The ecology of fleabane (*Conyza* spp.)

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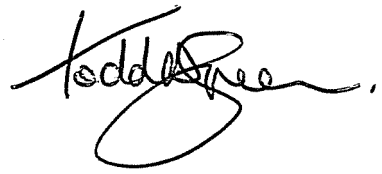
DECLARATION

I certify that the substance of this thesis has not already been submitted for any degree and is not currently being submitted for any other degree or qualification.

I certify that any help received in preparing this thesis, and all sources used, have been acknowledged in this thesis.



Todd Douglas Green

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ABSTRACT

Conyza bonariensis (L.) Cronquist, flaxleaf fleabane, originating from South America, is a major emerging weed threat for dry-land cropping systems in Australia. *Conyza bonariensis* is particularly increasing in importance within the northern cropping region of Australia, is one of the most difficult-to-control weeds in minimum tillage systems, and is tolerant to important herbicides. There is a need to expand the ecological knowledge of *C. bonariensis* in order to better understand its success in minimum tillage systems and to provide principles for the improved management of this weed.

Conyza bonariensis is common in fallows, thereby depleting the soil stored moisture, and has caused a doubling of control costs in certain areas of the northern cropping region. Control costs are likely to further increase due to the weed's rapid development of herbicide resistance. In addition, *C. bonariensis* is a problem weed within many field crops, including – cotton, chickpea, lucerne, maize, sorghum, soybean and wheat. *Conyza bonariensis* competes for water and nutrients, especially in wheat and dry-land sorghum crops. Control of *C. bonariensis* is greatly dependant on herbicides, thereby increasing the risk of herbicide resistance. There are currently glyphosate resistant populations of *C. bonariensis* in six countries and there have been reports of differential responses to glyphosate in southern Queensland populations.

In this study, ecological aspects of the key life stages of *C. bonariensis* were investigated, comprising of germination, emergence, growth and development, seed dispersal and seed longevity. All ecological findings were compared with a congeneric species, *C. sumatrensis* (Retz.) E. Walker (tall fleabane), which is currently not problematic in cropping systems in Australia, despite being present in the region within other ruderal sites (e.g. roadsides), as a way of determining what ecological characteristics in *C. bonariensis* may be responsible for its increase in the northern region cropping system.

Germination was limited by temperature, moisture and light. Seeds of *C. bonariensis* germinated between 10 and 30^{o}C, with optimal germination at 25^{o}C. *Conyza bonariensis*

seeds were able to germinate under moisture stress down to -0.8 MPa. Light was essential for germination of *C. bonariensis*. In a 90% shade environment, *C. bonariensis* germination was reduced by 80% compared with a full light environment. With adequate temperature, light and moisture, *C. bonariensis* seeds can germinate within 2 to 3 days. Soil type and stubble levels affected *C. bonariensis* emergence. Emergence was reduced in heavy black vertosol soil compared with lighter soils. There was no significant difference in emergence with 1.8 t ha^{-1} of stubble compared with no stubble.

Conyza bonariensis can emerge all-year-round, and there are differences in development and fecundity between emergence cohorts. More than 85 000 seeds were produced per plant in the overwintering cohort, which was 40% higher than the spring emerged plants. The root:shoot ratio at the time of stem elongation in overwintered *C. bonariensis* plants was 60% higher than spring emerged plants. This ecological feature makes the late-autumn cohort more difficult to control. There was a short period of six weeks between stem elongation and seed production in *C. bonariensis*, and with a slow response to herbicide, this adds to the success of this weed.

*Conyza bonariensis s*eed settling velocity and pappus geometry was affected by humidity. Settling velocity was 0.28 m s^{-1} at 30% humidity and increased to 0.33 m s^{-1} at 90% humidity. The pappus bristles of *C. bonariensis* seeds were closer together in environments of high humidity. *Conyza bonariensis* seeds were not able to emerge from burial depths of 0.5 cm or greater, although the length of time that the seed remained viable increased with burial depth. Seed longevity at 1 cm burial depth was 37 months and at 10 cm depth, this increased to 80 months. Seeds which enter a minimum tillage system typically remain on or near the soil surface, the preferred germination site for *C. bonariensis*, therefore adding to the weed's success in these systems.

In comparison with *C. sumatrensis*, *C. bonariensis* produced more seed, had a higher relative reproductive effort, developed more rapidly, could germinate in milder temperatures only and had a longer lived seed bank. These ecological findings are likely to account for the greater success of *C. bonariensis* in minimum tillage cropping systems. The effective long-term management of *C. bonariensis* requires an integrated approach to weed management,

in which herbicide use is complemented with non-chemical control measures. Through limiting soil disturbance, there will be a reduction in the burial of seed and thereby a more rapid depletion of the seed bank, assuming there is no further addition of seed to the soil seed bank from elsewhere. Where appropriate, cultivation could be used to bury the seeds of *C. bonariensis* and prevent germination or to perhaps kill overwintering plants with large taproots. Agricultural practices should also aim to maximise competition, including shade, against *C. bonariensis*. Diligent control is required to prevent seed set, especially for the overwintered plants which are more difficult to control and have a higher seed production.

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CHAPTER ONE

INTRODUCTION

Conyza bonariensis (L.) Cronquist (flaxleaf or hairy fleabane) is a cosmopolitan plant in temperate and sub-tropical climates, native to South America and a member of the Asteraceae (Everett 1990; Prieur-Richard et al. 2000). Its mode and timing of arrival to Australia is unknown; although, botanical collections in 1847 record widespread populations in Adelaide (Burry and Kloot 1982). *Conyza bonariensis* is reported as both an agricultural and environmental weed, with habitat preferences for disturbed sites, abandoned fields and roadsides (Thebaud and Abbott 1995; Prieur-Richard *et al.* 2000). *Conyza bonariensis* has become one of the most dominant emerging weed threats for dry-land cropping systems in Australia and is increasingly important in a range of locations across northern New South Wales (NSW), southern Queensland (QLD) (Wu *et al.* 2007) and southern Western Australia (WA) (Storrie 2007). Within cropping systems, *C. bonariensis* grows well in bare fallows, in cropping gaps, between wide rows and in poorly competitive crops (CRC for Australia Weed Management 2006). *Conyza bonariensis* is also problematic in crops such as cotton (Wu *et al.* 2007).

It is believed that the relatively recent success of *C. bonariensis* in Australian cropping systems is due to a shift in farming practices from conventional to conservation (zero or minimum) tillage systems and a reduced reliance on soil-applied residual herbicides (Storrie 2007). The incidence of minimum tillage methods in cropping and pasture lands in Australia has risen to 57% in 2008, from 26% in 2001, and is likely to continue increasing (ABS 2009). *Conyza bonariensis* is thought to be adapted for both germination and growth under reduced-tillage systems. The abundance of this weed may also be due to a tolerance to many of the herbicides commonly used in crops and fallows. Glyphosate resistant *C. bonariensis* was initially reported in South Africa in 2003 (Heap 2010).

The majority of weed problems are ecological in nature and therefore sustainable long-term control strategies must be based on an understanding of the biotic and abiotic factors which promote or suppress the establishment, growth and spread of weeds (Sindel 2000). The importance of ecological and life cycle studies of weeds to underpin effective management strategies has been well documented (Mortensen *et al.* 2000; Mohler 2001; Booth *et al.* 2003).

Knowledge on the biology and ecology of *C. bonariensis* in Australia is limited. The broad aims of this thesis were to better understand the ecology of *C. bonariensis* and to investigate the ecological reasons for the emerging threat of *C. bonariensis* in conservation tillage systems in the northern cropping region of Australia, and identify the potential management principles needed to manage the weed more effectively. The research tested ecological factors that influence seed germination, emergence, growth and development, spread and seed bank dynamics contributing to seed longevity.

As a means of better understanding the ecological reasons for the increased success of *C. bonariensis* in northern cropping systems, its ecology is contrasted in this thesis to that of a congeneric species, *C. sumatrensis* (Retz.) E. Walker (tall fleabane), which is less prominent and problematic in cropping systems in Australia despite being present in the various regions (e.g. along road sides and in grazing systems) and being one of the most dominant plant species globally (Prieur-Richard *et al.* 2000; Weaver 2001).

The literature is reviewed in a separate chapter (Chapter 2) and provides background information on invasive plant ecology, *Conyza* species taxonomy, morphology and distribution in Australia, current knowledge on *Conyza* species' biology and ecology and the agronomic impact and control of this weed. In Chapter 2, knowledge gaps and hypotheses of this thesis are also identified. The experimental program of this thesis is reported through Chapters 3 to 7. The focus of Chapter 3 is on germination; Chapter 4 on emergence; Chapter 5 on growth, development and fecundity; Chapter 6 on seed dispersal; and Chapter 7 on seed bank longevity. Chapter 8 covers general conclusions, including ecological reasons for the success of *C. bonariensis* in the northern cropping region, summary comparative ecology

between the two species, management principles necessary for long-term effective control of *C. bonariensis* and future research priorities.

Chapter Two: Literature Review

CHAPTER TWO

LITERATURE REVIEW

INTRODUCTION

This review covers the ecology of plant invasions, role of ecology in developing integrated weed management strategies, weed species shifts relating to farming practice changes, *Conyza* species taxonomy, morphology and distribution, current biological and ecological knowledge on *Conyza* species and the agronomic impact and control of *Conyza bonariensis* (L.) Cronquist. In the conclusion of this chapter I outline the specific project aims.

INVASIVE PLANT ECOLOGY

An invasion is defined as any geographical expansion of a species into an area that it has not previously occupied (Vermeij 1996). Invasive species can be either native or exotic. Invasion ecology includes the stages of the plant invasion process and factors impacting on success, characteristics of invasiveness and factors that may assist communities to inhibit invasion. Furthermore, it explores the impact of a successful invasion on existing communities.

Exotic plant invasion process

The terminology used to describe the invasion stages is not consistent in the literature and therefore the following definitions are offered which will be used throughout this thesis. Traditional terminology for invasive species involves introduction, colonisation and naturalisation (Groves 1986; Cousens and Mortimer 1995). However, Richardson *et al.* (2000), undertook a comprehensive review of definitions for invasive ecology and reported

the invasion process comprised of *introduction*, *naturalisation* and *invasion* stages.

Introduction is the initial stage of invasion and involves the species, or its propagule, being transported across a significant geographical barrier (Richardson *et al.* 2000; Booth *et al.* 2003). Anthropogenic means of transportation include both deliberate and accidental mechanisms – predominantly the former (Goodwin *et al.* 1999). Deliberate importation of exotic species has been for ornamental qualities (Humphries *et al.* 1991), use as forage, fibre, medicines and erosion control (Baker 1974). Accidental importation is predominantly due to increases in trade and travel (Humphries *et al.* 1991; Hodkinson and Thompson 1997) and includes vectors such as contaminants of food, soil, adhesion to livestock (Parsons and Cuthbertson 1992) and through ship ballast (Hockley 1974; Ruiz *et al.* 2000). Many losses occur in the transporting of exotic species or propagules to the destination and Goodwin *et al.* (1999) estimate that only 10% of the survivors will establish a self-sustaining population in the invaded ecosystem.

