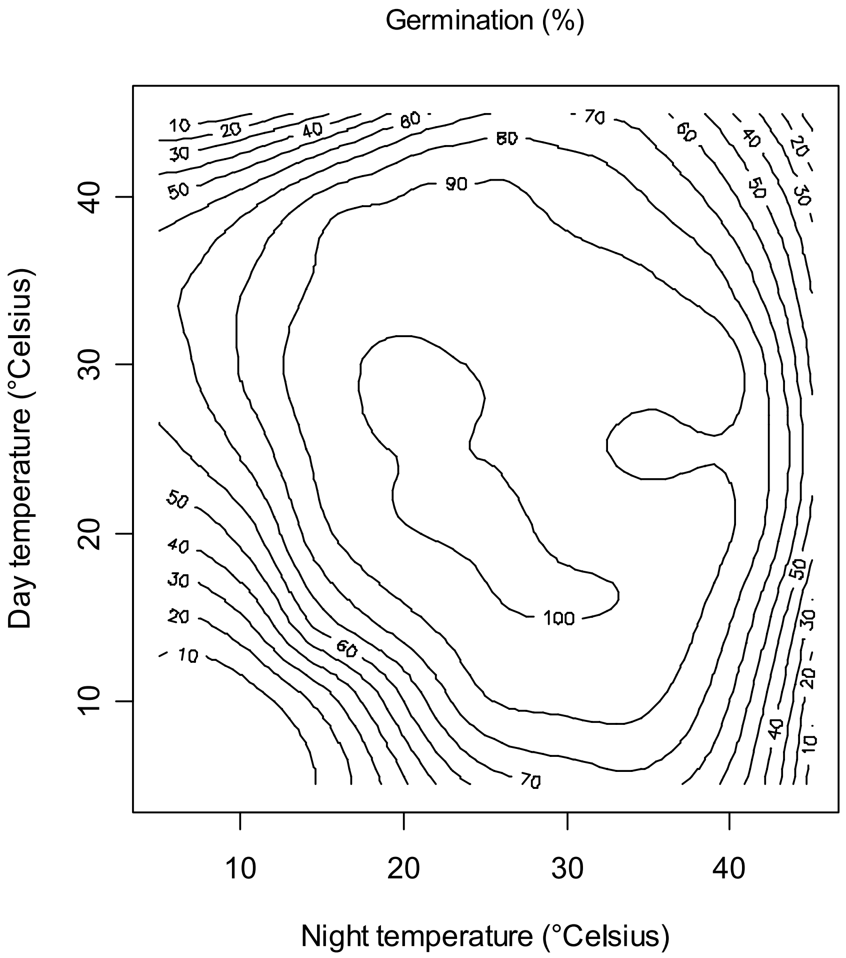

Figure 3.2 Germination of *H. hirta* at a range of diurnally alternating temperatures on a thermo-gradient plate. The percent of germinated viable seeds at 13 days after sowing is shown on a 0.5 C interpolated grid.

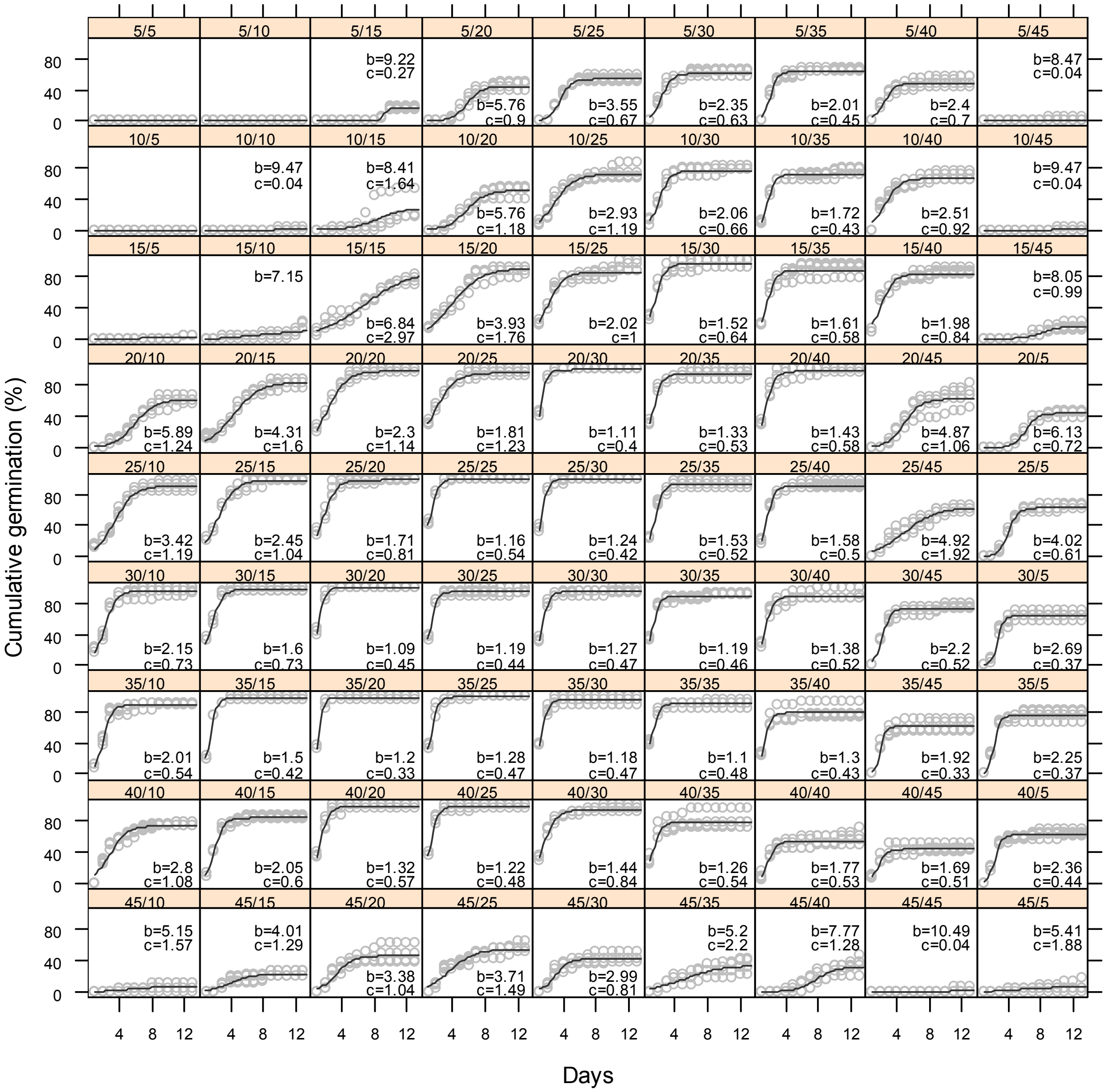

Figure 3.3 Effect of day/night temperature combinations (shown at the top of each panel) on *H. hirta* germination over time. The line represents the fitted logistic model; the regression parameter *b* shows the time taken to obtain 50% germination of the maximum. Plots with no *b* values had zero or little germination and an acceptable fit was not possible.

Effect of Light on Germination. *Hyparrhenia hirta* seed germinated well (≥ 80%) under all light regimes (8, 12, 16 h and 24 h darkness), but the maximum germination percent (92%) was reported at a 12 h photoperiod (Figure 3.4). The effect of light on germination was significant ($P < 0.001$), with the responses of the 8, 12 and 16 h light regimes being similar (~ 90%) but, in darkness, germination was 9% lower than the other treatments. The high level of germination in the absence of light indicates that *H. hirta* can germinate without a light trigger, although light may improve germination slightly (Gramshaw and Stern 1977, Baskin and Baskin 1998). These results indicate that *H. hirta* seeds can readily germinate within the soil, under a plant canopy or litter shade. This could be a contributing factor to its successful invasion under undisturbed ecosystems.

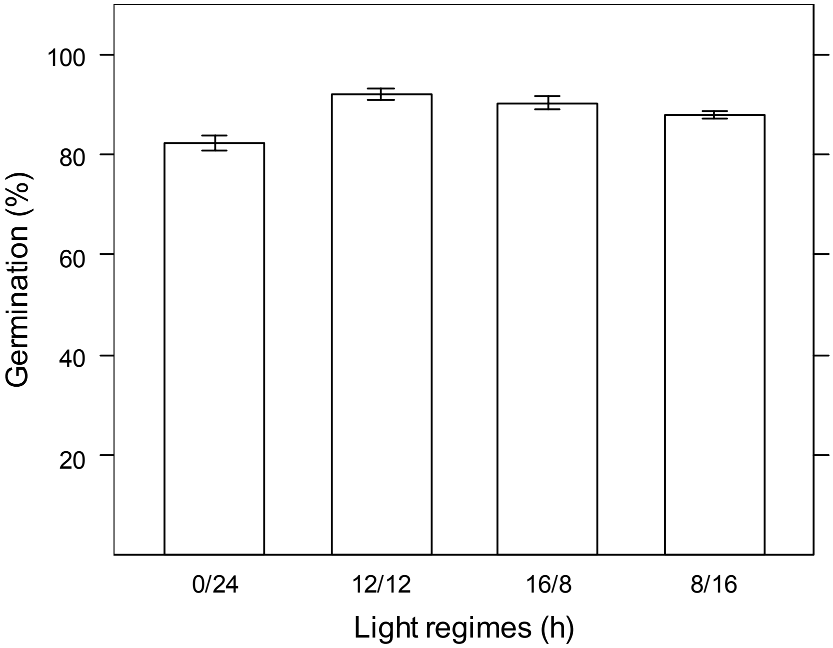

Figure 3.4 Effect of light/dark regimes on *H. hirta* germination. Mean and standard error are shown.

Effect of pH on Germination. Germination of *H. hirta* seeds decreased ($P < 0.001$) as the solution pH decreased or increased compared with the control (pH 6.45) and pH 7 (Figure 3.5). Greatest germination (93%) was recorded at pH 6.45 (control) and germination at neutral pH 7 was 92%. Moderately acidic or alkaline conditions (pH 5 and 9, respectively) reduced germination by about 10%, while strongly acidic or alkaline conditions (pH 4 and 10, respectively) gave an even larger reduction (about 38%). Although the reduction in germination at the pH extremes are substantial, the absolute level of germination was never below 56%. These results are similar to work on seeds of *Lolium rigidum* (Chauhan *et al.* 2006) and *Andropogon hallii* and *Panicum antidotale* (Stubbendieck 1974), which have been reported to germinate over a wide pH range, with more than 50% seeds being germinated at pH 4 and 10. We conclude that the pH of most soils found in Australia will not be a limiting factor in the spread and establishment of *H. hirta*.

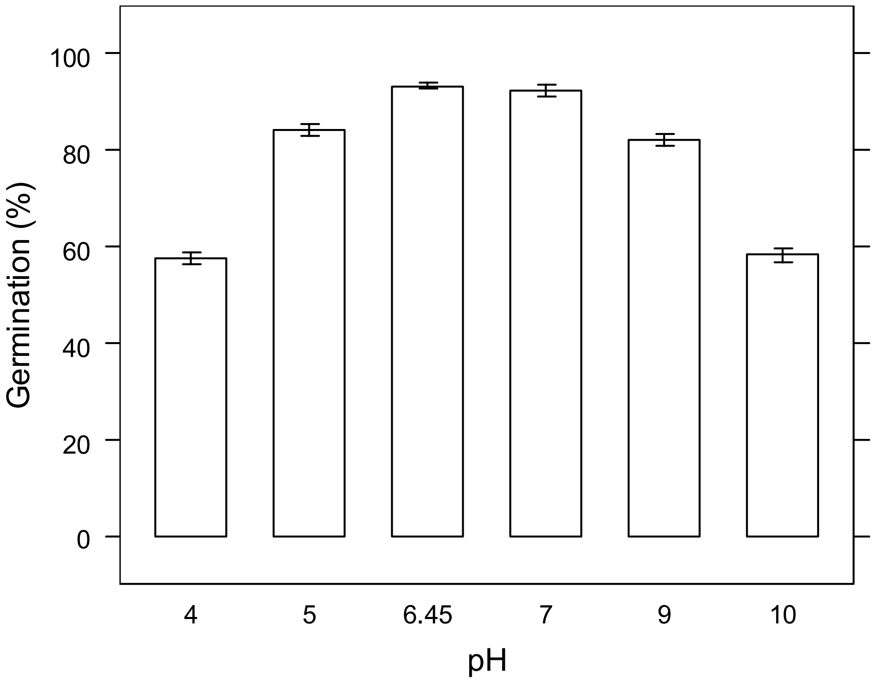

Figure 3.5 Effect of pH on germination of *H. hirta* seed incubated at 30/20 C day/night temperature with a 12 h photoperiod for eight days. Mean and standard error are shown.

Effect of Osmotic Stress on Germination. Germination of *H. hirta* decreased from 93% to 43% as osmotic potential decreased from 0 to -0.37 MPa (Figure 3.6). There was no significant difference in *H. hirta* germination between the control and -0.09 MPa treatment, whereas germination was reduced by 22% and 54% at -0.18 and -0.37 MPa, respectively. Germination at -0.37 MPa indicates that a moderate proportion of seeds of *H. hirta* can germinate under marginal water-stress conditions.

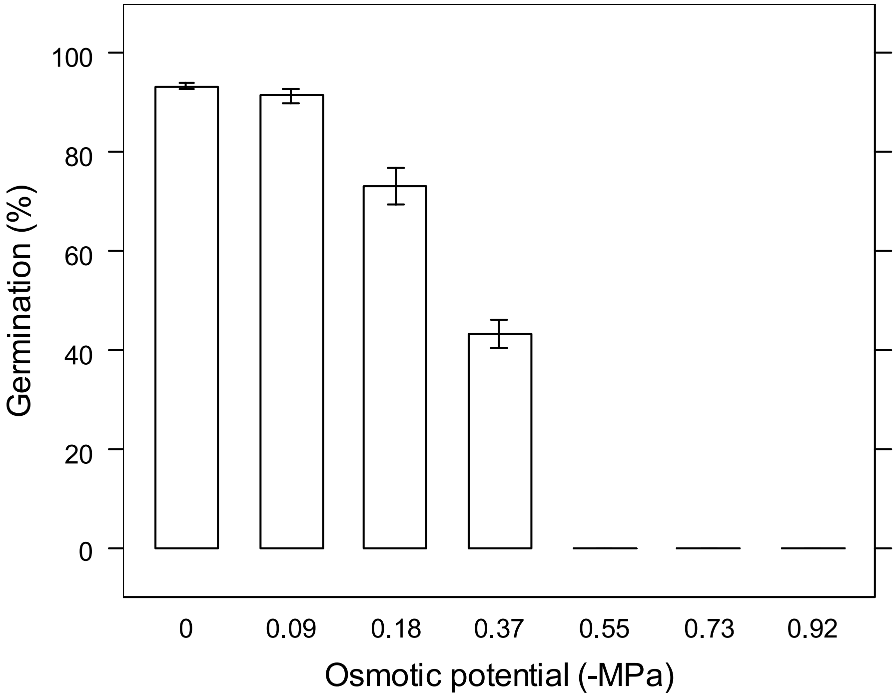

Figure 3.6 Effect of osmotic potential on germination of *H. hirta* seed incubated at 30/20 C day/night temperature with a 12 h photoperiod for eight days. Mean and standard error are shown.

Germination of *H. hirta* seeds was completely inhibited at osmotic potentials of -0.55 MPa or greater, indicating that *H. hirta* seeds were unable to germinate at low soil moisture, such as in winter in northern Australia. These findings are consistent with other studies on successful invaders of semi-arid regions such as, *L. rigidum*, and *Eragrostis curvula*, where tolerance of soil moisture stress provides a competitive advantage (Maze *et al.* 1993, Chauhan *et al.* 2006). Baruch and Bilbao (1999) reported seed germination in *Hyparrhenia rufa* up to on osmotic potential of -2.0 MPa. In contrast to *H. hirta*, germination in some Australian native grasses (e. g. *Bothriochloa macra*, *Chloris truncata*, and *Danthonia caespitos*) declined at -0.1 MPa (Maze *et al.* 1993). Watt (1982) found that in very wet conditions, native species have greater potential for successful establishment, whereas exotic species performed relatively better when available soil moisture was moderate or low. Germination of *H. hirta* below the limiting osmotic potentials for native grasses indicates greater tolerance of moisture stress at this stage of growth, which may be an important factor contributing to the establishment of this species under field conditions. The extent of drought tolerance of *H. hirta* needs to be confirmed in the field.

Statement of Originality:

All the work contained within this paper is the original research of the PhD candidate, Vinod Kumar Chejara.

Candidate:

[redacted]

Principal Supervisor:

Statement of Contribution by Others:

This paper has been prepared by the PhD candidate, Vinod Kumar Chejara. All coauthors are PhD supervisors (Paul Kristiansen, Wal Whalley, Brian Sindel, and Christopher Nadolny) and have only contributed to this paper to the extent that would normally be expected of such roles. All coauthors have given their consent for having their contributions to this paper included in the thesis and accept the student's contribution as indicated in the Statement of Originality.

Candidate:

[redacted]

Principal Supervisor:

CHAPTER FOUR

Vertical distribution and viability of *Hyparrhenia hirta* seeds and seedling emergence in soils of different textures

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Vertical distribution and viability of *Hyparrhenia hirta* seeds and seedling emergence in soils of different textures

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Abstract

Hyparrhenia hirta has become a serious invasive and environmental weed in Australia in recent decades. There is no published research on the vertical distribution, dormancy and viability of *H. hirta* seeds and its seedling emergence. However, the knowledge of the distribution and fate of *H. hirta* seeds particularly in different soils could assist in the development of effective weed control programs. A number of experiments were conducted to determine the vertical distribution of seeds in the soil profile in areas with long-term *H. hirta* infestations and to determine the effect of soil type, burial depth and time on dormancy, viability and emergence. The vertical distribution of seeds was assessed in the field in clay and sandy soils. In addition, the effect of burial depth and soil texture on dormancy and viability of *H. hirta* seed was studied in the field using seeds placed in litter bags for up to 12 months. Most (> 60%) of the seeds collected from *H. hirta* infestations in the field were found on or near the surface (0 – 2 cm), with deeper distribution in the clay soil than the sandy soil. The number of viable seeds recovered after burial was higher in sandy soil than clay soil. In the litter bag experiment, there was a linear decrease in seed dormancy and viability over time. Negligible dormancy and viability was observed at the final exhumation time (after 12 months), and seeds persisted slightly longer in the sandy soil. Seedling emergence was greatest at the 3 cm burial depth in both soil types but there was higher emergence in the clay soil with shallow seed burial but the trend was reversed with deeper burial. The rate of emergence and total emergence decreased with increased burial depth for both soil types. The results show that the seed bank for *H. hirta* in undisturbed habitats tends to be shallow, short-lived, with low innate dormancy and seedling emergence tend to be rapid. This suggests that there is potential to enhance *H. hirta* seed bank depletion by, for example, changing the vertical distribution of seed through specific tillage practices to increase germination and subsequent control (e.g. with herbicides) or by preventing further seed fall and soil disturbance altogether.

Nomenclature: Coolatai grass, thatching grass, *Hyparrhenia hirta* (L.) Stapf.

Key words: Buried seeds, germination, *Hyparrhenia hirta*, invasive weed, seed distribution, seed fate, seedling emergence, weed ecology.

4.1 Introduction

Hyparrhenia hirta (L.) Stapf (Coolatai grass, thatching grass) is a perennial grass, native to southern Africa and the Mediterranean Region. It has been introduced and become naturalized in many regions throughout the world with a Mediterranean or subtropical climate. The most rapid plant growth in this species occurs in late spring to mid-summer after rain (Faithful 2002), with a growth pattern typical of a warm-season sub-tropical species. In Australia, it was introduced in the 1890s to the Coolatai district of northern New South Wales, as a pasture plant and has more recently been used for erosion control (Hunt 2006), but it is now regarded as an invasive weedy species (McCormick *et al.* 1992) that is largely unpalatable to grazing cattle. It also has the potential to invade a wide range of rare native shaded grassy woodland and open grassland communities (Nadolny 1998, McArdle *et al.* 2004).

The occurrence, survival and emergence of seeds in the soil has important implications for the design of long-term weed control strategies (Bourdot and Hurrell 1992). The seeds of many successful pasture weeds have prolonged dormancy and viability, which enable them to survive through unfavorable conditions for plant growth (Altieri and Liebman 1988). Seed longevity and seedling emergence of many grass species is affected by burial depth (Alex 1980). However, no published information is available about the seed banks and seedling emergence of *H. hirta*. Such information is essential for understanding the population dynamics of this weed and for designing more effective management strategies.

The distribution of seeds, both horizontally and vertically controls the transition process from seed to plant (Chambers and MacMahon 1994). Processes that affect the vertical movement of seeds generally have a large influence on establishment and recruitment patterns of plants (Van der Wall and Joyner 1998). Hence, the fate of seeds after dispersal from a parent plant to the soil surface is of prime importance.

The vertical movement of seeds in soil can be significantly affected by physical processes that act on seeds after they reach the soil surface in the absence of tillage. Vertical movement of seeds into soil also depends on the interaction of seed morphology (size and shape) with soil surface characteristics and texture (Peart 1984, Thompson *et al.* 1993, Chambers 1995). Peart (1984) divided grass dispersal units into three main types: actively-awned, passively-awned and unawned. The active hygroscopic awns in many species of grass help to drill or to propel dispersal units into cracks across the soil surface (Peart 1979, 1984). The seeds of grasses that have awns can also be readily anchored and caused to germinate at the soil surface without developing a seed bank at greater depth in the soil (Peart 1984). The dispersal units of *H. hirta* have small, active-awns as well as inactive hairs, and may therefore be expected to be found at shallow depths in the soil profile. However, small compact seeds such as those of *H. hirta* may escape from processes that usually prevent penetration across the ground surface, such as germination, predation or secondary dispersal, and thus generally tend to have greater longevity than large seeds. The vertical movement of seeds in the soil may also depend on the ratio of seed size to soil particle size (Chambers *et al.* 1991). Fine-textured soils often experience pronounced alterations in their key physical properties throughout the year, developing cracks during the dry season of varying width and depth, which become closed during the wet season (Eswaran *et al.* 1999). *Hyparrhenia hirta* grows on a range of soil types from light textured granite soils to heavy black earths, but is said to prefer light textured soils (McCormick *et al.* 1992).

The current interest in forecasting and modelling seedbank dynamics has increased interest in the relationship between soil factors and weed seed dormancy and germination (Grundy *et al.* 1996, Buhler *et al.* 1997). It is now widely accepted that knowledge of the effects of climatic, ecological and agronomic factors on seedbank dynamics is important in direct and indirect weed control (Forcella *et al.* 1992). Benvenuti and Macchia (1998) found that deeply buried seed did not germinate primarily because of the limited soil gas diffusion, which is itself affected by soil texture (Radford and Greenwood 1970) and partly because of the lack of a light trigger. The emergence or recruitment of a seedling can also be affected by seed size, seedling morphology and soil compaction (Weller 1985, Maun and Lapierre 1986). Large-seeded species have much higher per-capita or per seed germination, emergence or establishment success than small-seeded species (Gross 1984, Dalling and Hubbell 2002). Seedlings from larger seeds are generally more likely to emerge from deeper in the soil than smaller seeds because of higher energy reserves and physical capacity for emergence (Watt and Whalley 1982a, Grundy 2003). The depth of seed burial also affects seed viability. Emergence has been reported from a wide range (0 to 15 cm) of soil depths (Balyan and Bhan 1986). The microsite requirements for some species can be extremely specific (Weaver and Cavers 1979, Boyd and Van Acker 2003). The seedling growth of grasses has been divided into two major forms: panicoid and festucoid type (Sargant and Arber 1915, Boyd and Avery 1936). *Hyparrhenia hirta* has panicoid seedling growth, with an elongated first and sub-coleoptile internode. The coleoptile serves to force a way upward through the soil while protecting the plumule bud within it (Hyder *et al.* 1971, Watt and Whalley 1982a). Benvenuti (2003) suggested that inhibition of seedling emergence at varying depths would be greater in a soil which has a higher percentage of clay than sandy soil. The seeds of *H. hirta* are small in size, so it was hypothesized that there would be little emergence from deep in either soil texture (clay and sandy) used in this study, but that emergence in clay would be less than in sand.

The aim of this study was to determine the vertical distribution, emergence pattern and viability of *H. hirta* seeds in the field and to determine the effect of soil type and depth of burial on seed viability and seedling emergence.

4.2 Materials and Methods

Experiment 1: Vertical Distribution of Seeds in the Field. To examine the vertical distribution of *H. hirta* seeds in the field, two sites heavily infested with *H. hirta* were selected on travelling stock routes at Armidale (30º 54′ S, 151º 88′ E, 1019 m elevation) and Yarrowyck (30º 47′ S, 151º 57′ E, 824 m elevation) on the Northern Tablelands of New South Wales, Australia. The mean annual temperature and precipitation at Armidale and Yarrowyck are 20 C and 23 C, and 790 and 766 mm, respectively. These study sites are surrounded by grazing country. Livestock grazing and disturbance (tillage practices) have not occurred at either site for at least 5 years. Soil texture was a meta-sedimentary clay (Chromosol) at Armidale and sandy granite (Tenosol) at Yarrowyck (Isbell 1996). In Autumn 2006 and 2007 when most of the seeds of *H. hirta* had dispersed from their parent plant at both sites, 10 soil cores (7 cm diameter and 10 cm depth) were collected randomly from each site. Each corer was forced into the soil until filled and then taken out of the soil and the ends sealed. The cores were then individually packed in plastic bags and taken to a laboratory.

Each core was separated into seven layers (0-1, 1-2, 2-3, 3-4, 4-5, 5-7, and 7-10 cm deep). Each sample was air dried and mixed by hand in the laboratory. Seeds of *H. hirta* were separated from the soil by sieving over 2, 1 and 0.5 mm sieves, removed with forceps and the number of seeds recovered from each layer was recorded. The recovered seeds for each layer were then incubated in Petri dishes in a controlled environment to determine germinability. The growth cabinet was set to alternate between 12 hours light at 30 C, and 12 hours dark at 20 C. Light was provided by two fluorescent tubes with a light intensity of 30 µmol m^{-2} s^{-1}. The number of seeds germinated on each dish was counted daily for 15 days and divided by the total number of seeds recovered to obtain the total percentage germination. Percent germination in each soil layer was also calculated.

Experiment 2: Effect of Depth of Burial on Seed Dormancy and Viability. To investigate the effect of burial depth and soil texture on seed dormancy and longevity, an experiment was established on August 2006, on two sites: one at Kirby Research Station (30º 43′ S, 151º 61′ E) and another at Trevanna (30º 29′ S, 151º 38′ E) on the campus of the University of New England (UNE), Armidale, NSW, Australia. The area has cold, relatively dry frosty winters, moist springs and warm summers. Average annual precipitation is 790 mm, falling mostly between August and October.

The soil types at the Kirby and Trevanna sites were sandy granite (Tenosol) and meta-sedimentary clay (Chromosol), respectively (Isbell 1996) with organic carbon contents of 1.2 and 1.6%, respectively. The vegetation on both sites consisted of native grasses with no *H. hirta*.

Hyparrhenia hirta seeds used in Experiments 2 and 3 were harvested from glasshouse grown plants at UNE, Armidale on 25th July 2006. The plants had been transplanted from a roadside *H. hirta* infestation near the University campus. The panicle dispersal units were harvested by running a thumb and forefinger along the length of mature inflorescences prior to shedding. Only fully developed caryopses, were used in these germination experiments and these were selected by squeezing dispersal units with forceps. Selected dispersal units (seeds) were then stored at room temperature until used in both experiments. Initial viability of this seed sample was tested in a growth cabinet (12 h light at 30 C, and 12 h dark at 20 C). The numbers of seeds germinated (radicle visibly protruding from the seed coat) were counted daily for 15 days. Any seeds that did not germinate were cut transversely slightly above the embryo and then tested with a 0.1% tetrazolium solution for viability, as described in Leist and Kramer (2003). The total viability of this seed sample was 80 ± 5%. The total germination achieved from the viable seed sample was 90 ± 5%.

Soil was collected from both sites where this experiment was conducted and air dried for 4 days and then sieved through a 1.0 mm mesh screen so that there would be good soil/seed contact when packed into the bags for burial. Soil was then steam-sterilized and stored at room temperature until used.

Twenty-five mature seeds of *H. hirta* were mixed with 120 g of steam sterilized soil and then placed in a 10 × 10 cm bag made of nylon mesh with a pore size of 500 micron. The experimental area was mowed before bags were buried at four depths, on the soil surface, 3 cm, 6 cm and 9 cm deep in the soil in a completely randomized design with four replications. Exhumation times were 2, 4, 8, and 12 months after the start of the experiment. Sixteen bags from each site were exhumed each time over the 12 month period.

After exhumation, the bags were taken to the laboratory. Soil of each bag was air dried and then seeds were separated from the soil by sieving over 2, 1 and 0.5 mm sieves. Seeds of *H. hirta* were removed using forceps. The number of seeds recovered from each bag was recorded separately. After this, seeds were tested for germinability in Petri dishes in a growth cabinet set to alternate between 12 h light at 30 C and 12 h dark at 20 C. The numbers of seeds germinated (radicle visibly protruding from the seed coat) were counted daily for 15 days. Any seeds that did not germinate were dissected and then tested with tetrazolium for viability. Seeds that were empty or soft or missing from the bags were counted as dead or lost. The number of viable seeds was the combined number of germinated and dormant seeds.

Experiment 3: Effect of Depth of Seed Burial on Seedling Emergence. The effect of seed burial on seedling emergence was studied in a growth cabinet at the UNE. Two soils of contrasting texture that were representative of soils infested with *H. hirta* were collected from UNE research farms as described in Experiment 2. One was a sandy granite derived soil (Tenosol) and the other was a meta-sedimentary clay (Chromosol) (Isbell 1996). The bulk densities of the clay and sandy soils were 1.36 and 1.33 g/ cm^3, respectively.

Twenty-five seeds of *H. hirta*, as collected in Experiment 2, were sown in plastic pots (8.5 cm diameter by 17 cm deep) at depths of 0, 3, 6 and 9 cm. These depths were selected on the basis of the maximum depth at which seeds were recovered in Experiment 1 (10 cm depth). The growth cabinet temperature and photoperiod settings were the same as for Experiment 1. Fluorescent lamps were used to produce a photosynthetic photon flux density of 600 µmol m^{-2} s^{-1}. Pots were placed on saucers and bottom-watered as needed (usually every second day) to maintain adequate soil moisture. Emergence was monitored over 35 days and successful emergence was achieved when the first leaf had emerged.

Statistical Analysis. The data on vertical distribution of seeds are presented as percentage of the total seeds recovered from all depths. Seedling emergence data (Experiment 3) are also presented as percentages. Analysis of variance was used to determine the significance of vertical distribution of seed, distribution of viable seeds, dormancy, viability and seedling emergence response to soil depth and texture with the statistical package R 2.2.0 (R Development Core Team 2006). Variances were checked by plotting residual vs. fitted values to confirm the homogeneity of the data, but no transformations were necessary. Standard errors were used to separate significantly different treatments (Webster and Payne 2002). Means and standard error bar plots were used to present the vertical distribution of seed, viability and dormancy data graphically. A logistic model, $y = a/(1+\exp((b-x)/c)$, was fitted to the data for emergence of *H. hirta* in contrasting soil textures over time, where y is the total emergence (%) at depth x, a is the maximum emergence (%), b is the time taken to obtain 50% of the maximum emergence, and c indicates the slope (MathSoft 1999).

4.3 Results and Discussion

Experiment 1: Vertical distribution of seeds in the field. The total densities of seeds of *H. hirta* recovered from Armidale and Yarrowyck sites were 32 441 and 31 584 m^{-2}, respectively. Significant differences ($P < 0.005$) between different depths were observed in the percent vertical distribution of *H. hirta* seeds, with most of the seeds (>60%) found in the 0-1 cm layer and a further 20% found in the 1-2 cm layer

(Figure 4.1). In contrast the number of seeds at 7-10 cm was negligible. Soil texture was also a significant factor in determining vertical distribution of seeds at depths greater than 2 cm where the number of seeds was significantly higher in the clay soil than the sandy soil.

The number of viable seeds of *H. hirta* also decreased with soil depth in line with the number of seeds recovered (Figure 4.1). The majority of viable seeds (~65%) were found at 0-1 cm and another 15% at 1-2 cm. No viable seed was recovered below 7 cm. There was no significant ($P = 0.571$) difference between soil textures in the number of viable seeds at any given depth.

The number of viable seeds as a proportion of seeds recovered in each soil layer was highest (>15%) at 0-1 cm (Figure 4.1). The proportion of viable seeds at 2-7 cm did not differ significantly ($P < 0.005$). The proportion of viable seeds in sandy soil was higher than clay soil, especially at 0-2 cm.

Seeds were recovered from all soil layers up to 10 cm depth, but in decreasing quantities as depth increased. The was similar to the results for *Sporobolus* spp. and *Scirpus litoral* (Andrews 1995, Espinar *et al.* 2005). Most seeds of *H. hirta* were recovered in the 0-2 cm soil layer as were those of other grass species such as *Sporobolus* spp. and *Stipa neesiana* on uncultivated soil (Bourdot and Hurrell 1992, Andrews 1995), with very few seeds collected from the lower soil depths. The entry of seeds into deep soil layers via cracks in dry soil during the period of seed rain can be a reason for this depth distribution of seeds (Eswaran *et al.* 1999, Espinar *et al.* 2005). The soil cracking tend to be much greater in the clay soil as compared to the sandy soil used in this study (Isbell 1996). Stamp (1984) suggests that seeds of grasses have the ability to move vertically for self-burial because of their hygroscopic awns. There were no significant differences in the proportion of seeds in the clay and sandy soil at upper depths (0-2 cm), whereas, at lower depths the proportion of seeds were significantly higher in clay soil than sandy soil. The influence of soil texture on vertical movement of seed may be associated with the colloidal component of the soil (Benvenuti 2007). High cohesive forces of smaller soil particles particularly clay soil particles form in the presence of bivalent and trivalent cations which help in the attraction particles to one another and therefore, form possible barriers to the raindrop-induced gravitational movement of seeds (Marshall *et al.* 1996, Benvenuti 2007). However the small and awned seeds of *H. hirta* may have a tendency to be self-buried in the soil and form a more persistent seed bank.

The viability of *H. hirta* seeds decreased as the soil depth increased (Figure 4.1). Perhaps seeds at shallow depths were produced more recently, whereas seeds from lower depths were possibly older and had taken some time to move down through the soil profile (Chambers and MacMahon 1994, Thompson *et al.* 1994, Rotundo and Aguiar 2004). Assuming that some proportion of the buried seed bank dies each year (Rice 1989), it is reasonable to expect that the seeds at lower soil depths will be less viable.