The *naturalisation* process commences as abiotic and biotic barriers to survival are conquered (Richardson *et al.* 2000; Booth *et al.* 2003). If the exotic species does establish and remains relatively localised around the introduction point, it is classed as established and non-invasive (Booth *et al.* 2003). Different traits are required for successful naturalisation within a natural community compared with an anthropogenic disturbed habitat (Sakai *et al.* 2001). Tilman (1997) reported that establishment pressures are greater for invasive plants attempting to establish in grassland habitats with high species richness.

For many species, prior to becoming invasive or undertaking rapid population growth after successfully establishing, there is a lag time (Humphries *et al.* 1991; Hobbs and Humphries 1995). Such a phase is often viewed as an ecological phenomenon – the lag phase in an exponential population growth curve (Sakai *et al.* 2001). A delay can be a result of evolutionary changes and adaptations which are necessary for the successful invasion of the new habitat (Kruger *et al.* 1986; Sakai *et al.* 2001). The period of lag phases vary significantly – Hobbs and Humphries (1995) reported the phase can last from 20 to 100 years.

The *invasion* stage is primarily defined in relation to spatial and temporal distribution

(Richardson *et al.* 2000; Kolar and Lodge 2001; Lambrinos 2004). Invasive status requires naturalised plants to produce reproductive offspring in areas that are distant from the initial introduction site – this has been defined as more than 100 metres in less than 50 years for seed based taxa (Richardson *et al.* 2000).

The Australian invasion experience

There has been approximately 28 000 exotic plant species brought into Australia since the first European settlers arrived (Humphries *et al.* 1991). More than 2 500 species have since become established and over 1 300 classified as agricultural, noxious or environmental weeds (Humphries *et al.* 1991). Introduced species in the Australian setting comprise approximately 10 to 15% of total vascular plant flora (Groves 1986; Humphries *et al.* 1991; Saunders *et al.* 1996). These figures are not large when compared globally; albeit the short time scale since settlement in Australia does raise concerns (Adamson and Fox 1982). Williamson (1999) reported that invasions are less problematic in Europe and China because agriculture originated there and the invasive problems follow the path of European agriculture adoption, for example in Australia.

Characteristics of a successful invader

The examination of characteristics that support successful invasion should not be viewed in isolation from the landscape ecology of the invasion site. Studying the invading species is one component; the other is exploring the habitat characteristics to establish invasibility (Maillet and Lopez-Garcia 2000). McIntyre *et al.* (1995) described a species' ability to successfully invade as a combined function of the ecological properties of the target environment, attributes of the plant and the disturbances (natural and anthropogenic) of the target land. There is a key restraint in attempting to answer questions regarding attributes for invasiveness and why some ecosystems are more invasible, which is the absence of data on failed invasion attempts (Rejmanek and Richardson 1996).

Invasibility refers to the "degree to which a community is susceptible to the establishment of external species, whether these are native or exotic" (Lavorel *et al.* 1999:41). A communities invasibility is a combination of the traits of the invasive species, the native species and the community (Sakai *et al.* 2001); therefore not all communities are equally invasible. There is no clear clarification available on why some regions are more prone than others. This is partly due to a lack of investigation into invasion mechanisms from an invaded community viewpoint (Lavorel *et al.* 1999). An invasive species may be such as a result of sharing traits with resident natives or the possession of different traits – enabling the occupation of available niches (Levine and D'Antonio 1999).

An extensive review of literature on diversity and invasion by Hector *et al.* (2001) reported diverse communities were more resistant to invasion. The increase in diversity reduces available resources for potential invaders through selection processes and niche-complementarity effects (Hector *et al.* 2001). This hypothesis was first proposed by Elton (1958); albeit, there is not uniform support for this hypothesis. Empirical studies both support (Palmer and Maurer 1997) and dispute (Tilman 1997) the native diversity and invasion relationship hypothesis. Subsequent studies reported that the species (Crawley *et al.* 1999) or functional group composition (Prieur-Richard *et al.* 2000) is more pertinent than richness in relation to invasion resistance.

Disturbance can also precede invasion through the change or removal of filters acting on the community (Booth *et al.* 2003). This results in alteration to habitat characteristics which could make it more conducive to invasion (Dukes and Mooney 1999). Disturbances can include both natural (e.g. wildfire) and anthropogenic (e.g. land clearing) modes.

Kolar and Lodge (2001) used data from the United States of America Plant Database to analyse characteristics of alien species which support successful invasion. Several features have been reported to be significant in supporting invasion, including the number of seeds produced (Newsome and Noble 1986; Reichard and Hamilton 1997), the history of invasion (Richardson *et al.* 1990; Scott and Panetta 1993; Reichard and Hamilton 1997), the family or genus' invasiveness (Scott and Panetta 1993; Reichard and Hamilton 1997), presence of vegetative reproduction (Richardson *et al.* 1990; Reichard and Hamilton 1997) and low

variability in seed crops (Richardson *et al.* 1990; Rejmanek and Richardson 1996). The method used for these findings were through the comparison with invasive to non-invasive species. Lodge (1993) described characteristics for successful invasion as high levels of genetic variability, phenotypic plasticity and dispersal capacities.

Through a study of successful invasions, Goodwin *et al.* (1999) identified several characteristics as key determinants of invasiveness. These include small, short-lived seeds (Thompson *et al.* 1995) that can germinate without pre-treatment, short juvenile periods and short intervals between large seed crops, vegetative reproduction and perfect flowers (Crawley 1987; Perrins *et al.* 1992; Rejmanek and Richardson 1996). Species colonising disturbed sites need to deal with higher levels of light and reduced levels of soil moisture (Baker 1967; Sutherland 2004). Therefore, plants tolerant to high levels of light and reduced soil moisture have a selective advantage over plants which are less tolerant (Baker 1967).

DEFINING A 'WEED'

There is a plethora of definitions for what constitutes a weed. Rao (2000) described weeds as unwanted plants that compete, from an anthropogenic viewpoint, with land and water resources. Furthermore, weeds grow where we either want other plants to grow or no plants to grow (Rao 2000). Baker (1965:147) defines a plant as a weed "if, in any specified geographical area, its populations grow entirely or predominantly in situations markedly disturbed by man (without, of course, being deliberately cultivated plants)".

The classification of a plant being a weed is more for convenience than an assessment of biological characteristics (Booth *et al.* 2003); this is not to say that certain features are not shared by many weeds. Several traits defining weediness have been offered (Baker 1974; Newsome and Noble 1986; Zimdahl 1999). However, they are not well understood and therefore unable to be used to declare a weed *a priori* (Noble 1989).

An introduced species needs to satisfy the classification requirement that they interfere with

human activity or have a detrimental effect upon the environment (Scott and Panetta 1993). It was estimated that 20 to 40% of naturalised plants in Australia will become weeds (Groves 1986). One means by which weeds are grouped is by habitat type, and these include agrestal (agricultural weed), ruderal (waste sites/disturbed sites), grassland, aquatic, forestry and environmental weeds (Holzner 1982).

Weed species shift due to changes in farming practices

Over recent years, the incidence of cultivation has decreased within Australia farming systems. It was estimated, in 2001, that 41% of cropping land in Australia was sown without prior soil disturbance (Chauhan *et al.* 2006), this has risen to 57% in 2008 (ABS 2009). The reduction of tillage in many other countries has been advanced by the adoption of glyphosate resistant crops (Cerdeira and Duke 2006). Benefits attributed to reduced tillage include an increase in soil moisture retention (Unger 1981; Hairston *et al.* 1984; Holland and Felton 1989; Coolman and Hoyt 1993), operating cost savings for labour and fuel (Frye 1984; Brown *et al.* 1989), reduction in soil erosion (Lee and Stewart 1983; Coolman and Hoyt 1993; Everitt and Keeling 2007) and reduced surface runoff of pesticides and fertilisers (Unger 1981).

Factors of concern in minimum tillage systems and impeding on some producers' uptake of this technology, is an increased cost of herbicides, the increased risk of herbicide resistant weeds (Coffman and Frank 1991), and the promotion of weed shifts (Swanton *et al.* 1999). Changes to a weed community are likely when an agroecosystem undergoes long-term cultural modifications (Clements *et al.* 1994). In minimum tillage systems, shifts toward grass, perennial, wind-disseminated weeds and volunteer crop plants have been reported (Swanton *et al.* 1993). The reduction of disturbance in minimum tillage systems allows the colonisation of species adapted to the modified environment (Swanton *et al.* 1993); this modified environment can provide safe sites for germination of weeds that were not associated with conventional farming systems (Clements *et al.* 1994). Weeds are evidence of

nature struggling to bring about ecological succession. For example, annual cropping systems hold back natural plant succession and provide a high percentage of bare ground – an ideal environment for annual weeds to prosper (Clements *et al.* 1994). With a reduction of soil disturbance in minimum tillage systems, weeds are expected to display a greater tendency to undergo succession (Swanton *et al.* 1993).

Importance of understanding a weed's ecology

Weed problems are typically ecological in nature and therefore effective long-term control strategies need to be formulated on a sound understanding of the conditions which promote or suppress their growth (Sindel 2000). A species' ability to invade is a combined function of the ecological properties of the target environment, attributes of the plant and the disturbances of the target land (McIntyre *et al.* 1995). Without ecological information, weed management ultimately may fail or make weed problems worse (Booth *et al.* 2003). Too often there has been strong reliance on a single solution to manage weeds, creating problems with weeds adapting to this management option. An ecological approach to managing weeds broadens the options available for management and therefore decreases the probability of failure (Booth *et al.* 2003). Increasing ecological knowledge of weeds provides a greater understanding of the interference mechanisms, expands crop loss prevention techniques and leads to more effective long-term management strategies (Uscanga-Mortera *et al.* 2007).

CONYZA SPECIES TAXONOMY, MORPHOLOGY AND DISTRIBUTION

Taxonomy

Conyza Less. genus is a member of the daisy family, Asteraceae, tribe Asteraceae and sub-

tribe Conyzinae. There are approximately 60 species of *Conyza* spread globally throughout temperate and sub-tropical climatic zones (Everett 1990; Thebaud and Abbott 1995), with presence in all continents except Antarctica. Some seven species are established in parts of Australia (Everett 1990; AVH 2010).

The *Conyza* species naturalised and now invasive in Australia include *C. bonariensis* (flaxleaf fleabane), *C. sumatrensis* (Retz.) E. Walker (tall fleabane), also known as *C. albida* Willd. Ex Sprengel and *C. floribunda* Kunth., *C. canadensis* (L.) Cronq. var. *canadensis* (Canadian fleabane), *C. leucantha* (D. Don) Ludlow and Raven, *C. chilensis* Sprengel, also known as *C. primulifola*; *C. parva* Cronq., also known as a variety of *C. canadensis* (*C. canadenis* var. *pusilla* (Nutt.) Cronq.) and *C. bilbaoana* E.J. Remy. (Everett 1990). Other species which herbarium records indicated as present in Australia include *C. aegyptiaca* (L.) Aiton, *C. pinnata* (L.f.) Kuntze and *C. scabrida* DC. (AVH 2010). A taxonomic key by Everett (1990) for the *Conyza* species naturalised in Australia is presented (Table 2.1).

Biogeographical and evolutionary studies on Erigeron and Asteraceae by Noyes (2000), reported that *Conyza* and several other genera are derived from within Erigeron. The *Conyza* genus has previously been treated as Erigeron; for example, *C. bonariensis* was previously *E. bonariensis* L. (Cronquist 1943). Cronquist (1943) made this taxonomic transfer based on the anatomical difference in ligule and corollas in *Conyza* species. The genus classification put forward by Cronquist (1943) described *Conyza* as having few central hermaphrodite flowers, numerous pistillate flowers, filiform corollas, ligules generally absent, if present: inconspicuous, shorter than the tubes and scarcely if at all exceeding the pappus.

Table 2.1 Taxonomic key for *Conyza* species established in Australia.

1			Involucral bracts densely hairy.	
	2		Leaves linear, oblong or narrow-oblanceolate; the whole plant appearing pale grey from the spreading septate hairs especially dense on the stems and around the axis……..	*C. bonariensis*
	2		Leaves lanceolate, oblanceolate or spathulate; plants hispid with short septate or glandular hairs, giving a yellowish green appearance.	
		3	Growth form widely branching below the diffuse infloresence; stems and leaves with dense yellow glandular hairs, as well as hispid hairs on the leaves……..	*C. leucantha*
		3	Growth from mainly a simple stem unbranched below a distinct inflorescene; stems and leaves hispid with septate hairs.	
		4	Inforescence of up to 7 heads; involucre darker than the florets; heads 8-12 mm long, 15-20 mm diameter……..	*C. chilensis*
		4	Infloresence of many heads; involucre pale, the same colour as the florets; heads 4-5 mm long, 3-4 mm diameter……..	*C. sumatrensis*
1			Involucral bracts glabrous or almost so.	
	5		Heads campanulate, outer florets with short, but visible, white ligules, involucral bracts pale cream on the inner surface.	
		6	Stems conspicuously but not densely hairy with long, spreading septate hairs, margins of lower leaves usually toothed, flat; involucral bracts without an apical red spot……..	*C. canadensis*
		6	Stems not conspicuously hairy, leaf margins entire or crenate, recurved; involucral bracts usually with an apical red dot……..	*C. parva*
	5		Heads hemispherical, outer florets filiform, involucral bracts orange or reddish on the inner surface……..	*C. bilbaoana*

Source: Everett (1990:198)

Cytotaxonomy

Conyza species have a basic chromosome number of nine: diploid, triploid, tetraploid and hexaploid configurations have been reported (Goldblatt 1985; Razaq *et al.* 1994; Thebaud

and Abbott 1995; Carr *et al.* 1999). Configurations for *Conyza* species include *C. canadensis* (2*n* = 18) (Thebaud and Abbott 1995) and *C. chilensis* (2*n* = 18) (Solbrig *et al.* 1964). There is evidence of allopolyploidy existing within *C. sumatrensis* (2*n* = 54) (Goldblatt 1985) and *C. bonariensis* (Thebaud and Abbott 1995) (2*n* = 54) from four separate analyses of cytology (Goldblatt 1985; Razaq *et al.* 1994; Carr *et al.* 1999; Baltisberger and Widmer 2006). Polyploidy is a trait common to many successful invasive plant species (Clegg and Brown 1983), and is most common in chromosome basic numbers 6 and 9 (Solbrig *et al.* 1964). A correlation for polyploid species with spatial distribution and ecological preferences has been demonstrated (Manton 1949; Solbrig *et al.* 1964). Ehrendorfer (1980) reported polyploid species are more vastly distributed than diploids within Europe.

Through a quantitative trait and isozyme analysis, Thebaud and Abbott (1995) reported *C. bonariensis* as being 90% similar to *C. sumatrensis* and that less than 40% similarity existed between these two species and *C. canadensis*. This finding is also supported on a taxonomic level, as illustrated in Table 2.1, with a separation of *C. canadensis* from *C. bonariensis* and *C. sumatrensis* occurring on the first division, based on glabrous or hairy involucral bracts respectively. Furthermore, both *C. sumatrensis* and *C. bonariensis* have polyploidy (Goldblatt 1985; Thebaud and Abbott 1995). This genetic similarity, however, is not supported on a biogeographical level.

Morphology

The morphology of the *Conyza* genus is described as:

> *"Erect more or less pubescent herbs. Leaves alternate, basal and cauline, entire or toothed. Heads hemispherical to campanulate, pedunculate in large terminal corymbs or panicles; involucral bracts linear to lanceolate, herbaceous with scarious margins, imbricate, becoming reflexed receptacle naked, pitted, flat. Outer florets female, filiform or ligulate; ligules very short, white to pink or absent. Disc florets bisexual, few or many, tubular, usually yellow. Anthers obtuse at base. Style branches with*

terminal appendages. Achenes flattened with marginal ridges, glabrous or pubescent; pappus of numerous capillary bristles." (Everett 1990:197-198)

A comparative morphology matrix for the seven *Conyza* species established in Australia has been compiled (Table 2.2), and photographs of different life stages and anatomy of *C. bonariensis* presented (Figure 2.1).

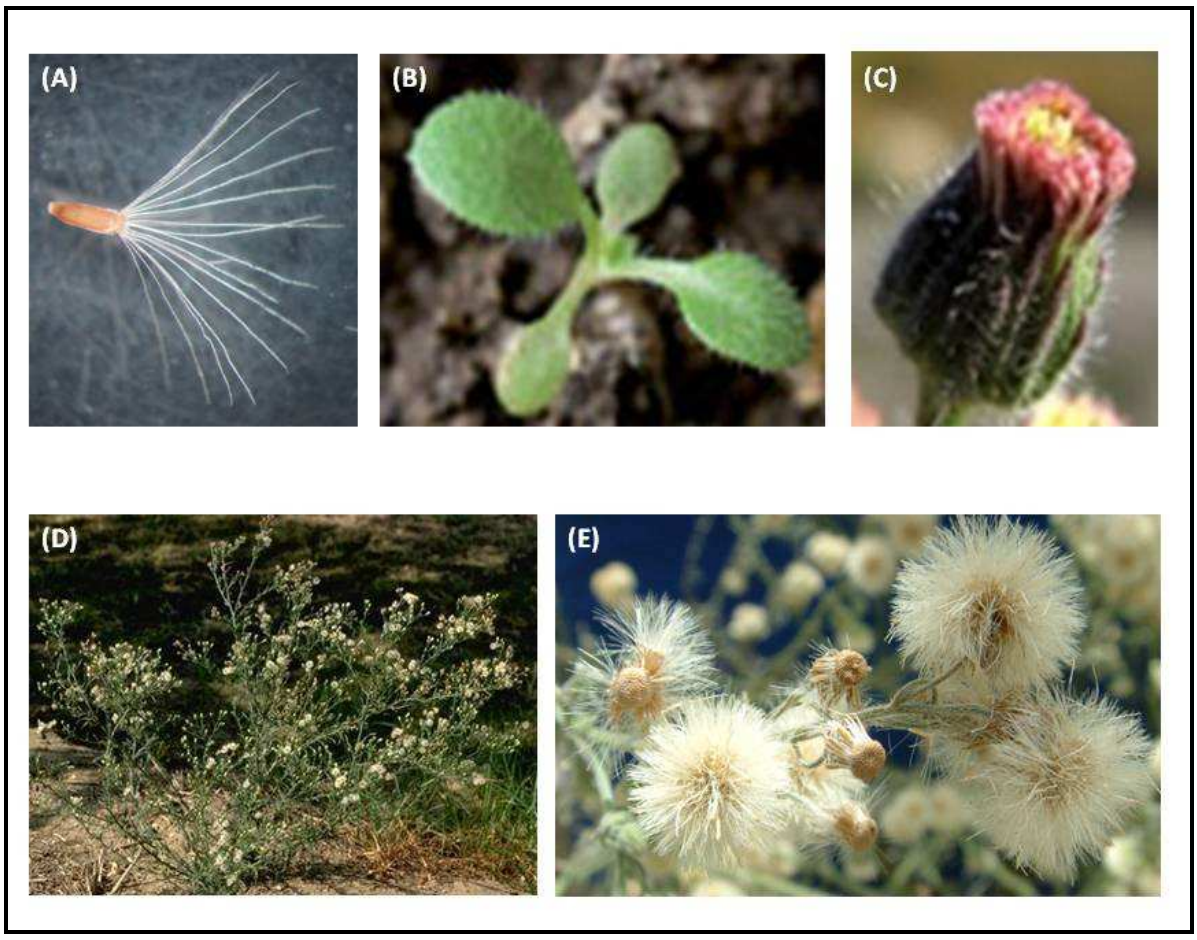

Figure 2.1 Photographs of *C. bonariensis* – (A) seed, (B) seedling, (C) capitulum, (D) mature plant and (E) mature seeds on capitula and receptacles of dispersed seeds.

Table 2.2 Comparative morphology of *Conyza* species established in Australia.

Feature	*C. bonariensis*	*C. sumatrensis*	*C. canadensis*	*C. parva*	*C. bilbaoana*	*C. chilensis*	*C. leucantha*
Leaves	hispid, hairy.	basal lanceolate to oblanceolate, hispid with short hairs. Upper leaves lanceolate to linear.	long spreading antrorse septate hairs, basal oblong to oblanceolate. Upper leaves elliptic to linear.	linear to oblong.	glabrous with antrorse bristles on margins, basal leaves oblanceolate to linear. Upper leaves oblong to linear.	oblanceolate to spathulate, densely hispid.	lanceolate, yellow hairs, sessile.
Leaf dimensions	4-9 cm long, 5-15 mm wide.	4-10 cm long, 5-12 mm wide.	2-10 cm long, 3-8 mm wide.	3-4.5 cm long, 1-5 mm wide.	2-5 cm long, 1-8 mm wide.	15-25 cm long, 12-35 mm wide.	7-10 cm long, 12-18 mm wide.
Height on maturity	1 m	2 m	1.5 m	0.5 m	2 m	0.8 m	2 m
Achenes	oblong, pappus white to pink bristles 3 mm long.	ovoid, sparsely hairy; pappus of gold minutely barbellate bristles 3 mm long.	oblong, pale; pappus of creamy bristles 4 mm long.	elliptic, sparsely hairy; pappus of creamy minutely barbellate bristles 2-3 mm long.	oblong, sparsely hairy, red-brown with paler thickened margins; pappus of free golden bristles 2-3 mm long.	oblong, hairs only at apex; pappus of cream, minutely barbellate bristles 5 mm long.	ovoid, sparsely hairy; pappus of cream to purplish barbellate bristles 3 mm long.
Inflorescence	pyramidal or corymbiform panicle; heads hemispherical 5-6 mm long, 8-12 mm diameter.	extended panicle with numerous heads; heads broad-campanulate, 4-6 mm long, 6-10 mm diameter.	extensive pyramidal panicle; heads campanulate to hemispherical, 3-4 mm long, 3-4 mm diameter.	1-several spike-like panicles; branches of panicle short with up to 10 heads each; heads campanulate, 3-4 mm long, 3-5 mm diameter.	many cylindrical panicles, each with numerous heads; heads hemispherical or oblong when young, 2.5-4 mm long, 3 mm diameter.	small, up to 7 heads; heads hemispherical, 8-12 mm long, 15-20 mm diameter.	rounded panicle; heads broad-campanulate to globose, 5-6 mm long, 5-7 mm diameter.
Floret colour	white-to-pink	straw	cream	white or tinged mauve	red-brown	yellowish	reddish

Source: after Everett 1990

Origin and distribution in Australia

The majority of naturalised *Conyza* species in Australia are of South American origin: *C. bonariensis* (Michael 1977), *C. chilensis*, *C. parva* and *C. bilbaoana* (Everett 1990). *Conyza canadensis* is native to North America, *C. sumatrensis* native to Indonesia and *C. leucantha* native to Nepal (Everett 1990). The most widespread species on a global basis are *C. canadensis* and *C. sumatrensis* (Thebaud and Abbott 1995).