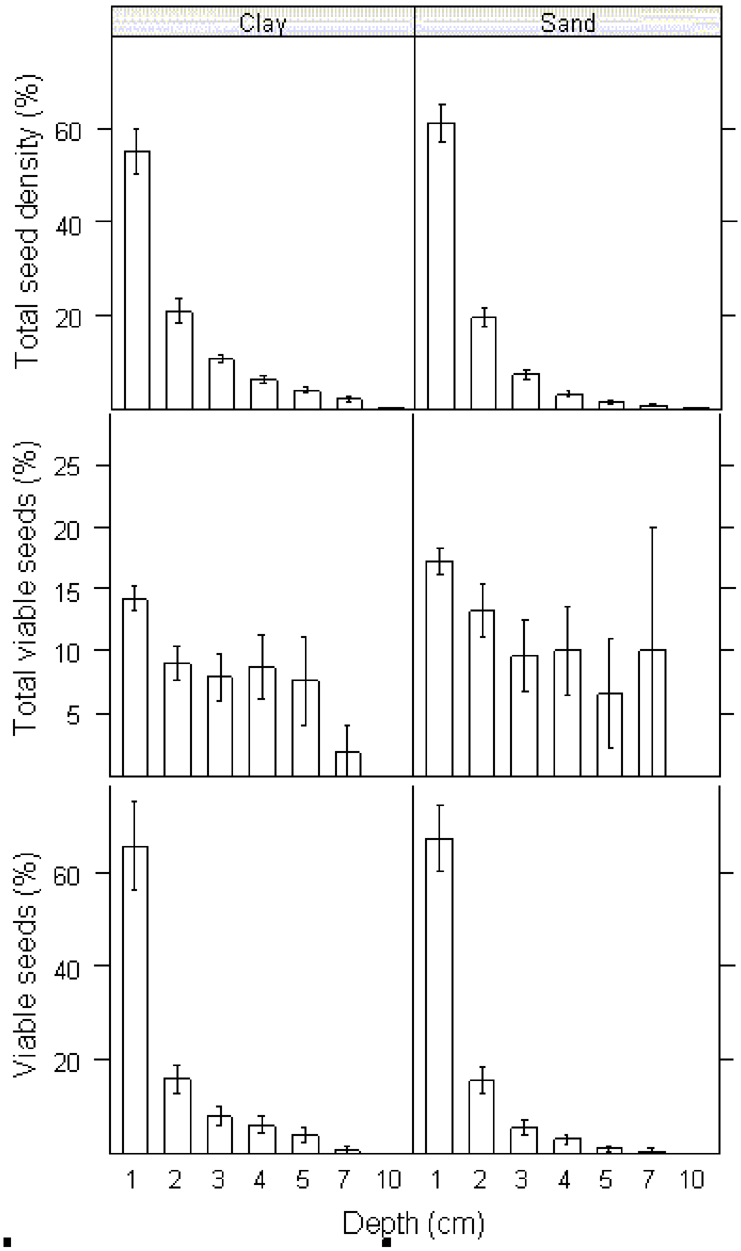

Figure 4.1 Percentage of *H. hirta* seeds recovered from infested field sites with sandy or clay soil. The top plot shows the total percentage of seeds recovered, the middle plot shows the percentage of viable seeds at each depth and the bottom plot shows the percentage viability of seeds recovered at each depth. Means and standard errors are shown.

Experiment 2: Effect of depth of burial on seed dormancy and viability. The proportion of dormant *H. hirta* seeds in the field was significantly influenced by the soil texture and exhumation time interaction (P = 0.007). Burial depth was not significant (P = 0.911) as a main term or in any interactions. The proportion of dormant seeds declined over time and was greater in sandy soil than clay soil (Figure 4.2). In clay soil there were no dormant seeds recovered at 8 or 12 months from 0 or 3 cm depths and none at 12 months at 6 and 9 cm, whereas in sandy soil dormancy was retained in a small proportion of seeds until 12 months at 3 and 6 cm depths.

Germinability of buried seeds was significantly (P = 0.008) affected by the interaction between soil type, soil depth and time of exhumation (Figure 4.2). The proportion of germinable seeds declined over the 12 month period of exhumation. In the first two exhumations of seed burial, germination was significantly higher in clay soil than sandy soil at shallow depths. Whereas, at deeper depths it was greater in sandy soil. Most of the seeds lost their viability within 8 months of burial except for a few seeds which were still viable after 12 months, particularly at 6 and 9 cm depths.

Hyparrhenia hirta seeds used in the depth burial study had very little innate (primary) dormancy, resulting in 90 ± 5% germination in the laboratory. Buried seeds are most likely to maintain their longevity longer because of the presence of dormancy enforced in a large portion of the seed bank by unfavorable environments around the buried seed. The proportion of dead and lost seeds in the buried bags rapidly increased in each of the depth treatments over time (Figure 4.2). Irrespective of the depth at which the seed was buried, the seed either decayed or disappeared from the seed bag or it remained as an empty seed coat. In addition, the possibility of microbial decay, predation by microorganisms and pathogens can not be ruled out.

Similar results had also been reported by Trotter (2006) in *Nassella trichotoma* where more than 80% of seeds were reported dead after 19 months of burial.

The dormancy of buried seeds decreased at all depths over time. Seeds of *H. hirta* can retain their dormancy and viability up to 8 months in the field. The observed viability in buried seeds up to 8 months suggests that seed may have acquired dormancy because of inhibitory factors, such as darkness and the lack of suitable edaphic conditions for germination (Omami *et al.* 1999). Seeds buried in clay soil lost their dormancy and viability faster than those in sandy soil possibly because of several factors including the higher organic carbon content, increasing soil biological activity and decomposition processes (Van *et al.* 2005). In clay soil at surface and shallow depth (3 cm) dormancy was retained for less time than at greater depths, suggesting that a mechanism for inducing dormancy was most likely less effective in seeds placed in shallow depths or on the soil surface (Omami *et al.* 1999, Baskin *et al.* 2004). Germinability in the laboratory after exhumation declined at all depths over time (Figure 4.1). By the final exhumation (12 months after burial), germinability (in both soil types) was higher in seed stored in deeper layers (6 and 9 cm), which could be due to lack of a light trigger and oxygen at lower depths (Benvenuti 2003, Benvenuti *et al.* 2005).

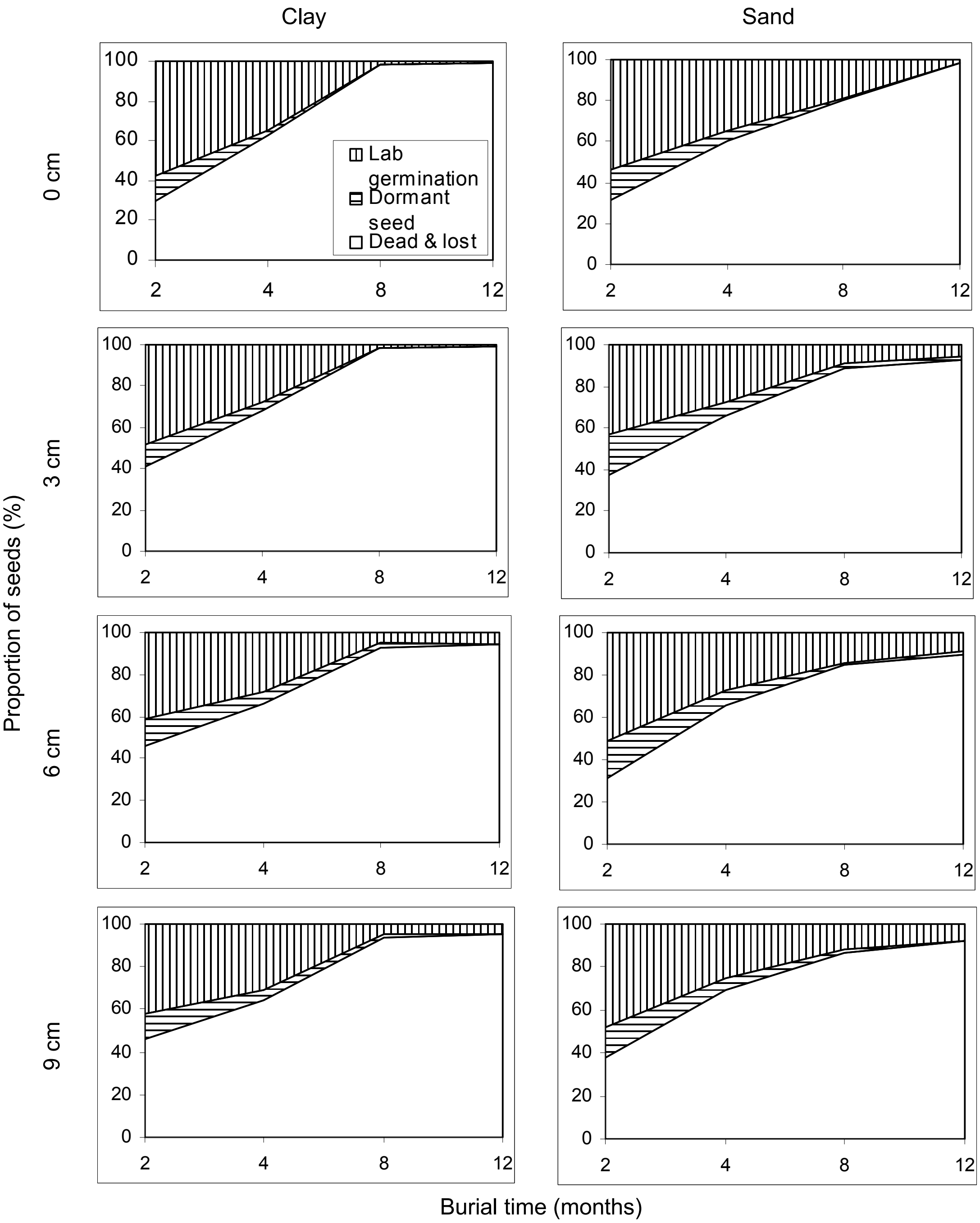

Figure 4.2 The fate of *H. hirta* seeds buried at 0, 3, 6 and 9 cm over a 12 month period in two different soil textures (clay and sand).

Experiment 3: Effect of depth of seed burial on seedling emergence. A logistic function was fitted to determine the effect of depth of seed burial on emergence (%) of *H. hirta* over time in two contrasting soil types (Figure 4.3). The highest number of seedlings emerged from the shallow depth (3 cm) but then decreased significantly as the planting depth increased. Seedling emergence at the soil surface was significantly ($P < 0.05$) less than the shallow depth (3 cm).

At the shallow depths (surface and 3 cm), the estimated seedling emergence was greater in clay soil than sandy soil whereas, at deeper depths (below 3 cm) seedling emergence was higher in sandy soil than clay soil. Seedling emergence was the greatest (~ 90%) at burial depth 3 cm in clay soil. In sandy soil, seedling emergence was also highest (~ 80%) at planting depth 3 cm, but at 6 cm, was 30% more than clay soil. Seedling emergence at 9 cm was 3 and 11% in clay and sandy soil, respectively.

The emergence rate, indicated by *b* (time to 50% of estimated maximum emergence), was least at depth 3 cm, where *b* was about 5.5 days in sandy soil and 6.5 days in the clay soil. In sandy soil, the emergence rates at 0, 3 and 6 cm were not significantly different (*b* = 5-7 days) to each other, but the rate of emergence at 9 cm depth was significantly lower (*b* = 12 days) than other depths. In both soils, the fastest emergence occurred at 3 cm followed by the 6, 0 and 9 cm depths.

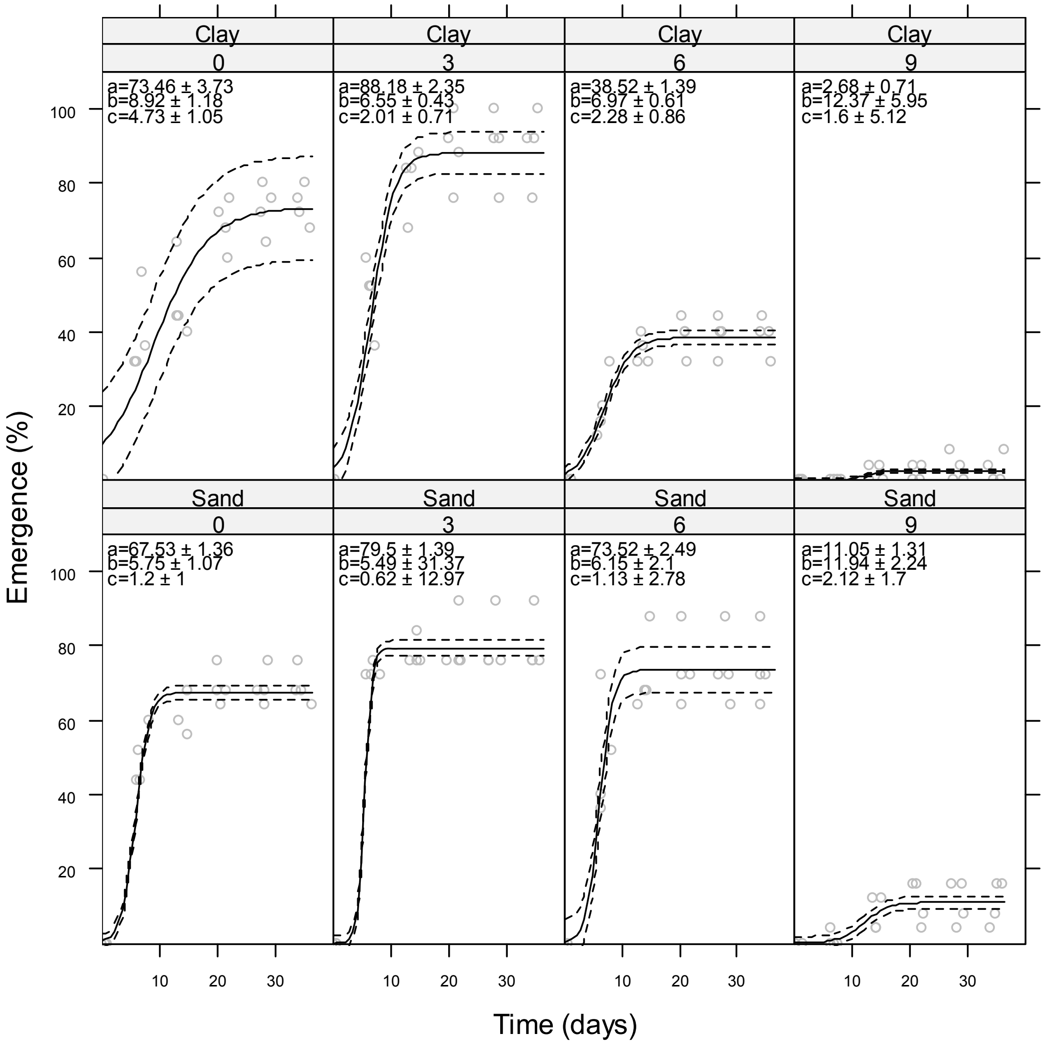

Figure 4.3 Effect of soil type (clay and sand) and planting depth (0, 3, 6 and 9 cm) on emergence of *H. hirta* seedlings in a growth cabinet at 30/20 C day/night temperature with a 12 h photoperiod for 35 days after planting. Logistic regression curves (continuous lines) of the form $y = a/(1+\exp((b-x)/c)$, are shown with 95% confidence limits (dashed lines) and model parameters (± standard error).

Seeds can often germinate faster in sandy soil than clay soil because of less soil compaction, lower bulk density and better oxygen transport (Refsgaard *et al.* 1991, Sun and Dickinson 1996). For example, higher seedling emergence of *Astrebla* *lappacea* occurs in sandy soil than in clay soil (Lambert *et al.* 1990). Greater seed germination and seedling emergence at shallow depth of burial is normally due to good soil-seed contact and moisture availability at the shallow depths (Ghorbani *et al.* 1999). Benvenuti (2003) suggested that the major cause of the reduction in seedling emergence from deep in the soil is fatal germination and failure of germinated seeds to reach the surface. Increasing soil depth also retards the early development of the secondary root system (Lambert *et al.* 1990). Once a seed has germinated, its size, vertical position within the soil profile, seedling morphology, soil type and compaction play an important role in emergence of seedlings (Sheldon 1974, Maun and Lapierre 1986). Seedlings from larger seeds have generally more chance to emerge from depth in the soil than smaller seeds because of higher energy reserves and physical capacity (Watt and Whalley 1982a, Grundy 2003). It is believed that panicoid type seedlings have less capability to emerge from depth than festucoid seedlings (Hyder and Sneva 1963, Watt and Whalley 1982a). *Hyparrhenia hirta* has panicoid seedling morphology. Deeper planting of a panicoid grass can only hinder its establishment, due to the greater risk of restricted secondary root development as the surface soil dries out (Hyder and Sneva 1963, Watt and Whalley 1982a, Lambert *et al.* 1990). Watt and Whalley (1982b) also found a similar trend of emergence and establishment of some native (*Bothriochloa macra*, *Dichanthium sericeum*) and exotic grasses (*Panicum coloratum*, *Pennisetum clandestinum*). The negligible seedling emergence from 9 cm can be due to soil compaction (Sheldon 1974) and unavailability of oxygen for seed respiration (Refsgaard *et al.* 1991). Decreased emergence due to increased planting depth has also been reported in other grasses as well; for example *Lolium rigidum* (Chauhan *et al.* 2006), *B. macra*, *D. sericeum*, *P. coloratum*, and *P. clandestinum* (Watt and Whalley 1982a).

The speed of seedling emergence, like emergence itself, was greatest at 3 cm in sandy and clay soil, while better soil-seed contact, soil moisture and oxygen transport may improve germination and emergence (Refsgaard *et al.* 1991, Ghorbani *et al.* 1999). The small seeded grasses like *H. hirta* have poor physical capacity to emerge fast upward from the deeper depths in the soil (Watt and Whalley 1982a). Panicoid type grass seedling emergence and establishment can be slow if seed is planted deeper in the soil due to restricted secondary root development (Hyder *et al.* 1971, Lambert *et al.* 1990).

The relatively short life-expectancy of *H. hirta* seeds has major implications for the control of this weed. The results on seed biology of *H. hirta* indicate that if all existing plants at a site are destroyed and all emerged seedlings are killed before seed set next year, it is likely that this species could be eradicated from the site. These results explain why there has been very little re-infestation of sites on travelling stock routes near Manilla, where infestations of *H. hirta* had been controlled by spot spraying in the recent past (Chejara *et al.* 2006).

Statement of Originality:

All the work contained within this paper is the original research of the PhD candidate, Vinod Kumar Chejara.

Candidate:

Principal Supervisor:

Statement of Contribution by Others:

This paper has been prepared by the PhD candidate, Vinod Kumar Chejara. All coauthors are PhD supervisors (Paul Kristiansen, Wal Whalley, Brian Sindel, and Christopher Nadolny) and have only contributed to this paper to the extent that would normally be expected of such roles. All coauthors have given their consent for having their contributions to this paper included in the thesis and accept the student's contribution as indicated in the Statement of Originality.

Candidate:

Principal Supervisor:

CHAPTER FIVE

Seedbank and seedling dynamics in *Hyparrhenia hirta* as affected by management factors

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Seedbank and seedling dynamics in *Hyparrhenia hirta* as affected by management factors

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Abstract

Hyparrhenia hirta has become highly invasive in Australia where it has become a serious environmental weed in recent decades. Understanding seed and seedling dynamics of weeds and how various management treatments (e.g. mowing, herbicide and no management) affect these may assist in identifying the conditions and management strategies required to limit invasion. The population dynamics of *H. hirta* have not been studied previously. A two year field study was conducted to determine the seedbank, pattern of seedling emergence and survival of *H. hirta* at three sites in northern New South Wales, Australia, under three treatments: an unmanaged (control), mown and herbicide treatments. *Hyparrhenia hirta* seedlings were assessed at monthly intervals in permanent quadrats (0.5 × 0.5 m) to determine seedling emergence from January 2006 to December 2007. The density of *H. hirta* seeds in the soil at each experimental site under different treatments was measured in December 2005, and December 2006 before the application of treatments and again at the end of the trial in December 2007 by taking ten randomly placed soil cores from each plot, outside the monitoring quadrats. Seedling emergence occurred on many occasions during the two year period of the trial in each treatment and at all sites but the main seedling flushes were observed in the warmer months from midsummer to early autumn. In 2007, at all sites, seedling emergence declined by more than 90% in mown and herbicide treated plots compared with the control plots. Seedling survivorship was greater in mown and herbicide treatments than the control. The seedling cohorts emerging in winter had lower survival. *Hyparrhenia hirta* seedlings are moderately sensitive to frost and low temperatures. This study showed that *H. hirta* may have a large viable seedbank, dependent on the level of infestation and climatic conditions, but that the seedbank declines rapidly when seed addition is prevented. Therefore, some form of direct control of *H. hirta* in combination with providing good pasture competition and grazing management, will assist in the control of *H. hirta*.

Keywords: alien species, disturbance, establishment, *Hyparrhenia hirta*, seed dynamics, seedling dynamics,

5.1 Introduction

Biological invasions, particularly by introduced grasses, have become a major threat to agriculture, natural ecosystems and biodiversity world-wide (Mack *et al.* 2000, Williams and Baruch 2000). Control of invasive plant species is often expensive, labour intensive and has limited success (Myers *et al.* 2000). Management outcomes are also influenced by environmental variations (Hansen and Wilson 2006). Therefore, effective long-term weed control strategies must be based on a sound understanding of the population dynamics of the weed, with an understanding of conditions that promote or suppress establishment and growth of the weed in a particular environment (Sindel 2000).

Hyparrhenia hirta (L.) Stapf (Coolatai grass) is a summer-active, C4 perennial grass, native to southern Africa and the Mediterranean region. It grows in open savannas, extending into the dry tropics, particularly in highland regions (Clayton

1969). It was introduced in the 1890s to the Coolatai district of northern New South Wales (NSW), Australia, as a pasture plant and has more recently been used for erosion control (Hunt 2006); it now invades areas of native flora, particularly roadsides, travelling stock reserves and pastures (Nadolny 1998, McArdle *et al.* 2004). The population dynamics of *H. hirta* have not been studied previously. Earlier studies have highlighted the importance of understanding the effects of various management treatments (e.g. grazing, mowing, herbicide application, no management) on population dynamics of weedy plants (Grace *et al.* 1999, Meyer and Schmid 1999, Lamoureaux and Bourdot 2002, Hansen and Wilson 2006).

Defoliation by clipping and mowing had been used in many studies to simulate grazing which is often integral to grassland management (Milchunas and Noy-Meir 2002, Verrier and Kirkpatrick 2005). Verrier and Kirkpatrick (2005) found that mowing produced a greater cover of rare or threatened species, greater native plant cover and lower exotic grass cover in Tasmania than an unmown (control) treatment. Mowing may remove biomass and prevent seed production as well as addition of seeds to the soil seed bank (Meyer and Schmid 1999). On the other hand, mowing can reduce vegetation cover sufficiently to allow seeds of some species to germinate and grow, potentially forming new populations (Gross 1980). For example, Trotter (2006) found that slashing encouraged the seedling survival of *Nassella trichotoma* on the Northern Tablelands of NSW, and suggested that disturbance created by slashing a pasture is not an adequate method to control this weed.

Herbicides are the primary method for controlling invasive species in most rangeland systems (DiTomaso 2000). Currently, control of *H. hirta* in Australia is based on slashing and spraying with glyphosate (Lodge *et al.* 1994, Luckens 2002). There are also off-label permits for its control using glyphosate and flupropanate in north-west NSW. However, continuous use of a single herbicide can select for resistance in the target weed species and can also potentially harm native species (DiTomaso 2000, Reever-Morghan *et al.* 2003), which may limit its value for the long-term control of invasive species.

The aim of this research was to determine the impact of herbicide application and mowing on the seed bank, emergence and survival of *H. hirta* compared with unmanaged vegetation or control.

5.2 Materials and methods

Study species

Hyparrhenia hirta is a perennial, hermaphrodite tussock grass, 1-2 m tall at flowering, with a 3 m deep root system (Humphries 1965). The growing period is controlled by temperature and rainfall, with most annual dry matter production occurring in the Northern Tablelands of NSW, Australia, between October and April, and peak growth rates between December to February (Chris Nadolny *pers. comm.*). In Mediterranean climates in Australia, flowering starts in midsummer, from December to January; however, in parts of South Australia, flowering has been reported to occur year-round (Warner 2004). Robinson and Potts (1950) indicated that this species is sensitive to frost, and may be killed in a harsh winter in the subtropical environment of Florida. They stated that it produces seeds well in to late summer and autumn.

Diaspores are mainly hairy seeds with long awned husks that are capable of catching on people, animals and vehicles that move past the plant. Human activities such as slashing or vehicular traffic can assist in spreading the weed, particularly along roadsides (Luckens 2002). The long, robust, hygroscopic awns of grasses such as *H. hirta* generally promote self-burial of seeds into the soil and form a large seed bank (Benvenuti 2007). Dispersed seeds remain dormant for 12 months (see Chapter

4) and can germinate over a range of temperatures between 5 - 45 ºC, with a peak at 25 - 30 ºC (Chejara *et al.* in press).

Study sites

To study the population dynamics of *H. hirta*, three experimental field sites were established in highly invaded travelling stock routes on the north-west slopes and New England Tableland region of New South Wales (NSW), Australia (Figure 5.1). All three sites had only been lightly grazed at most, in the past five years and occurred in grassy-woodland communities. The soil was a meta-sedimentary clay (Chromosol) at Armidale and Manilla, and a sandy granite (Tenosol) at Yarrowyck (Isbell 1996). The topsoils were very low in available phosphorus, nitrogen and total sulphur (Table 5.1).

The Manilla site (30º 50′ S, 150º 47′ E, 492 m altitude) was surrounded by cropping and grazing land. This region has a warm temperate climate with a mean maximum air temperature of 24.5 ºC in summer and 9.8 ºC in winter (Bureau of Meteorology 2007). The mean annual rainfall is 675 mm, with rain occurring throughout the year but with slight summer dominance (Bureau of Meteorology 2007). The weather recordings for all study sites during the trial period are shown in Figure 5.2.

The Armidale site (30º 54′ S, 151º 88′ E, 1019 m altitude) was surrounded by grazing properties with areas of grassland dominated by grasses, *H. hirta*, *Poa sieberana*, *Bothriochloa macra*, *Dichanthium sericeum*, *Phalaris aquatica* and scattered *Eucalyptus* trees. This region has a temperate climate with a mean maximum air temperature of 19.5 ºC in summer and 7.2 ºC in winter and a mean minimum air temperature of 13 ºC in summer and 1 ºC in winter with an average of 94 frosts a year. The mean annual rainfall is 790 mm (Bureau of Meteorology 2007, Burr 2007).

The Yarrowyck site (30º 47′ S, 151º 57′ E, 824 m altitude) has long term average annual precipitation of 766 mm (Bureau of Meteorology 2007). The vegetation community of this site is grassy-woodland dominated by *H. hirta*, *Aristida ramosa*, *Chrysocephalum apiculatum*, *Carex inversa* and various *Eucalyptus* species, such as *E. blakelyi*.

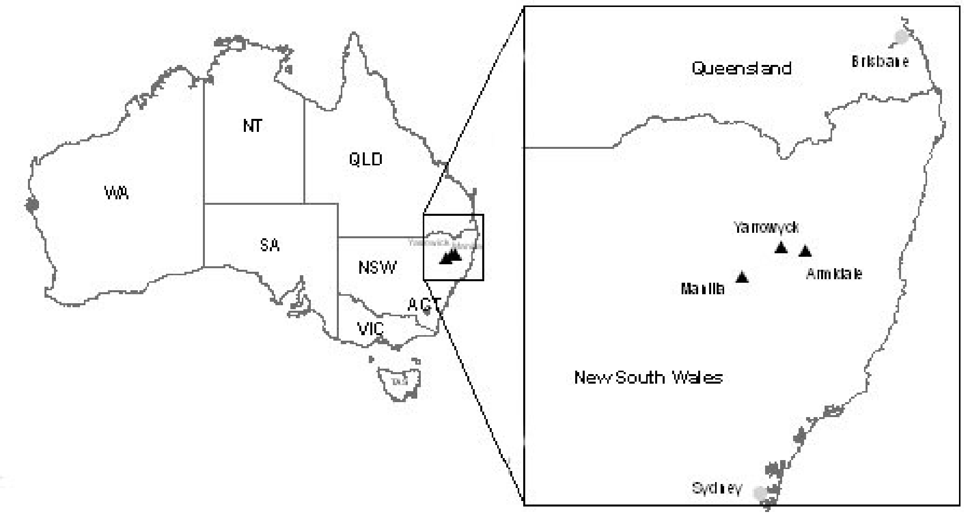

Figure 5.1 Location of the three field sites in northern NSW, Australia ▲.

Experimental treatments

The studies were carried out between December 2005 and December 2007. In December 2005, three treatments were applied at each of the three sites: control (unmanaged), herbicide application and mowing. Plots were fenced and kept ungrazed throughout the experimental period. Each treatment was applied in 2 × 2 m plots, leaving a 0.5 m buffer zone to minimise edge effects. Four replicate plots were used at each site in a completely randomised design. Permanent quadrats (0.5 × 0.5 m) were set up at the centre of each plot for monitoring *H. hirta* seedling emergence and survival monthly.

The control treatment had existing vegetation and was left undisturbed. The herbicide treatment had Roundup Bioactive (360g/L a.i. glyphosate) applied at a rate of 4 kg a.i./ha (Lodge *et al.* 1994) with a hand-held pneumatic sprayer in the second week of December 2005 and at the same week in 2006. Grazing was simulated by mowing by using a lawn mower and removing all biomass 3 - 6 cm above ground level in December 2005 and December 2006. These plots were also trimmed using a hand-held electric shears further three times a year to prevent the addition of new seeds of *H. hirta*.

Table 5.1 Soil parameters for the three experimental sites

Parameter (method of analysis*) [units]	Experimental site		
	Manilla	Armidale	Yarrowyck
pH (1:5 water)	6.5	6.8	6.6
organic carbon [%]	1.8	2.4	0.97
nitrate nitrogen [mg/kg]	1.1	1.8	1.3
sulfate sulfur (KCl40) [mg/kg]	< 1.0	2.0	< 1.0
phosphorus (Colwell) [mg/kg]	12	8.1	8.3
potassium (AmAc) [meq/100g]	0.62	0.47	0.21
calcium (AmAc) [meq/100g]	6.5	6.0	2.5
magnesium (AmAc) [meq/100g]	2.6	2.1	0.82

*abbreviations: AmAc = ammonium acetate, KCl = potassium chloride

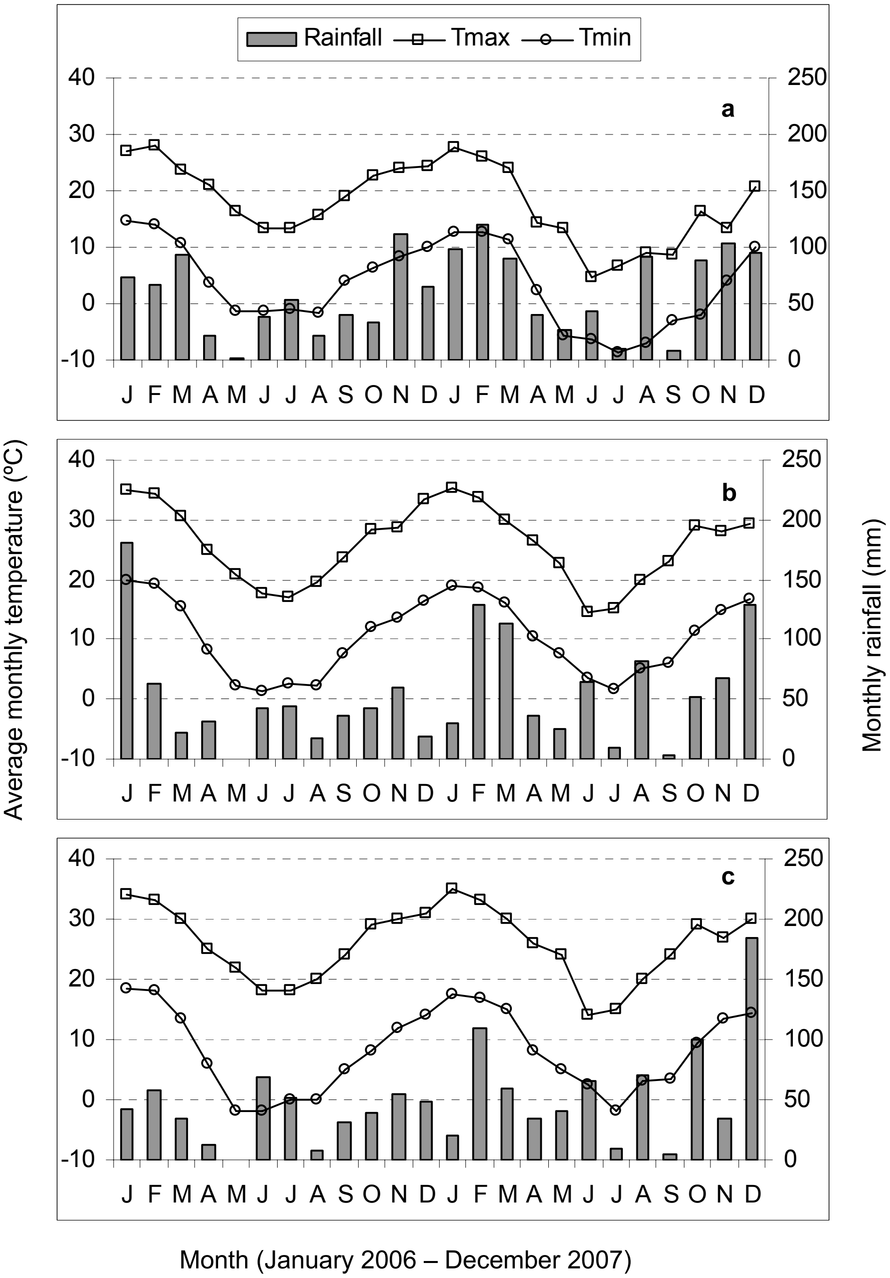

Figure 5.2 Weather conditions during the experimental period at (a) Armidale, (b) Manilla and (c) Yarrowyck. Bars show total monthly rainfall (right axes), and lines show mean monthly maximum (Tmax) and minimum (Tmin) temperatures (left axes). Data source: (Bureau of Meteorology 2007, Burr 2007).

Measurements

Seedbank

The density of *H. hirta* seeds in the soil at each experimental site was measured in December 2005 and December 2006 before the application of treatments and at the end of the trial in December 2007 by taking ten randomly placed soil cores from each plot, outside the permanent monitoring quadrats. Soil cores were 50 mm in diameter and 100 mm in depth. The total number of seeds in each core was determined by washing the core through sieves with a 0.5 mm mesh size.

The recovered seeds from each core were then incubated in Petri dishes lined with moistened Whatmans No. 1 filter paper in a controlled environment to determine germinability. The growth cabinet was set to alternate between 12 hours light at 30 ºC, and 12 hours dark at 20 ºC. Fluorescent lamps were used to produce a light intensity of 85 µmol m^{-2} s^{-1}. The number of seeds germinated on each dish was counted daily for 15 days and divided by the total number of seeds recovered to obtain the total number of germinable seeds. Any complete seeds that did not germinate were cut transversely slightly above the embryo and then tested with a 0.1% tetrazolium solution for viability (Leist and Kramer 2003).

Seedling emergence and survival

Hyparrhenia hirta seedlings were assessed at the end of each month throughout the experimental period in the permanent quadrats. All new seedlings of *H. hirta* that emerged within the month were counted and marked with a coloured pin representative of the month of emergence. Surviving seedlings from previous months were also identified and counted. Pins which were no longer associated with a living seedling were removed and counted.

Biomass production

To measure biomass and species composition, vegetation was clipped at ground level in three 0.2 × 0.2 m randomly placed quadrats using electric shears. These samples were taken before the application of treatments in 2005 and 2006 and a final sample taken at the end of experiment in December, 2007. Plants were identified, dried at 40 ºC for 48 hours and weighed. Each biomass sample was categorised into four groups: perennial grasses, annual grasses, legumes and other forbs. Only *H. hirta* biomass data are presented here.

Statistical analysis

All analyses were performed using the statistical package R 2.2.0 (R Development Core Team 2006). Analyses of variance (ANOVA) were performed on the total number of emerged seedlings, seedling survival, seedbank and biomass production per meter square. The cumulative seedling emergence data were plotted (Figure 5.3) using the `loess` smoothing function in R (R Development Core Team 2006). The data on survival of seedlings were presented using survivorship curves. In this approach the interval-specific survivorship (number of seedlings emerged in a particular census period minus dead seedlings from that period) was plotted using line graphs in Microsoft Excel. Variances were checked by plotting residual vs. fitted values to confirm the homogeneity of the data. Data for emergence, mortality and survival against site, year and treatments were square root transformed prior to analysis. Significantly different treatments were separated using orthogonal contrasts.

5.3 Results

Seedling emergence

The pattern of seedling emergence of *H. hirta* varied significantly ($P < 0.05$) between year, sites and treatments. Throughout the experimental period, the greatest number of seedlings emerged at the Armidale site followed by Manilla and Yarrowyck (Figure 5.3). The control treatment had the greatest seedling recruitment followed by the mowing and herbicide treatments. Seedlings emerged throughout the year but the main seedling flushes were in the warmer months, from October to March.

At Armidale in 2006, the density of emerged seedlings was 106, 79 and 53 m^{-2} in the control, mown and herbicide treatments, respectively. In 2007, seedling emergence was 16, 98 and 90% lower in the control, herbicide and mown treatments, respectively compared with 2006. After 14 months, there was no further recruitment recorded in the herbicide and mowing treatments.

At Manilla in 2006, the highest emergence occurred in the control treatment (90 seedlings/m^2) followed by the herbicide and mown treatments where emergence was 55 and 50 seedlings/m^2, respectively. In 2007, seedling recruitment was 11, 91 and 88% lower compared with 2006 under the control, herbicide and mown treatments, respectively. In the herbicide and mown treatments, further seedling emergence did not occur after 16 months.

At Yarrowyck, the total number of seedlings emerged in 2006 was 80, 32 and 59 seedlings/m^2 in the control, herbicide and mown treatments, respectively, while in 2007, emergence diminished by 14, 97 and 93% in the control, herbicide and mown treatments compared with emergence in 2006. There was no further emergence after 10 and 16 months in the herbicide and mown treatments, respectively.

Survivorship of seedlings

Survival curves describing the number of seedlings recruited at a month and the length of time over which these cohorts of seedlings survived are shown in Figures

5.4. The ANOVA showed that survival pattern of *H. hirta* seedlings varied significantly ($P < 0.05$) between sites, year and treatments. Seedling mortality was high in all treatments, mostly occurring in winter. In 2006 at all sites and in all treatments, seedlings that emerged in early summer had maximum survival rates.

The survival rate was highest at Manilla followed by Yarrowyck and Armidale. In 2006, the herbicide treatment had the greatest seedling survival compared with the other two treatments.

Armidale site

At Armidale, the overall seedling survival rate in 2006 was highest (38%) in the herbicide treatment followed by the control (31%) and mown (30%) treatment. However, in 2007 it was highest (30%) in the control treatment. Seedling recruitment in the control treatment occurred in 22 occasions (Figure 5.4). The largest cohorts of seedlings emerged between January and March each year. In January 2006, 19 seedlings emerged in the control treatment but only one seedling survived throughout the study period. The highest seedling survivorship (3 seedlings/m^2) observed was from the September 2006.

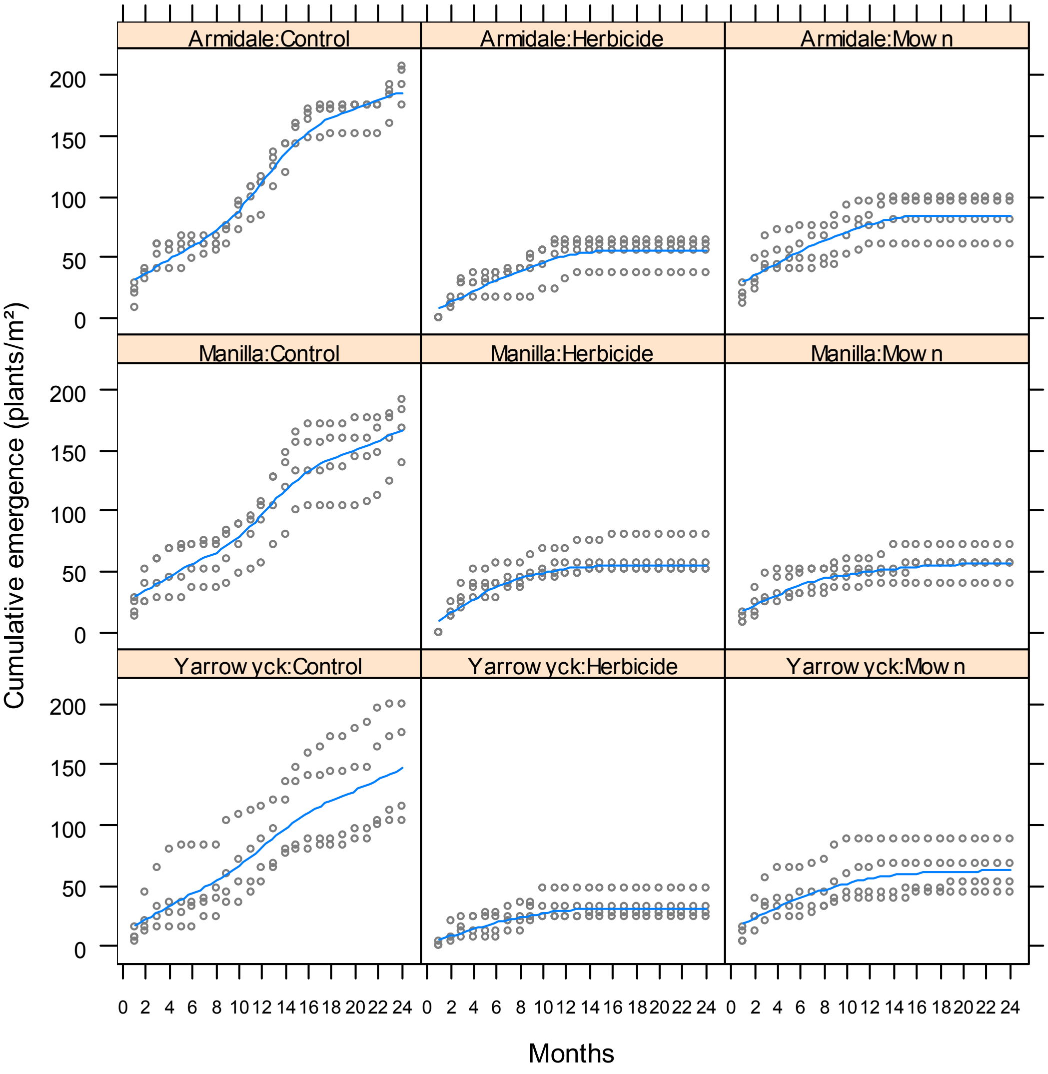

Figure 5.3 Cumulative seedling emergence of *H. hirta* over two years (January 2006 – December 2007), shown as months (January 2006 = 1) under three management treatments; control, herbicide and mown at three study sites; Armidale, Manilla and Yarrowyck. Lines represent the pattern of cumulative emergence and circles represent data points in four replicates.

Twelve cohorts occurred in the mown treatment at the Armidale site (Figure 5.4). Nineteen seedlings were observed in January 2006 and four of them survived until the next mown treatment in December 2006. Most of the mortality of the January 2006 cohort occurred between February and July 2006. Two further seedling cohorts emerged in January 2007 but did not survive longer than four months.

The herbicide treatment had the lowest seedling recruitment for the duration of the study (Figure 5.4). Twelve cohorts were observed in the herbicide treatment, with the largest cohorts occurring in the February and March 2006. Fifty percent of the total recruits died from March to June 2006. The number of seedlings surviving from the February and March 2006 cohorts was three and two, respectively. In the September to November 2006 cohorts, three to five seedlings survived until the next treatment application in December 2006.

Manilla site

At Manilla, in 2006, the seedling in the herbicide treatment had the greatest total survival rate (42%) followed by those in the control (40%) and mown (34%) treatments (Figure 5.4), while in 2007, seedlings in the mowing treatment had greater (67%) survival than the other treatments.

The control treatment at Manilla had new cohorts in 21 of the 24 months (Figure 5.4). Cohorts emerging in February 2006 and between January to March 2007 had the highest survival, with four to five seedlings/m^2 surviving the period of study.

Fifteen cohorts were observed in the mowing treatment (Figure 5.4), emerging in every season over the two-year study period. Cohorts emerging from January to April in both years survived throughout the period of the trial while other cohorts did not persist each year.

The herbicide treatment had twelve cohorts during the trial (Figure 5.4), the largest (16 seedlings/m^2) emerging in February 2006 with 37.5% seedling survivorship in the first year. The January and February 2007 cohort had two seedlings recruitment with 50% survivorship at until the end of trial.

Yarrowyck site

Seedling cohorts in the control treatment at Yarrowyck occurred in every month of the trial (Figure 5.4). Cohorts recruited during the warmer months (September – March) had higher survival than those recruited in cooler months (April – August). The largest flush of seedlings (16 seedlings/m^2) was observed in February 2007, but only 19% survived until the end of the trial.

Thirteen cohorts emerged in the mown treatment in the two years (Figure 5.4). The largest cohort recruited in February 2006, with four seedling surviving throughout the trial. In the second year, only one seedling emerged in February and it survived until the end of trial.

The herbicide treatment had the lowest number of cohorts recruited at Yarrowyck (Figure 5.4). Cohorts emerging in April, and July to October had longer survivorship than other cohorts.

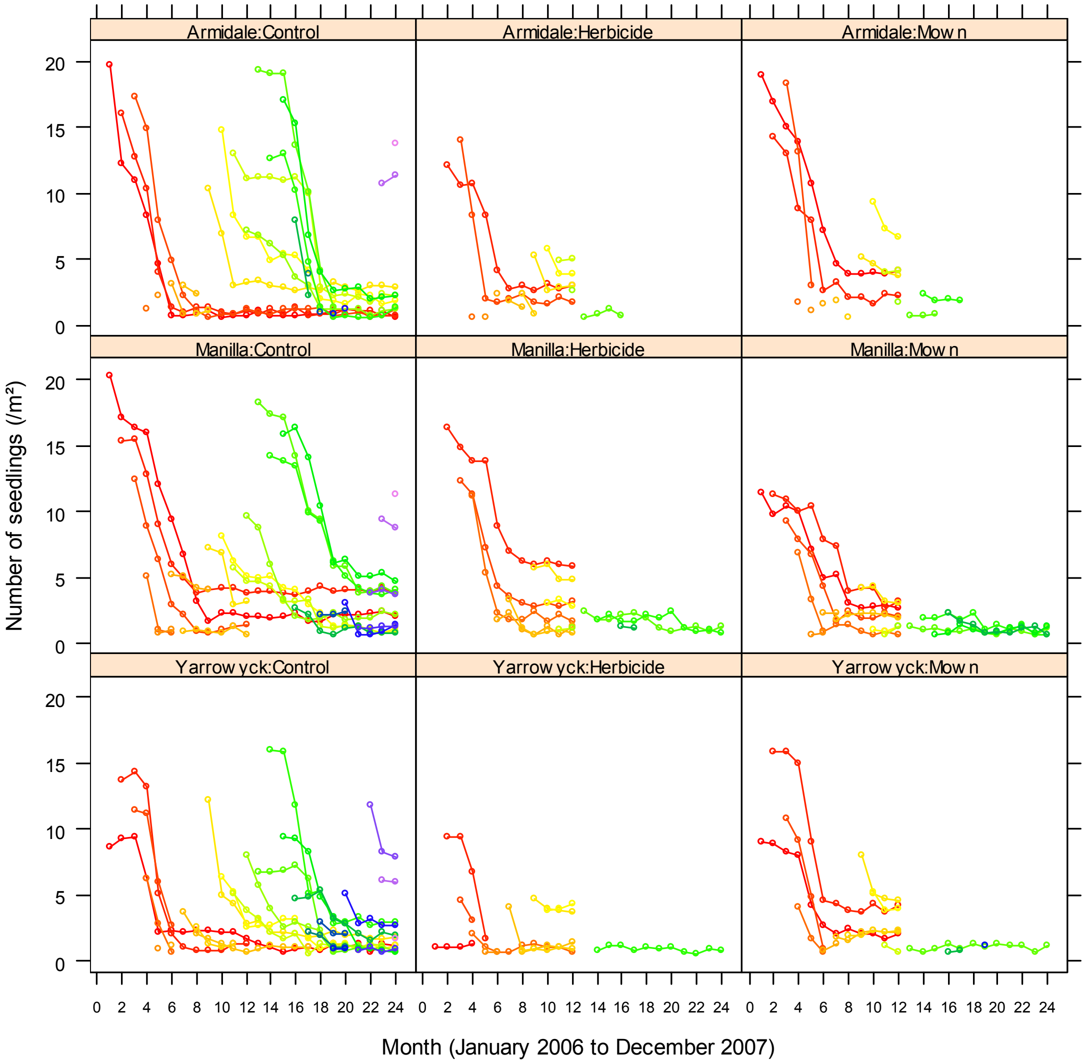

Figure 5.4 Seedling survival curves of *H. hirta* over two years (January 2006 – December 2007), shown as months (January 2006 = 1) under three management treatments; control, herbicide and mown at three study sites; Armidale, Manilla and Yarrowyck. Lines represent the survival pattern of seedlings for different cohorts. Age of cohorts varies from red to violet colour as the age of cohorts increased.

Seedbank

The seedbank of *H. hirta* varied between sites, years and treatments ($P < 0.05$), although there was no significant difference in the number of seeds between treatments at any of the sites in 2005 at the start of the trial (Figure 5.5). Throughout the experimental period, Armidale had the most seeds followed by Manilla and Yarrowyck. In 2006 and 2007, the greatest number of seeds were recovered from the control treatment while there was no significant difference in the seedbanks between the herbicide and mown treatments at any of the sites. The average number of seeds collected from the Armidale site was 14 837 seeds/m^2. In 2006, the seedbank declined by 74 and 76% in herbicide and mown treatments, respectively, whereas in 2007 it had declined by about 95% from 2005 densities in both treatments. The seedbank at Manilla declined by 92 and 94% in herbicide and mown treatment plots over the two years. At Yarrowyck, the seedbank declined by up to 98% in plots treated with herbicide or mowing in comparison with the seedbank in 2005.

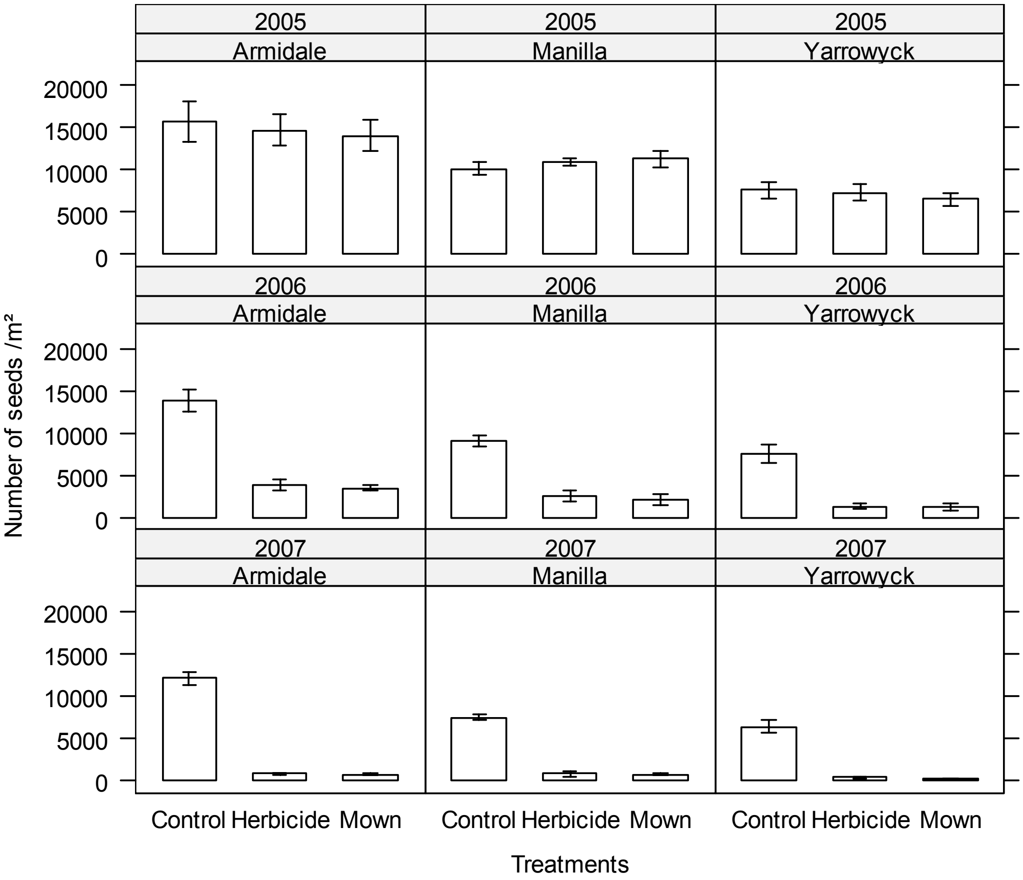

Figure 5.5 The changes in the *H. hirta* seedbank over two years (December 2005 – December 2007), under three management treatments; control, herbicide and mown at three study sites; Armidale, Manilla and Yarrowyck. Year 2005 represents the *H. hirta* seedbank before treatment applications. Means and standard errors are shown.

Viable seedbank

The viable seed bank of *H. hirta* varied significantly between sites, years and treatments (P = 0.003). In 2005, the greatest number of viable seeds was found at Yarrowyck (25.6%), followed by Manilla (19.5%) and Armidale (19.0%) (Figure 5.6). In 2006 at Armidale, the percent viable seedbank in mown and herbicide treated plots decreased by 79 and 84%, respectively. In 2007, the percentage of viable seedbank in the control plots at Armidale was 19.2%, while in the herbicide and mown treatments, no viable seed was recovered from the soil seedbank. Similarly, at Manilla, the percentage of viable seeds in the herbicide and mown treatments was 2.5% and zero, respectively. No viable seeds were recovered from the treated plots at the Yarrowyck site in 2007.

Biomass production

At Armidale in 2007, *H. hirta* biomass production in the control plots increased by 67.4% compared with 2005 (Figure 5.7). In the herbicide and mown treatments, biomass production decreased by 93.4 and 32.3%, respectively between 2005 and 2007. Herbage production in the control plots at the Manilla site, increased by 62% but declined by 84 and 4% in the herbicide and mown treatments, respectively. At Yarrowyck, herbage production increased by 91% in control plots but declined by 97.4 and 2% in herbicide and mown treatments.

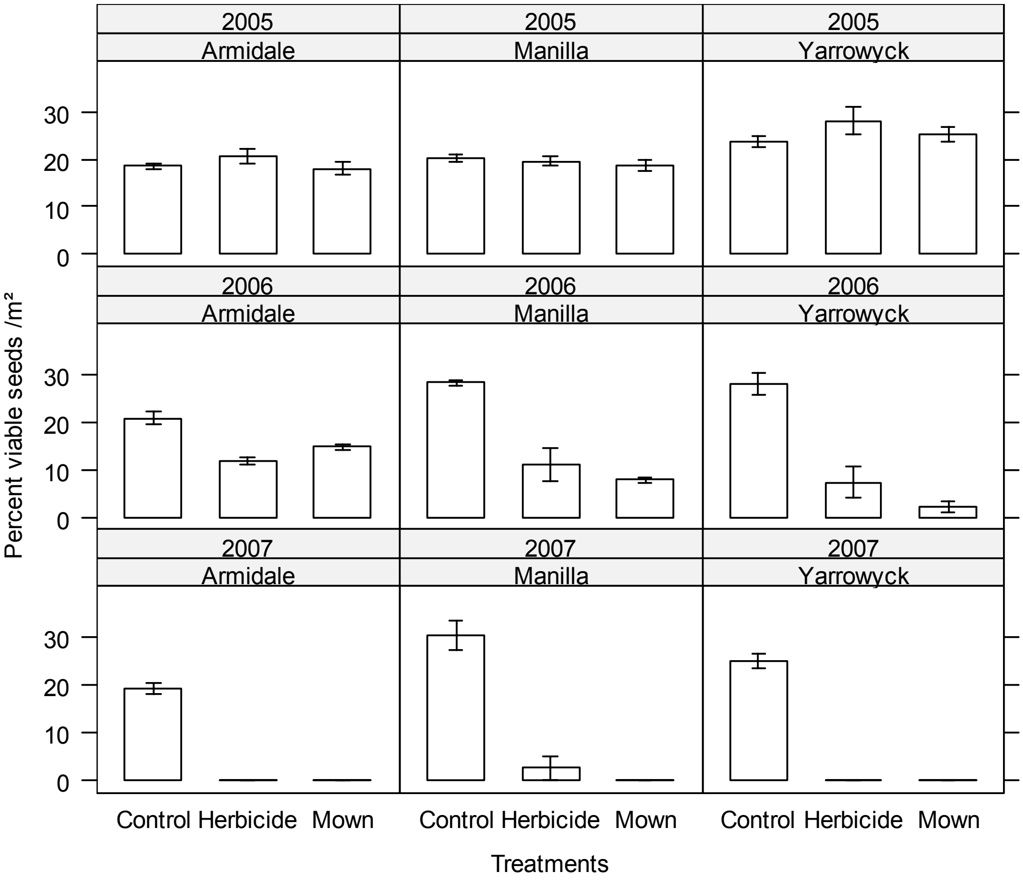

Figure 5.6 The changes in the viable seedbank of *H. hirta* over two years (December 2005 – December 2007), under three management treatments; control, herbicide and mown at three study sites; Armidale, Manilla and Yarrowyck. Year 2005 represents the *H. hirta* seedbank before treatment applications. Means and standard errors are shown.

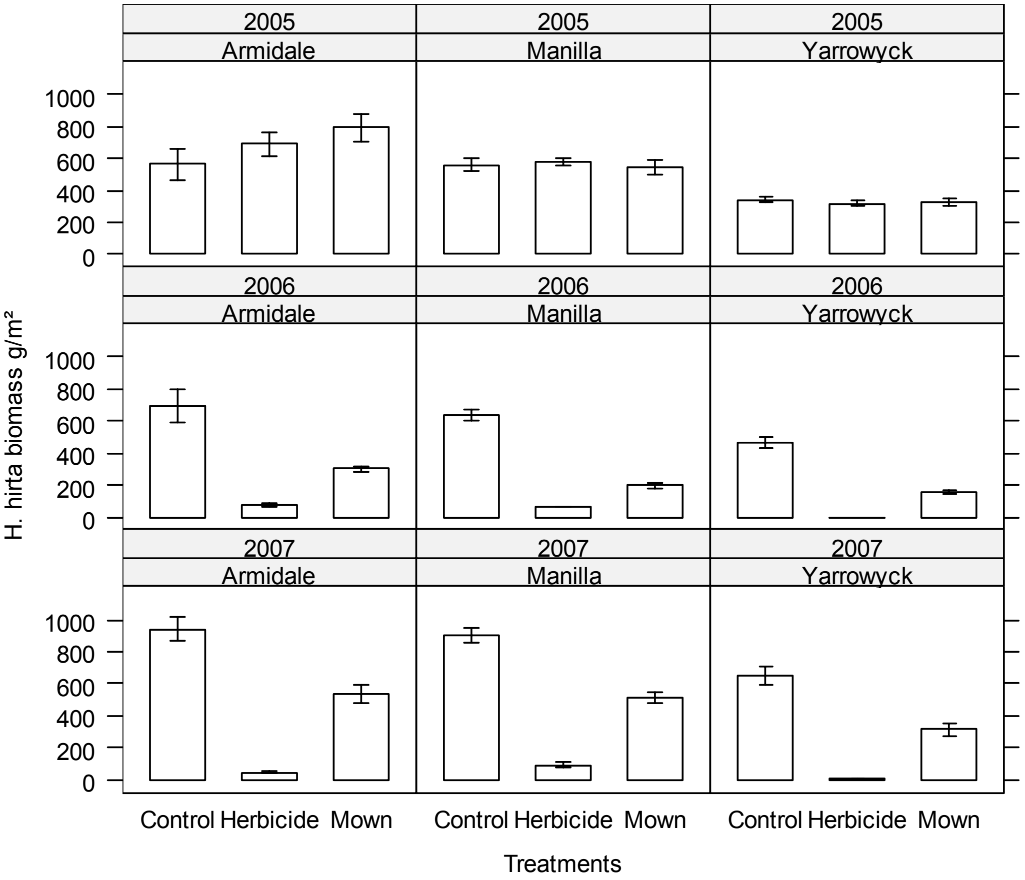

Figure 5.7 The changes in the biomass production of *H. hirta* over two years (December 2005 – December 2007), under three management treatments; control, herbicide and mown at three study sites; Armidale, Manilla and Yarrowyck. Year 2005 represents the *H. hirta* seedbank before treatment applications. Means and standard errors are shown.

5.4 Discussion

Seedling recruitment

Seedling recruitment of *H. hirta* occurred throughout the two-year trial in each treatment at all sites, but the main seedling flushes were observed in the warmer and wetter months of the year, from October to March. Emergence declined with the onset of cooler weather and lower rainfall. In South Australia, Warner (2004) observed that most seedlings of *H. hirta* were recruited in warmer months with sufficient rainfall at densities of 380 seedlings/m^2. Similarly, Lodge (1981) found that the most favourable period for the emergence and successful establishment of warm-season perennial grasses was from midsummer to early autumn on the north-west slopes of NSW, Australia. The temperature at these times of emergence are consistent with the temperature ranges (20-30 ºC) for optimum germination and growth of *H. hirta* (McWilliam *et al.* 1970, Chejara *et al.* in press). During this time, the mean monthly minimum temperature was above 10 ºC. There is also generally adequate rainfall during this period, with flushes of emergence usually following a rainfall event of greater than 30 mm. *Hyparrhenia hirta* is widely distributed in regions of its home range with a sub-tropical, warm temperate or Mediterranean climate. It includes areas receiving low to relatively high rainfall, with maximums in summer or winter. This supports the results of this study that *H. hirta* is able to germinate and establish under a wide range of climatic conditions.

The higher seedling emergence at Armidale may be due to the larger seed pool and higher plant density or biomass at this site. The higher seedling emergence of *H. hirta* in the control treatment was likely to result from the continued addition of seed from mature plants. Evidence from South Australia and the north-west Slopes of NSW, Australia, indicates that *H. hirta* flowering can occur year-round (Steve Clarke and Chris Nadolny *pers. comm.* 2005), but the flowers produced in some months do not necessarily result in viable seeds.

Higher seedling emergence in the control plots indicates that *H. hirta* does not require disturbance for emergence and establishment, giving its ability to invade undisturbed ecosystems. Warner (2004) reported that plant litter cover did not inhibit

H. hirta emergence. In the mown and herbicide treated plots, seed inputs were excluded thus reducing the level of emergence.

Survivorship of seedlings

Seedling mortality was high in all treatments, particularly for cohorts that emerged in winter. *Hyparrhenia hirta* seedlings are moderately frost sensitive (McCormick *et al.* 1992) and during winter in 2006 and 2007, the minimum temperature of all sites declined to below 0 ºC, especially in Armidale. Growth chamber experiments evaluating the germination and early growth of *H. hirta* indicated that seedlings do not survive at temperatures < 10 ºC or > 40 ºC (V. Chejara, unpub. data). Also there are longer periods without rain in winter, or with very low rainfall in these regions.

Manilla had the highest survivorship among all sites with maximum survival in cohorts emerging between January and March. This result is likely to be due to more favourable temperatures and moisture availability during these months. Seedling survival depends on the emergence timing, speed of seed germination after effective rains and on the desiccation tolerance of seedlings (Kigel 1995, Verdu and Mas 2006). Factors affecting germination and early seedling growth are often the primary determinants of the competition and the successful establishment of adult plants (De Villiers *et al.* 2001, Johnson and Sindel 2005). Manilla received around 30 mm rainfall in January 2007 and the temperature (20/35 ºC day/night) was very suitable for the germination and growth of *H. hirta* seedlings (McWilliam *et al.* 1970, Chejara *et al.* in press). The rapid germination of *H. hirta* (1 – 2 days after sowing) provides a competitive advantage in rapidly imbibing soil moisture from summer rainfall, especially in sandy soils where *H. hirta* has been very successful (Chejara *et al.* in press). However, the work on root development in *H. hirta* seedlings, speed of emergence, and architecture needs to be explored. Van Kleunen and Johnson (2007) found that rapid and profuse seedling emergence plays an important role in invasion into new areas for several Iridaceae species from South Africa.

The highest survivorship of seedlings during the first year of the trial occurred in the herbicide treated plots at all experimental sites, presumably because of the significant reduction in resource competition from other plants. Lodge (1981) reported that seedling emergence and survival were highest for various grass species that germinated in the open inter-tussock spaces. This is likely to be due to higher availability of light and less intra-specific competition from neighbouring mature plants whose phenology would be synchronized with those of the seedlings (Harper 1977, Lodge 1981), as well as from inter-specific competition from rapidly growing annual species (Harradine and Whalley 1980). High intra-specific competition in *H. hirta* seedlings has been found in a pot trial exploring competition between *H. hirta* and the native grass *Bothriochloa macra* (see Chapter 6).

Seedbank

The soil seedbank is an important influence on the invasive potential of a plant species (Rees 1995), with seed input (Garrido *et al.* 2007) and seed longevity (Forcella *et al.* 2000) playing important roles in the seedling emergence pattern or spatial variation at various scales. The soil seedbank of *H. hirta* varied between sites, years and treatments.

Our results show that both herbicide and mown treatments reduced the *H. hirta* seedbank to a low level after two years. Andrews *et al.* (1996) found a significant reduction in the seedbank of *Sporobolus indicus* var. *major* in bare plots compared with vegetated plots. The highly significant change in the seedbank in herbicide and mown plots is likely to be due to exclusion of further seed input and facilitation of extra emergence due to sufficient light and less intra- and inter-specific competition in treated plots compared with control plots during the trial period.

The abundance of germinable seeds did not always satisfactorily predict seedling emergence and population density. The relationship between the numbers of viable seeds and numbers of emerged seedlings largely varies from species to species (Rebollo *et al.* 2001). Seedling survivorship of *H. hirta* did not depend on the size of the viable seeds in the seedbank, with the largest seedbank occurring at Armidale but the greatest seedling survivorship occurring at Manilla. There was a very low number of viable seeds recovered from the treated plots after two years, supporting the results of our study on seed viability indicating that *H. hirta* seed does not remain viable for much more than one year (see Chapter 4).

In conclusion, seedling emergence was low in treated plots where new seed production was restricted over the trial period. The ideal time for seedling emergence in the studied areas was between October and March; however, recruitment occurred throughout the year. From the point of view of weed control, it seems important to prevent seedling establishment of *H. hirta* during the period corresponding to the main flush of seedling emergence (between October to March). The results of this study also indicate that emergence in *H. hirta* can be seed-limited. The disturbance associated with herbicide and mown treatments promotes seedling emergence and survival and, as a consequence, can potentially promote population growth in the weed. Therefore, disturbance such as mowing and herbicide application created an ideal environment for seedling establishment and survival. Seedling survival in the mown and herbicide treatments at all three sites was longer than in control plots. It is therefore important to control individual tussocks along with providing good pasture competition and integrated weed management, including grazing, to manage *H. hirta*.

The seedbank, including the viable seedbank, became depleted in mown and herbicide treated plots during the two year period of the trial. These results suggest that removing the whole tussock and preventing the further ingress of seed in the soil seedbank for a couple of years can be helpful in controlling this species.

Statement of Originality:

All the work contained within this paper is the original research of the PhD candidate, Vinod Kumar Chejara.

Candidate:

Principal Supervisor:

Statement of Contribution by Others:

This paper has been prepared by the PhD candidate, Vinod Kumar Chejara. All coauthors are PhD supervisors (Paul Kristiansen, Brian Sindel, Christopher Nadolny and Wal Whalley) and have only contributed to this paper to the extent that would normally be expected of such roles. All coauthors have given their consent for having their contributions to this paper included in the thesis and accept the student's contribution as indicated in the Statement of Originality.