There is no information available regarding the exact location or arrival mode for *Conyza* species to Australia. However, diary entries of Captain Phillip Parker King describe observations of a *Conyza* species on 25 February 1818 on the east coast (Lee 2003). Initial botanical collections in South Australia, carried out in 1847, reported *C. bonariensis* as widespread in the Adelaide area (Burry and Kloot 1982). When weeds establish in a new geographic area, they generally come from a location with approximately comparable climatic conditions (Baker 1972).

Conyza bonariensis occurs in all states of Australia (Everett 1990; AVH 2010) (Figure 2.2). The incidence in cropping systems is mainly prevalent in northern and central New South Wales, southern Queensland (Wu 2007) and southern Western Australia (Storrie 2007). *Conyza canadensis* is not reported to exist in all states; Everett (1990) reported that Northern Territory and Western Australia have zero recordings, although the Australia Virtual Herbarium records indicated that Northern Territory, South Australia and Tasmania have no reported incidence (AVH 2010). The predominant populations of *C. canadensis* are along the east coast of Australia (AVH 2010). *Conyza sumatrensis* is present in all states and territories, except Northern Territory (Figure 2.2), with the greatest collections having occurred in Victoria and Queensland (AVH 2010).

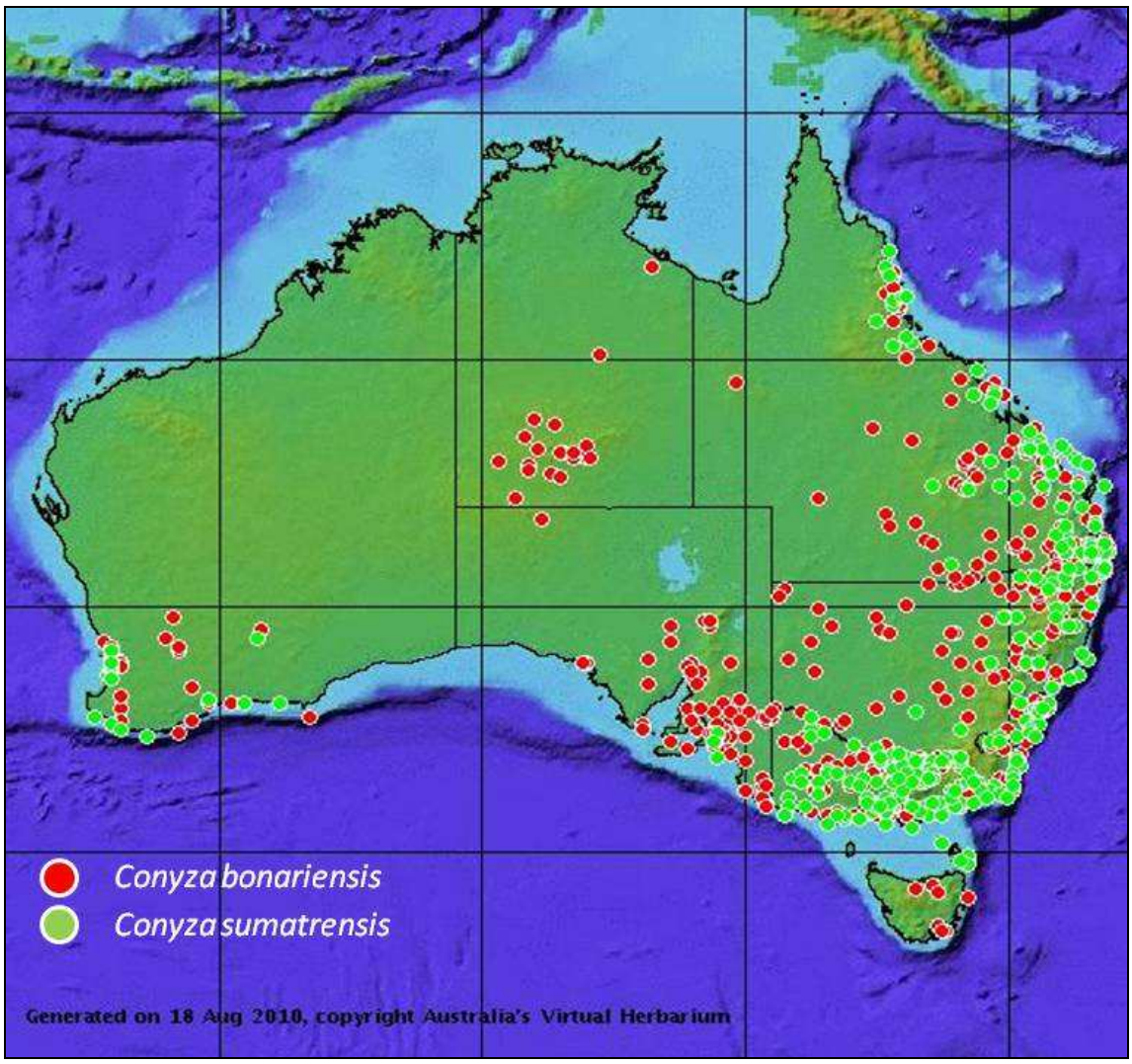

Figure 2.2 Distribution of *C. bonariensis* and *C. sumatrensis* in Australia.

Source: AVH (2010).

Distribution of *Conyza* species in relation to preference for habitat types is summarised in Table 2.3. This habitat preference summary indicates referenced sightings of the species within the stated habitats and does not testify that the weed is unable to invade non-listed habitats.

Table 2.3 Habitat preferences for *Conyza* species established in Australia.

Species	Habitat type	Reference
C. bilbaoana	Roadsides and other disturbed sites.	Everett 1990.
C. bonariensis	Cultivation, ruderal and roadside. Major weed of cropping systems in northern cropping region of Australia. Minimum tillage agriculture.	Everett 1990; Thebaud and Abbott 1995. Wu *et al.* 2007. Somervaille and McLennan 2003.
C. canadensis	Disturbed sites. Minimum tillage agriculture. Roadsides, field edges, abandoned fields. Agrestal and ruderal.	Everett 1990. Buhler *et al.* 1997; Brown and Whitwell 1988; Weaver 2001. Weaver 2001; Steckel *et al.* 2006; Dauer *et al.* 2007. Thebaud and Abbott 1995.
C. chilensis	Roadsides.	Everett 1990.
C. leucantha	Roadsides and disturbed sites.	Everett 1990.
C. parva	Sandy soil.	Everett 1990.
C. sumatrensis	Cultivation, grazing, ruderal, roadside.	Everett 1990; Thebaud and Abbott 1995.

Most *Conyza* species present in Australia are restricted to certain climatic zones (Table 2.4). The exception is *C. bonariensis* which has been reported to occur in all climatic zones. All tropical infestations of *Conyza* species, apart from *C. bonariensis*, are limited to the east coast of Australia (AVH 2010).

Table 2.4 *Conyza* species distribution by climatic zones in Australia.

	Climatic zones						
	Temperate			Sub-tropical			Tropical
Species	Winter rainfall (mainly moderate)	Winter rainfall (moderate to heavy)	Uniform rainfall	Arid (winter / non season rainfall)	Arid (mainly summer rainfall)	Summer rainfall	Summer rainfall
C. bilbaoana	✓		✓			✓	
C. bonariensis	✓	✓	✓	✓	✓	✓	✓
C. canadensis	✓	✓	✓			✓	✓ (*)
C. chilensis			✓			✓	
C. leucantha						✓	✓(*)
C. parva		✓	✓			✓	✓(*)
C. sumatrensis	✓	✓	✓			✓	✓(*)

*refers to infestations only reported on the east coast of Australia

Source: after AVH (2010)

CONYZA SPECIES BIOLOGY AND ECOLOGY

Seed bank dynamics

Observations made on soil seed banks commenced with Darwin in 1859, when he noticed seedlings emerged from mud sampled from a pond. The first published research was in 1882, by Putersen, where the occurrence of seeds at different soil depths was measured

(Roberts 1981). There are several definitions offered to encapsulate the concept of a 'reservoir of seeds' or 'seed bank'. Roberts (1981) equates seed bank to the viable seed reservoir present in soil. This is extended to viable seeds present or mixed in soil and/or soil debris by Leck *et al.* (1989). As a fluid entity, there are both inflows and outflows to the system.

The composition of species within a seed bank is the combined result of seed production, germination and mortality (Hoffman *et al.* 1998). This is extended in agronomic settings to include crop management practices (Hoffman *et al.* 1998), e.g. tillage and pesticide use. Importantly, the soil seed bank is the first stage of life for annual plant species (Christoffoleti and Caetano 1998). There has been a range of estimates published on the approximate number of viable seeds existing in the soil. This range is variable due to the numerous methods employed, time of year sampled, different habitats and species (Roberts 1981; Fenner 1985; Gross 1990). Bilalis *et al.* (2001) reported that the reservoir of seeds in soil can exceed billions per hectare. Fenner (1985) reported seed volumes in three key habitats, viz., 10^2 to 10^3 seeds m^{-2} in forest, 10^3 to 10^6 seeds m^{-2} in grassland and 10^3 to 10^5 seeds m^{-2} in arable land.

Conyza **species seed viability and longevity**

Seed viability refers to a seed that is capable of germination given suitable conditions (Bradbeer 1988). This also includes seeds which are viable, yet dormant (Bradbeer 1988). From an ecological perspective, seed viability, in addition to germination, allows for the possibility of the seedling to establish in its environment (Bradbeer 1988). Seed longevity in soil depends on numerous interactions, including dormancy of seed, environmental conditions (e.g. temperature, light, water and gases) and biotic activity (e.g. bacteria, fungi, predation and allelopathy) (Fenner 1985). Thompson *et al.* (1997) described three temporal categories to define seed longevity: transient (<1 yr), short-term (1 to 4 yrs) and long-term (>4 yrs).

Wu *et al.* (2007) measured differences in seed viability for *C. bonariensis* between two soil

types, light sodosol and heavy black vertosol. Buried seeds in the light sodosol maintained significantly higher viability than the heavy black vertosol during the two year experimental period. Results after a full two years of burial showed 8% viable seeds in sodosol and 2% in vertosol (Wu *et al.* 2007). *Conyza canadensis* seeds are reported to remain viable for at least 1 to 2 years (Weaver 2001). Longevity within a laboratory setting has been measured as 2 to 3 years for *C. sumatrensis* and *C. canadensis* (Hayashi 1979).