Candidate:

Principal Supervisor:

CHAPTER SIX

Density based competition between Australian native grass *Bothriochloa macra* and introduced grass *Hyparrhenia hirta*

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Density based competition between Australian native grass *Bothriochloa macra* and introduced grass *Hyparrhenia hirta*

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Abstract

Hyparrhenia hirta has invaded a large area of cropping, grazing and nature reserve land since it was introduced to Australia. *Bothriochloa macra* is a native grass species that grows in areas invaded by *H. hirta* in the north-west slopes of New South Wales, Australia. Intra- and inter-specific competition between *H. hirta* and *B. macra* at an early growth stage was investigated to evaluate the influence of the invasive perennial grass on the growth of a native perennial grass, *B. macra*. A glasshouse experiment was conducted using a factorial bivariate design with monocultures (1, 2, 4, 6 and 8 plants/pot of each species) and mixtures (2:6, 4:4 and 6:2 *H. hirta*:*B. macra* and the converse) where plants were grown at an overall density of eight plants per pot, providing combinations of the two species from 8:0 and 0:8. Competition indices of relative crowding coefficient (*K*), relative yield totals (*RYT*), and intra- and inter-specific competition were calculated from the root and shoot dry weight data. For both roots and shoots, *K* of *H. hirta* towards *B. macra* was much higher than *B. macra* over *H. hirta*, which indicated a high competitive ability of *H. hirta*. Relative yield total values of both species more than one, indicated some degree of resource complementarity. Intra-specific competition in *H. hirta* was increased as the plant density increased, whereas it was decreased in *B. macra* when density increased more than 6 plants per pot. This indicates that increasing density of plants can intensify the intra-specific competition in *H. hirta*. Inter-specific competition of *H. hirta* over *B. macra* for both roots and shoots was three- to seven-fold higher than vice versa. In conclusion, the results indicated that *H. hirta* was competitively aggressive over *B. macra* and may inhibit its early growth and establishment when growing within *H. hirta* invaded areas.

Keywords: *Bothriochloa macra*; Coexistence; *Hyparrhenia hirta*; Inter-specific competition; Intra-specific competition; Invasion mechanism

6.1 Introduction

Invasive species may invade native vegetation through a number of mechanisms including ecological adaptation, allelopathy, plant competition and changes in ecosystem processes such as geomorphology, hydrology, biogeochemistry and disturbance (Mallik and Prescott 2001, Heirro and Callaway 2003, Levine *et al.* 2003). Competition between plants for natural resources (e.g. moisture, light and nutrients) is one of the most important mechanisms. Depending on local conditions, plant species show different resource capture patterns, which enable them to compete efficiently for limiting resources (Gleeson and Tilman 1994, Schippers and Olff 2000). Although inter-specific competition has been suggested as an important tool in Integrated Weed Management (IWM) systems (Michalk *et al.* 1999, Warwick *et al.* 2005), there has been little integration of research on the importance of competition mechanisms between native grasses and weedy introduced grasses in grasslands and grassy woodlands (Fowler 1995, Wedin and Tilman 1996, Navas *et al.* 2002, Groves *et al.* 2003, Warwick *et al.* 2005).

Hyparrhenia hirta (L.) Stapf (Coolatai grass) is a summer-active, C4 perennial grass, native to southern Africa and the Mediterranean region. It grows in open savannas, extending into the dry tropics, particularly in highland regions (Clayton 1969). It was introduced in the 1890s to the Coolatai district of northern New South Wales, Australia, as a pasture and erosion control plant (Hunt 2006), but now invades areas of native flora, particularly roadsides, travelling stock reserves and native pastures (Nadolny 1998, McArdle *et al.* 2004).

Hyparrhenia hirta can grow on a range of soil types from light textured granite soils to heavy black earths, but it is more common on light textured soils (McCormick *et al.* 1992). The root system of *H. hirta* can reach depths of up to 3 m (Humphries 1965). Plant roots have many functions but their primary function is the acquisition of soil-based resources, primarily water and nutrients, and to provide anchorage (Fitter 1996). This deep root system gives *H. hirta* the ability to explore water available at depth, contributing to its tolerance to drought and providing a competitive advantage through summer, especially in recently emerged seedlings (Bokhari *et al.* 1987, McCormick *et al.* 1992). Fetene (2003) found that *H. hirta* was competitively aggressive towards *Acacia etbaica* and would inhibit the growth of tree seedlings when the latter were planted within the grass community. In a study on the impacts of *H. hirta* on native species richness, McArdle *et al.* (2004) reported that *Bothriochloa macra* was the most frequently recorded species in *H. hirta* infested plots.

In the absence of defoliation (grazing pressure), soil disturbance and at high native grass plant densities, it might be expected that *H. hirta* would be less competitive than the Australian native C4 perennial grasses such as *B. macra*. If true, then this would be important for the management of *H. hirta*. In this study, the competitive relationship between *H. hirta* and *B. macra* was investigated in a glasshouse experiment where greater control over substrate and environmental factors could be achieved (Gibson *et al.* 1999) than in field trials.

Two main designs have been commonly used in pot experiments to measure inter- and intra-specific competition, i.e. the replacement series and the additive design with both designs having their own limitations. These limitations have been well described in Snaydon (1991). In this study, a bivariate factorial design (Snaydon 1991) was used to investigate the inter- and intra-specific competition between the introduced *H. hirta* and the native *B. macra*. Both grasses have similar physiognomy (Wheeler *et al.* 2002), and are phylogenetically close within the tribe Andropogoneae (Mathews *et al.* 2002).

The following questions were addressed: (1) what is the degree of inter- and intra-specific competition of *H. hirta* and *B. macra* when grown in mixtures of variable proportions and (2) how do the relative shoot and root competitive abilities of the two species vary?

6.2 Experimental design

The experiment was conducted using a completely randomised design with four replicates where both species (*H. hirta* and *B. macra*) were planted at several densities in a bivariate factorial design in pots in a glasshouse experiment. For evaluating intra-specific competition, monocultures of each species were planted in increasing densities (1, 2, 4, 6 and 8 plants per pot), while inter-specific competition was investigated by planting both species together in different proportions (2:6, 4:4 and 6:2) at a constant overall density (8 plants/pot).

Plant growth conditions and measurements

The experiment was conducted in a temperature-controlled glasshouse at the University of New England (UNE), Armidale, New South Wales, Australia. The glasshouse conditions were kept at approximately 26/17 ºC (day/night). *Hyparrhenia hirta* seeds used were harvested from glasshouse grown plants at UNE, on 5th October 2006. The plants had been transplanted from a roadside *H. hirta* infestation near the UNE. The seeds of *B. macra* were purchased from Native Seeds Pty Ltd, Australia.

The seeds of both species were germinated in Petri dishes on filter paper in a growth cabinet and were transplanted at the two-leaf stage to plastic pots (200 mm diameter and 190 mm depth) filled with a sandy granite-derived soil, a Tenosol, (Isbell 1996), which is a common soil type in areas where *H. hirta* has become naturalised. The soil used in this experiment was very low in available phosphorus, nitrogen and total sulphur. Plants were watered every alternate day to maintain soil moisture and 100 ml of Aquasol solution (N23:P4:K18) was applied weekly.

Plants were harvested 12 weeks after planting at the flowering stage. The harvested material was separated into component species. Soil was washed from the roots, and the shoots and roots were separated, put in paper bags and oven dried at 60ºC for 48 hours. From the root and shoot biomass data, the competition indices were calculated.

Competition indices

To investigate the competitive relationship between species, four indices were used: (1) relative crowding coefficient (K), (2) relative yield total (RYT), (3) index of intra-specific competition (R_{hh} and R_{bb}) and (4) index of inter-specific competition (R_{hb} and R_{bh}) (de Wit and van den Bergh 1965, Snaydon 1991, Sackville Hamilton 1994, Jolliffe 2000).

Relative crowding coefficient (K)

Relative crowding coefficient (*K*) is a measure of the relative dominance of one species over the other in a mixture (de Wit 1960). *K* was calculated as described by Firbank and Watkinson (1985):

$$K_{hb} = Y_{hb}F_b / (Y_{hh} - Y_{hb})F_h \qquad \text{and} \qquad K_{bh} = Y_{bh}F_h / (Y_{bb} - Y_{bh})F_b$$

where K_{hb} and K_{bh} are the respective relative crowding coefficients of species *h* (*H. hirta*) over species *b* (*B. macra*) and *b* towards *h*; Y_{hh} and Y_{bb} are the respective monoculture dry weight yields per pot (either shoots or roots as specified); Y_{hb} and Y_{bh} are the respective yields of species in the mixtures and F_h and F_b are the relative proportions of species *h* and *b*, respectively.

Relative yield total (*RYT*)

The relative yield total measures the resource complementarity between species (de Wit and van den Bergh 1965). This is calculated as follows:

$$RYT = Y_{hb} / Y_{hh} + Y_{bh} / Y_{bb}$$

Where, in two species mixtures, an *RYT* value close to 1.0 indicates that both species make the same demands for the same limiting resources. Relative yield total values greater than 1.0 indicate that species still compete for the same resources but may also make demands on different resources. Relative yield total values less than 1.0 indicate mutual antagonism (Bi and Turvey 1994).

Intra- and inter-specific competition (R_{hh}, R_{bb} and R_{hb}, R_{bh})

In an additive and replacement series experiment, it is necessary to assess the relative importance of intra- and inter-specific competition in determining the yield of each species in the experiment. Intra- and inter-specific competition indices were calculated as follows (Jolliffe *et al.* 1984):

$$R_{hh} = (Y_{hp} - Y_{hh}) / Y_{hp}\,; \qquad R_{bb} = (Y_{bp} - Y_{bb}) / Y_{bp}$$

and

$$R_{hb} = (Y_{bb} - Y_{bh}) / Y_{bb} \; ; \qquad R_{bh} = (Y_{hh} - Y_{hb}) / Y_{hh}$$

where R_{hh} and R_{bb} are the relative effects of intra-specific competition on species *h* and *b*, respectively, and R_{hb} and R_{bh} are the relative inter-specific competition effects from species *h* on *b* and *b* over *h*, respectively. Y_{hp} and Y_{bp} represent the projected yield of species *h* and *b*, respectively, which are expected yields of that species at a given density in the absence of intra- and inter-specific competition. Projected yield can be calculated as the product of the species density and the yield of the species when grown as a single plant in a pot.

Statistical analysis

Analysis of variance (ANOVA) was used to determine the overall significance of treatments on root and shoot competition of *H. hirta* and *B. macra* using the statistical package R 2.2.0 (R Development Core Team 2006). Variances were checked by plotting residual vs. fitted values to confirm the homogeneity of the data. No transformations were necessary. The differences between the treatment means were considered significant when $p \leq 0.05$. The standard errors of the means of different competition indices were calculated using formulae described by the US Census Bureau (2003).

6.3 Results

Relative crowding coefficients and relative total yields

The relative crowding coefficients (*K*) and the relative yield total (*RYT*) of the two species are presented in Table 6.1. For both root and shoot, the *K* of *H. hirta* over *B. macra* (K_{hb}) was much greater than the converse (K_{bh}), where the mean value of all density proportions of K_{hb} and K_{bh} are 1.61 and -11.6, respectively. The *K* value of *H. hirta* for root biomass was 5.6% greater than for shoot biomass. The mean *RYT* values of the both species for root and shoot were greater than 1.0, but *RYT* for root biomass was 10% higher than for shoot biomass.

Table 6.1 Relative crowding coefficient (*K*) and relative yield total (*RYT*) values for both shoot and root of *Bothriochloa macra* and *Hyparrhenia hirta*.

B/H	K_{bh}	K_{hb}	*RYT*
Root			
2/6	-27.30 (6.50)	3.84 (1.21)	1.69 (0.38)
4/4	-5.00 (3.68)	0.92 (0.11)	1.73 (0.51)
6/2	-2.50 (1.82)	0.06 (0.01)	1.31 (0.36)
Mean	-11.60	1.61	1.58
Shoot			
2/6	14.13 (8.36)	3.75 (1.98)	1.38 (0.23)
4/4	-6.40 (2.92)	0.74 (0.05)	1.61 (0.31)
6/2	-1.84 (0.40)	0.04 (0.01)	1.33 (0.28)
Mean	1.96	1.51	1.44

The replacement series *B/H* represents the density of *B. macra* as the first species versus *H. hirta* in each pot. K_{bh} is the crowding coefficient of *B. macra* against *H. hirta* and K_{hb} is the crowding coefficient of *H. hirta* against *B. macra*. *RYT* is the relative yield total of each species combination. Values in parentheses are standard errors of the mean.

Intra-specific competition

The intra-specific competition of both species increased as the density of plants increased per pot (Figure 6.1). The increasing pattern of intra-specific competition in *H. hirta* continued until four plants/pot and then plateaued as density increased further. However, in *B. macra*, intra-specific competition decreased when the plant density increased to more than six plants per pot. Intra-specific competition for the roots was greater than for shoots in *H. hirta*, but it did not vary significantly. Intra-specific competition for roots in *H. hirta* at a density of eight plants per pot (0.89 ± s.e. 0.03) was significantly greater than at four plants per pot (0.80 ± s.e. 0.07). Similarly, the competition for shoots in *H. hirta* was significantly higher at a density of eight (0.85 ± s.e. 0.02) than four plants/pot (0.77 ± s.e. 0.02). There were no significant differences in intra-specific competition between roots and shoots of *B. macra*. In *B. macra*, intra-specific competition was reduced by 13 and 10% for roots and shoots, respectively, when the plant density increased to more than six plants per pot.

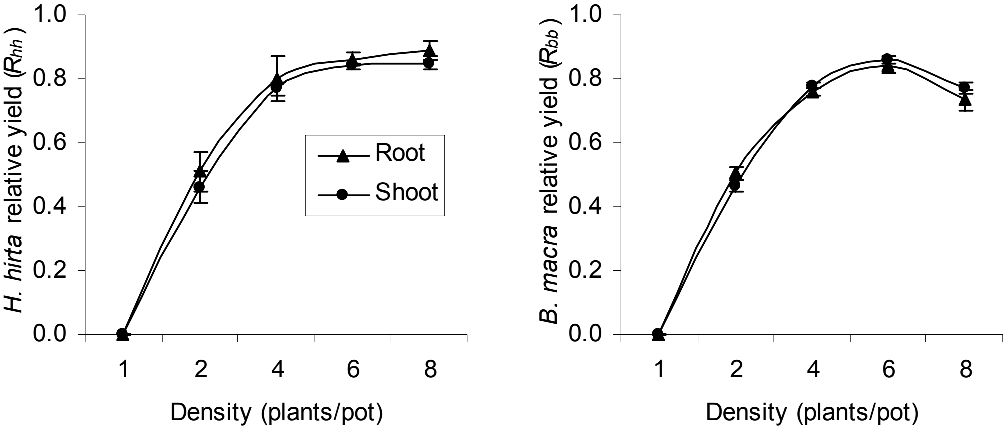

Figure 6.1 The relative effects of intra-specific competition on the root and shoot yields of *Bothriochloa macra* (R_{bb}) and *Hyparrhenia hirta* (R_{hh}). Vertical lines are standard errors.

Inter-specific competition

The relative effect of inter-specific competition from *H. hirta* on *B. macra* was three- to seven-fold greater than that of *B. macra* over *H. hirta* (Figure 6.2). Inter-specific competition from *H. hirta* over *B. macra* did not vary for root and shoot yields. There was an increasing trend as *H. hirta* density increased. Inter-specific competition from *B. macra* towards *H. hirta* for shoots was 29.4% greater at higher densities than for roots.

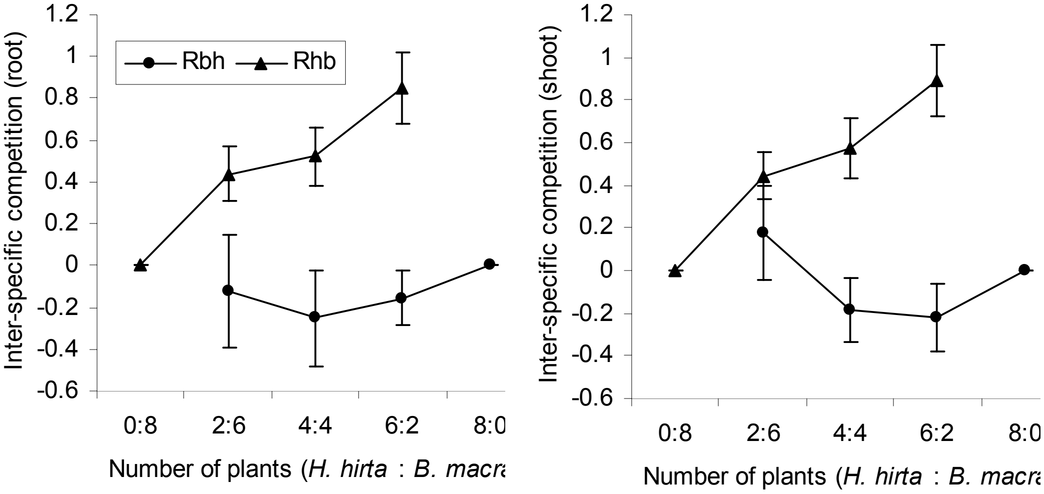

Figure 6.2 The relative effects of inter-specific competition from *Bothriochloa macra* on *Hyparrhenia hirta* (R_{bh}) and from *H. hirta* on *B. macra* (R_{hb}) for both roots and shoots. Vertical lines are standard errors.

A significant interaction of species and density was found for root and shoot yield of both species ($p < 0.05$). *Hyparrhenia hirta* produced significantly higher root and shoot yields when the two species were grown in mixtures (Figure 6.3). The root and shoot yields of *H. hirta* did not change significantly as the weed's proportion increased in the mixture. The root and shoot yield of *B. macra* was significantly reduced as its proportion decreased in the mixture. The increase was greater for shoot yield than root yield for both species.

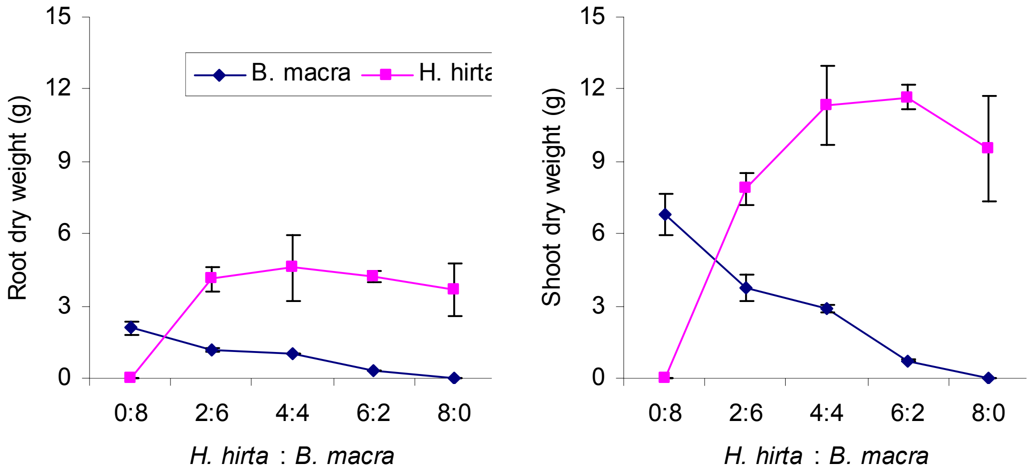

Figure 6.3 Root and shoot dry weights of *Bothriochloa macra* and *Hyparrhenia hirta* in their various proportions within the replacement series. Vertical lines are standard errors.

6.4 Discussion

Competition among plant species is important in determining species co-existence and the relative abundance of co-occurring species, and an important tool to the development of IWM (Navas *et al.* 2002, Warren *et al.* 2002). In this study, we investigated density-based competition between *H. hirta* and *B. macra* because both species have an intermediate type of response to fertilizers, especially nitrogen and phosphorus (Wedin and Tilman 1996, Prober *et al.* 2002).

The results of this study showed that, in terms of competitiveness, *H. hirta* was more aggressive against *B. macra* than the converse. The competitiveness of *H. hirta* was reflected by its value of *K* towards *B. macra* (K_{hb}) which were much higher than K_{bh} for roots and shoots (Table 6.1). The average *RYT* of the mixture of both species for roots and shoots was 1.58 and 1.44, respectively. This indicates that while both species were competing for resources, there was also some degree of resource complementarity between them. Similarly, *H. hirta* has been found to be competitively aggressive against *A. etbaica* at the seedling stage (Fynn *et al.* 2005b).

Other studies on competition have attributed high values of *RYT* to the use of different resources, mainly nitrogen and phosphorus, in addition to differences in root and shoot characteristics (Bi and Turvey 1994, Lodge 2000, Fetene 2003, Wang *et al.* 2008). Slightly higher (5.6%) values of the K_{hb} of *H. hirta* for root yield than shoot yield, indicate that its roots had higher competitiveness than its shoots. This supports the idea that root competition starts as soon as the root system of one plant intermingles with that of the other, which usually occurs before leaf canopies are sufficiently developed to induce competition for light (Aspinall 1960, Dhima *et al.* 2007). In this study, high K_{hb} values for roots and shoots of *H. hirta* indicated that the competitiveness of *H. hirta* depended on the combined effects of root and shoot competition. The competitiveness of one species towards another may depend on plant strategies and trait trade-offs which facilitate the capture of resources in competition (Aspinall 1960). Fynn *et al.* (2005b) found that of tall and narrow-leaved species, *H. hirta* was the most competitive in infertile subplots in comparison with *Themeda triandra* and *Panicum maximum*. The ecophysiological attributes of the African grasses such as *H. hirta* with high biomass allocation to leaves, high growth rate, deep root system, and high leaf-level gas exchange rates also have important consequences (Fynn *et al.* 2005b).

The intra-specific competition of *H. hirta* (R_{hh}) increased as the density increased until four plants per pot and plateaued as density increased above this, whereas in *B. macra* (R_{bb}), it decreased when plant density was more than 6 plants per pot (Figure 6.1). These results indicate that *H. hirta* development and growth can be influenced by increasing intra-specific competition. Chauvel *et al.* (2000) found that, due to intra-specific competition, growth and seed production of *Alopecurus myosuroides* was affected negatively as the density increased.

Inter-specific competition of *H. hirta* (R_{hb}) on the root and shoot yield of *B. macra* was significantly higher than that of *B. macra* on *H. hirta* (Figure 6.2). Similarly, greater inter-specific competition of *H. hirta* on *A. etbaica* were reported by Fetene (2005). The higher (three- to seven-fold) inter-specific competitive ability of *H. hirta* indicated that it would aggressively compete with the Australian native grass, *B. macra*, and inhibit growth when growing in *H. hirta* invaded areas. The inter-specific competition or aggressiveness of *H. hirta* in well-watered pots under glasshouse conditions may have been intensified. The competitive exclusion of *B. macra* by *H. hirta* in the pots is similar to that which we have observed in field studies (Fetene 2003, McArdle *et al.* 2004).

In conclusion, the results of this study indicate that aggressiveness or competitive ability of *H. hirta* is one of the mechanisms through which it is invading native vegetation. Differences in the use of resources between *H. hirta* and *B. macra* as indicated by their *RYT* above 1.0 may in part explain why native grasses, such as *B. macra*, can reclaim some nutrient deficient sites on which *H. hirta* had successful early establishment and growth, as observed by Fynn *et al.* (2006).

<u>Statement of Originality:</u>

All the work contained within this paper is the original research of the PhD candidate, Vinod Kumar Chejara.

Candidate:

Principal Supervisor:

Statement of Contribution by Others:

This paper has been prepared by the PhD candidate, Vinod Kumar Chejara. All coauthors are PhD supervisors (Paul Kristiansen, Wal Whalley, Brian Sindel, and Christopher Nadolny) and have only contributed to this paper to the extent that would normally be expected of such roles. All coauthors have given their consent for having their contributions to this paper included in the thesis and accept the student's contribution as indicated in the Statement of Originality.

Candidate:

Principal Supervisor:

CHAPTER SEVEN

Effect of *Hyparrhenia hirta* and *Phalaris aquatica* aqueous extracts and plant residues on two native grasses

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Effect of *Hyparrhenia hirta* and *Phalaris aquatica* aqueous extracts and plant residues on two native grasses

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Abstract

Both *Hyparrhenia hirta* and *Phalaris aquatica* can be highly invasive in Australia, infesting native grasslands, grassy woodlands and travelling stock reserves, often producing virtually monospecific stands. We investigated the allelopathic effects of *H. hirta* and *P. aquatica* on the germination and early growth of two co-occurring native grass species, *Bothriochloa macra* and *Dichanthium sericeum* using root and shoot aqueous extracts in a laboratory bioassay experiment and plant residues in a glasshouse pot trial. In the laboratory experiment, aqueous extracts of chopped plant material soaked in deionized water (1:10 w/v) for 48 h at room temperature were diluted to 0.1, 1 and 10%. A control treatment contained deionized water only. In the pot experiment, the target species were grown with and without above-ground plant residues of *H. hirta* and *P. aquatica*. Seed germination of both target species was significantly inhibited by the aqueous extracts of both invasive species and more so at high concentrations. The *H. hirta* shoot extract had a greater effect than the root extract of this species, and this was comparable to the inhibition of germination by the *P. aquatica* extract. With respect to seedling growth, root length in *B. macra* and *D. sericeum* was similar for all extracts, but shoot length of *D. sericeum* was more sensitive than that of *B. macra* to all extracts. In the pot experiment, presence of plant residues reduced the seedling emergence and root/shoot ratios of both target species. Emergence of *B. macra* and *D. sericeum* was reduced by about 61% by *H. hirta* residues and 67% by *P. aquatica*. While *H. hirta* clearly has allelopathic potential, its allelopathic effect in the field will be determined by extract concentrations in the soil, which, at this stage, are unknown.

Keywords: Allelopathy, biological invasion, *Bothriochloa macra*, *Dichanthium sericeum* germination, *Hyparrhenia hirta*, *Phalaris aquatica*, plant residue.

7.1 Introduction

Alien invasive species can affect native plant communities by reducing the diversity and relative abundance of native plant species and altering successional dynamics (Parker *et al.* 1999, Mack *et al.* 2000, Fynn *et al.* 2005b). A number of mechanisms may be involved including competition for water, mineral nutrients or light, changes to nutrient cycling, hydrology, biogeochemistry, disturbance and allelopathy (Woitke and Dietz 2002, Heirro and Callaway 2003). Allelopathy, the production of chemicals by one species that are detrimental to neighbouring species, may allow an invading species to dominate regardless of disturbance history (Levine *et al.* 2003) and resource availability (Heirro and Callaway 2003). The community structure in a variety of ecosystems has been altered in this way (Doria 1998, Nilsson *et al.* 2000, Kohli *et al.* 2001, Wardle 2002).

Allelopathy can be important in grassland ecosystems where various grasses possess secondary metabolites such as phenolic compounds, hydroxamic acids, and flavonoids (Wardle 2002). These chemicals can be released into the environment by leaching from above-ground plant parts, root exudation, stem flow, volatilization, microbial activity, dry residue decomposition, and the incorporation of plant residues into the soil (Rice 1984, Sanchez-Moreiras *et al.* 2003). Orr *et al.* (1984) found that leaf extracts of *Lolium arundinaceam* inhibited the seedling emergence of *Elaeagnus umbellate*. Chung and Miller (2005) found that allelochemicals from grass residues affected *Medicago sativa* growth and development. Plant extracts of *Imperata cylindrica* were reported to inhibit the germination of *Phalaris minor* and *Echinochloa colonum* (Chung and Miller 1995), while shoot leachates of *Lolium perenne* inhibited the radicle, shoot and root growth of *Carduus nutans* (Tripathi and Vaishya 1997). Nevertheless, laboratory experiments investigating allelopathy have limitations and the results are often complex and difficult to explain mechanistically. Also under laboratory conditions, the influence of many other factors are not taken into account such as climate and soil, soil microbial ecology, nutrient dynamics, life cycle pattern, density, and other biotic characteristics of the aggressive plant (Wardle *et al.* 1996).

Hyparrhenia hirta has become a dominant weed in a wide range of vegetative communities, from pastures to roadside reserves and remnant woodlands where its dense growth of leaf and stem material may suppress ground-strata flora and form monocultures on sites with diverse land-use histories and bio-physical characteristics (Inderjit and Weston 2000). It is therefore possible that *H. hirta* has an allelopathic potential to inhibit the germination and seedling emergence of other species in the community. Boughey *et al.* (2004) and Munro (1966), cited in Clayton (1964), found that some species of *Hyparrhenia* secrete a toxin which suppresses the growth of nitrifying bacteria. Previous work by Warner (1969, Warner 2004) on the allelopathic potential of *H. hirta* with low concentrations (< 10%) of *H. hirta* shoot extract indicated that *H. hirta* extracts may have some inhibitory effect on an invasive specie's *Lolium rigidum* root growth. On this basis, we investigated the allelopathic potential of *H. hirta* on native grasses using aqueous root and shoot extracts in a seed germination bioassay.

This experiment also compared the allelopathic potential of *H. hirta* leaf extract with that of another introduced grass, *Phalaris aquatica,* known to adversely affect germination, radicle growth and nodulation in a variety of plants (Halsall *et al.* 1995, Warner 2004). *Phalaris aquatica* was introduced into Australia in 1887, probably from Italy, and has been cultivated in Australia since 1904 (Leigh *et al.* 1995). While still being regarded as a valuable pasture species, it has become highly invasive in non-pasture situations including conservation reserves, urban parkland, travelling stock routes and remnant woodland (Trumbel 1933). The target species chosen, *Bothriochloa macra* and *Dichanthium sericeum* were native grasses that declined in abundance in sites invaded by *H. hirta* (Nadolny, C., pers. comm.).

The research addressed the following questions. (1) Does *H. hirta* inhibit native grasses? (2) Are native grass species differentially inhibited? (3) Does inhibition depend upon the source and concentration of the aqueous extracts? (4) Is *H. hirta* more or less allelopathic than *P. aquatica*? The allelopathic potential of *H. hirta* and *P. aquatica* plant residues were also determined in a pot experiment with soil in a glasshouse.

7.2 Methods

Laboratory Experiment

Live *Hyparrhenia hirta* and *Phalaris aquatica* plants were collected in August 2006 from a travelling stock route at Stingybark Hill (30º 28′ S, 151º 40′ E, 1019 m elevation) near Armidale, New South Wales, Australia. This travelling stock route was heavily infested with *H. hirta.* Plants were then divided into roots and shoots, coarsely chopped into small pieces (~ 2 cm) and soaked in deionized water for 48 h at room temperature in a ratio of 1:10 w/v of plant material to water (Satsangi *et al.* 2002, Rafiqul Hoque *et al.* 2003, Stoner *et al.* 2004). The aqueous extracts were filtered through Whatmans Number 40 filter paper and the filtrates stored at 4 ºC prior to use. Both root and shoot extracts of *H. hirta* were used while only the shoot extract of *P. aquatica* was used. The following dilutions of each extract were made: control (deionized water only), 0.1, 1 and 10 % (w/v). Extract concentrations of greater than 10% were not considered because concentrations of that magnitude are unlikely to occur under field conditions. The osmotic potentials (OP) of extracts of both species were measured using a vapour pressure osmometer (Model 5500, Wescor Inc., Logan, UT, USA).

Seeds of the two native grass target species, *Bothriochloa macra* and *Dichanthium sericeum*, were purchased from Native Seeds Pty. Ltd. Their germination percentages were both greater than 80 ± 5%. Twenty seeds of a target species were placed in a 9 cm diameter Petri dish lined with Whatmans Number 1 filter paper and covered with a glass lid. The aqueous extracts were applied (3 ml) every alternate day to keep the filter paper moist. The Petri dishes were incubated for 15 days at 12 h light (30º C) and 12 h dark (20º C). Each treatment was replicated four times and the dishes arranged in a completely randomised design in the growth cabinet.

The number of germinated seeds (with radicle ≥ 1 mm) at 1, 3, 5, 7, 9, 11, 13 and 15 days after the start of the experiment were counted. Root and shoot lengths were determined 15 days after the start of the experiment by measuring four representative seedlings.

Glasshouse Experiment

The experiment was conducted in a temperature-controlled glasshouse (28/17 ºC day/night) at the University of New England, Armidale, New South Wales, Australia. Fresh above-ground *H. hirta* and *P. aquatica* plant residues were collected in August 2007 from the same site as described in the laboratory experiment and the same seed samples of *B. macra* and *D. sericeum* were again used.

Twenty five seeds of *B. macra* and *D. sericeum* were sown in plastic pots (150 mm diameter) at 25 mm depth below residues of *H. hirta* and *P. aquatica* and in a non-residue containing control, as described by Lovett and Jessop (2007). Pots were filled with a sandy granite-derived soil, a Tenosol, (Lovett and Jessop 1982), which is a common soil type in areas where *H. hirta* has become naturalized in Australia. The residues were chopped to 1-2 cm maximum length pieces and spread on the surface of the soil at a rate equivalent to 7.5 t ha^{-1}. The rate of residues was equivalent to *H. hirta* residues collected at the infested field site. All the treatments were replicated four times and pots were watered every second day to maintain soil moisture at field capacity.

Seedling emergence was recorded at weekly intervals for 5 weeks. Plants were harvested at 8 weeks after sowing, soil washed from the roots, and the shoots and roots separated, put into paper bags and oven dried at 60º C for 48 h before being weighed.

Statistical analysis

The germination data for the laboratory experiment were expressed as the percentage of the total seed germinated out of the total seeds minus the number of dead seeds at the end of experiment 15 days after sowing. Analysis of variance (ANOVA) was used to determine the overall significance of treatments on germination, root length and shoot length responses to different concentrations of *H. hirta* (root and shoot extract) and *P. aquatica* (shoot extract) using the statistical package R 2.2.0 (Isbell 1996). Variances were checked by plotting residual vs. fitted values to confirm the homogeneity of the data. No transformations were necessary. The data from the repeated experiments were pooled because there were no time effects or time × treatment interactions. Standard errors were used to separate significantly different treatments (R Development Core Team 2006). Means and standard error bar plots were used to present the seed germination, root length and shoot length data graphically.

7.3 Results

Laboratory Experiment

Osmotic Potential

The OPs of *H. hirta* and *P. aquatica* aqueous extracts (Table 7.1) were not significantly different from each other ($P = 0.261$) at any concentration, as determined by ANOVA. However, the OP increased within each species as concentrations increased. The OPs measured for the *H. hirta* and *P. aquatica* aqueous extracts were below 100 mOsm/kg H_2O, which is low enough not to affect seed germination or seedling growth of many plant species (Smith 1989, Webster and Payne 2002).

Table 7.1. Osmotic potential (mOsm/kg H_2O) of *H. hirta* and *P. aquatica* aqueous extracts at different concentrations

	Extract concentration (% w/v)			
	0	0.1	1	10
H. hirta	22.0	23.7	26.5	33.5
P. aquatica	22.0	24.0	27.0	34.7

Germination

The similar response was observed for all extracts and both native perennial grasses with the germination generally decreasing as the extract concentration increased (Figure 7.1). At 10% *H. hirta* shoot extract concentration, germination was inhibited in *B. macra* and *D. sericeum* by 25 and 30%, respectively, as compared with the control (deionized water). However, at 10% *P. aquatica* shoot extract concentration, it declined by 28 and 18% in *B. macra* and *D. sericeum*, respectively. A 1% dilution of all extracts generally resulted in significant reductions in germination, with the exception that 1% Phalaris shoot extract did not significantly reduce germination of D. *sericeum* seed. *Bothriochloa macra* was more sensitive than *D. sericeum* to *H. hirta* and *P. aquatica* shoot extracts.

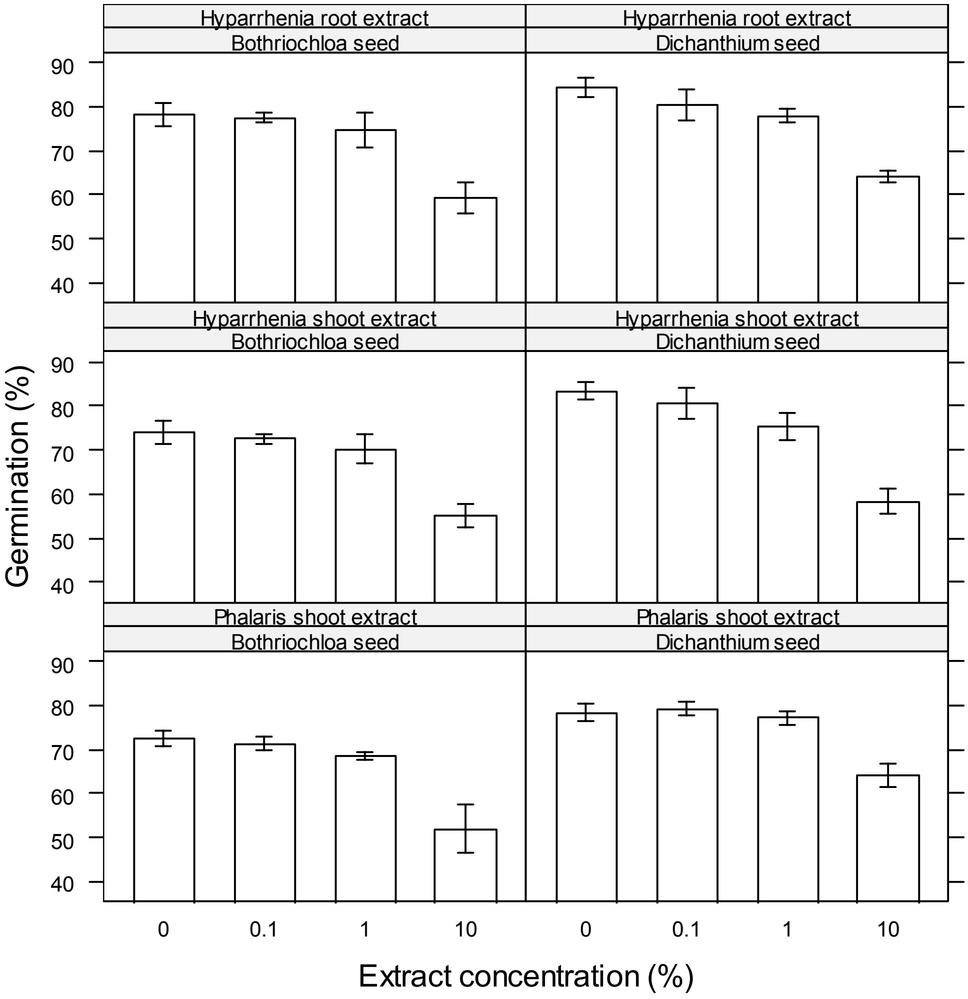

Figure 7.1 Effect of *Hyparrhenia hirta* root and shoot, and *Phalaris aquatica* shoot aqueous extracts on germination of *Bothriochloa macra* and *Dichanthium sericeum*. Mean and standard error are shown.

Root Length

The extracts generally reduced the root length of both species as the concentration of extracts increased (Figure 7.2). At 10% concentration of *P. aquatica* shoot extract, the root length inhibition of *B. macra* was greater than for *D. sericeum,* although there was no significant reduction of *B. macra* root growth at 1%. The *H. hirta* shoot extract generally had a greater effect on root length than the *P. aquatica* shoot extract.

In general, the root length of *B. macra* and *D. sericeum* responded similarly to all extracts.

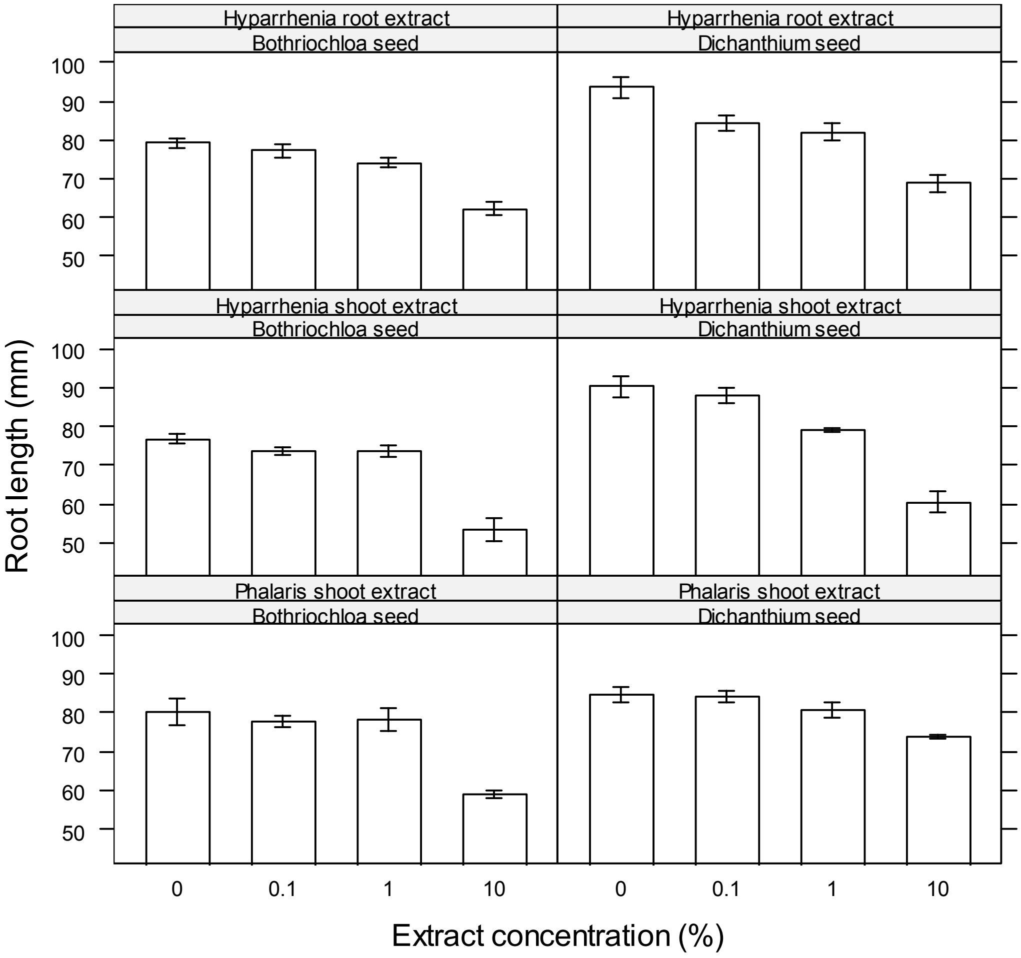

Figure 7.2 Effect of *Hyparrhenia hirta* root and shoot, and *Phalaris aquatica* shoot aqueous extracts on root length of *Bothriochloa macra* and *Dichanthium sericeum*. Mean and standard error are shown.

Shoot Length

Shoot length of both species generally declined as the concentration of all extracts increased (Figure 7.3). The greatest shoot length reduction was observed in the *H.*

hirta shoot extract followed by the *H. hirta* root extract and the *P. aquatica* shoot extract. At 10% concentration, *H. hirta* shoot extract reduced the shoot length of *B. macra* and *D. sericeum* by 45 and 60%, respectively, as compared with the control (deionized water), while *P. aquatica* shoot extract reduced shoot length of *B. macra* and *D. sericeum* by 16 and 17%, respectively. For shoot length, *D. sericeum* was more sensitive than *B. macra* to all extracts.

Glasshouse Experiment

Seedling Emergence

The cumulative seedling emergence percent of *B. macra* and *D. sericeum* in the pots with soil was significantly ($P < 0.001$) decreased by both the *H. hirta* and *P. aquatica* plant residues applied on the soil surface (Figure 7.4). The overall emergence of *D. sericeum* was lower than *B. macra*. At day 35, the maximum seedling emergence of *B. macra* and *D. sericeum* in the control treatment was 92% and 77%, respectively. The reduction of seedling emergence of *B. macra* in the *H. hirta* and *P. aquatica* plant residue treatments in comparison with the control was 63% and 65%, respectively, whereas in *D. sericeum,* it was 60% and 69%. Both target species responded similarly to *H. hirta* and *P. aquatica* residues.

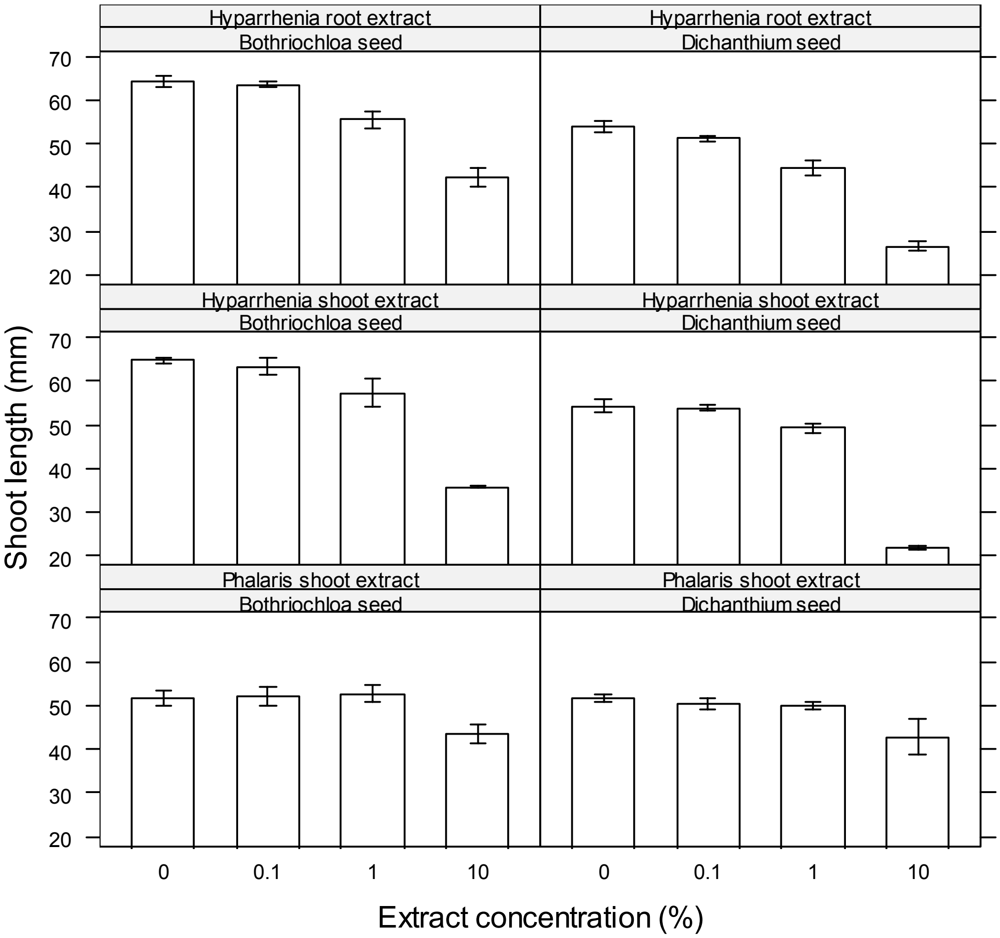

Figure 7.3 Effect of *Hyparrhenia hirta* root and shoot, and *Phalaris aquatica* shoot aqueous extract on shoot length of *Bothriochloa macra* and *Dichanthium sericeum*. Mean and standard error are shown.

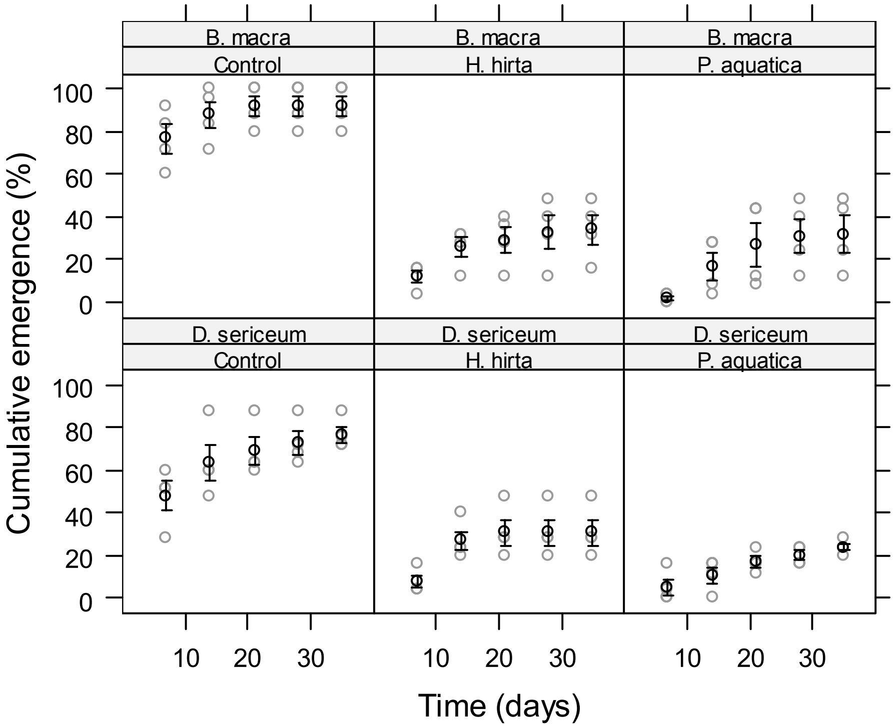

Figure 7.4 Effect of *Hyparrhenia hirta* and *Phalaris aquatica* plant residues on seedling emergence of *Bothriochloa macra* and *Dichanthium sericeum*. The light circles are the individual data points, with means represented with dark circles and standard errors indicated by the bars.

Root / shoot Ratio

The root/shoot ratio (Figure 7.5) of both target species *B. macra* and *D. sericeum* was significantly ($P < 0.001$) reduced by *H. hirta* and *P. aquatica* residues relative to the control. The maximum root/shoot ratio of *B. macra* (0.61) and *D. sericeum* (0.49) was observed in the control pots. The reduction of root: shoot ratio of *B. macra* due to the application of *H. hirta* and *P. aquatica* residues was 56% and 37%, respectively, whereas in *D. sericeum,* it was 43% and 84%. However, a greater reduction in the root/shoot ratio of *B. macra* was caused by *H. hirta* rather than the *P. aquatica* residue.

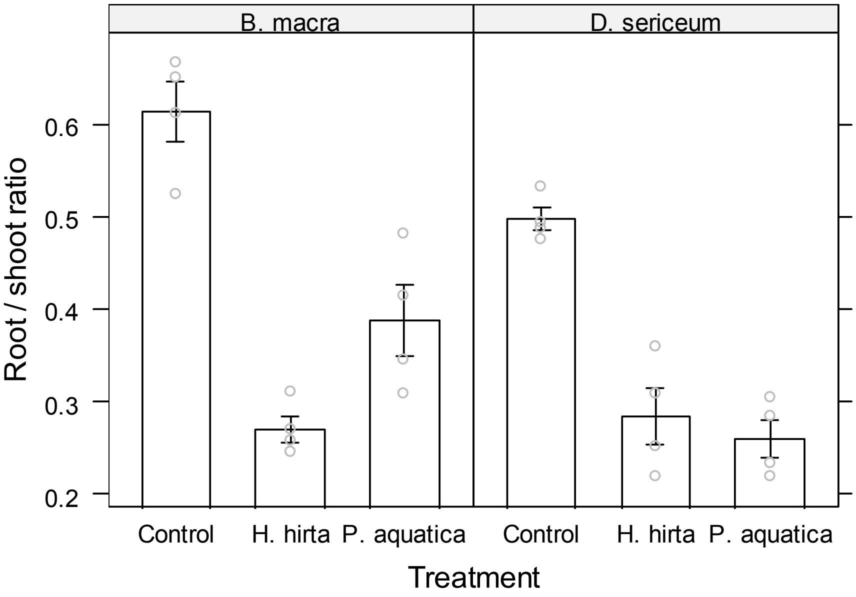

Figure 7.5 Effect of *Hyparrhenia hirta* and *Phalaris aquatica* plant residues on root biomass/ shoot biomass ratio of *Bothriochloa macra* and *Dichanthium sericeum*. The light circles are the individual data points, with means and standard errors.

7.4 Discussion

The root and shoot aqueous extracts of *H. hirta* were inhibitory to germination, and root and shoot growth of both native grasses, *B. macra* and *D. sericeum*, and more so at higher concentrations, indicating that extracts of *H. hirta* contain allelopathic compounds. The shoot extracts of *H. hirta* were generally more inhibitory than the root extracts. In general, leaves and leaf litter are the most consistent source of allelochemicals, whereas, roots generally have few allelochemicals and are less potent (Wanjura and Buxton 1972).

Plant residues of *H. hirta* and *P. aquatica* both reduced root length in comparison with the control in the pot experiment. Shoot dry weight however was not significantly reduced by the *H. hirta* plant residues compared with the control. This result supports the argument that the developing root system is highly sensitive to the presence of allelochemicals (Rice 1979).

Contrasting results of the allelopathic potential of a species between laboratory and field experiments are frequently reported (Lovett and Jessop 1982, Inderjit and Weston 2000, Inderjit 2006). The phytotoxic activity of allelochemicals in soil depends on the concentration in soil water, and this may be influenced by various soil and environmental factors affecting adsorption, desorption and degradation in the soil (Kobayashi 2004, Zaller 2006). For example, Zaller (1996) found an allelopathic effect of *Rumex obtusifolius* leaf extracts at lower concentrations on germination of some grassland species under controlled conditions, but there was no significant inhibitory effect under natural soil situations.

At the concentrations tested, the allelopathic effect of *H. hirta* shoot extract was generally slightly greater than that of the *P. aquatica* shoot extract, which has well known allelopathic potential. For example, Leigh *et al.* (2006) reported in a field study that *P. aquatica* litter reduced seedling numbers and dry matter production of *Trifolium subterraneum* while Halsall *et al.* (1995) found that an inhibitory effect of *P. aquatica* on germination, root and shoot growth of a variety of plants was caused by allelochemicals contained in its plant residues.

In conclusion, these results indicate that *H. hirta* has an allelopathic potential inhibiting germination and early growth of *B. macra* and *D. sericeum*, particularly at the higher concentration (10%). In this work, the effect of *H. hirta* on the two native grasses was consistent between aqueous extracts and the plant residues in pots which support the claim that *H. hirta* may be allelopathic under field conditions, though a purely physical effect of plant residue on seedling emergence has not yet been ruled out. Since the inhibitory effect of *H. hirta* and *P. aquatica* aqueous extracts at low concentrations (≤ 10%) is relatively small, concentrations in field soil would need to high for allelopathy to significantly contribute to the invasive process. Warner (1995) found that *H. hirta* leaf aqueous extract at lower concentrations (< 10%) actually stimulated the root growth of *Lolium rigidum* seedlings. The significance of allelopathy in the field is generally determined by aqueous concentrations found in the soil, but common levels found in the field are at this stage unknown. If those factors are low, then other factors such as resource competition, propagule pressure, rapid germination characteristics and differential climatic adaptations (e.g. drought and frost escaping strategies) may be more likely to influence the invasion of *H. hirta* into native plant communities. The ecophysiological attributes (e.g. high biomass allocation to leaves, high growth rate, and high leaf-level gas exchange rates) of African grasses such as *H. hirta* have important consequences for their successful invasion (Warner 2004). These results suggest that allelopathy could be one driver in *H. hirta* invasion, although further research is needed to separate the effects of allelopathy from the influence of these other factors, and to determine the effect of different conditions, such as soil moisture and soil fertility, on allelopathy.

Statement of Originality:

All the work contained within this paper is the original research of the PhD candidate, Vinod Kumar Chejara.

Candidate:

Principal Supervisor:

Statement of Contribution by Others:

This paper has been prepared by the PhD candidate, Vinod Kumar Chejara. All coauthors are PhD supervisors (Paul Kristiansen, Wal Whalley, Brian Sindel, and Christopher Nadolny) and have only contributed to this paper to the extent that would normally be expected of such roles. All coauthors have given their consent for having their contributions to this paper included in the thesis and accept the student's contribution as indicated in the Statement of Originality.

Candidate:

Principal Supervisor:

CHAPTER EIGHT

The current and future potential geographical distribution of *Hyparrhenia hirta*

Manuscript to be submitted to *Weed Research*

The current and future potential geographical distribution of *Hyparrhenia hirta*

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Abstract

Hyparrhenia hirta has become highly invasive in several parts of the world, including Australia where it has become a serious environmental weed in recent decades. Knowledge of the likely potential distribution and relative abundance of this invasive species under current and future climate scenarios will help biosecurity and weed control authorities to plan better strategies to manage the invasion. The CLIMEX modelling package was used to investigate the impacts of climate change in the potential global distribution of *H. hirta*. The world-wide potential distribution of *H. hirta* under current climatic conditions is vast, and far greater than the current distribution with suitable climate conditions extending over much of the tropics and subtropics. Under future climates, the range of *H. hirta* is likely to expand into areas currently too cold for its survival, and contract from areas which are projected to become drier under climate change. The effects of likely climatic scenarios on the global potential distribution of *H. hirta* are sufficiently great that they should be considered routinely in strategic control plans for biotic invasions. Changes in the potential range of an invasive organism under global warming scenarios, will mean that different plant invasion management agencies may become affected by *H. hirta*.

Key words: biological invasion, climate change, CLIMEX, *Hyparrhenia hirta*, modelling, range shift, weed

8.1 Introduction

Biological invasions, habitat disturbance and climate change are three of the greatest environmental challenges that we face in the 21st Century (Dukes and Mooney 1999, Williams and Baruch 2000, Kriticos *et al.* 2006). The management of plant invasions and their attendant impacts on biodiversity and crop productivity continues to challenge scientists and land managers alike. Recent discussions of biosecurity risk management have focused attention on issues of how to manage these threats through a greater emphasis on threat avoidance and early intervention (Mack *et al.* 2000). One of the challenges facing researchers is to quantify and predict the impacts each weed will have on biodiversity and production at global and local levels under current and future climates (Vitousek *et al.* 1996, Norby *et al.* 2001, Biosecurity Council 2003, Gallagher *et al.* 2006, Kriticos *et al.* 2006). Some of the most immediate effects of recent climate change are becoming apparent through impacts on biodiversity. These changes have the potential to cause significant ecological and economic damage. A rapidly changing climate can favour invasive species that can extend or shift their ranges quickly or species that can tolerate a wide range of climatic conditions and may have greater competitive success than most native species (Kriticos *et al.* Submitted). The factors affecting growth and distribution of plant species include increased concentrations of atmospheric carbon dioxide (CO_2) and changes in water availability, salinity and temperature. For instance, increased CO_2 can create favorable conditions for species invasion by increasing productivity, soil moisture and nitrogen uptake (Dukes 2003).

Many invasive species benefit from habitat disturbances because they are better dispersers and breeders than most native species. Therefore, climate change can be expected to favour invasive plants over established native vegetation (Weltzin *et al.* 2003, Hilbert *et al.* 2007), especially if accompanied by an increase in extreme conditions such as droughts alternating with very wet years. Grasses, especially C4 grasses, exhibit fundamentally different responses to temperature and CO_2 compared with C3 plants (Walker 1991, Hilbert *et al.* 2007). C4 grasses assimilate CO_2 efficiently, and they have high water-use efficiencies (Collatz *et al.* 1998). While the warm-season C4 grasses dominate tropical and temperate areas where mean monthly temperatures exceed 22 ºC for at least one month of the year (Clark *et al.* 2001), the literature linking climate change to geographic distribution of invasive weeds shows a general poleward trend for a range of species under future scenarios (Collatz *et al.* 1998, Kriticos *et al.* 2003, Kriticos *et al.* 2006).

Hyparrhenia hirta (L.) Stapf (Coolatai grass, thatching grass) is a summer-active, C4 perennial grass, native to southern Africa and the Mediterranean Region. It originally grew in open savannas, extending into the dry tropics, particularly in highland regions (Kriticos *et al.* 2003a) receiving low to relatively high rainfall, with a maximum in summer or winter. In southern Africa, Coolatai grass occurs in undisturbed ecosystems and is widespread in native pastures, but also colonises degraded grasslands. It is naturalised in America and many European countries but is not currently reported as a significant weed there. It was introduced in the 1890s to the Coolatai district of northern New South Wales (NSW), Australia, as a pasture species and to control erosion (Clayton 1969), and has subsequently invaded areas of native flora, particularly roadsides, travelling stock reserves and native pastures (Hunt 2006). *Hyparrhenia hirta* often forms monocultures with its dense growth of leaf and stem biomass, and has been shown to greatly reduce the diversity of native plants in areas it has invaded (Nadolny 1998).

Ecology of *Hyparrhenia hirta*

In Australia, *H. hirta* grows most rapidly in late spring or midsummer after rain (McArdle *et al.* 2004), which is typical of a subtropical species. However, most recordings of large stands of *H. hirta* in Australia and overseas occur between the 175-600 mm annual rainfall isohyets (Rubin and Palmer 1996, Faithful 2002). Perkins *et al.* (1988) reported that in the subtropical region of South Africa it prefers relatively open *Acacia* wooded grasslands, but will grow in a wide range of warm temperate habitats from full-sun to semi-shade. McWilliam *et al.* (1999) suggest that *H. hirta* is exapted (McWilliam *et al.* 1970) to survive in Australia's Mediterranean environment which has periods of drought in the summer, and reported that in Western Australia, flowering occurs in midsummer, from December to January. Anecdotal evidence from South Australia and the North West Slopes of NSW, Australia, suggests that *H. hirta* can flower year-round (Steve Clarke and Chris Nadolny *pers. comm.* 2005), but that the flowers produced in some months do not necessarily result in viable seeds. Robinson and Potts (1982) found that *H. hirta* can produce seeds in late summer and autumn in the subtropical environment of Florida, USA.

Hyparrhenia hirta has a breeding system that enables new populations to arise from a single plant (Robinson and Potts 1950). Large, established populations can produce sufficient seed to spread rapidly in spite of the apparently low proportion of seed that is viable (McWilliam *et al.* 1970, Chejara 2008). *Hyparrhenia hirta* spreads by means of tiny, hairy and awned dispersal units that adhere to clothing, animals, vehicles and roadside machinery (Chejara 2008). Human activities such as slashing or road traffic help in spreading the weed. In pastures and travelling stock routes, livestock disperse *H. hirta* seed.

Seed can germinate readily over a wide range of temperatures, light regimes and pH levels, and under marginal water stress (Luckens 2002). The fast germinating character of *H. hirta* in relatively warm conditions provides a competitive advantage in rapidly capturing soil moisture from summer rainfall, especially in sandy soils where it has been very successful (Chejara *et al.* in press). *Hyparrhenia hirta* can grow on a range of soil types from light textured granitic soils to heavy black earths, but it prefers light textured soils (Chejara *et al.* in press). In a field trial conducted in south-western Australia, *H. hirta* was reported as a moderately salt tolerant pasture species (McCormick *et al.* 1992).

The current distribution of *Hyparrhenia hirta*

Global distribution

Hyparrhenia hirta is widely distributed in regions with a subtropical, warm temperate or Mediterranean climate (Figure 8.1). It occurs in the Mediterranean region, extending throughout the Middle East to Afghanistan and Pakistan. To the west, its southern limit lies in the Cape Verde Islands and Hoggar massif (Algeria), but in the south it extends through Egypt to northern Tanzania. It is apparently absent from West Africa, and uncommon in the Congo and Zambesi regions, but appears in South Africa (Rogers and Bailey 1963). It has also been reported in North America, north-eastern states of South America, Madagascar and throughout Australia (Clayton 1969).

Australian distribution

There are populations of *H. hirta* throughout all Australian states except Tasmania (Figure 8.1), in a wide range of climatic conditions (Global Biodiversity Information

Facility 2007). It was introduced into Australia as a pasture species because of its fast, resilient growth and adaptation to a wide range of climatic conditions. Faithful (Faithful 2002, 2006) suspected that at least 10 races of *H. hirta* were sourced from Iraq to Portugal and South Africa and were introduced by the CSIRO in the 1960s for pasture trials. Many different ecotypes have since been recognized within Australia (Jackson and Jacobs 1985, Faithful 2002) making it clear that several introductions from various locations have been made and this may contribute to its wide distribution in Australia. Since then, it has been spreading rapidly on the North West Slopes and Northern Tablelands of NSW, and now occurs on the Central West Slopes, South West Slopes, North West Plains and Central and North Coast of that state (Jackson and Jacobs 1985). It has spread rapidly throughout NSW and south-east Queensland, where it has invaded large areas of grazing country, roadsides and travelling stock routes (Wheeler *et al.* 2002). It is also present in the south-west region of Western Australia (McCormick *et al.* 1992) where it was introduced in 1943 to control soil erosion (Humphries 1959, Lloyd and Moore 2002).

Modelling species potential ranges

The early prediction of biological invasions can only be made using scientific climate based modelling tools that provide information relevant to a decision-maker's needs (Humphries 1959, Rastetter 1996). Bioclimatic models are widely used tools for assessing the potential distribution of a species on the basis of its ecology and climate profile (Kriticos *et al.* 2003). Such commonly used bioclimatic models include ANUCLIM/BIOCLIM, CLIMATE, CLIMEX, DOMAIN, GARP, HABITAT and MaxEnt (Beaumont *et al.* 2005). All the models work on the assumption that climate is the primary determinant of the distribution of plant species (Kriticos and Randall 2001, Kriticos *et al.* 2003). Different models, however, have different capacities to model the effects of novel climates such as those encountered on new continents and under global warming. Research investigating the potential distribution of invasive plant species in relation to climate change in Australia is limited except for the work of Kriticos *et al*. (2000, 2003, Kriticos *et al.* 2003a, 2006) and Dunlop *et al.* (2003a). In a comparative study of different systems to analyse potential weed distribution, Kriticos and Randall (2006) found that CLIMEX (Sutherst and Maywald 1985, Kriticos and Randall 2001) was one of the most suitable climate modelling programs for undertaking weed risk analyses because it included a conformal global database, and it can support model-fitting to a known plant distribution, and can be used with confidence to assess the climatic suitability of habitats under both current and future climate scenarios.

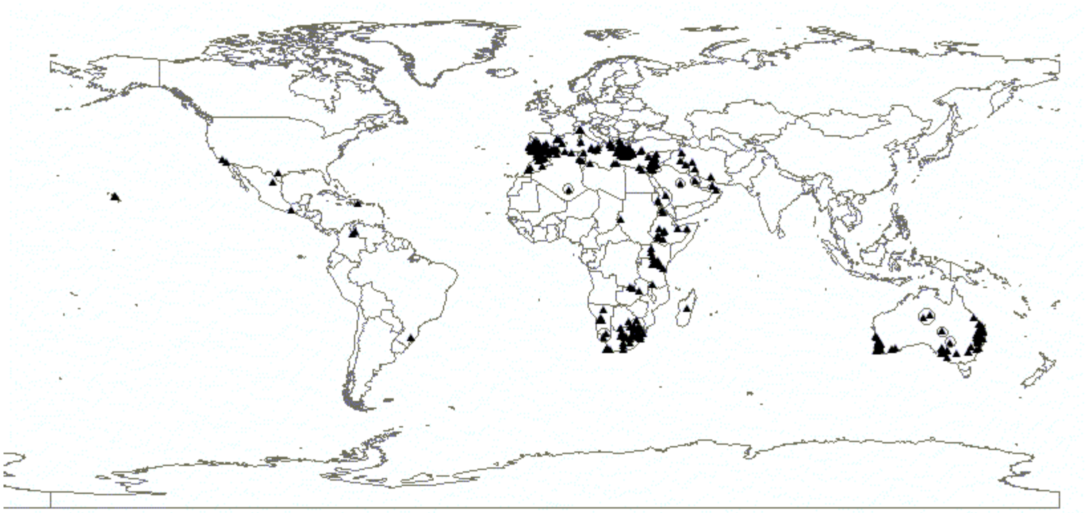

Figure 8.1 The current global distribution of *H. hirta* (▲). Records regarded as doubtful or non-current are circled (database from Australia's Virtual Herbarium 2006, Clayton, 1969 and Global Biodiversity Information Facility 2007).

The objectives of this study were to develop a model of the climate responses of *H. hirta* based upon its eco-physiological characteristics and its naturalised distribution world-wide. Specific goals were to: (i) Develop climatic parameters describing *H. hirta*'s response to climatic variables, based on its world-wide distribution (ii) predict the potential distribution of *H. hirta* under current climatic conditions, and (iii) predict its distribution in relation to various climate change scenarios for the 2080s.

8.2 Materials and methods

The ecological modelling software, CLIMEX for Windows Version 3 ((Sutherst and Maywald 1985), was used in this study to develop a predictive model of the potential distribution of *H. hirta* under various climatic conditions in Australia. This program is based on an eco-physiological growth model that assumes that a population experiences a favourable season with positive growth and an unfavourable season that causes negative population growth (Dunlop *et al.* 2006, Sutherst *et al.* 2007). This package has been widely used to predict the potential distribution of many species, including weeds (2003, Kriticos *et al.* 2003a, Lawson *et al.* 2004, Sutherst *et al.* 2004, Kriticos *et al.* 2005, Kriticos *et al.* 2006, Scott and Batchelor 2006). CLIMEX allows a user to infer the population response of plants and poikolothermal animals to climate from the species' geographic range, and to apply these response functions to novel climates to project the species potential range in these new regions or climate scenarios (Woodward 1987, Scott and Batchelor 2006).

CLIMEX uses various growth and stress-related indices to asses the potential growth and survival of a population at a given location (Kriticos *et al.* 2003). The program uses the weekly response of temperature (TI) and moisture (MI) to calculate the weekly growth index (GI_W), which is integrated across the year to give the annual growth index (GI_A). The annual growth index indicates the potential suitability of the climatic conditions for growth of a population throughout the year. A series of stress indices (cold, wet, hot, dry, hot-wet, hot-dry, cold-wet, and cold-dry) can play an important role in the estimation of the response of the species to adverse climatic conditions. The stress indices play the biggest part in defining the species' range boundaries, whilst the growth indices play a larger role in defining the species' relative abundance within its geographic range. The growth and stress indices are estimated weekly and combined into an annual Ecoclimatic Index (EI) which, scaled from 0 to 100, describes the climatic suitability of a species in a given location. In practice, EI values of 100 can only be found in highly stable environments such as equatorial environments, and maximum values of 50-70 are more typical. In order to de-emphasise the apparent precision afforded by the percentage scaling, the EI values have been arbitrarily grouped into four classes: unfavourable habitats (0-0.49), marginally favourable (0.50 – 9.99), favourable (10 – 19.99) and highly favourable (>20).