Seed production and dispersal

Conyza species are prolific seed producers (Kempen and Graf 1981; Wu *et al.* 2007; Hao *et al.* 2009). A range of seed production levels has been reported for *C. bonariensis*, including up to 375 561 per plant (Kempen and Graf 1981) and *C. sumatrensis* more than 60 000 (Hao *et al.* 2009). *Conyza canadensis* is reported to produce 200 000 seeds per plant, with a positive correlation between plant height and total fecundity (Weaver 2001; Shields *et al.* 2006). The relationship between plant density and seed production levels has been explored in *C. canadensis* by Bhowmik and Bekech (1993), with a reported increase in the number of seeds produced per plant as plant densities decreased – 100 000 seeds at 200 plants m^{-2} and 200 000 seeds at 10 plants m^{-2}. This result is consistent with an earlier finding on intraspecific competition in *C. canadensis* (Palmblad 1968). Seeds are dispersed within 1 to 2 days from mature capitula, dependent on climate (Thebaud *et al.* 1996). Seeds of *Conyza* species are dispersed with a fully developed embryo and can easily absorb water (Karlsson and Milberg 2007).

Chambers and MacMahon (1994) described two separate phases of seed dispersal. Phase I, is the transit from parent plant to the soil surface and Phase II involves subsequent horizontal or vertical movements (Chambers and MacMahon 1994). Phase I, or primary dispersal, for *Conyza* species is via wind, an abiotic means (Wu 2007). Wind dispersal (anemonochory) is one of the most studied seed dispersal vectors. Johnson *et al.* (1981) determined distance travelled by a wind dispersed seed using the release height (*H*), wind speed (*U*) and the propagule terminal velocity (settling velocity) in cm s^{-1} (V_s). The formula is represented as $d=HU/V_s$ (Johnson *et al.* 1981). This function assumes zero turbulence and a steady wind speed at all heights (Cousens and Mortimer 1995). Andersen (1992) calculated

the mean settling velocity for *C. bonariensis* as 29.11 cm s^{-1}. Structural features of a seed which reduces the speed it falls, for example; a pappus of a high surface area to volume ratio, increases the likelihood of lateral transportation by air currents (Chambers and MacMahon 1994; Cousens and Mortimer 1995).

Small seeds, as in *Conyza* species, typically have a lower survival and competitive ability than larger seeds, albeit the dispersal ability and extent is greater (Harper *et al.* 1970). The achene volume has been calculated as 0.006 mm^3 for *C. bonariensis* and 0.011 mm^3 in *C. canadensis* (Andersen 1993). The seed weight of *C. canadensis* is reported by Milberg *et al.* (1996) as 0.04 mg. In addition to small seed size aiding dispersal, *Conyza* species, and many other Asteraceae members, have a pappus attached to the achene (Fenner 1985; Dauer *et al.* 2007) – such structures act as a drag-enhancing parachute (Andersen 1993). Pappus lengths for the *Conyza* species in Australia range from 2 to 5 mm (Everett 1990). It is reported in numerous Asteraceae species that the pappus alters its geometry in varying levels of humidity (Sheldon 1974).

The concept of enhanced dispersal ability based on morphology is supported by experiments undertaken by Shields *et al.* (2006) where *C. canadensis* seeds were discovered between 41 and 140 m above ground level, therefore placing them into the Planetary Boundary Layer (from 2.5 times the canopy height up to approximately 2 km from ground level) (Shields *et al.* 2006). Wind speeds in this layer can reach 20 m s^{-1}, with a dispersal distance of up to 500 km achievable for aerial biota (Shields *et al.* 2006). Dauer *et al.* (2007) determined that *C. canadensis* seeds were often dispersed at least 500 m from the source, although 99% of the seed was found within 100 m.

Phase II or secondary dispersal – the movement down or along the soil after landing – is not well understood for many species, including *Conyza* species. This dispersion can continue until a seed germinates, it becomes permanently entrapped, or until certain structures that enable dispersion deteriorate (Johnson and Fryer 1992). *Conyza* species seed morphology with an attached pappus gives rise to a large surface area to volume ratio which makes it difficult for the seed to passively move down cracks in the soil (Bekker *et al.* 1998) or be buried by earth-worms (Van der Reest and Rogaar 1988). Seeds landing on an area with no resident vegetation are more capable of being further transported via winds along the surface soil, whereas areas with vegetation restrict the horizontal wind dispersion (Zimdahl

1999). Secondary dispersion can significantly change the seed shadow created after primary dispersal (Harper 1977; Chambers and MacMahon 1994) and is more effective in conditions with a smooth surface, minimal obstacles and high wind velocities close to the ground (Monteith and Unsworth 1990).

Seed dormancy

The definition of seed dormancy involves ambiguity, despite the level of research it has received (Bewley 1997). It is generally agreed that seed dormancy refers to a failure of a viable seed to complete germination under favourable conditions (Fenner 1985; Bradbeer 1988; Baskin and Baskin 1989; Bewley 1997). Many seeds undergo a period of dormancy after dispersal – such a period could be a few days to many decades or longer (Fenner 1985) – e.g., *Malva neglecta* Walir. (common mallow) seeds can remain viable for over 100 years (Kivilaan and Bandurski 1981). Harper (1977) described three types of seed dormancy – innate, enforced and induced. Such classifications all relate to the means by which the dormancy has ensued. Baskin and Baskin (2004) undertook more recent work to arrive at a global classification system of dormancy. Under this classification, five classes of dormancy are used: physiological dormancy (PD), morphological dormancy (MD), morphophysiological dormancy (MPD), physical dormancy (PY) and combinational dormancy (PY + PD) and within these classes exist differing levels and types (Baskin and Baskin 2004).

Dormancy, or delayed germination, can be disadvantageous when fast colonisation is required (Lavorel *et al.* 1994). An absence of dormancy can also be a disadvantage due to the reduction of dispersal opportunities (Fenner 1985). Lavorel *et al.* (1994) reported dormancy is an advantage in environments where adult populations are destroyed by disturbance. Thebaud *et al.* (1996) reported that *Conyza* species lack any dormancy, although Karlsson and Milberg (2007) undertook after-ripening experiments on *C. bonariensis* and *C. canadensis* and reported non-deep physiological dormancy (PD) existed.

Factors affecting *Conyza* species germination

Temperature

Main *et al.* (2006) reported *C. canadensis* emergence was highly variable and found no strong correlation with air temperature (r^2=0.45). Research into optimal germination temperatures have been conducted (not across all species), with *Conyza* species generally germinating between 10 and 25^{o}C (Zinzolker *et al.* 1985). The optimal temperature for *C. bonariensis* germination was estimated to be 20^{o}C with a base temperature (temperature below which development ceases) of 4.2^{o}C (Wu *et al.* 2007) using seeds from southern Queensland populations. This base temperature is eight degrees lower than that reported for *C. canadensis*, 12.5^{o}C (Steinmaus *et al.* 2000). The highest level of germination reported for *C. canadensis* was at 28.2^{o}C (Shontz and Oosting 1970). Nandula *et al.* (2006) investigated *C. canadensis* germination using day/night temperatures. The combination of 24^{o}C (day) and 20^{o}C (night), with a 13 hr photoperiod, achieved the highest germination result of 61% after 10 days (Nandula *et al.* 2006). Fresh seeds of *C. canadensis* were not able to germinate at 15^{o}C (day) and 5^{o}C (night) with light, whilst *C. bonariensis* seeds did germinate (Karlsson and Milberg 2007).

Light

The findings on light requirements for germination of *Conyza* species were mixed. Gorski (1975) and Nandula *et al.* (2006) reported that *C. canadensis* does not require any light, while others have reported that *Conyza* species had a requirement for light to germinate (Michael 1977; Zinzolker *et al.* 1985; Wu *et al.* 2007). The experiments to determine light requirements, however, have typically been of limited experimental design, i.e., light or no light. This was expanded by Milberg *et al.* (1996), but only for *C. canadensis*, where short-duration light exposure was tested. It was reported that *C. canadensis* was able to successfully germinate when exposed to only five seconds of light followed by complete darkness (Milberg *et al.* 1996). Some plant species have been reported to germinate with

only one second of daylight (Milberg *et al.* 1996). The relationship between seed size and dependence on light for germination has been investigated, with a direct correlation (p<0.0001) reported when studying 54 species, which included *C. canadensis* (Milberg *et al.* 2000).

Moisture

Main *et al.* (2006) reported that *C. canadensis* germination had only a weak correlation with rainfall (r^2=0.32). Flood tolerance testing by Stoecker *et al.* (1995) reported a significant effect of flooding on *C. canadensis* growth, survival and total biomass production, with a 50% reduction in survival, 26% reduction in height after 14 days, resulting in biomass 2% of the control group 56 days post flooding (Stoecker *et al.* 1995). Water stress experiments have also been reported for *C. canadensis*, with 25% germination at 0 MPa (distilled water), reducing to 2% at –0.8 MPa (Nandula *et al.* 2006), suggesting germination is possible in a moderately water stressed environment. Wu *et al.* (2007) reported that significant rain events stimulate emergence of *C. bonariensis*.

Soil

There is limited information available on the effect of soil types on germination and as with other ecological factors, information is devoid of comparisons between species. Wu *et al.* (2007) investigated burial depth impact on *C. bonariensis* emergence in the field using a heavy black vertosol soil and light sodosol. They reported no emergence in the heavy soil from any depth, while in the light soil, seedlings only emerged from the minimal depth of 0 to 2 cm (Wu *et al.* 2007). The lack of emergence in heavy soils reported by Wu *et al.* (2007) contrasts to an earlier investigation on *C. canadensis* which reported high emergence (>60%) in sandy, heavy and peaty soils (Shontz and Oosting 1970).

Seed size is a major determinant of ability to emerge from depth – small seeds can lack sufficient reserves to emerge (Hoffman *et al.* 1998). The impact of pH on germination of

C. canadensis was examined by Nandula *et al.* (2006) who reported higher rates of germination under neutral-to-alkaline conditions. In relation to salt content in soil, Nandula *et al.* (2006) reported *C. canadensis* achieved 4% germination at 160 mM sodium chloride (NaCl). Main *et al.* (2006) reported *C. canadensis* germination showed no strong correlation with soil temperature (r^2=0.21).

Other factors

Palmblad (1968) reported that the germination rate of *C. canadensis* decreased as the intraspecific competition increased – 87% germination with five seed per Petri-dish density down to 54% at a density of 100 seeds.

In an investigation of pesticide effects on weed germination, it was reported that germination time and total number of *C. canadensis* seeds germinating was significantly reduced with dimethoate, a foliar-feeding insect control (Gange *et al.* 1992).

The effect of crop residue on seed germination has been documented for *C. canadensis* in relation to several crops (Burke *et al.* 2003), with 77% less emergence reported after a corn or cotton crop, compared with no previous crop. A proposed hypothesis for this observation is that the crops with a late-season canopy physically prevent seeds from settling on the soil (Burke *et al.* 2003).