The principal assumptions within CLIMEX are that the geographical distribution of a species is primarily determined by climate (Sutherst and Maywald 2005, Sutherst *et al.* 2007), and that the geographic range of the species includes at least some records where the species is in dynamic equilibrium with its climatic tolerance limits for temperature and soil moisture. One of the clear advantages of this model over many other systems is that it can easily cope with modelling species distributions where the species is not generally at equilibrium with its environment, which is usually the case for invasive species. This system does not cover other biophysical factors such as soil, land use, vegetation cover, disturbance activities and the ability of a species to disperse in a new area (Sutherst and Maywald 1985, Sutherst *et al.* 1999, Lawson *et al.* 2004), though these factors can be considered in a stepwise fashion after the climate modelling has been completed.

Meteorological databases and climate change

CLIMEX uses five meteorological variables: mean monthly maximum and minimum temperature, rainfall and relative humidity at 0900 and 1500 hours. A regular gridded dataset of climate normals for 1961-1990 (Sutherst *et al.* 1999, Mitchell *et al.* 2004) was used to get the best fit of the parameters. The climate normals dataset consisted of 67 420 points spaced on a 0.5º latitude × 0.5º longitude regular grid of precipitation, mean temperature, diurnal temperature range and vapour pressure for significant land areas worldwide.

The TYN SC 2.0 (http://www.cru.uea.ac.uk/~timm/grid/TYN_SC_2.0.html) dataset also includes climate change scenario outputs from five Global Climate Models (GCM's). We used three models in this exercise: CSIRO-Mk2a (Mitchell *et al.* 2004), ECHAM4 (Hirst *et al.* 2000) and HadCM3 (Zhang *et al.* 1998). The change surfaces in the TYN SC 2.0 datasets were taken from GCMs run with four emission scenarios described in the Special Report on Emission Scenarios (SRES) (Gordon *et al.* 2000). The A1 scenario was used to run the CSIRO-Mk2a and ECHAM4, whereas for HadCM3 the most extreme scenario A1F1 was selected to represent the range of possible future climate suitability for *H. hirta* in the 2080s (IPCC 2000). The A2 and B families of SRES scenarios were ignored for this exercise after considering the results of Rahmstorf *et al.* (2007), which indicated that the observed global temperature increases in recent times were hotter than the hottest SRES scenarios and because we are more interested in the effects of the larger temperature increases that are likely. Prior to being used for the modelling exercise, the climate scenario datasets were extracted and manipulated to generate a set of surfaces of monthly averages for daily minimum temperature, maximum temperature and total rainfall and to estimate relative humidity at 0900 and 1500 hours based on the vapour pressure data as per described in detail by Stephens *et al.* (2007).

Fitting parameters

The parameters used in the CLIMEX model are fully described in Sutherst *et al.* (2007) and the general procedure for fitting these parameters has been clearly illustrated by Yonow and Sutherst (Yonow and Sutherst 1998, 2007). The resulting parameter values for *H. hirta* are described in Table 8.1. The native and global range of *H. hirta* current distribution was used to infer its climatic limits. The native range represents the species *realised* niche *sensu* Hutchinson (1998). When released from the effects of its natural enemies (Hutchinson 1957), a species may expand the climatic space occupied, more fully exploring its *fundamental* niche (Keane and Crawley 2002). Observations of this effect led to the recommendation to include consideration of the exotic range of a species when modelling its potential range (Davis *et al.* 1998). The capacity for substantial range expansion has clearly been demonstrated (Kriticos and Randall 2001). Each of the parameters were adjusted iteratively until maps of the stress indices matched favourably with the known distribution of *H. hirta* in its native range (Africa) and introduced ranges including Australia. The resulting parameters were also checked against knowledge of the plant's biology as a form of reasonability check.

Growth indices

CLIMEX analyses weekly and annual indices to determine suitability of each location for population growth (Sutherst and Maywald 1985, Wharton and Kriticos 2004). The temperature and moisture indices are combined multiplicatively to give the growth index GI_A, scaled from 0 to 100 (Kriticos *et al.* 2003, Sutherst *et al.* 2004).

Temperature index

The minimum (DV0) and maximum (DV3) temperature thresholds for *H. hirta* were adjusted from germination and growth experiments discussed in McWilliam *et al.* (2004). Germination did not occur below 5 ºC nor above 45 ºC although it has been observed that *H. hirta* grows well at moderate temperatures, especially in the frosty winter season in the Northern Tableland regions of NSW, Australia. In these regions and seasons however, it is likely that the plant is growing only during the warmest part of the day. Therefore, in the model, DV0 and DV3 were set at 13 ºC and 38 ºC respectively. The minimum and upper temperature thresholds for optimum growth (DV1 and DV2) were set at 26 and 30 ºC respectively based on experiments evaluating the germination and early growth of *H. hirta* between 20 and 40 ºC temperature (V. Chejara, unpub. data).

Table 8.1 CLIMEX parameter values used for *Hyparrhenia hirta* analysed from climatic data related with known distribution outside and in Australia taken from Sutherst *et al.* (1970)

Index	Parameter	Value*
Temperature	**DV0** = lower temperature threshold	13 ºC
	DV1 = lower optimum temperature	26 ºC
	DV2 = upper optimum temperature	30 ºC
	DV3 = upper temperature threshold	38 ºC
Moisture	**SM0** = lower soil moisture threshold	0.1
	SM1 = lower optimum soil moisture	0.4
	SM2 = upper optimum soil moisture	0.75
	SM3 = upper soil moisture threshold	1.4
Cold stress	**TTCS** = temperature threshold	0 ºC
	THCS = stress accumulation rate	-0.001 week^{-1}
Heat stress	**TTHS** = temperature threshold	40 ºC
	THHS = stress accumulation rate	0.001 week^{-1}
Dry stress	**SMDS** = threshold soil moisture	0.1
	HDS = stress accumulation rate	-0.006 week^{-1}
Wet stress	**SMWS** = threshold soil moisture	1.4
	HWS = stress accumulation rate	0.0015 week^{-1}
Degree-days	**PDD** = degree-days per generation	1390 ºC days

*Values without units are dimensionless proportions

Moisture index

Hyparrhenia hirta is a C4 type plant. These plants generally have high water-use efficiency (Sutherst *et al.* 2004). It has the capacity to survive periods of drought in the summer in a Mediterranean climate of Australia (Clark *et al.* 2001), partly due to the deep root system (McWilliam *et al.* 1970). The lower moisture threshold (SM0) was set as low as possible (0.1) which approximates the permanent wilting point, and allows sufficient growth to be simulated in the driest conditions of Saudi Arabia where *H. hirta* grows well (Humphries 1965). The lower and upper optimum moisture thresholds (SM1 and SM2) were set at 0.4 and 0.75 respectively to attain the best suitable moisture conditions in general for optimum plant growth. The upper soil moisture threshold (SM3) was set (1.4) to allow *H. hirta* to grow under conditions experienced in the coastal areas of central Italy where high temperature is followed by very high rainfall usually exceeding 1100 mm year^{-1} (Bokhari *et al.* 1987).

Stress indices

CLIMEX uses stress indices to limit the potential growth of a population in a given location. A value of 0 represents "no stress" and a value of 100 reflects "lethal" conditions (Pietro and Blasi 2002).

Cold stress

The cold stress function may not influence the potential distribution of a warm season species if extreme frost events occur in areas that are already unsuitable due to an insufficient thermal accumulation rate (Sutherst *et al.* 2004). However, cold stress is included to evaluate the distribution pattern of the species in climate change scenarios. The cold stress threshold (TTCS) and accumulation rate (THCS) were set at 0 ºC and -0.001 week^{-1} respectively because the plant is susceptible to frost damage (Kriticos *et al.* 2003). These parameters were adjusted to allow it to barely persist in Armidale (30º 54′ S, 151º 88′ E, 1019 m elevation), NSW, Australia, where it grows naturally, and where the minimum winter temperature regularly goes well below 0 ºC. A long-term monthly average of daily minimum temperature of 0 °C indicates that there are likely to be several severe frosts each week.

Heat stress

McWilliam *et al.* (2003) found that *H. hirta* seedlings can grow at temperatures up to 40 ºC. In another study conducted in Saudi Arabia (McWilliam *et al.* 1970), *H. hirta* was tolerant of high temperatures and very dry conditions. The heat stress threshold

(TTHS) was set at 40 ºC to coincide with the temperature above which growth ceases. The heat stress accumulation rate (THHS) was adjusted to -0.001 week^{-1} to match the distribution of *H. hirta* in Africa (Figure 8.1) and its distribution limit in Dubbo, NSW, Australia, where summer temperatures can exceed 40 ºC.

Dry stress

The dry stress threshold (SMDS) was set at 0.1. It was fixed at the same level as the lower soil moisture threshold (SM0) because soil moisture-related stresses were assumed to begin at the same soil moisture levels where growth stops (Bokhari *et al.* 1987). Dry stress accumulation rate (HDS) was adjusted on the basis of *H. hirta* distribution in Valladolid, Spain (Lat. 41º 39′ N, Long. 4º 46′ W), Santa Maria, California (Lat. 32º 44′N, Long. 117º 10′ W) and in some dry places of Namibia.

Wet stress

The wet stress threshold (SMWS) was set at 1.4 and the accumulation rate (HWS) set at 0.0015. This rate shows the inability of *H. hirta* to grow in waterlogged conditions. However, this rate will allow *H. hirta* to grow in high rainfall areas like the Tyrrhenian district of central Italy (Kriticos *et al.* 2003), and in the Maclean and Nymboidia districts of NSW (Australia).

8.3 Results

Current climate

The areas projected to be suitable for *H. hirta* invasion under current world-wide climatic conditions are illustrated in Figure 8.2. The projected distribution of *H. hirta* corresponds closely with the current global distribution of *H. hirta*, as well as showing a good fit within its native range in Africa, except for some areas that are circled in Figure 8.1. We checked these circled distribution points and found that these were either present under wet micro-sites that are not represented by climatic conditions, or are no longer present at those sites. The climatic conditions are projected to be suitable for *H. hirta* throughout much of the tropics and subtropics with the exception of desert areas where excessive dry stress and/or heat stress limit its distribution. It also conforms well to the Australian distribution where the model projects optimal environments in eastern Queensland, northern NSW and no climate suitability in the central part of Australia, predominantly because of dry and heat stresses. Optimal environments also occur in large parts of South America, Central America, sub-Saharan Africa, south-eastern USA, Madagascar, the Indian subcontinent, and most of the Pacific Islands. Climatic conditions are projected to be marginal in many warm temperate areas of the world, such as southern Mediterranean Europe and northern New Zealand.

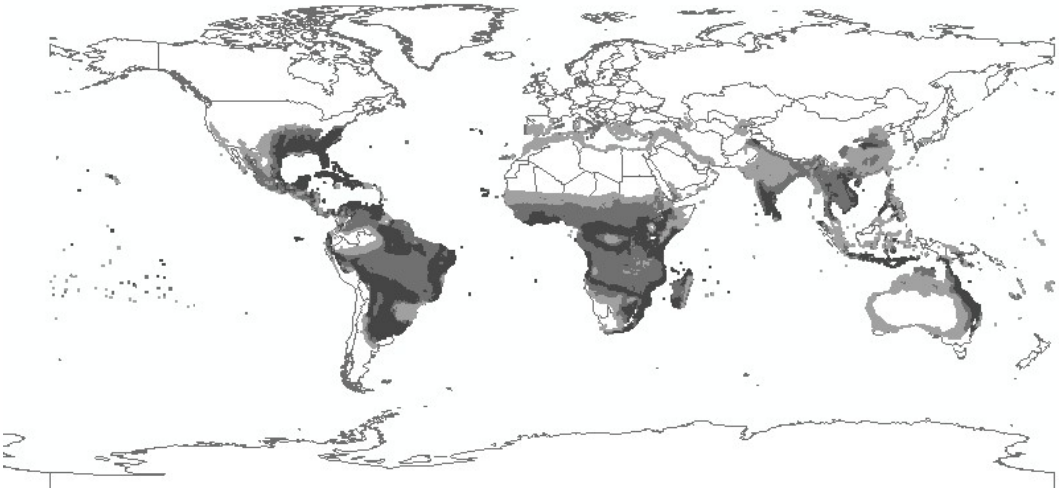

Figure 8.2 The climate suitability (EI) for *H. hirta* under the reference climate (1960-1990 averages) projected using CLIMEX^{TM} (□ , unsuitable (0.00-0.49); ░ , marginal (0.50-9.99); ▒ , suitable (10.00-19.99); ■ , optimal (20.00+).

Future climate

The overall impact of future climate on the potential distribution of *H. hirta* is that the distribution will likely expand poleward and into higher altitudes into areas that are currently too cool (Figure 8.3, Figure 8.4, Figure 8.5). Under current climatic conditions, suitable habitat in the USA only occurs in the southern part but under future climate change scenarios, the suitable range extends throughout the USA. The optimal range of *H. hirta* invasion also extends towards the north-eastern cropping areas of the USA. In some regions of South America, the projected warming under future climate scenarios may decrease the invasion threat from *H. hirta*. Under current climate conditions, suitable to optimal conditions for *H. hirta* extend through much of Brazil, Venezuela, Guyana, Surinam, Paraguay and Uruguay. Under the HadCM3 GCM with the most extreme SRES emission scenario (A1F1), suitable conditions for *H. hirta* invasion of this region decrease and extend toward coastal areas (Figure 8.5). Climate change scenarios indicate that South America is likely to become hotter and wetter (Pietro and Blasi 2002). The projected geographic range of optimal climates for *H. hirta* in Africa and inland Australia reduces as the climate is projected to become drier. In Europe, the potential range for *H. hirta* is projected to extend northward, with climatically suitable or marginal conditions occurring in much of Spain, Portugal, Italy and the south of France and Russia. Climate change scenarios indicate that the arctic is likely to become warmer. In Asia, the projected potential range also expands polewards, although projected conditions in South East Asia for *H. hirta* decrease because of increasing wet stress in New Guinea, and heat stress around Myanmar and Thailand. In China, the optimal range for *H. hirta* invasion is projected to extend towards north-eastern areas. Under each of the future climate scenarios examined here, the climatic suitability of much of Europe, the USA, South East Asia, south Pacific Islands including New Zealand, and NSW (Australia) increases substantially, with some areas becoming climatically optimal including some regions of Australia, the USA, southern India, eastern China, some European countries, and New Zealand that are presently used for grain, grazing and horticultural purposes. Under moderate SRES A1 scenarios the optimal suitability (EI > 20.00) of *H. hirta* on the basis of potential distribution counts used in the Figures 8.3 – 8.5 showed 41% increase compared to potential distribution under current climate. Whereas, under most extreme SRES A1F1 scenario the potential distribution counts for optimal suitability decreased by 45%.

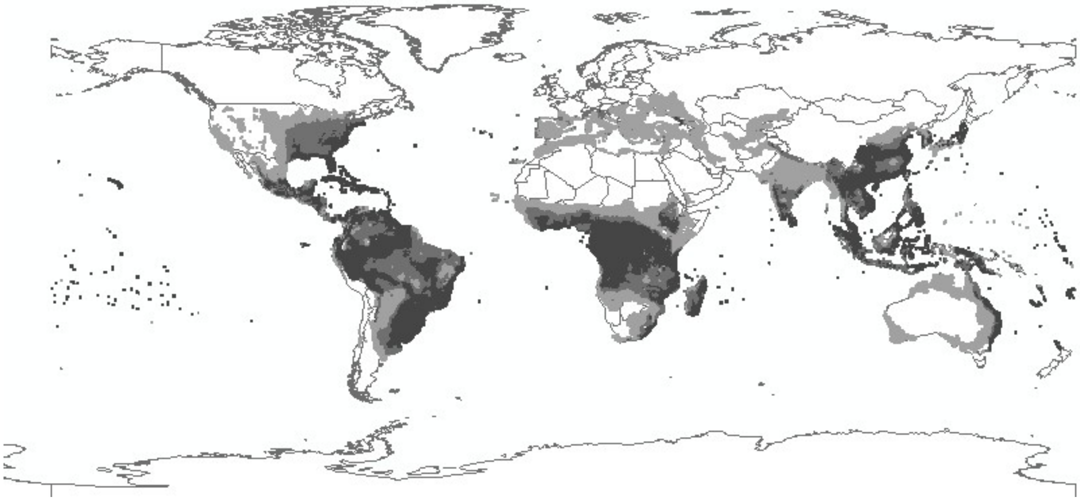

Figure 8.3 The climate (EI) for *H. hirta* in the 2080s projected using CLIMEX (□ , unsuitable (0.00-0.49); ░ , marginal (0.50-9.99); ▓ , suitable (10.00-19.99); ■ , optimal (20.00+). Source meteorological data adjusted using the CSIRO Mark 2 GCM (Stephens *et al.* 2007) running the SRES A1 scenario.

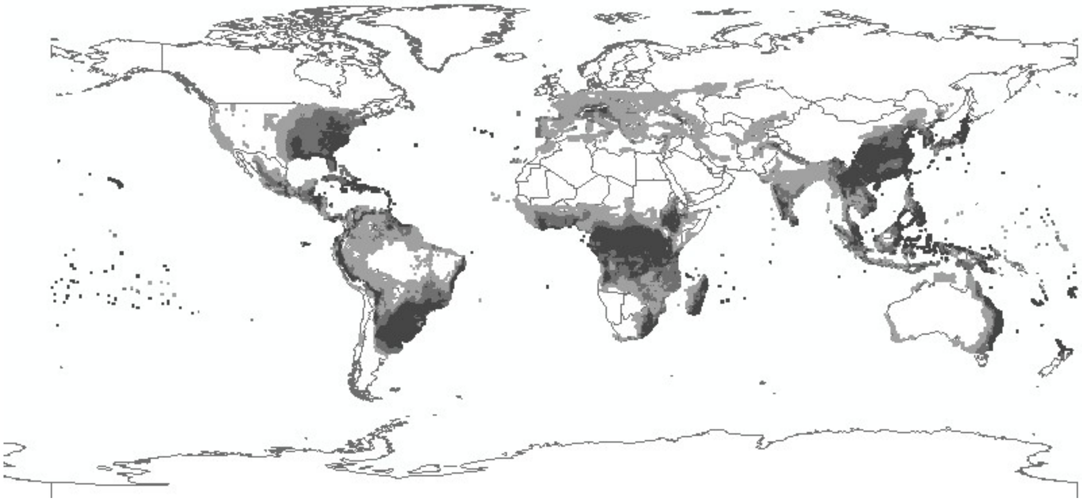

Figure 8.4 The climate (EI) for *H. hirta* in the 2080s projected using CLIMEX (□ , unsuitable (0.00-0.49); ■ , marginal (0.50-9.99); ■ , suitable (10.00-19.99); ■ , optimal (20.00+). Source meteorological data adjusted using the ECHAM 4 GCM (Hirst *et al.* 2000) running the SRES A1 scenario.

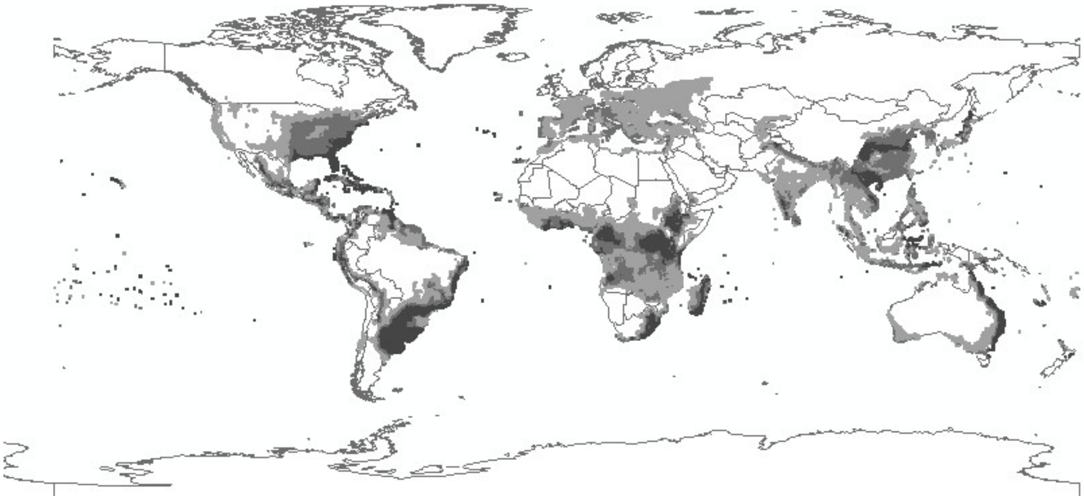

Figure 8.5 The climate (EI) for *H. hirta* in the 2080s projected using CLIMEX (□ , unsuitable (0.00-0.49); ■, marginal (0.50-9.99); ■, suitable (10.00-19.99); ■ , optimal (20.00+). Source meteorological data adjusted using the HadCM3 GCM (Zhang *et al.* 1998) running the most extreme SRES A1F1 scenario.

8.4 Discussion

The results presented here should be considered indicative of the directions and likely magnitudes of the expected changes in the potential range of *H. hirta* invasion in response to climate change, highlighting areas where more detailed risk assessments may be worthwhile. The results identify areas of the world that will be vulnerable to invasion by *H. hirta* as a consequence of climate change unless adequate control measures prevent further dispersal. This information can be used to alert public administrators and land managers to the invasion threat posed by this plant. The area at risk of invasion by *H. hirta* under current climate conditions greatly exceeds the current distribution, with suitable to optimal habitat covering much of the tropics and subtropics world-wide (Figure 8.2). Projected climate changes will most probably increase the area at risk of invasion, most noticeably in the most productive zones of the USA, Europe, South East Asia, India, Australia and Pacific Islands including New Zealand (Figure 8.3, Figure 8.4, Figure 8.5). The large potential for further invasion under both current and future climates justifies concerns that the invasion of this plant can be a great threat world-wide.

Hyparrhenia hirta is projected to be able to invade throughout the tropics and subtropics. Given its wide ecological range it will shift its distribution in relation to climate changes. While cold stress is the primary limiting factor, hot and dry stress prevent its establishment in the Sahara, inland Australia and parts of the Middle East. Areas of particular invasion risk include Central and South America, sub-Saharan Africa, coastal Queensland, most of parts of NSW, Mexico, the Caribbean and the south-eastern USA. These areas include wetter parts of the tropics and subtropics which tend to be naturally forested. *Hyparrhenia hirta* generally does not colonize areas beneath dense tree cover as well as it colonizes open areas (Gordon *et al.* 2000).

However, within that climatic zone, *H. hirta* may be capable of invading many grazed areas where tree cover has been artificially reduced.

Under future climates, the range of *H. hirta* is likely to expand into areas currently too cold for its survival, and contract from areas which are projected to become drier under climate change. Under moderately warmer scenario (CSIRO-Mk2a), a 41% increase in the potential distribution of *H. hirta* compared to its potential distribution under current climatic conditions suggests that the range of *H. hirta* is likely to expand into areas currently too cold. Under the more extreme scenario (HadCM3) the 45% decrease in potential distribution shows that its range is likely to be contracted overall if hot and dry stresses become too severe. The agricultural value of these areas is likely to decrease as they become drier, and the threat of this invasive grass would become even more accentuated. Where conditions become warmer and wetter (e.g. Brazil) there is a tendency for the climate suitability to decrease, and under the extreme scenario, there is even a range contraction. These results support the claim of Dukes (2004) that a rapidly changing climate can favour invasive species such as *H. hirta* that can extend or shift their ranges quickly or that can tolerate a wide range of climatic conditions and therefore have greater competitive success than native species. Under a changing climate the individual factors that have been investigated include increased CO_2 which can create favourable conditions for species invasion by increasing productivity, soil moisture and nitrogen uptake (Dukes 2003). Invasive species benefit greatly from habitat disturbances because they are better dispersers and breeders; characteristics that are likely to make them benefit from climate change (Weltzin *et al.* 2003).

CLIMEX models that predict the potential distribution of organisms in new areas under current or future climates based on their responses to climate in their native or exotic ranges, ignore dispersal and interactions among species, such as resource competition (Hilbert *et al.* 2007), biophysical factors such as soil, land use (Baker *et al.* 2000), vegetation cover, disturbance or the dispersal ability of a species to a new area. However, *H. hirta* expresses a range of traits that indicates that biophysical factors such as soil and resource competition are unlikely to limit its invasion into new areas. *Hyparrhenia hirta* is adapted to a wide range of climatic or biophysical conditions. As previously mentioned, *H. hirta* can survive periods of drought in the summer (Sutherst *et al.* 1999). It can grow on a range of soil types from light textured granitic soils to heavy black earths and it is a moderately salt tolerant species (McWilliam *et al.* 1970, McCormick *et al.* 1992). *Hyparrhenia hirta* was reported the most competitive species among five perennial C4 grass species particularly in infertile study plots in Mediterranean climatic conditions in South Africa (Rogers and Bailey 1963). Fetene (2005b) suggested that *H. hirta* was competitively aggressive towards *Acacia etbaica* and may inhibit the growth of tree seedlings when the latter are planted within the grass community.

Projecting climate changes using GCMs is an inexact procedure. Stephens *et al.* (2003) identified three major sources of uncertainty of using GCM models. Firstly, there are uncertainties in future greenhouse gas and aerosol emissions. Secondly, there are uncertainties in global climate sensitivity, because of differences in the way each GCM portrays physical processes. Finally, there are uncertainties in regional climate changes, which appear as regional differences in projections in response to similar emissions scenarios and mean global warming. The results presented here do not represent most of the accepted uncertainty due to the future socio-economic conditions that underpin the SRES emission scenarios. Due to the recent publication by Rahmstorf *et al.* (2007), showing unexpectedly large increases in global warming, we have explored the warmer scenarios to better examine the risks that could result from more accelerated climate change. Whilst most of the GCMs indicate similar results at the global level, there are significant regional differences. Therefore, for critical decision making, it is important to consider the sensitivity of the affected system to the probable full range of expected climatic changes (Rahmstorf *et al.* 2007).

The large potential for further spread of *H. hirta* and increased mitigation costs under both current and expected future climatic conditions, means that it may be worthwhile investing in efforts to prevent further spread of this species. The future range shift or extension of *H. hirta* poleward into areas that are currently too cool (Figure 8.3, Figure 8.4, Figure 8.5) appears to be a fairly robust projection that accords with previous climate change modelling (Kriticos *et al.* 2003, Kriticos *et al.* 2006, Stephens *et al.* 2007) and field observations (Kriticos *et al.* 2003a). The weed biosecurity authorities in these jurisdictions should be aware of its introduction into new areas. A crucial element in this response strategy will be adequate public awareness about the threat posed by *H. hirta*, its identification and control techniques. Maps such as those produced here can play an important element in planning and allocating resources to build community and management support and capacity to manage existing infestations, and to prevent further invasion. In the context of an active biotic invasion, changes in climate may significantly alter the area at risk of invasion (potential range) and the spatial pattern of abundance of the invader (Parmesan *et al.* 1999). Where climate change results in an expansion of the potential range of an invasive organism compared with that under the current climate, new agencies will become concerned with managing the invasion as the regions for which agencies are responsible for pest management come under greater threat. Likewise, cultural adaptation techniques and strategies based on the estimated potential distribution under current climate may be rendered less effective under climate change.

Statement of Originality:

All the work contained within this paper is the original research of the PhD candidate, Vinod Kumar Chejara.

Candidate:

Principal Supervisor:

Statement of Contribution by Others:

This paper has been prepared by the PhD candidate, Vinod Kumar Chejara. All coauthors are PhD supervisors (Paul Kristiansen, Darren Kriticos, Wal Whalley, Brian Sindel, and Christopher Nadolny) and have only contributed to this paper to the extent that would normally be expected of such roles. All coauthors have given their consent for having their contributions to this paper included in the thesis and accept the student's contribution as indicated in the Statement of Originality.

Candidate:

Principal Supervisor:

CHAPTER NINE

General conclusions

General conclusions

9.1 Introduction

Hyparrhenia hirta is becoming of increasing importance as a weed of natural environments throughout NSW and other Australian states, due to its dominating and competitive nature. It can be highly invasive, infesting native grasslands, grassy woodlands, pastures and travelling stock reserves, often creating mono-specific stands. Little research has been conducted on the biology and ecology of *H. hirta*, particularly in northern NSW where it was originally introduced. Therefore, this has limited the ability of land managers to develop effective control and management techniques.

This project was designed to improve the understanding of the key aspects of seed ecophysiology, population dynamics and community ecology of *H. hirta* on the Northern Tablelands which would be of value for the planning and implementation of management techniques. The key findings and implications for management are summarised in this chapter.

9.2 Seed Germination

Factors affecting seed germination

An understanding of the seed germination ecology of *H. hirta* will help us to understand its current distribution, predict potential spread into new areas and be useful in developing effective control strategies. The results of this study suggest that *H. hirta* seeds have the ability to germinate under a wide range of diurnal temperatures, different light regimes, pH levels and under marginal water stress (Chapter 3). *Hyparrhenia hirta* seeds can germinate over a wide range of temperature combinations from 5 – 45 ºC. The seeds germinate quickly, with a high rate (> 80%)

of germination one – two days after sowing, thus providing a competitive advantage by rapidly imbibing soil moisture from summer rainfall, especially in sandy soils where *H. hirta* has been very successful. The ability of *H. hirta* to germinate rapidly over a wide range of temperatures also provides a partial explanation for the establishment of this species throughout much of Australia. The slow spread of *H. hirta* in the cooler Tableland region of New South Wales, Australia is likely due to low germination in the lower temperatures from late summer to early autumn, and to frost.

The high level of germination in the absence of light indicates that *H. hirta* can germinate without a light trigger, although light may improve germination slightly. These results indicated that *H. hirta* seeds can readily germinate in soil and under plant canopy and litter shade. Germination of *H. hirta* at moderately acidic or alkaline conditions (pH 5 and 9, respectively) showed that the pH of most soils found in Australia will not be a limiting factor in its spread and establishment. Germination at -0.37 MPa indicates that a moderate proportion of seeds of *H. hirta* can germinate under marginal water-stress conditions. However, higher water-stress greatly reduces germination confirming that *H. hirta* is unlikely to successfully invade arid regions. Germination of *H. hirta* below the limiting osmotic potentials for native grasses indicates greater tolerance of moisture stress at this stage of growth, which may be an important factor contributing to the establishment of this species under field conditions.

9.3 Vertical distribution and viability of seeds and seedling emergence in soils of different textures

Hyparrhenia hirta seeds were more abundant at greater depths in clay soil than in sandy soil, but their emergence was lower at shallow depths in sandy soil possibly due to the lower porosity of the clay soil improving water availability to the seed. Since this species comes from Mediterranean climatic regions of Africa, the self-burial specialisation could be an evolutionary strategy to avoid the hot and semi-arid environment and to prevent biotic disturbance (e.g. seed predation) and abiotic disturbance such as fire.

Seeds can retain their dormancy and viability for about 12 months, and is greater in sandy soil than in clay soil. Differences in dormancy and viability due to soil types possibly related to the higher organic carbon content of the clay soil, increasing soil biological activity and decomposition processes (Kriticos *et al.* 2003a, Van *et al.* 2005).

The majority of the viable seeds were recovered from shallow depths. Perhaps seeds at shallow depths were produced more recently, whereas seeds from lower depths were possibly older and had taken some time to move down through the soil profile. Assuming that some proportion of the buried seed bank dies each year, it is reasonable to expect that the seeds at lower soil depths will be less viable.

The rapid emergence of *H. hirta* at shallow depths provides a competitive advantage in rapidly capturing soil moisture and nutrients, which tend to be more mobile in sandy soils where *H. hirta* has been very successful.

These results suggest that there is potential to enhance *H. hirta* seed bank depletion by, for example, changing the vertical distribution of seed through specific tillage practices to increase germination and subsequent control (e.g. with herbicides), or by preventing further seed fall through mowing, slashing or grazing and soil disturbance altogether. The relative short viability (≤ 12 months) of *H. hirta* seeds is an important attribute of the species that can be exploited in the design of weed control programs.

9.4 Seed and seedling population dynamics

Seed dynamics and seedling establishment of *H. hirta* in the field

A two-year field study of seedling recruitment, survival and seedbank density under different treatments (control, mowing and herbicide) has helped to develop an understanding of the population dynamics of *H. hirta*.

The seedlings of *H. hirta* recruited in most months during the two-year trial in each treatment at all sites. The main seedling flushes occurred in the warmer months of the year, from midsummer to early autumn and declined with the onset of cooler weather and lower rainfall. These results support the findings of the temperature experiment on seed germination in Section 9.2. Mowing and herbicide application significantly excluded the seed input into the seedbank, so emergence in the second year of the study was low in comparison with the control (unmanaged) plots.

The soil seedbank of *H. hirta* was extremely variable between sites and treatments during the study period. The Armidale site had the highest seed density (~14 837/m^2). This large seedbank may have resulted from the higher plant density and biomass production that was found at this site. In 2005, the highest number of seeds(~16 000/m^2) was collected from the control plots. During the two years, the seedbank declined by more than 90% due to the application of herbicide and mowing treatments. Hence, if seed can be prevented from entering a site for two years, the seedbank is likely to be depleted to low levels.

Seedling survival of *H. hirta* was influenced by climate and pasture competition. Seedling cohorts that emerged in winter had less survivorship, demonstrating that *H. hirta* seedlings are highly sensitive to low temperatures and frost. The highest survival rate occurred in cohorts emerging in the warm season from January to March. Manilla had the highest survivorship among sites. This was due to more favourable temperatures and moisture availability during these months. Manilla received around 30 mm of rainfall in January 2007 and the temperature (20/35 ºC day/night) was very suitable for the germination and growth of *H. hirta* seedlings. These results are in close conformity to the findings in Section 9.2.

The highest survivorship of seedlings during the first year of the trial was observed in the herbicide treated or mown plots at all sites. This result is presumed to be due to less intra- and inter-specific competition in the treated plots compared with the untreated control plots. Seedling emergence and survival are more likely to be highest for various grass species that germinate in the open between inter-tussock spaces due to higher availability of light and less intra-specific competition from neighbouring mature plants whose phenology would be synchronized with those of the seedlings (Harper 1977, Van *et al.* 2005), as well as from inter-specific competition from rapidly growing annual species (Lodge 1981). Therefore, some form of direct control of *H. hirta*, in combination with providing competitive pasture species and strategic grazing management to discourage seedling survival will assist in management, especially in summer when most *H. hirta* seedlings emerge.

9.5 Competitive and allelopathic interactions

Density based competition between the Australian native grass *B. macra* and *H. hirta*

The findings of this glasshouse study demonstrate that the competitive ability of *H. hirta* is likely to assist its invasion of native vegetation. For both roots and shoots, relative crowding coefficient of *H. hirta* towards *B. macra* was much higher than *B. macra* over *H. hirta*, which indicated a high competitive ability of *H. hirta*. Intra-specific competition in *H. hirta* was increased as the plant density increased, whereas it was decreased in *B. macra* when density increased more than 6 plants per pot. This indicates that increasing density of plants can intensify the intra-specific competition in *H. hirta*. Inter-specific competition of *H. hirta* over *B. macra* for both roots and shoots was three to seven fold higher than vice versa, showing that *H. hirta* may inhibit *B. macra* early growth and establishment when growing within *H. hirta* invaded areas.