Growth, development and reproduction

Conyza bonariensis follows a winter or summer annual life cycle (Wu 2007; Wu *et al.* 2007); yet it has been reported as a biennial weed (Prieur-Richard *et al.* 2000). In the northern cropping region of Australia, *C. bonariensis* emergence is predominantly in autumn and early winter, forming a basal rosette over winter and producing seeds in the following spring or summer (Wu *et al.* 2007).

An individual *C. bonariensis* plant flowers sequentially and the flowering period can span 1 to

4 months (Thebaud *et al.* 1996). Vernalisation requirements have not been determined, although DNA isolation and polymerase chain reaction (PCR) amplification of *C. canadensis* found similarities in species known to require vernalisation (Rudnoy *et al.* 2002). Plant age at bolting has been reported for *C. bonariensis*, *C. canadensis* and *C. sumatrensis* as 11, 13.6 and 11 weeks respectively, with the age at flowering of 13.9, 22.4 and 19.8 weeks respectively (Thebaud and Abbott 1995), using seeds sampled from European populations. The number of florets per head has also been reported for *C. bonariensis*, *C. canadensis* and *C. sumatrensis* as 210.5, 68.3 and 94.6 respectively (Thebaud and Abbott 1995). These quantitative measurements support the notion that different *Conyza* species have different time scales for each life stage. This research does not however, explore the impact on such temporal scales of edaphic, climatic or other ecological factors.

Conyza species reproduce autogamously, are self compatible, and as a result have a reduced pollen-to-ovule ratio compared with xenogamous reproducers (Cruden 1976). Phylogenetic data obtained by Noyes (2000), supported that autogamy has evolved independently in *Conyza* species. With no requirement to attract a pollinator, the flower size is small compared with an outbreeder, thus enabling efficient energy use (Ornduff 1969). The pollen-to-ovule ratio has been reported for *C. sumatrensis* as 98.8 (Hao *et al.* 2009), this contrasts to 988.6 in a xenogamous Asteraceae species, *Bidens leptocephala* Sherff. (Cruden 1976).

In a study which explored why *C. sumatrensis* and *C. canadensis* differed in their invasive abilities, Thebaud *et al.* (1996) reported that the catalyst initiating bolting is more related to resource availability than to light in both species. Although the catalyst for bolting was similar in both species, there were significant differences in bolting time, *C. sumatrensis* consistently bolted earlier than *C. canadensis* (Thebaud *et al.* 1996). A shorter time to stem elongation could provide a competitive advantage in vegetated areas (Thebaud *et al.* 1996). Flowering in *C. bonariensis* is favoured by a long photoperiod, such as 14 hrs (Amsellem *et al.* 1993). Following a wildfire in 1963 in the Wichita Mountains of Oklahoma (USA), plots were observed from 1964 to 1966 to investigate plant succession. It was reported that within the ungrazed plots, *C. canadensis* reached peak coverage during the second year after the fire, and was absent thereafter (Penfound 1968).

Competition effects on growth

Research on competition has been based on observations and limited experimental variables. It is common for invading species to establish in areas of low competition with established vegetation (Crawley 1987). Thebaud *et al.* (1996) reported that the ability to absorb and utilise both water and nutrient resources within a competitive environment was greater in *C. sumatrensis* than *C. canadensis* during experiments conducted on previously cultivated fields in France. Furthermore, they reported that *C. sumatrensis* established and persisted in fields uncultivated for up to 30 years, while *C. canadensis* was restricted to recently disturbed habitats (Thebaud *et al.* 1996).

Lavorel *et al.* (1999) reported that impact on functional group composition varied across life stages of *C. bonariensis* and *C. canadensis*. Survival of *C. bonariensis* and *C. canadensis* increased with an increase in Asteraceae species richness (Lavorel *et al.* 1999). Biomass and reproduction of *C. bonariensis* and *C. canadensis* decreased in the presence of higher annual grass species richness but increased in the presence of annual legumes (Lavorel *et al.* 1999). This reported increase in biomass, when grown in the presence of legumes, is likely due to the increase in nitrogen availability (Palmer and Maurer 1997).

Palmblad (1968) undertook an investigation into the effect of density for a range of weedy species, including *C. canadensis*, and reported an increase in above ground vegetative dry weight relative to density, albeit the amount of the increase in biomass reduced as the density increased. In addition to the biomass effect, it was reported that *C. canadensis* flowered later under high-density conditions (Palmblad 1968). *Conyza canadensis* was also reported to be more affected by competition in sandy soil compared with heavy clay soil in greenhouse experiments (Shontz and Oosting 1970).

Predation effects on growth

Although exotic plants typically arrive in a new country without their native herbivores, this does not exclude the possibility of generalist herbivores in the new habitat from predating these plants (Case and Crawley 2000). In an investigation in south east Queensland,

C. bonariensis plant density was reportedly increased with cattle grazing, whilst *C. sumatrensis* and *C. canadensis* showed no change (McIntyre *et al.* 2003). The response recorded for *C. bonariensis* is idiosyncratic of an exotic invasive species. Case and Crawley (2000) reported rabbit herbivory reduced seedling recruitment, plant height and total number of *C. sumatrensis* plants at flowering stage in field studies in Berkshire (United Kingdom). Neave and Tanton (1989) examined grazing effects of the grey kangaroo in grasslands within the Australian Capital Territory, and reported *C. bonariensis* was present only in plots that excluded grazing by kangaroos. In addition to the grazing of *C. bonariensis,* vegetative biomass, seeds and flowers, are consumed by birds (Lepschi 1993).

Allelopathic effects on growth

The main allelochemicals that can have inhibitory effects on crops include alkaloids, terpenoids, flavonoids, steroids, tannins and phenolic compounds (Whittaker and Feeny 1971). Current knowledge of allelochemicals in *Conyza* species is limited, although it is well documented on a worldwide basis that many weed species possess allelopathic potential (Shaukat *et al.* 1985; Khalid *et al.* 2002). On a general level, the *Conyza* genus is reported to be rich in terpenoids (Chaudhry *et al.* 2001). As well as weeds impacting on neighbouring plants through chemical means, there is also opportunity for the management of weed species through the use of allelochemicals.

Shaukat *et al.* (2003) investigated the effect of aqueous extract of *C. canadensis* on several crops and identified the phenolic components. They reported the aqueous shoot extract caused significant ($p<0.01$) inhibition of germination for all test plants (tomato > radish > corn = mungbean > wheat > bulrush millet); tomato germination was reported to be reduced to 0% at 75% extract concentration (Shaukat *et al.* 2003). Khalid *et al.* (2002) reported a germination and growth impact on corn from *C. canadensis*. The phenolic compounds identified through chromatography in *C. canadensis* were reported to be gallic acid, vanillic acid, catechol and syringic acid (Shaukat *et al.* 2003).

Chaudhry *et al.* (2001) examined *C. bonariensis* extracts for anti-fungal and anti-bacterial properties. They reported the methanol extract of *C. bonariensis* showed significant

antifungal activity when tested against *Cladosporium cucumerinum* and antibacterial activity against *Sarcina leutea* (Chaudhry *et al.* 2001).

AGRONOMIC IMPACT AND CONTROL

Impact

Conyza bonariensis is listed as both an agricultural and environmental weed (Thebaud and Abbott 1995). It is a weed of pasture systems and many field crops, including maize, soybean, sorghum, cotton, chickpea, wheat, and lucerne (Wu 2007). Managing *Conyza bonariensis* has doubled fallow weed control costs in certain areas of the northern cropping region of Australia (Wu *et al.* 2007). There are reports of herbicide resistance biotypes of *C. bonariensis* in eight countries, across a range of mode of action groups, including glyphosate (Heap 2010). There have been differential responses to glyphosate reported in *C. bonariensis* populations in southern Queensland, with populations from cropping paddocks more tolerant than populations from non-agricultural situations (Walker and Robinson 2008). *Conyza bonariensis* is also reported to host several pests, diseases and viruses (Costa 1955; Helms *et al.* 1961; Ferraz 1985; Xie and Yao 1989; Chaves *et al.* 2003).

Herbicide resistant biotypes in *Conyza* species

The first recorded incidence of glyphosate resistant *Conyza* species was *C. canadensis* in Delaware in 1999 (VanGessel 2001). *Conyza canadensis* is reported to have a high level of natural tolerance to glyphosate, possibly a factor aiding the evolution of greater resistance (Cerdeira and Duke 2006), and is placed on the list of top ten most important herbicide-resistant weed species (Heap 2010). Resistant populations are now estimated to be present in 44 000 ha, within 12 states of the United States of America (Heap 2010). This spread occurred within five years of the first reporting of a resistant population (Dauer *et al.* 2007). Initial reports of glyphosate resistant *C. bonariensis* occurred in South Africa in 2003 (Heap

2010).

Fuerst *et al.* (1985) reported a paraquat-resistant biotype of *C. bonariensis,* originating from Egypt, with a proposed resistance mechanism through exclusion of paraquat from its site of action in the chloroplast by a rapid sequestration mechanism (Fuerst *et al.* 1985). Shaaltiel *et al.* (1988) reported the Mendelian inheritance of paraquat resistance in *C. bonariensis* as involving one dominant gene. Triazine-resistant biotypes of *C. canadensis* were reported in Hungary (Lehoczki *et al.* 1985), Switzerland and the United Kingdom (Warwick 1991). The mechanism of resistance for *C. canadensis* is reported to be that of reduced translocation (Feng *et al.* 2004). With predominantly self-pollination in *Conyza* species, the movement of seed is the main source of resistance spread (Smisek *et al.* 1998). This factor is coupled with the production of large seed numbers and wind dispersal in *Conyza* species. A summary of herbicide resistant *Conyza* species, including the mode of action group and country of affected populations is provided (Table 2.5).

Table 2.5 Summary of reported herbicide resistant *Conyza* species biotypes.

Species	Mode of action group	Location
C. bonariensis	Glycines (M)	Brazil, Colombia, South Africa, Spain, Israel, USA.
	Photosystem I inhibitors (L)	Egypt, Japan, South Africa, USA.
	Photosystem II inhibitors (C)	Israel, Spain.
	ALS inhibitors (B)	Israel.
C. canadensis	Glycines (M)	Brazil, China, USA, Czech Republic, Spain.
	Photosystem I inhibitors (L)	Belgium, Canada, Japan, USA,
	Photosystem II inhibitors (C)	Belgium, Czech Republic, France, Hungary, Poland, Spain, Switzerland, United Kingdom, USA, Israel.
	ALS inhibitors (B)	Israel, Poland, USA.
	Ureas and amides	France, USA.
C. sumatrensis	Glycines (M)	Spain.
	Photosystem I inhibitors (L)	Japan, Malaysia, Sri Lanka, Taiwan.
	ALS inhibitors (B)	Spain (Osuna and De Prado 2003).

Source: Heap (2010)

Control

An important objective for the control of *C. bonariensis* is the prevention of seed set (Wu *et al.* 2007). Control needs to be multi-faceted, including within the crop and fallow, the seed bank and the various growth stages of the weed. Management should also extend to include the control of neighbouring seed sources, such as roadsides, channels, and edges of fields. An additional complication in designing effective weed management strategies and timings is that the emergence of *C. bonariensis* is not seasonally uniform.

Chemical

Chemical control is more effective at the early rosette stage, with the control efficacy decreasing as the plant age increases (Wu *et al.* 2007). There are several post-emergent herbicide mixes registered for application on *C. bonariensis* in winter fallow, although few of these provide 100% control (Werth and Walker 2007). Werth *et al.* (2010) reported a "double knock" approach for effective control of *C. bonariensis*, with glyphosate plus 2,4-D as the initial application and a follow-up application of paraquat and diquat, provided the most effective control on *C. bonariensis* – the follow-up application occurring five to seven days after the initial application (Werth *et al.* 2010).

Biological

There is no published evidence of successful biological control for any *Conyza* species, although Hoeft *et al.* (2001) investigated the use of *Pseudomonas syringae* pv. *tagetis* (PST) as a biological control for *Cirsium arvense* (L.) Scop. (Canada thistle) and suggested PST as a possible benefit in controlling *C. canadensis*.

In a minimum tillage system, crop residue remains on the soil surface. The effect of residue on seed germination of *C. canadensis* has also been examined, with 77% fewer emergences reported after a cotton crop compared with no previous crop (Main *et al.* 2006). They reported that crops with a late-season canopy physically prevented seeds from settling on the soil (Main *et al.* 2006).

Mechanical

Within the crop, inter-row cultivation can assist the control of smaller plants of *C. bonariensis* and the burial of any soil surface seeds will greatly reduce germination incidence (Taylor *et al.* 2002). Large plants, however, are quite woody and have a deep taproot and therefore may not be successfully controlled by inter-row cultivation (Taylor *et*

al. 2002). In fallow, cultivation is a more effective measure for *C. bonariensis* control.

Cultural

Using crop rotations and cover crops are strategies by which weeds can be reduced (Liebman and Dyck 1993). The success of such strategies on weed suppression is reported to involve the varying patterns of resource competition, allelopathic interference, soil disturbance and mechanical damage (Liebman and Dyck 1993). The use of winter cover crops in minimum tillage systems are reported to increase soil carbon; reduce soil erosion and increase water availability and infiltration (Saini *et al.* 2005). Furthermore, weed suppression can be achieved through physical and chemical allelopathic effects (Nagabhushana *et al.* 2001).

CONCLUSIONS

The increasing incidence of minimum tillage cropping systems is increasing the reliance on herbicides and causing weed species shifts. The reliance on herbicides, or a single control method, will not provide effective long-term control. It is important to understand the ecology of problem weeds and their success in formulating effective management strategies.

In the literature review I have highlighted that the majority of biological and ecological knowledge on *Conyza* species is on *C. canadensis*, Canadian fleabane. However, it is *C. bonariensis* which is becoming increasingly important in minimum tillage systems within the northern cropping region of Australia. Furthermore, some of the ecological knowledge on *C. bonariensis* is based on overseas populations and research gaps exist in some areas: particularly the effect of soil types and emergence cohorts. Knowledge of certain attributes of *C. bonariensis* ecology could greatly improve the understanding of its success in minimum tillage system and improve the management and control of this weed.

Specific aims of the project

The first two aims addressed in this thesis relate to gaining a greater understanding of germination and emergence ecology of *C. bonariensis*, viz.:

(1) ***Determine the germination requirements (temperature, moisture and light) of* C. bonariensis *and determine if its prevalence in the northern cropping region of Australia, particularly minimum tillage systems, is related to its germination requirements*** (Chapter 3), and

(2) ***Determine the effect of different soil types and stubble loads on the emergence of* C. bonariensis** (Chapter 4).

The next research aim addresses the research gap of the effect of different emergence cohorts on *C. bonariensis* population dynamics:

(3) ***Determine the emergence cohort effect on growth and fecundity of* C. bonariensis *and whether this adds to its success in the northern cropping region*** (Chapter 5).

With predominantly self-pollination in *C. bonariensis*, the movement of seed is the main source of herbicide resistance spread; therefore a greater understanding of dispersal ecology is critical for effective long-term management. The next research aim relates to seed settling velocities and the effect of humidity on seeds:

(4) ***Determine the effect of humidity on* C. bonariensis *seed and seed dispersal and whether this adds to its success in the northern cropping region*** (Chapter 6).

The final research aim is about the length of time seeds of *C. bonariensis* can remain viable after they have been dispersed:

(5) Determine the effect of seed burial depth on seed longevity of* C. bonariensis *and whether this adds to its success in the northern cropping region (Chapter 7).

As previously mentioned, all experiments contrasted *C. bonariensis* ecology with that of the congeneric species, *C. sumatrensis,* which is less problematic in cropping systems in Australia, as a way of better identifying what characteristics of *C. bonariensis* may be responsible for its increasing incidence in minimum tillage cropping systems in the northern cropping region of Australia.

Chapter Three: Germination

CHAPTER THREE

GERMINATION

This chapter has been written in journal paper format, containing an Abstract and a combined Results and Discussion section. The bullet-point Conclusion section has been added for thesis consistency.

ABSTRACT

Fleabanes are problem weeds in disturbed sites within temperate climates in Australia and other parts of the world. Flaxleaf fleabane, or hairy fleabane, is becoming increasingly important in minimum tillage systems, with some populations being tolerant to important herbicides. Three experiments were conducted to determine if germination response to environmental factors differs between flaxleaf fleabane and the widespread but less common fleabane in crops, tall fleabane, to determine what ecological factors could be causing flaxleaf fleabane to increase in importance. The effect of constant temperature (5, 10, 15, 20, 25, 30 and 35^{o}C), shading (0, 50, 70, 90 and 100%) and moisture (-0.2, -0.4, -0.6, -0.8, -1.2, -1.4 and -1.6 MPa) on fleabane germination was tested. The optimal temperature for germination in both species was 25^{o}C, with no germination occurring at 5^{o}C. Tall fleabane had a greater tolerance to shade. Neither species germinated in full darkness or under osmotic potentials of less than -0.80 MPa. These results indicate that tall fleabane may be more prevalent in competitive environments, such as roadsides and pastures, because of its tolerance to shading. Other ecological factors, such as time to flower, or factors not yet explored, appear to give flaxleaf fleabane an advantage in cropping systems. Furthermore, the results support the use of shade as a control method for flaxleaf fleabane.

INTRODUCTION

Conyza species are annual, herbaceous plants belonging to the Asteraceae. There are seven exotic *Conyza* species naturalised in Australia, with infestations of one or more species in every state and territory and major climatic zone (Everett 1990). *Conyza sumatrensis* (Retz.) E. Walker, tall fleabane, previously known as *C. albida,* and *Conyza bonariensis* (L.) Cronquist, flaxleaf or hairy fleabane, indigenous to Indonesia and South America respectively (Everett 1990), are the two most prevalent species in Australia (AVH 2010). They typically invade disturbed sites, including roadsides, wastelands and crop edges. *Conyza bonariensis* has the broader geographic distribution of the two in Australia, tolerating a range of climates and habitats (Everett 1990). It is the most common *Conyza* species in dry-land cropping systems, and is an increasing problem in summer fallows and crops, such as cotton, increasing weed control costs (Wu *et al.* 2007).

Conyza bonariensis is believed to have increased in prevalence in dry-land cropping systems as a result of a shift towards conservation (zero or minimum) tillage practices and reduced reliance on soil-applied residual herbicides (Storrie 2007). The viability of *Conyza* species seed generally increases with soil burial depth (Wu *et al.* 2007), and under these tillage systems, seeds remain on or near the soil surface in favourable conditions for germination. While *Conyza canadensis* (L.) Cronquist, Canadian fleabane, and *C. sumatrensis* are the most dominant *Conyza* species within agroecosytems on a global basis (Prieur-Richard *et al.* 2000; Weaver 2001), it is not clear why *C. bonariensis* is emerging as the main fleabane weed in Australian cropping systems when *C. sumatrensis* is also present in the region.

Due to the weak dormancy of *Conyza* species seeds (Karlsson and Milberg 2007), most non-buried seed will germinate, given sufficient moisture, light and suitable temperatures, though Main *et al.* (2006) found that *C. canadensis* emergence was highly variable, with no strong correlation to temperature. *Conyza* species generally germinate between 10 and 25^{o}C (Zinzolker *et al.* 1985). Fresh seeds of *C. canadensis* were not able to germinate at 15^{o}C (day) and 5^{o}C (night) with constant light, whilst *C. bonariensis* seeds were successful under these conditions (Karlsson and Milberg 2007).

Light is not always a requirement for successful germination. The findings on light requirements for *Conyza* species germination are mixed. Gorski (1975) and Nandula *et al.* (2006) reported that *C. canadensis* does not require light to trigger germination, while other authors have found it necessary for *Conyza* species germination (Michael 1977; Zinzolker *et al.* 1985; Karlsson and Milberg 2007; Wu *et al.* 2007). Generally, there is a direct correlation between seed size and dependence on light for germination across a wide range of species (Milberg *et al.* 2000). Within the agroecosytem, shading is affected by management practices, including tillage. Under a minimum or no-till regime, crop residues can create a shaded microsite. Within conventional tillage, seeds are often buried below the soil surface and therefore the level of light that seeds experience is reduced. Steckel *et al.* (2006) found that C_3 species, such as *Conyza*, are influenced more by shade then C_4 species.

Moisture is critical to successful germination, with the imbibition of water being the first step in the germination process. While rainfall events appear to stimulate emergence of fleabane in the Australian landscape (Wu *et al.* 2007), moisture stress reduced germination of *C. canadensis* from 25% at 0 MPa to 2% at -0.8 MPa pressure (Nandula *et al.* 2006).

The objectives of this chapter are to determine and contrast the optimal germination conditions for two species of *Conyza*, namely *C. bonariensis* and *C. sumatrensis*, to better understand why *C. bonariensis* more successfully invades crops in Australia than *C. sumatrensis.* Such information will assist in designing better weed control strategies and in predicting what other weed species may invade areas under conservation farming. The experiments reported here form part of a larger study to understand the reasons for the invasion of *C. bonariensis* in Australian cropping systems by comparing its ecology with the less invasive *C. sumatrensis*. In this chapter, aspects of germination are examined, given that the success of *Conyza* species is aided by its prolific seed production (Kempen and Graf 1981; Wu *et al.* 2007). Light, moisture and temperature may all be critical for the germination of *Conyza* species seeds.

METHODS

Three experiments were conducted to assess the differences between three environmental factors (temperature, shading and moisture) on the germination of *C. bonariensis* and *C. sumatrensis*.

Seed collection and viability testing

To ensure similar maturation conditions, *C. bonariensis* and *C. sumatrensis* seeds were collected from the same roadside site 50 km east of Moree in Northern New South Wales, Australia (29^{o}32' S, 150^{o}14' E) on the same day in January 2008. The capitula of 50 sampled plants of each species were placed in paper bags and gently shaken to remove mature seeds, air-dried and stored in closed paper bags at room temperature prior to use. The temperature experiment was conducted in April 2008 and repeated in June 2008, and moisture and shading experiments were conducted in July 2008. Initial seed viability was assessed using 0.5% 2,3-5-triphenyltetrazolium chloride (TTC) (Freeland 1976). The tetrazolium bioassay used four replicates of 100 seeds for each species. The TTC solution was poured into each replicate Petri-dish with the 100 seeds and left for five hours at room temperature. After this time, seeds which turned red in colour were classed as viable.