Effect of *H. hirta* and *P. aquatica* aqueous extracts and plant residues on two native grasses

Both *H. hirta* and *Phalaris aquatica* can be highly invasive throughout Australia, infesting native grasslands, grassy woodlands and travelling stock reserves, often leading to a monoculture. It is reported that both of these species have allelopathic potential which inhibit the germination and early growth of native grasses in bioassays. The results of our study showed that the seed germination and early growth of target species, *B. macra* and *Dichanthium sericeum* were significantly inhibited by the aqueous extracts of both invasive species at high concentrations (≥ 1%) but generally not affected at low concentrations (≤ 1%). While, *H. hirta* may have allelopathic potential, the importance of these effects in the field are unknown, especially in comparison to the effects of resource competition.

9.6 CLIMEX modelling

The current and future potential geographical distribution of *H. hirta*

Knowledge of the likely potential distribution of *H. hirta* under current and future climate scenarios will help biosecurity and weed control authorities to plan strategies to manage invasion. The CLIMEX modelling package was used to determine suitable climatic parameters to explain current *H. hirta* distribution and to investigate the impacts of climate change on the potential global distribution of *H. hirta*.

The world-wide potential distribution of *H. hirta* under current climatic conditions includes suitable optimal habitat covering much of the tropics and subtropics. While cold stress is the primary limiting factor, hot and dry stress prevent its establishment in the Sahara, inland Australia and parts of the Middle East. Areas of particular invasion risk include Central and South America, sub-Saharan Africa, coastal Queensland, most of parts of NSW, Mexico, the Caribbean and the south-eastern USA. Range expansion is likely to be limited by land-use management factors.

Projected climate changes will most probably increase the area at risk of invasion, most noticeably in the most productive zones of the USA, Europe, South East Asia, India, Australia and the Pacific Islands including New Zealand. Given its wide ecological range it will shift its distribution in response to climate changes.

Under future climates, the range of *H. hirta* is likely to expand into areas currently too cold for its survival, and to contract from areas which are projected to become drier under climate change. Under moderately warmer scenario (CSIRO-Mk2a), a 41% increase in the potential distribution of *H. hirta* compared to its potential distribution under current climatic conditions suggests that the range of *H. hirta* is likely to expand into areas currently too cold. Under the more extreme scenario (HadCM3) the 45% decrease in potential distribution shows that its range is likely to be contracted overall if hot and dry stresses become too severe. The effects of likely climatic scenarios on the global potential distribution of *H. hirta* are sufficiently great that they should be considered routinely in strategic control plans for biotic invasions. Where climate change results in an expansion of the potential range of an invasion of *H. hirta* compared with that under the current climate, new agencies will become concerned with managing the invasion as the regions for which agencies are responsible for pest management come under greater threat.

9.7 Future research

Several areas for future research have arisen from work in this thesis. Aspects of the biology and ecology of *H. hirta* were examined in glasshouse and field situations specific to the northern NSW. However, little is know about its biological and ecological behaviour in other Australian ecosystems including under winter dominant rainfall conditions. Factors affecting germination of *H. hirta* studied in the laboratory need to be confirmed in field situations as well. Research on effect of environmental factors on *H. hirta* life cycle (e.g. growth habit, timing of flowering and seed production) would also be useful.

Hyparrhenia hirta was competitive against *B. macra* and has slight allelopathic potential to inhibit the germination and early growth of native grasses. These effects need to be examined under field conditions, especially the relative contribution of resource competition versus allelopathy in invasion.

Although some aspects of the population dynamics of *H. hirta* were examined, little is know about its seed production. There is disagreement over seed production in this species. Humphries (1980), Robinson and Potts (1965) and McCormick and Lodge (1950) have noted that *H. hirta* is a poor seed producer with a high degree of variability between plants in their ability to set seed, whereas, Luckens (1991) found that *H. hirta* was a prolific seeder. The timing and amount of seed production need to be assessed under a range of biophysical and management conditions.

References

Adams, R. M., Rosenzweig, C., Peart, R. M., Ritchie, J. T., McCarl, B. A., Glyer, J. D., Curry, R. B., Jones, J. W., Boote, K. J., and Allen, L. H. (1990). Global climate change and US agriculture. *Nature* **345**, 219-224.

Adkins, S. W., Bellairs, S. M., and Loch, D. S. (2002). Seed dormancy mechanisms in warm season grass species. *Euphytica* **126**, 13-20.

Agarwal, A. R., Gahlot, A., Verma, R., and Rao, P. B. (2002). Effects of weed extracts on seedling growth of some varieties of wheat. *Journal of Environmental Biology* **23**, 19-23.

Alex, J. F. (1980). Emergence from buried seed and germination of exhumed seed of fall panicum. *Canadian Journal of Plant Science* **60**, 635-642.

Altieri, M. A., and Liebman, N. (1988). Weed Management in Agro-ecosystems: Ecological Approaches. CRC Press, Florida.

Andrews, T. S. (1995). The population biology of giant *Sporobolus* R. Br. species as an aid to their management in pastures on the North Coast of New South Wales. Ph D Thesis, Department of Botany, University of New England, Armidale.

Andrews, T. S., Jones, C. E., and Whalley, R. D. B. (1997). Factors affecting the germination of Giant Parramatta grass. *Australian Journal of Experimental Agriculture* **37**, 439-446.

Andrews, T. S., Whalley, R. D. B., and Jones, C. E. (1996). Seed production and seedling emergence of Giant Parramatta grass on the North Coast of New South Wales. *Australian Journal of Experimental Agriculture* **36**, 299-308.

Arnon, D. I., and Johnson, C. M. (1942). Influence of hydrogen ion concentrations on the growth of higher plants under controlled conditions. *Plant Physiology* **17**, 525-539.

Aspinall, D. (1960). An analysis of competition between barley and white persicaria. *Annals of Applied Biology* **48**, 637-654.

Auld, B. A., and Coote, B. G. (1981). Prediction of pasture invasion by *Nassella trichotoma* (Gramineae) in south east Australia. *Protection Ecology* **3**, 271-277.

Australia's Virtual Herbarium 2006. *Royal Botanic Gardens Melbourne*. 30th December, 2006. <http://www.rbg.vic.gov.au/avh/>.

Badgery, W. B., Kemp, D. R., Michalk, D. L., and King, W. M. (2002). Competition between native grasses and serrated tussock (*Nassella trichotoma*) at low fertility - initial results. *Plant Protection Quarterly* **17**, 95-98.

Badgery, W. B., Kemp, D. R., Michalk, D. L., and King, W. M. C. G. (2005). Competition for nitrogen between Australian native grasses and the introduced weed *Nassella trichotoma*. *Annals of Botany* **96**, 799-809.

Baker, R. H. A., Sansfors, C. E., Jarvis, C. H., Cannon, R. J. C., MacLeod, A., and Walters, K. F. A. (2000). The role of climatic mapping in predicting the potential geographic distribution of non-indigenous pests under current and future climates. *Agriculture Ecosystems Environment* **82**, 57-71.

Balyan, R. S., and Bhan, V. M. (1986). Germination of horse purslane (*Trianthema portulacastrum*) in relation to temperature, storage conditions, and seedling depths. *Weed Science* **34**, 513-515.

Baruch, Z., and Bilbao, B. (1999). Effects of fire and defoliation on the life history of native and invader C_4 grasses in a Neotropical savanna. *Oecologia* **119**, 510-520.

Baskin, C. C., and Baskin, J. M. (1998). Ecology of seed dormancy and germination in grasses. *In* "Population Biology of Grasses" (G. P. Cheplick, ed.), pp. 30-83. Cambridge University Press, Cambridge.

Baskin, C. C., Milberg, P., Andersson, L., and Baskin, J. M. (2004). Germination ecology of seeds of the annual weeds *Capsella bursa-pastoris* and *Descurainia sophia* originating from high northern latitudes. *Weed Research* **44**, 60-68.

Bazzaz, F. A. (1990). Plant-plant interactions in successional environments. *In* "Perspectives on Plant Competition" (J. B. Grace and D. Tilman, eds.), pp. 239-263. Academic Press, San Diego.

Beaumont, L. J., Hughes, L., and Poulsen, M. (2005). Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. *Ecological Modelling* **186**, 250-269.

Begon, M., and Mortimer, M. (1986). Population Ecology a Unified Study of Animals and Plants. 2nd/Ed. Sinauer Associates Inc., Sunderland Massachusetts.

Bekker, R. M., Bakker, J. P., Grandin, U., Kalamees, R., Milberg, P., Poschlod, P., Thompson, K., and Willems, J. H. (1998). Seed size, shape and vertical distribution in the soil: indicators of seed longevity. *Functional Ecology* **12**, 834-842.

Benech-Arnold, R. L., Sanchez, R. A., Forcella, F., Kruk, B. C., and Ghersa, C. M. (2000). Environmental control of dormancy in weed seed banks in soil. *Field Crops Research* **67**, 105-122.

Benefield, C. B., DiTomaso, J. M., Kyser, G. B., Orloff, S. B., Churches, K. R., Marcum, D. B., and Nader, G. A. (1999). Success of mowing to control yellow starthistle depends on timing and plant's branching form. *California Agriculture* **53**, 17-21.

Benvenuti, S. (2003). Soil texture involvement in germination and emergence of buried weed seeds. *Agronomy Journal* **95**, 191-198.

Benvenuti, S. (2007). Natural weed seed burial: effect of soil texture, rain and seed characteristics. *Seed Science Research* **17**, 211-219.

Benvenuti, S., Dinelli, G., Bonetti, A., and Catizone, P. (2005). Germination ecology, emergence and host detection in *Cuscuta campestris*. *Weed Research* **45**, 270-278.

Benvenuti, S., and Macchia, M. (1998). Phytochrome mediated germination control of *Datura stramonium* L. seeds. *Weed Research* **38**, 199-205.

Bewley, J. D. (1997). Seed germination and dormancy. *The Plant Cell* **9**, 1055-1066.

Bewley, J. D., and Black, M. (1994). Seeds. *In* "Physiology of Development and Germination", pp. 445. Plenum, New York.

Bhowmik, P. C. (1997). Weed biology: importance to weed management. *Weed Science* **45**, 349-356.

Bi, H., and Turvey, N. D. (1994). Inter-specific competition between seedlings of *Pinus radiata*, *Eucalyptus regnans* and *Acacia melanoxylon*. *Australian Journal of Botany* **42**, 61-70.

Biosecurity Council (2003). Tiakina Aotearoa Protect New Zealand: The Biosecurity Strategy for New Zealand. The Biosecurity Council, Wellington.

Blackshaw, R. E., Stobbe, E. H., Shaykewich, C. F., and Woodbury, W. (1981). Influence of soil temperature and soil moisture on green foxtail (*Setaria viridis*) establishment in wheat (*Triticum aestivum*). *Weed Science* **29**, 179-184.

Bokhari, U. G., Faisal, A., and Al-Nori, M. (1987). Adaptive strategies of desert grasses in Saudi Arabia. *Journal of Range Management* **40**, 19-22.

Booth, B. D., Murphy, S. D., and Swanton, C. J. (2003a). Ecology of weeds. *In* "Weed Ecology in Natural and Agricultural Systems", pp. 1-13. CABI Publishing, Wallingford.

Booth, B. D., Murphy, S. D., and Swanton, C. J. (2003b). From seed to seedling. *In* "Weed Ecology in Natural and Agricultural Systems", pp. 81-99. CABI Publishing, Wallingford.

Boughey, A. S., Munro, P. E., Meiklejohn, J., Strang, R. M., and Swift, M. J. (1964). Antibiotic relations between African savanna species. *Nature* **203**, 1302-1303.

Bourdot, G. W., and Hurrell, G. A. (1992). Aspects of the ecology of *Stipa neesiana* Trin. & Rupr. seeds. *New Zealand Journal of Agricultural Research* **35**, 101-108.

Boyd, L., and Avery, G. S. (1936). Grass seedling anatomy: the first internode of *Avena* and *Triticum*. *Botanical Gazette* **97**, 765-779.

Boyd, N. S., and Van Acker, R. C. (2003). The effects of depth and fluctuating soil moisture on the emergence of eight annual and six perennial plant species. *Weed Science* **52**, 725-730.

Brown, J. R., and Carter, J. (1998). Spatial and temporal patterns of exotic shrub invasion in an Australian tropical grassland. *Landscape Ecology* **13**, 93-102.

Buckland, S. M., Thompson, K., Hodgson, J. G., and Grime, J. P. (2001). Grassland invasions: effects of manipulations of climate and management. *Journal of Applied Ecology* **38**, 301-309.

Buhler, D., Hartzler, R. G., and Forcella, F. (1997). Implications of weed seedbank dynamics to weed management. *Weed Science* **45**, 329-336.

Bureau of Meteorology 2007. *New South Wales Climate Averages*. 25/12/2007. <http://www.bom.gov.au/climate/averages/tables/ca_nsw_names.shtml>.

Burke, I. C., Thomas, W. E., Spears, J. F., and Wilcut, J. W. (2003). Influence of environmental factors on broadleaf signalgrass (*Brachiaria platyphylla*) germination. *Weed Science* **51**, 683-689.

Burr, P. 2007. *Bureau of Meteorology weather station in East Armidale*. 30/12/2007. <http://www-personal.une.edu.au/~pburr/weather/datafiles.htm>.

Callaway, R. M. (2002). The detection of neighbors by plants. *Trends in Ecology and Evolution* **17**, 104-105.

Campbell, M. H. (1998). Biological and ecological impact of serrated tussock (*Nassella trichotoma* (Ness) Arech.) on pastures in Australia. *Plant Protection Quarterly* **13**, 80-86.

Campbell, M. H., Dellow, J. J., Keys, M. J., and Gilmour, A. R. (1985). Use of herbicides for the selective removal of *Eragrostis curvula* (Schrad.) Nees from a

Phalaris aquatica pasture. *Australian Journal of Experimental Agriculture* **25**, 665-671.

Campbell, M. H., and Gilmour, A. R. (1979). Effect of time and rate of application of herbicides on serrated tussock (*Nassella trichotoma*) and improved pasture species. *Australian Journal of Experimental Agriculture and Animal Husbandry* **19**, 472-475.

Chachalis, D., and Reddy, K. N. (2000). Factors affecting *Campsis radicans* seed germination and seedling emergence. *Weed Science* **48**, 212-216.

Chambers, J. C. (1995). Relationship between seed fates and seedling establishment in an alpine ecosystem. *Ecology* **76**, 2124-2133.

Chambers, J. C., and MacMahon, J. A. (1994). A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. *Annual Review Ecological Systems* **25**, 263-292.

Chambers, J. C., MacMahon, J. A., and Haefner, J. H. (1991). Seed entrapment in alpine ecosystems: effects of soil particle size and diaspore morphology. *Ecology* **72**, 1668-1677.

Chauhan, B. S., Gill, G., and Preston, C. (2006). Influence of environmental factors on seed germination and seedling emergence of rigid ryegrass (*Lolium rigidum*). *Weed Science* **54**, 1004-1012.

Chauvel, B., Guillemin, J. P., and Letouze, A. (2005). Effect of intra-specific competition on development and growth of *Alopecurus myosuroides* Hudson. *European Journal of Agronomy* **22**, 301-308.

Chejara, V. K. (2008). Ecological studies of *Hyparrhenia hirta* (L.) Stapf in northern New South Wales. PhD, University of New England, Armidale.

Chejara, V. K., Kristiansen, P., Whalley, R. D. B., Sindel, B. M., and Nadolny, C. (in press). Factors affecting seed germination of Coolatai grass (*Hyparrhenia hirta*). *Weed Science*.

Chejara, V. K., Nadolny, C., Kristiansen, P., Whalley, R. D. B., and Sindel, B. M. (2006). Impacts of *Hyparrhenia hirta* (L.) Stapf (Coolatai grass) on native vegetation in a travelling stock route in northern New South Wales. *In* "15th Australian Weeds Conference" (C. Preston, J. H. Watts and N. D. Crossman, eds.), pp. 207-210, Weed Management Society of South Australia, Adelaide.

Chung, I. M., and Miller, D. A. (1995). Allelopathic influence of nine forage grass extracts on germination and seedling growth of alfalfa. *Agronomy Journal* **87**, 767-772.

Clark, J. S., Grimm, E. C., Lynch, J., and Mueller, P. G. (2001). Effects of holocene climate change on the C_4 grassland/woodland boundary in the northern plains, USA. *Ecology* **82**, 620-636.

Clayton, W. D. (1969). A revision of the genus *Hyparrhenia*. *Kew Bulletin* **2**, 1-196.

Collatz, G. J., Berry, J. A., and Clark, J. S. (1998). Effects of climate and atmospheric CO_2 partial pressure on the global distribution of C_4 grasses: present, past, and future. *Oecologia* **114**, 441-454.

Conn, J. S., Beattie, K. L., and Blanchard, A. (2006). Seed viability and dormancy of 17 weed species after 19.7 years of burial in Alaska. *Weed Science* **54**, 464-470.

Connell, J. H. (1990). Apparent versus "Real" Competition in Plants. *In* "Perspectives on Plant Competition" (J. B. Grace and D. Tilman, eds.), pp. 9-26. Academic Press Inc., San Diego.

Cook, G. D., and Dias, L. (2006). It was no accident: deliberate plant introductions by Australian government agencies during the 20th century. *Australian Journal of Botany* **54**, 601-625.

Cook, T. (2003). Perennial Grass Weeds: An Overview of Management Options. *In* "12th Biennial Noxious Weeds Conference and Expo Conference Program and Papers", Taree, Australia.

Cousens, R., and Mortimer, M. (1995). Processes involved in the regulation of population density. *In* "Dynamics of Weed Populations", pp. 86-134. Cambridge University Press, Cambridge.

Crawley, M. J. (1986). Plant Ecology. Blackwell Scientific, Oxford.

Dalling, J. W., and Hubbell, S. P. (2002). Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *Journal of Ecology* **90**, 557-568.

Davis, A. J., Jenkinson, L. S., Lawton, J. H., Shorrocks, B., and Wood, S. (1998). Making mistakes when predicting shifts in species range in response to global warming. *Nature* **391**, 783-786.

Dawson, J. H., and Bruns, V. F. (1975). Longevity of barnyard grass, green foxtail, and yellow foxtail seeds in soil. *Weed Science* **23**, 437-40.

De Villiers, A. J., Van Rooyen, M. W., and Theron, G. K. (2001). The role of facilitation in seedling recruitment and survival patterns, in the Strandveld Succulent Karoo, South Africa. *Journal of Arid Environments* **49**, 809-821.

de Wit, C. T. (1960). On competition. *Verslagen van Landbouwkundige Onderzoekingen* **66**, 1-82.

de Wit, C. T., and van den Bergh, J. P. (1965). Competition between herbage plants. *Netherlands Journal of Agricultural Science* **13**, 212-221.

Devlin, R. M., and Witham, F. H. (1983). Absorption and translocation of water. *In* "Plant Physiology", pp. 53-71. Prindle, Weber and Schmidt, Boston.

Dhima, K. V., Lithourgidis, A. S., Vasilakoglou, I. B., and Dordas, C. A. (2007). Competition indices of common vetch and cereal intercrops in two seeding ratio. *Field Crops Research* **100**, 249-256.

DiTomaso, J. M. (2000). Invasive weeds in rangelands: species, impacts and management. *Weed Science* **48**, 255-265.

DiTomaso, J. M., Kyser, G. B., and Hastings, M. S. (1999). Prescribed burning for control of yellow starthistle (*Centaurea solstitialis*) and enhanced native plant diversity. *Weed Science* **47**, 233-242.

Doria, R. G. (1998). Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. *Ecological Applications* **8**, 975-989.

Dukes, J. S. (2003). Hotter and weedier? Effects of climate change on the success of invasive species. *In* "Global Climate Change and Biodiversity" (R. Green, M. Harley, L. Miles, J. Scharlemann, A. Watkinson and O. Watts, eds.), pp. 25, Tyndall Centre for Climate Change Research.

Dukes, J. S., and Mooney, H. A. (1999). Does global change increase the success of biological invaders? *Trends in Ecology and Evolution* **14**, 135-139.

Dunlop, E. A., Wilson, J. C., and Mackey, A. P. (2006). The potential geographic distribution of the invasive weed *Senna obtusifolia* in Australia. *Weed Research* **46**, 404-413.

El-Khatib, A. A., Hegazy, A. K., and Galal, H. K. (2003). Allelopathy in the rhizosphere and amended soil of *Chenopodium murale* L. *Weed Biology and Management* **4**, 35-42.

Engler, R., Guisan, A., and Rechsteiner, L. (2004). An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology* **41**, 263-274.

Espinar, J. L., Thompson, K., and Garcia, L. V. (2005). Timing of seed dispersal generates a bimodal seed bank depth distribution. *American Journal of Botany* **92**, 1759-1763.

Eswaran, H., Beinroth, F. H., Reich, P. F., and Quandt, L. A. (1999). Vertisols : their properties, classification, distribution and management. United States Department of Agriculture, Lincoln, Nebraska.

Facelli, J. M., and Pickett, S. T. A. (1991). Plant litter and effects on plant community structure. *Botanical Review* **57**, 1-32.

Faithful, I. (2002). Weed watch warning tambookie grass *Hyparrhenia hirta*. In Under Control No. 19, March 2002, Dept. of Natural Resources and Environment, Victoria, pp. 10-11.

Fenner, M. (1987). Seedlings. *New Phytologist* **106 (Suppl.)**, 35-47.

Fetene, M. (2003). Intra- and inter-specific competition between seedlings of *Acacia etbaica* and a perennial grass (*Hyparrhenia hirta*). *Journal of Arid Environments* **55**, 441-451.

Firbank, L. G., and Watkinson, A. R. (1985). On the analysis of competition within two species mixtures of plants. *Journal of Applied Ecology* **22**, 503-517.

Fitter, A. (1996). Characteristics and functions of root systems. *In* "Plant Roots: The Hidden Half" (W. Yoav, E. Amram and K. Uzi, eds.), pp. 1-20. Marcel Dekker, Inc., New York.

Forcella, F., Benech-Arnold, R. L., Sanchez, R., and Ghersa, C. M. (2000). Modeling seedling emergence. *Field Crops Research* **67**, 123-139.

Forcella, F., Wilson, R. G., Renner, K. A., Dekker, J., Harvey, R. G., Alm, D. A., Buhler, D. D., and Cardina, J. (1992). Weed seedbank of the U.S. Corn Belt: Magnitude, variation, emergence and application. *Weed Science* **40**, 636-644.

Fowler, N. L. (1995). Density-dependent demography in two grasses: a five-year study. *Ecology* **76**, 2145-2164.

Fynn, R. W. S., Morris, C. D., and Edwards, T. J. (2005a). Long-term compositional responses of a South African mesic grassland to burning and mowing. *Applied Vegetation Science* **8**, 5-12.

Fynn, R. W. S., Morris, C. D., and Kirkman, K. P. (2005b). Plant strategies and trait trade-offs influence trends in competitive ability along gradients of soil fertility and disturbance. *Journal of Ecology* **93**, 384-394.

Gallagher, R., Beaumont, L., Downey, P. O., Hughes, L., and Leishman, M. R. (2006). Assessing the potential impacts of climate change on weeds in New South Wales: establishing priorities. *In* "15th Australian Weeds Conference" (C. Preston, J. H. Watts and N. D. Crossman, eds.), pp. 35-39, Weed Management Society of South Australia, Adelaide.

Gallandt, E. R. (2006). How can we target the weed seedbank? *Weed Science* **54**, 588-596.

Gardener, M. R. (1998). The biology of *Nassella neesiana* (Trin. & Rupr.) Barkworth (Chilean needle grass) in pastures on the Northern Tablelands of New South Wales: weed or pasture? PhD, The University of New England, Armidale.

Gardener, M. R., Sindel, B. M., Whalley, R. D. B., and Earl, J. M. (2005). Can *Nassella neesiana*, Chilean needle grass, be incorporated into a grazing management system in Australia? *Plant Protection Quarterly* **20**, 36-40.

Gardener, M. R., Whalley, R. D. B., and Sindel, B. M. (2003). Ecology of *Nassella neesiana*, Chilean needle grass, in pastures on the Northern Tablelands of New South Wales. II. Seedbank dynamics , seed germination, and seedling recruitment. *Australian Journal of Agricultural Research* **54**, 621-626.

Garnier, L. K. M., and Dajoz, I. (2001). The influence of fire on the demography of a dominant grass species of West African savannas, *Hyparrhenia diplandra*. *Journal of Ecology* **89**, 200-208.

Garrido, J. L., Rey, P. J., and Herrera, C. M. (2007). Regional and local variation in seedling emergence, mortality and recruitment of a perennial herb in Mediterranean mountain habitats. *Plant Ecology* **190**, 109-121.

Gasque, M., and Garcia-Fayos, P. (2003). Seed dormancy and longevity in *Stipa tenacissima* L. (Poaceae). *Plant Ecology* **168**, 279-290.

Ghorbani, R., Seel, W., and Leifert, C. (1999). Effects of environmental factors on germination and emergence of *Amaranthus retroflexus*. *Weed Science* **47**, 505-510.

Gibson, D. J., Connolly, J., Hartnett, D. C., and Weidenhamer, J. D. (1999). Essay review: designs for greenhouse studies of interactions between plants. *Journal of Ecology* **87**, 1-16.

Gilfedder, L., and Kirkpatrick, J. B. (1994). Climate, grazing and disturbance and the population dynamics of *Leucochrysum albicans* at Ross, Tasmania. *Australian Journal of Botany* **42**, 417-430.

Gill, G. S., and Davidson, R. M. (2000). Weed Interference. *In* "Australian Weed Management Systems" (B. M. Sindel, ed.), pp. 61-80. R J and F J Richardson Publications, Melbourne.

Gleeson, S. K., and Tilman, D. (1994). Plant allocation, growth rate and successional status. *Functional Ecology* **8**, 543-550.

Global Biodiversity Information Facility 2007. *Online Database*. April 20, 2007. <http://www.gbif.org/>.

Goldberg, D. E. (1990). Components of resource competition in plant communities. *In* "Perspectives on Plants Competition" (J. B. Grace and D. Tilman, eds.), pp. 27-49. Academic Press, San Diego.

Goldberg, D. E., and Landa, K. (1991). Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *Journal of Ecology* **79**, 1013-1030.

Gordon, C., Cooper, C., Seniour, C. A., Banks, H., Gregory, J. M., Johns, T. C., Mitchell, J. F. B., and Wood, R. A. (2000). The simulation of SST, sea Ice extents and ocean heat transports in a version of the Hadley Centre Coupled Model without flux adjustments. *Climate Dynamics* **16**, 147-168.

Gould, S. J., and Vrba, E. S. (1982). Exaptation - a missing term in the science of form. *Paleobiology* **8**, 4-15.

Grace, B. S., Sheppard, A. W., Whalley, R. D. B., and Sindel, B. M. (2002). Seedbanks and seedling emergence of saffron thistle (*Carthamus lanatus*) in eastern Australian pastures. *Australian Journal of Agricultural Research* **53**, 1327-1334.

Grace, B. S., Sindel, B. M., Sheppard, A. W., and Whalley, R. D. B. (1999). Ecology, population dynamics and management of *Carthamus lanatus* in eastern Australian pastures. *In* "11th European Weed Research Society Symposium", pp. 78, Basel.

Gramshaw, D., and Stern, W. (1977). Survival of annual ryegrass (*Lolium rigidum* Gaud.) seed in a Mediterranean type environment. II: effects of short-term burial on persistence of viable seed. *Australian Journal of Agricultural Research* **28**, 93-101.

Grice, A. C. (2000). Weed management in Australian rangelands. *In* "Australian Weed Management Systems" (B. M. Sindel, ed.), pp. 431-458. R J and F J Richardson Publications, Melbourne.

Grime, J. P. (1979). Plant Strategies and Vegetation Processes. John Wiley and Sons, Chichester.

Gross, K. L. (1980). Colonization of *Verbascum thapsus* (Mullein) in an old field in Michigan: the effects of vegetation. *Journal of Ecology* **68**, 919-927.

Gross, K. L. (1984). Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *Journal of Ecology* **72**, 369-387.

Groves, R. H., Austin, M. P., and Kaye, P. E. (2003). Competition between Australian native and introduced grasses along a nutrient gradient. *Austral Ecology* **28**, 491-498.

Grundy, A. C. (2003). Predicting weed emergence: a review of approaches and future challenges. *Weed Research* **43**, 1-11.

Grundy, A. C., Mead, A., and Bond, W. (1996). Modelling the effect of weed-seed distribution in the soil profile on seedling emergence. *Weed Research* **36**, 375-384.

Guardia, R., Raventos, J., and Caswell, H. (2000). Spatial growth and population dynamics of a perennial tussock grass (*Achnatherum calamagrostis*) in a badland area. *Journal of Ecology* **88**, 950-963.

Guisan, A., and Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8**, 993-1009.

Gutterman, Y. (2000). Maternal effects on seeds during development. *In* "Seeds: The Ecology of Regeneration in Plant Communities" (M. Fenner, ed.), pp. 59-84. CAB International, Wallingford.

Halsall, D. M., Leigh, J. H., Gollasch, S. E., and Holgate, M. (1995). The role of allelopathy in legume decline in pastures. II. Comparative effects of pasture, crop and weed residues on germination, nodulation and root growth. *Australian Journal of Agricultural Research* **46**, 189-207.

Hansen, M. J., and Wilson, S. D. (2006). Is management of an invasive grass *Agropyron cristatum* contingent on environmental variation? *Journal of Applied Ecology* **43**, 269-280.

Harper, J. L. (1977). The Population Biology of Plants. Academic Press, London.

Harradine, A. R., and Whalley, R. D. B. (1980). Reproductive development and seedling establishment of *Aristida ramosa* R. Br. in Northern New South Wales. *Australian Rangeland Journal* **2**, 124-135.

Hattersley, P. W. (1983). The distribution of C3 and C4 grasses in Australia in relation to Climate. *Oecologia* **57**, 113-128.

Heirro, J. L., and Callaway, R. M. (2003). Allelopathy and exotic plant invasion. *Plant and Soil* **256**, 29-39.

Hilbert, D. W., Hughes, L., Johnson, J., Lough, J. M., Low, T., Pearson, R. G., Sutherst, R. W., and Whittaker, S. (2007). Biodiversity conservation research in a changing climate. *In* "Workshop report: research needs and information gaps for the implementation of the key objectives of the National Biodiversity and Climate Change Action Plan". Department of the Environment and Water Resources, Commonwealth of Australia.

Hirst, A. C., O'Farrell, S. P., and Gordon, H. B. (2000). Comparision of a coupled ocean-atmosphere model with and without oceanic eddy-induced advection. 1. Ocean spin-up and control integration. *Journal of Climate* **13**, 139-163.

Humphries, A. W. (1959). *Hyparrhenia hirta*- a promising pasture species. *Journal of the Australian Institute of Agricultural Sciences* **25**, 334-336.

Humphries, A. W. (1965). *Hyparrhenia hirta* (L.) Stapf - a novel pasture species for a mediterranean type environment. *CSIRO Australian Plant Introduction Review* **2**, 17-18.

Hunt, S. (2006). Utilisation of pastures dominated by Coolatai grass (*Hyparrhenia hirta*). *In* "Stipa" (D. Bonnington, ed.), pp. 36-42. Native Grasses Association Inc, Dubbo.

Hutchinson, G. E. (1957). Concluding remarks. Cold Spring Symposium on Quantitative Biology. pp. 415–427. Yale University, New Haven, Connecticut.

Hyder, D. N., Everson, A. C., and Bement, R. E. (1971). Seedling morphology and seeding failure with blue grama. *Journal of Range Management* **24**, 287-292.

Hyder, D. N., and Sneva, F. A. (1963). Morphological and physiological factors affecting the grazing management of crested wheatgrass. *Crop Science* **31**, 267.

Ida, H., and Nakagoshi, N. (1996). Gnawing damage by rodents to the seedlings of *Fagus crenata* and *Quercus mongolica* var. *grosseserrata* in a temperate Sasa grassland-deciduous forest series in southwestern Japan. *Ecological Research* **11**, 97-103.

Inderjit (2006). Experimental complexities in evaluating the allelopathic activities in laboratory bioassays: A case study. *Soil Biology and Biochemistry* **38**, 256-262.

Inderjit, and Bhowmik, P. C. (2004). Sorption of benzoic acid onto soil colloids and its implications for the allelopathy studies. *Biology and Fertility of Soils* **40**, 345-348.

Inderjit, and Weston, L. A. (2000). Are laboratory bioassays for allelopathy suitable for prediction of field responses? *Journal of Chemical Ecology* **26**, 2111-2118.

IPCC (2000). Special Report on Emissions Scenarios: A Special Report of Working Group III of the Intergovernmental Panel on Climate Change Cambridge University Press, Cambridge.

Isbell, R. F. (1996). The Australian Soil Classification. CSIRO Publishing, Melbourne.

Jackson, D. L., and Jacobs, S. W. L. (1985). Australian Agricultural Botany. Sydney University Press, Sydney.

Johnson, S. B., and Sindel, B. M. (2005). Recruitment potential from asexual and sexual reproduction in *Polymeria longifolia*. *Weed Research* **45**, 279-288.

Jolliffe, P. A. (2000). The replacement series. *Journal of Ecology* **88**, 371-385.

Jolliffe, P. A., Minjas, A. N., and Runeckles, V. C. (1984). A reinterpretation of yield relationships in replacement series experiments. *Journal of Applied Ecology* **21**, 227-243.

Kanchan, S. D., and Jayachandra (1980). Allelopathic effects of *Parthenium hysterophorus* L. IV. Identification of inhibitors. *Plant and Soil* **55**, 67-75.

Keane, R. M., and Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* **17**, 164-170.

Keeley, J. E. (1988). Allelopathy. *Ecology* **69**, 293-294.

Kemp, D. R., King, W. M., Michalk, D. L., and Alemseged, Y. (1999). Weed proofing pastures: how can we go about it? *In* "12th Australian Weeds Conference" (A. C. Bishop, M. Boerama and C. D. Barnes, eds.), pp. 138-143. Tasmanian Weeds Society, Inc., Davenport, Tasmania.

Kigel, J. (1995). Seed germination in arid and semiarid regions. *In* "Seed Dormancy and Germination" (J. Kigel, ed.), pp. 645-700. Marcel Dekker, Inc., NY.

Kitajima, K., and Fenner, M. (2000). Ecology of seedling regeneration. *In* "Seeds" (M. Fenner, ed.). Cabi Publishing, Wallingford.

Kobayashi, K. (2004). Factors affecting phytotoxic activity of allelochemicals in soil. *Weed Biology and Management* **4**, 1-7.

Koger, C. H., Reddy, K. N., and Poston, D. H. (2004). Factors affecting seed germination, seedling emergence, and survival of texaweed (*Caperonia palustris*). *Weed Science* **52**, 989-995.

Kohli, R. K., Singh, H. P., and Batish, D. R. (2001). Allelopathy in Agroecosystems. Haworth Press Inc, Binghamton, NY.

Korhammer, S. A., and Haslinger, E. (1994). Isolation of a biologically active substance from rhizomes of quackgrass [*Elymus repens* (L.) Gould]. *Journal of Agriculture and Food Chemistry* **42**, 2048-2050.

Kriticos, D. J. (1996). The role of ecological modelling in weed management. *In* "11th Australian Weeds Conference" (R. C. H. Shepherd, ed.), pp. 560-568. Weed Science Society of Victoria Inc., Melbourne.

Kriticos, D. J., Alexander, N. S., and Kolomeitz, S. M. (2006). Predicting the potential geographic distribution of weeds in 2080. *In* "15th Australian Weeds Conference" (C. Preston, J. H. Watts and N. D. Crossman, eds.), pp. 27-34, Weed Management Society of South Australia, Adelaide.

Kriticos, D. J., and Randall, R. P. (2001). A comparison of systems to analyse potential weed distributions. *In* "Weed Risk Assessment" (R. H. Groves, F. D. Panetta and J. G. Virtue, eds.), pp. 61-79. CSIRO Publishing, Melbourne.

Kriticos, D. J., Sutherst, R. W., Brown, J. R., Adkins, S. W., and Maywald, G. F. (2003). Climate change and the potential distribution of an invasive alien plant: *Acacia nilotica* spp. *indica* in Australia. *Journal of Applied Ecology* **40**, 111-124.

Kriticos, D. J., Sutherst, R. W., Brown, J. R., Adkins, S. W., and Maywald, G. F. (2003a). Climate change and biotic invasions: a case history of a tropical woody vine. *Biological Invasions* **5**, 145-165.

Kriticos, D. J., Watt, M. S., Potter, K. J. B., and Leriche, A. (Submitted). Predicting growth rates of invasive alien plant species using a climatic habitat suitability model. *Journal of Applied Ecology*.

Kriticos, D. J., Yonow, T., and McFadyen, R. E. (2005). The potential distribution of *Chromolaena odorata* (Siam weed) in relation to climate. *Weed Research* **45**, 246-254.

Lacey, J. R., Wallender, R., and Olson-Rutz, K. (1992). Recovery, germinability and viability of leafy spurge (*Euphorbia esula*) seeds ingested by sheep and goat. *Weed Technology* **6**, 559-602.

Lambert, F. J., Bower, M., Whalley, R. D. B., Andrews, A. C., and Bellotti, W. D. (1990). The effects of soil moisture and planting depth on emergence and seedling morphology of *Astrebla lappacea* (Lindl.) Domin. *Australian Journal of Agricultural Research* **41**, 367-76.

Lamoureaux, S., and Bourdot, G. (2002). *Nassella trichotoma* (Nees) Arechav.: seedling recruitment and survival in New Zealand *In* "13th Australian Weeds Conference" (H. S. Jacob, J. Dodd and J. H. Moore, eds.), pp. 533-536. Plant Protection Society of Western Australia, Perth.

Larsen, A. L. (1971). Two-way thermogradient plate for seed germination research: construction plans and procedures. United States Department of Agriculture, Washington.

Lawson, B. E., Bryant, M. J., and Franks, A. J. (2004). Assessing the potential distribution of buffel grass (*Chenchrus ciliaris* L.) in Australia using a climate-soil model. *Plant Protection Quarterly* **19**, 155-163.

Lee, J. M., and Hamrick, J. L. (1983). Demography of two natural populations of musk thistle (*Carduus nutans*). *Journal of Ecology* **71**, 923-936.

Leigh, J. H., Halsall, D. M., Muller, W. J., Oram, R. N., Edlington, J. P., and Geissler, A. E. (1995). The role of allelopathy in legume decline in pastures. III. Tolerance of subterranean clover lines to the allelopathic compounds released from Phalaris residues. *Australian Journal of Agricultural Research* **46**, 1039-1049.

Leist, N., and Kramer, S. (2003). ISTA Working Sheets on Tetrazolium Testing. *In* "Agricultural, Vegetable and Horticultural Species, ISTA", Vol. 1, pp. 176, Bassersdorf.

Leon, R. G., Knapp, A. D., and Owen, M. D. K. (2004). Effect of temperature on the germination of common waterhemp (*Ameranthus tuberculatus*), giant foxtail (*Setaria faberi*), and velvetleaf (*Abutilon theophrasti*). *Weed Science* **52**, 67-73.

Levine, J. M., Vila, M., D'Antonio, C. M., Dukes, J. S., Grigulis, K., and Lavorel, S. (2003). Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of Biological Science* **270**, 775-781.

Lloyd, S. G., and Moore, J. (2002). Coolatai grass or tambookie grass (*Hyparrhenia hirta* (L.) Stapf) - an introduced pasture grass with environmental weed potential. *In* "13th Australian Weeds Conference" (H. S. Jacob, J. Dodd and J. H. Moore, eds.), pp. 549-551. Council of Australian Weed Science Societies, Perth.

Lodge, G. M. (1981). The establishment of warm- and cool-season native perennial grasses on the north-west slopes of New South Wales. I. Dormancy and germination. *Australian Journal of Botany* **29**, 121-133.

Lodge, G. M. (2000). Competition among seedlings of perennial grasses, subterranean clover, white clover, and annual ryegrass in replacement series mixtures. *Australian Journal of Agricultural Research* **51**, 377-383.

Lodge, G. M. (2004). Seed dormancy, germination, seedling emergence, and survival of some temperate perennial pasture grasses in northern New South Wales. *Australian Journal of Agricultural Research* **55**, 345-355.

Lodge, G. M., McCormick, L. H., and Harden, S. (2005). Grazing studies of a *Hyparrhenia hirta* (Coolatai grass) pasture in northern New South Wales. *Australian Journal of Experimental Agriculture* **45**, 1603-1611.

Lodge, G. M., McMillan, M. G., McCormick, L. H., and Cook, A. S. (1994). Effects of glyphosate, flupropanate and 2,2-DPA on *Hyparrhenia hirta* (L.) Stapf (Coolatai grass). *Australian Journal of Experimental Agriculture* **34**, 479-85.

Lovett, J. V., and Jessop, R. S. (1982). Effects of residues of crop plants on germination and early growth of wheat. *Australian Journal of Agricultural Research* **33**, 909-916.

Luckens, R. J. (2002). Proclamation of Coolatai grass (*Hyparrhenia hirta*). pp. 11pp. Animal and Plant Control Board, Salisbury, Australia.

Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., and Bazzaz, F. A. (2000). Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* **10**, 689-710.

Mackey, A. P. (1997). The biology of Australian weeds. 29. *Acacia nilotica* spp. *indica* (Benth.) Brenan. *Plant Protection Quarterly* **12**, 7-17.

Mallik, A. U., and Prescott, C. E. (2001). Growth inhibitory effects of salal on western hemlock and western red cedar. *Agronomy Journal* **93**, 85-92.

Marshall, T. J., Holmes, J. W., and Rose, C. W. (1996). Soil Physics. Cambridge University Press, Cambridge.

Mathews, S., Spangler, R. E., Mason-Gamer, R. J., and Kellogg, E. A. (2002). Phylogeny of Andropogoneae inferred from phytochrome B, GBSSI, and NDHF. *International Journal of Plant Sciences* **163**, 441-450.

MathSoft (1999). S-PLUS 2000 Guide to Statistics. Vol. 1. Data Analysis Products Division, MathSoft, Seattle.

Maun, M. A., and Lapierre, J. (1986). Effects of burial by sand on seed germination and seedling emergence of four dune species. *American Journal of Botany* **73**, 450-455.

Maze, K. M., Koen, T. B., and Watt, L. A. (1993). Factors influencing the germination of six perennial grasses of central New South Wales. *Australian Journal of Botany* **41**, 79-90.

McArdle, S. L., Nadolny, C., and Sindel, B. M. (2004). Invasion of native vegetation by Coolatai grass *Hyparrhenia hirta*: impacts on native vegetation and management implications. *Pacific Conservation Biology* **10**, 49-56.

McCormick, L. H., and Lodge, G. M. (1991). Coolatai Grass — Friend or Foe? New South Wales Agriculture and Fisheries, Orange.

McCormick, L. H., and Lodge, G. M. (1998). Coolatai Grass Field Day. New South Wales Agriculture, Manilla.

McCormick, L. H., McMillan, M. G., and Lodge, G. M. (1992). Coolatai grass (*Hyparrhenia hirta*) control. *Australian Weeds Research Newsletter* **41**, 36-38.

McWilliam, J. R., Shanker, K., and Knox, R. B. (1970). Effects of temperature and photoperiod on growth and reproductive development in *Hyparrhenia hirta*. *Australian Journal of Agricultural Research* **21**, 557-569.

Meyer, A. H., and Schmid, B. (1999). Seed dynamics and seedling establishment in the invading perennial *Solidago altissima* under different experimental treatments. *Journal of Ecology* **87**, 28-41.

Michalk, D., Kemp, D. R., Campbell, M. H., and McLaren, D. A. (1999). Control of serrated tussock - problems in developing IWM systems. *In* "Proceedings of the Twelfth Australian Weeds Conference" (A. C. Bishop, M. Boersma and C. D. Barnes, eds.), pp. 20-24. Tasmanian Weeds Society, Devonport, Tasmania.

Michel, B. E. (1983). Evaluation of the water potentials of solutions of polyethylene glycol 8000 both in the absence and presence of other solutes. *Plant Physiology* **72**, 66-70.

Milberg, P. J., Andersson, L., and Thompson, K. (2000). Large-seeded species are less dependent on light for germination than small-seeded ones. *Seed Science Research* **10**, 99-104.

Milchunas, D. G., and Noy-Meir, I. (2002). Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos* **99**, 113-130.

Miller, R. W., and Donahue, R. L. (2004). Soil water properties. *In* "Soils in Our Environment", pp. 62-97. Prentice Hall, Upper Saddle River, NJ.

Miller, S. D., and Nalewaja, J. D. (1990). Influence of burial depth on wild oats (*Avena fatua*) seed longevity. *Weed Technology* **4**, 514-517.

Mitchell, T. D., Carter, T. R., Jones, P. D., Hulme, M., and New, M. (2004). A comprehensive set of climate scenarios for Europe and the globe: the observed record (1900-2000) and 16 scenarios (2000-2100). *Tyndall Working Paper* **55**, 33.

Mousseau, T. A., and Fox, C. W. (1998). The adaptive significance of maternal effects. *Trends in Ecology and Evolution* **13**, 403-407.

Mullahey, J. J., West, S. H., and Cornell, J. A. (1996). Effects of simulated drought by polyethylene glycol on bahiagrass germination. *Seed Science and Technology* **24**, 219-224.

Murdoch, A. J., and Ellis, R. H. (1992). Longevity, viability and dormancy. *In* "Seeds: The Ecology of Regeneration in Plant Communities" (M. Fenner, ed.), pp. 193-229. CAB International, Wallingford.

Murdoch, A. J., and Ellis, R. H. (2000). Dormancy, viability and longevity. *In* "Seeds: The Ecology of Regeneration in Plant Communities" (M. Fenner, ed.), pp. 183-214. CAB International, Wallingford.

Myers, J. H., Simberloff, D., Kuris, A. M., and Carey, J. R. (2000). Eradication revisited: dealing with exotic species. *Trends in Ecology and Evolution* **15**, 316-320.

Nadolny, C. (1998). Towards integrating farming and conservation: the role of native pastures. *Pacific Conservation Biology* **4**, 70-78.

Nandula, V. K., Eubank, T. W., Poston, D. H., Koger, C. H., and Reddy, K. N. (2006). Factors affecting germination of horseweed (*Conyza canadensis*). *Weed Science* **54**, 898-902.

Navas, M. L., Garnier, E., Austin, M. P., Viaud, A., and Gifford, R. M. (2002). Seeking a sound index of competitive intensity: application to the study of biomass production under elevated CO_2 along a nitrogen gradient. *Austral Ecology* **27**, 463-473.

Nicholls, N., and Collins, D. (2006). Observed change in Australia over the past century. *Energy and Environment* **17**, 1-12.

Nilsson, M., Zacrisson, O., Sterner, O., and Wallstedt, A. (2000). Characterization of the differential effects of two boreal dwarf shrub species. *Oecologia* **123**, 122-128.

NLWRA (2001). Australian Agriculture Assessment 2001. National Land and Water Resources Audit, Braddon.

Norby, R. J., Kobayashi, K., and A, K. B. (2001). Rising CO_2 - future ecosystems. *New Phytologist* **150**, 215-221.

Olson, B. E. (1999). Grazing and weeds. *In* "Biology and Management of Noxious Rangeland Weeds" (R. L. Sheley and J. K. Petroff, eds.), pp. 85-96. Oregon State University Press, Corvallis.

Omami, E. N., Haigh, A. M., Medd, R. W., and Nicol, H. I. (1999). Changes in germinability, dormancy and viability of *Amaranthus retroflexus* as affected by depth and duration of burial. *Weed Research* **39**, 345-354.

Orr, S. P., Rudgers, J. A., and Clay, K. (2005). Invasive plants can inhibit native tree seedlings: testing potential allelopathic mechanisms. *Plant Ecology* **181**, 153-165.

Pandy, D. K. (1994). Inhibition of salvinia (*Salvinia molesta* Mitchell) by parthenium (*Parthenium hysterophorus* L.). II. Relative effect of flower, leaf, stem, and root residue on salvinia and paddy. *Journal of Chemical Ecology* **20**, 3123-3131.

Panetta, F. D. (1993). A system of assessing proposed plant introductions for weed potential. *Plant Protection Quarterly* **8**, 10-14.

Panetta, F. D., and Mitchell, N. D. (1991). Homoclime analysis and the prediction of weediness. *Weed Research* **31**, 273-284.

Panetta, F. D., and Timmins, S. (2004). Evaluating the feasibility of eradications for terrestrial weed incursions. *Plant Protection Quarterly* **19**, 5-11.

Parker, I. M., Simberloff, D., Lonsdale, W. M., Goodell, K., Wonham, M., Kareiva, P. M., Williamson, M. H., Von Holle, B., Moyle, P. B., Byers, J. E., and Goldwasser, L. (1999). Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* **1**, 3-19.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W. J., Thomas, J. A., and Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**, 579-583.

Peart, M. H. (1979). Experiments of the biological significance of the morphology of seed-dispersal units in grasses. *Journal of Ecology* **67**, 843-863.

Peart, M. H. (1984). The effects of morphology, orientation and position of grass diaspores on seedling survival. *Journal of Ecology* **72**, 437-453.

Perkins, L., Bredenkamp, G. J., and Granger, J. E. (1999). The phytosociology of the incised river valley and dry upland savanna of southern KwaZullu-Natal. *South African Journal of Botany* **65**, 321-330.

Pietro, R. D., and Blasi, C. (2002). A phytosociological analysis of abandoned olive-grove grasslands of Ausoni mountains (Tyrrhenian district of Central Italy). *Lazaroa* **23**, 73-93.

Prober, S. M., Thiele, K. R., and Lunt, I. D. (2002). Identifying ecological barriers to restoration in temperate grassy woodlands: soil changes associated with different degradation states. *Australian Journal of Botany* **50**, 699-712.

Putnam, A. R. (1985). Weed allelopathy. *In* "Weed Physiology: Reproduction and Ecophysiology" (S. O. Duke, ed.), Vol. 1, pp. 131-155. CRC Press, Boca Raton.

Quayyum, H. A., Malik, A. U., Leach, D. M., and Gottardo, C. (2000). Growth inhibitory effects of nutgrass (*Cyperus rotundus*) on rice (*Oryza sativa*) seedlings. *Journal of Chemical Ecology* **26**, 2221-2231.

R Development Core Team (2006). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Radford, P. J., and Greenwood, D. J. (1970). The simulation of gaseous diffusion in soils. *European Journal of Soil Science* **21**, 305-313.

Rafiqul Hoque, A. T. M., Ahmed, R., Uddin, M. B., and Hossain, M. K. (2003). Allelopathic effect of different concentration of water extracts of *Acacia auriculiformis* leaf on some initial growth parameters of five common agricultural crops. *Pakistan Journal of Agronomy* **2**, 92-100.

Rahmstorf, S., Cazenave, A., Church, J. A., Hansen, J. E., Keeling, R. F., Parker, D. E., and Somerville, R. C. J. (2007). Recent climate observations compared to projections. *Science* **316**, 709.

Rastetter, E. B. (1996). Validating models of ecosystem response to global change. *Bioscience* **46**, 190-197.

Rebollo, S., Perez-Camacho, L., Garcia-de Juan, M. T., Rey Benayas, J. M., and Gomez-Sal, A. (2001). Recruitment in a Mediterranean annual plant community: seed bank, emergence, litter, and intra- and inter-specific interactions. *Oikos* **95**, 485-495.

Redmann, R. E., and Abouguendia, Z. M. (1979). Germination and seedling growth on substrates with extreme pH-Laboratory evaluation of buffers. *Journal of Applied Ecology* **16**, 901-907.

Rees, M. (1995). Community structure in sand dune animals: is seed weight a key quantity? *Journal of Ecology* **83**, 857-863.

Reever-Morghan, K. J., Leger, E. A., and Rice, K. J. (2003). Clopyralid effects on yellow starthistle (*Centaurea solstitialis*) and nontarget species. *Weed Science* **51**, 596-600.

Refsgaard, J. C., Christensen, T. H., and Ammentrop, H. C. (1991). A model for oxygen transport and consumption in the unsaturated zone. *Journal of Hydrology* **129**, 349-369.

Rey, P. J., and Alcantara, J. M. (2000). Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. *Journal of Ecology* **88**, 622-633.

Rice, E. L. (1964). Inhibition of nitrogen-fixing and nitrifying bacteria by seed plants *Ecology* **45**, 824-837.

Rice, E. L. (1979). Allelopathy- an update. *Botanical Review* **45**, 15-119.

Rice, E. L. (1984). Allelopathy. Academic Press Inc., Orlando, Florida.

Rice, K. J. (1989). Impacts of seed banks on grassland community structure and population dynamics. *In* "Ecology of Soil Seed Banks" (V. T. Parker, M. A. Leck and R. L. Simpson, eds.), pp. 211-230. Academic Press, Sydney.

Ridenour, W. M., and Callaway, R. M. (2001). The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. *Oecologia* **126**, 444-450.

Robinson, B. P., and Potts, R. C. (1950). The history of *Hyparrhenia hirta* and studies of its flowering habits and seed production. *Agronomy Journal* **42**, 395-397.

Rogers, A. L., and Bailey, E. T. (1963). Salt tolerance trials with forage plants in south-western Australia. *Australian Journal of Experimental Agriculture and Animal Husbandry* **3**, 125-130.

Rotundo, J. L., and Aguiar, M. R. (2004). Vertical seed distribution in the soil constrains regeneration of *Bromus pictus* in a Patagonian steppe. *Journal of Vegetation Science* **15**, 512-522.

Roundy, B. A., and Biedenbender, S. H. (1996). Germination of warm-season grasses under constant and dynamic temperatures. *Journal of Range Management* **49**, 425-431.

Rubin, F., and Palmer, A. R. (1996). The physical environment and major plant communities of the Karoo National Park, South Africa. *Koedoe* **39**, 25-52.

Russo, S. E., and Augspurger, C. K. (2004). Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. *Ecological Letters* **7**, 1058-1067.

Sackville Hamilton, N. R. (1994). Replacement and additive designs for plant competition studies. *Journal of Applied Ecology* **31**, 599-603.

Sanchez-Moreiras, A. M., Weiss, O. A., and Roger-Reigosa, M. J. (2003). Allelopathic evidence in the Poaceae. *The Botanical Review* **69**, 300-319.

Sargant, E., and Arber, A. (1915). The comparative morphology of the embryo and seedling in the *Gramineae*. *Annals of Botany* **24**, 161-222.

Satsangi, G. P., Shrivastava, J. N., Kumari, S., and Gangwar, N. (2002). Allelopathic response of *Parthenium hysterophorus* L. on germination and seedling vigour in *Sorghum vulgare* L. and *Cajanus cajan* L. and control measures for the weed. *In* "13th Australian Weeds Conference" (H. S. Jacob, J. Dodd and J. H. Moore, eds.), pp. 564-568. Council of Australian Weed Science Societies, Perth.

Schippers, P., and Olff, H. (2000). Biomass partitioning, architecture and turnover of six herbaceous species from habitats with different nutrient supply. *Plant Ecology* **149**, 219-231.

Schoener, T. W. (1983). Field experiments on interspecific competition. *The American Naturalist* **122**, 240-285.

Scott, J. K., and Batchelor, K. L. (2006). Climate-based prediction of potential distributions of introduced *Asparagus* species in Australia. *Plant Protection Quarterly* **21**, 91-98.

Sheldon, J. C. (1974). The behaviour of seeds in soil. III. The influence of seed morphology and behaviour of seedlings on the establishment of plants from surface lying seeds. *Journal of Ecology* **62**, 47-66.

Sheley, R. L., Kedzie-Webb, S., and Maxwell, B. D. (1999). Integrated weed management on rangeland. *In* "Biology and Management of Noxious Rangeland Weeds" (R. L. Sheley and J. K. Petroff, eds.), pp. 57-68. Oregon State University Press, Corvallis.

Shipley, B. (1993). A null model competitive hierarchies in competition matrices. *Ecology* **74**, 1693-1699.

Shipley, W., and Keddy, P. A. (1994). Evaluating the evidence for competitive hierarchies in plant communities. *Oikos* **69**, 340-345.

Sindel, B. M. (2000). Weeds and their impact. *In* "Australian Weed Management Systems" (B. M. Sindel, ed.), pp. 3-16. RJ and FJ Richardson, Melbourne.

Slattery, W. J., Conyers, M. K., and Aitken, R. L. (2001). Soil pH, aluminium, manganese and lime requirement. *In* "Soil Analysis: an Interpretation Manual" (K. I. Peverill, L. A. Sparrow and D. J. Reuter, eds.), pp. 103-108. CSIRO Publishing, Collingwood.

Smith, A. E. (1989). The potential allelopathic characteristics of bitter sneezeweed (*Helenium amarum*). *Weed Science* **37**, 665-669.

Smith, P. L., Wilson, B., Nadolny, C., and Lang, D. (2000). The Ecological Role of the Native Vegetation of New South Wales. Native Vegetation Advisory Council of New South Wales, Department of Land and Water Conservation, Sydney.

Snaydon, R. W. (1991). Replacement or additive designs for competition studies? *Journal of Applied Ecology* **28**, 930-946.

Stamp, N. E. (1984). Self-burial behaviour of *Erodium cicutarium* seeds. *Journal of Ecology* **72**, 611-620.

Stephens, A. E. A., Kriticos, D. J., and Leriche, A. (2007). The current and future potential geographical distribution of the oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae). *Bulletin of Entomological Research* **97**, 369-378.

Stevens, K. L. (1986). Allelopathic polyacetylenes from *Centaurea repens* (Russian knapweed). *Journal of Chemical Ecology* **12**, 1205-1211.

Stoner, J., Adams, R., and Simmons, D. (2004). Exotic grass fuel in south eastern Australia. *In* "14th Australian Weeds Conference" (B. M. Sindel and S. B. Johnson, eds.), pp. 207-209. Weed Society of New South Wales, Wagga Wagga.

Stubbendieck, J. (1974). Effect of pH on germination of three grass species. *Journal of Range Management* **27**, 78-79.

Sun, D., and Dickinson, G. R. (1996). The competition effect of *Brachiaria decumbens* on the early growth of direct seeded trees of *Alphitonia petriei* in tropical north Australia. *Biotropica* **28**, 272-276.

Sutherst, R. W., and Maywald, G. (2005). A climate model of the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae): implications for invasion of new regions, particularly Oceania. *Environmental Entomology* **34**, 317-335.

Sutherst, R. W., and Maywald, G. F. (1985). A computerized system for matching climates in ecology. *Agriculture Ecosystems Environment* **13**, 281-299.

Sutherst, R. W., Maywald, G. F., Bottomley, W., and Bourne, A. (2004). CLIMEX v2. Hearne Scientific Software Pty Ltd, Melbourne.

Sutherst, R. W., Maywald, G. F., and Kriticos, D. J. (2007). CLIMEX v3. User's Guide. Hearne Scientific Software Pty Ltd, Melbourne.

Sutherst, R. W., Maywald, G. F., Yonow, T., and Stevens, P. M. (1999). CLIMEX: Predicting the Effects of Climate on Plants and Animals. CSIRO Publishing, Collingwood, Victoria.

Swaine, M. D. (1996). Rainfall and soil fertility as factors limiting forest species distributions in Ghana. *Journal of Ecology* **84**, 419-428.

Tan, D. K. Y., Daley, A. T., and Wu, H. (2007). Allelopathic potential of lippia (*Phyla canescens*) on germinating seeds. *Allelopathy Journal* **19**, 257-266.

Taylor, I. N., Walker, S. R., and Adkins, S. W. (2005). Burial depth and cultivation influence emergence and persistence of *Phalaris paradoxa* seed in an Australian sub-tropical environment. *Weed Research* **45**, 33-40.

Teeri, J. A., and Stowe, L. G. (1976). Climatic patterns and the distribution of C4 grasses in North America. *Oecologia* **23**, 1-12.

Thompson, K., Band, S. R., and Hodgson, J. G. (1993). Seed size and shape predict persistance in soil. *Functional Ecology* **7**, 236-241.

Thompson, K., Green, A., and Jewels, A. M. (1994). Seeds in soil and worm casts from a neutral grassland. *Functional Ecology* **8**, 29-35.

Tieszen, L. L., Senyimba, M. M., Imbamba, S. K., and Troughton, J. H. (1979). The distribution of C3 and C4 grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. *Oecologia* **37**, 337-350.

Tilman, D. (1986). Resources, competition and the dynamics of plant communities. *In* "Plant Ecology" (M. J. Crawley, ed.), pp. 51-75. Blackwell Scientific Publications, Oxford.

Tilman, D. (1990). Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition. *In* "Perspectives on Plant Competition", Vol. 42, pp. 117-141. Academic Press, Inc, San Diego.

Tokeshi, M. (1999). Species Coexistence: Ecological and Evolutionary Perspectives. Blackwell Science, Oxford, Malden, MA.

Tripathi, J. S., and Vaishya, R. D. (1997). Allelopathic effects of fresh plant extracts on germination of weed seeds. *Indian Journal of Weed Science* **29**, 192-193.

Trotter, T. F. (2006). The ecology and management of *Nassella trichotoma* on the Northern Tablelands of New South Wales. PhD thesis, The University of New England, Armidale.

Trumbel, H. C. (1933). The agricultural features of *Phalaris tuberosa* and allied forms. *Journal of the Department of Agriculture (South Australia)* **37**, 400-425.

US Census Bureau (2003). Census of Population and Housing, 2000: Public Use Microdata Sample. U. S. Department of Commerce, Washington DC.

Van der Reest, P. J., and Rogaar, H. (1988). The effect of earthworm activity on the vertical distribution of plant seeds in newly reclaimed polder soils in the Netherland. *Pedobiologia* **31**, 211-218.

Van der Wall, S. B., and Joyner, J. W. (1998). Secondary dispersal by the wind of winged pine seeds across the ground surface. *American Midland Naturalist* **139**, 365-373.

Van Gils, H. (1988). Mid-altitudinal vegetation of the Macaronesian Island Santo Antao (Cabo Verde). *Vegetatio* **74**, 33-38.

Van Kleunen, M., and Johnson, S. D. (2007). South African Iridaceae with rapid and profuse seedling emergence are more likely to become naturalized in other regions. *Journal of Ecology* **95**, 674-681.

Van, T. K., Rayamajhi, M. B., and Center, T. D. (2005). Seed longevity of *Melaleuca quinquenervia*: a burial experiment in South Florida. *Journal of Aquatic Plant Management* **43**, 39-42.

Verdu, A. M. C., and Mas, M. T. (2006). Cohort-dependent seedling recruitment, survival and reproductive capacity of *Tribulus terrestris*. *Weed Research* **46**, 371-378.

Verrier, F. J., and Kirkpatrick, J. B. (2005). Frequent mowing is better than grazing for the conservation value of lowland tussock grassland at Pontville, Tasmania. *Austral Ecology* **30**, 74-78.

Vitousek, P. M., D'Antonio, C. M., Loope, L. L., and Westbrooks, R. (1996). Biological invasions and global environmental change. *American Scientist* **84**, 468-478.

Wagner, W. L., Herbst, D. R., and Sohmer, S. H. (1999). Manual of the Flowering Plants of Hawaii. Vol. 2, pp. 83. Bishop Museum Special Publication, Honolulu.

Walker, B. H. (1991). Ecological consequences of atmospheric and climate change. *Climate Change* **18**, 301-316.

Wang, J. H., Wang, S. P., Schnug, E., Haneklaus, S., Patton, B., and Nyren, P. (2008). Competition between *Stipa grandis* and *Cleistogenes squarrosa*. *Journal of Arid Environments* **72**, 63-72.

Wanjura, D. F., and Buxton, D. R. (1972). Water uptake and radicle emergence of cottonseed as affected by soil moisture and temperature. *Agronomy Journal* **64**, 427-431.

Wardle, D. A. (2002). Communities and Ecosystems: Linking the Aboveground and Belowground Components. Princeton University Press, Princeton, NJ.

Wardle, D. A., Nicholson, K. S., Ahmed, M., and Rahman, A. (1996). Use of a comparative approach to identify allelopathic potential and relationship between allelopathy bioassays and "competition" experiments for ten grassland and plant species. *Journal of Chemical Ecology* **22**, 933-948.

Warner, S. (2004). Ecological studies of Coolatai grass (*Hyparrhenia hirta* (L.) Stapf.): an invasive weed on the Adelaide Plains. Honours Thesis, University of Adelaide, Adelaide.

Warren, J., Wilson, F., and Diaz, A. (2002). Competitive relationships in a fertile grassland community-does size matter? *Oecologia* **132**, 125-130.

Warren, P. H., Law, R., and Weatherby, A. J. (2006). Invasion biology as a community process: messages from microcosms. *In* "Conceptual Ecology and Invasions Biology: Reciprocal Approaches to Nature" (M. W. Cadotte, S. M. McMahon and T. Fukami, eds.), pp. 343-367. Springer, Dordrecht.

Warwick, B. B., David, R. K., David, L. M., and Warren, M. C. G. K. (2005). Competition for nitrogen between Australian native grasses and the introduced weed *Nassella trichotoma*. *Annals of Botany* **96**, 799-809.

Watson, L., and Dallwitz, M. J. (1992). The Grass Genera of the World. CAB International, Wallingford.

Watt, L. A. (1982). Germination characteristics of several grass species as affected by limiting water potentials imposed through a cracking clay soil. *Australian Journal of Agricultural Research* **33**, 223-231.

Watt, L. A., and Whalley, R. D. B. (1982a). Effect of sowing depth and seedling morphology on establishment of grass seedlings on cracking black earths. *Australian Rangeland Journal* **4**, 52-60.

Watt, L. A., and Whalley, R. D. B. (1982b). Establishment of small-seeded perennial grasses on black clay soils in north-western New South Wales. *Australian Journal of Botany* **30**, 611-623.

Weaver, S. E., and Cavers, P. B. (1979). Dynamics of seed populations of *Rumex crispus* and *Rumex obtusifolius* (Polygonaceae) in disturbed and undisturbed soil. *Journal of Applied Ecology* **16**, 909-917.

Webster, R., and Payne, R. W. (2002). Analysing repeated measurements in soil monitoring and experimentation. *European Journal of Soil Science* **53**, 1-13.

Wedin, D. A., and Tilman, D. (1996). Influence of nitrogen loading and species composition on the carbon balance of grasslands. *Science* **274**, 1720-1723.

Weller, S. G. (1985). Establishment of *Lithospermum caroliniense* on sand dunes: the role of nutlet mass. *Ecology* **66**, 1893-1901.

Weltzin, J. F., Belote, R. T., and Sanders, N. J. (2003). Biological invaders in a greenhouse world: will elevated CO_2 fuel plant invasions? *Frontiers in Ecology and the Environment* **1**, 146-153.

Weston, L. A., Burke, B. A., and Putnam, A. R. (1987). Isolation, characterization and activity of phytotoxic compounds from quackgrass [*Agropyron repens* (L.) Beauv.]. *Journal of Chemical Ecology* **13**, 403-421.

Wharton, T. N., and Kriticos, D. J. (2004). The fundamental and realized niche of the Monterey Pine aphid, *Essigella californica* (Essig) (Hemiptera: Aphididae): implications for managing softwood plantations in Australia. *Diversity and Distributions* **10**, 253-262.

Wheeler, D. J. B., Jacobs, S. W. L., and Whalley, R. D. B. (2002). Grasses of New South Wales. The University of New England, Armidale, New South Wales.

Williams, D. G., and Baruch, Z. (2000). African grass invasion in the Americas: ecosystem consequences and the role of ecophysiology. *Biological Invasions* **2**, 123-140.

Williams, N. S. G. (2005). Management strategies for preventing invasion in urban grasslands. *Plant Protection Quarterly* **20**, 12-16.

Woitke, M., and Dietz, H. (2002). Shifts in dominance of native and invasive plants in experimental patches of vegetation. *Perspectives in Plant Ecology, Evolution and Systematics* **5**, 165-184.

Woodward, F. I. (1987). Climate and Plant Distribution. Cambridge University Press, Cambridge.

Yamamoto, Y. (1995). Allelopathic potential of *Anthoxanthum odoratum* for invading *Zoysia*-grassland in Japan. *Journal of Chemical Ecology* **21**, 1365-1373.

Yonow, T., and Sutherst, R. W. (1998). The geographical distribution of the Queensland fruit fly, *Bactrocera* (*Dacus*) *tryoni*, in relation to climate. *Australian Journal of Agricultural Research* **49**, 935-953.

Young, J. A., Palmquist, D. E., and Blank, R. R. (1998). The ecology and control of perennial pepperweed (*Lepidium latifolium* L.). *Weed Technology* **12**, 402-405.

Zaller, J. G. (2006). Allelopathic effects of *Rumex obtusifolius* leaf extracts against native grassland species. *Journal of Plant Diseases and Protection* **20**, 463-470.

Zhang, X. H., Oberhuber, J. M., Bacher, A., and Roeckner, E. (1998). Interpretation of interbasin exchange in an isopycnal ocean. *Climate Dynamics* **14**, 725-740.

Zimdahl, R. L. (1999). Fundamentals of Weed Science. Academic Press, San Diego.