General experimental methods

Germination tests were carried out in incubators at the University of New England, Armidale, Australia. For each species and treatment there were eight replicates, each of 100 seeds, except the temperature treatments, which involved four replicates, each of 100 seeds, repeated over time. Seeds were placed into 9 cm Petri-dishes lined with Whatman's No. 1 filter paper for each treatment. To control fungal growth on seeds, filter papers were dusted with Thiram (a.i. Thiram 80% w/w) fungicide powder (Barmac Industries Pty Ltd). Thermostats maintained temperature to ± 1^{o}C of the desired temperature, and as a check,

mercury thermometers were placed inside each incubator and read on a regular basis. Seeds were defined as germinated when the radicle or shoot extended greater than 1 mm beyond the seed coat (Steinmaus *et al.* 2000). The position of Petri-dishes within the incubators was changed daily.

Temperature effects on germination

Seven incubators were set to constant temperatures of 5, 10, 15, 20, 25, 30, and 35^{o}C. For the repeat experiment, the same incubators were used but the temperatures were interchanged. The light intensity within each incubator was maintained at 6.8 µmol m^{-2} sec^{-1} with fluorescent lighting. Each Petri-dish had 5 ml of deionised water added at the start of the experiment, with additional water provided as required to maintain moist conditions throughout the treatment period. Petri-dishes were sealed with parafilm to reduce evaporation. Seedlings were counted on a daily basis at the same time of day, then removed, throughout the 21 day treatment period.

Shading effects on germination

Five shade treatments were applied to *C. bonariensis* and *C. sumatrensis* seeds – 0, 50, 70, 90 and 100% shade. Shade cloth (Shade Australia, Moorebank, Australia) manufactured to shading levels of 50, 70 and 90% were used – these levels were confirmed with a photometer. Full darkness was achieved by wrapping the Petri-dishes in aluminium foil and parafilm was used to prevent evaporation on these treatments which remained unopened for the experimental period. The shade cloth was cut into two 60 by 60 cm pieces for each of the three shade levels. Petri-dishes were placed between the two pieces of cloth for each of the 50 to 90% shade levels. All treatments were placed in an incubator set at 25^{o}C with a constant light supply and organised in a randomised complete block design. Each Petri-dish had 5 ml of deionised water added at the start of the experiment. Petri-dishes were sealed with parafilm to reduce evaporation. No additional water was provided to the 100% shade

treatments. All others had additional watering to maintain moist conditions throughout the treatment period. Germination was recorded daily in all treatments except 100% shade.

Moisture effects on germination

To examine the influence of moisture stress on germination, a total of eight osmotic potentials were used: -0.2, -0.4, -0.6, -0.8, -1.0, -1.2, -1.4 and -1.6 MPa. The osmotic potentials were prepared using potassium chloride (KCl), as calculated by Robinson and Stokes (2002). The KCl was added to deionised water and potato dextrose agar (15 g L^{-1}). The mixture was stirred thoroughly, autoclaved at 121^{o}C for one hour, then placed in a 60^{o}C water bath and subsequently poured into Petri-dishes. Seeds were added and each Petri-dish was sealed with parafilm to prevent evaporation. All dishes were arranged in a randomised complete block design within an incubator set at 25^{o}C with constant light. Germinated seeds were counted at the end of the 21 day treatment period. Prior to using KCl for osmotic potentials, polyethylene glycol (PEG 8000) was tested using the methods of Michel (1983). No seeds of either *Conyza* species germinated in any osmotic potential tested (-0.2 to -1.6 MPa) when PEG was used. Lagerwerff *et al.* (1961) reported that not all seeds can germinate with PEG and one reason is a reduction in oxygen availability (Mexal *et al.* 1975).

Statistical analysis

All significant differences referred to are $p<0.05$, unless otherwise stated and all means reported are accompanied by their standard error (±S.E.). There were no significant differences between repeat experiments for temperature treatments or the interaction of repeat experiment and treatment, therefore the data were combined. All data sets had levels of skewness within two standard errors and therefore no transformations were performed. Treatment effects were analysed using ANOVA, in the statistical package SPSS v. 17.0 to a confidence level of $\alpha=0.05$. Where the ANOVA returned a significant finding, significant differences between pairs of treatments were detected to a confidence interval of

α=0.05 using a Tukey multiple comparison for temperature and moisture and a Dunnett multiple comparison for shading, which included a control (0% shade). The base temperature (T_{base}), the temperature below which phenological development ceases (Steinmaus *et al.* 2000), for both species was estimated by regressing germination rate on sub-optimal temperatures and computing an x-intercept from the linear equation (Holt and Orcutt 1996).

RESULTS AND DISCUSSION

This suite of experiments was designed to test differences in germination response to environmental factors between *C. bonariensis* and *C. sumatrensis* and thereby to help explain differences in the ecological niches occupied by the two species in Australia. Initial seed viability levels for *C. bonariensis* and *C. sumatrensis* were 78.9% (±6.7%) and 83.1% (±5.3%) respectively.

Temperature effects on germination

Analysis of variance returned species, temperature and the interaction as significant (Table 3.1). Tukey multiple comparison showed that when comparing the two species, all treatment combinations were significantly different except *C. sumatrensis* at 35^{o}C which was not different to all *C. bonariensis* treatments. Germination for both species peaked at 25^{o}C (Figure 3.1), with *C. bonariensis* reaching 33.7% (±8.4%) and *C. sumatrensis* 78.4% (±4.7%). However, the 25^{o}C germination results were not significantly different to the 15 or 20^{o}C in *C. bonariensis*. There was no germination in either species at a constant 5^{o}C, although *C. bonariensis* is capable of germinating in a 15^{o}C/5^{o}C environment (Karlsson and Milberg 2007). Germination of *C. sumatrensis* remained relatively high from 10^{o}C to 30^{o}C, whereas germination of *C. bonariensis* had a distinct peak at 20 to 25^{o}C and dropped away more rapidly above and below these temperatures than *C. sumatrensis* (Figure 3.1). In *C. sumatrensis*, 13.7% (±3.7%) of seeds also germinated at 35^{o}C, with zero germination of

C. bonariensis seeds at this temperature. These differences in peak and overall ranges between the species suggest that *C. sumatrensis* may have a greater capacity to emerge in a broader diversity of climatic environments, compared with *C. bonariensis* which may need the milder temperatures of autumn and spring.

As well, *C. sumatrensis* germinated more rapidly after imbibition than *C. bonariensis* across the range of temperatures tested (Figure 3.2), which may help it to compete more vigorously with other species, such as along roadsides, where it is commonly seen, but may also make it more vulnerable to early post-emergence herbicide applications in a cropping environment. The two species did not differ significantly in original seed viability and yet *C. sumatrensis* was able to germinate at higher levels at all temperatures tested, excepting 5^{o}C. *Conyza bonariensis* is reported to possess no innate dormancy (Wu *et al.* 2007), however, Karlsson and Milberg (2007) reported that *C. bonariensis* seeds possess non-deep physiological dormancy, which Baskin and Baskin (2004) reported allow seeds to germinate at lower temperatures with age. The seed used is these experiments were up to six months old and therefore considered relatively fresh. Base temperatures (T_{base}) were calculated as 4^{o}C and 5^{o}C for *C. bonariensis* and *C. sumatrensis* respectively.

Table 3.1 Analysis of variance results for temperature (r^2=0.843).

Source	df	MS	F	p
Corrected Model	11	0.573	36.134	<0.05
Intercept	1	12.064	761.174	<0.05
Species	1	3.564	224.899	<0.05
Temperature	5	0.265	16.742	<0.05
Species*Temperature	5	0.054	3.387	<0.05
Error	74	0.016		
Total	86			
Corrected Total	85			

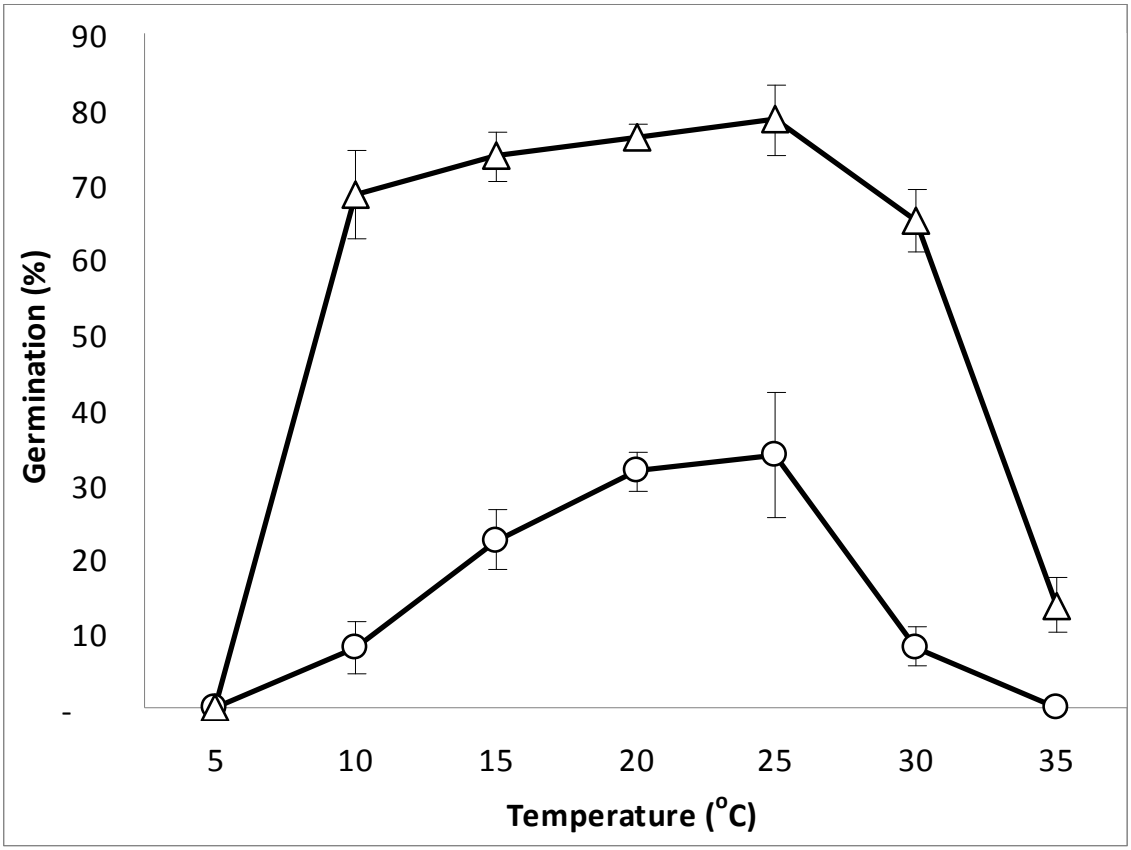

Figure 3.1 Total germination for *C. bonariensis* (○) and *C. sumatrensis* (Δ) with standard error bars (⌶) after 21 days treatment period under different temperatures.

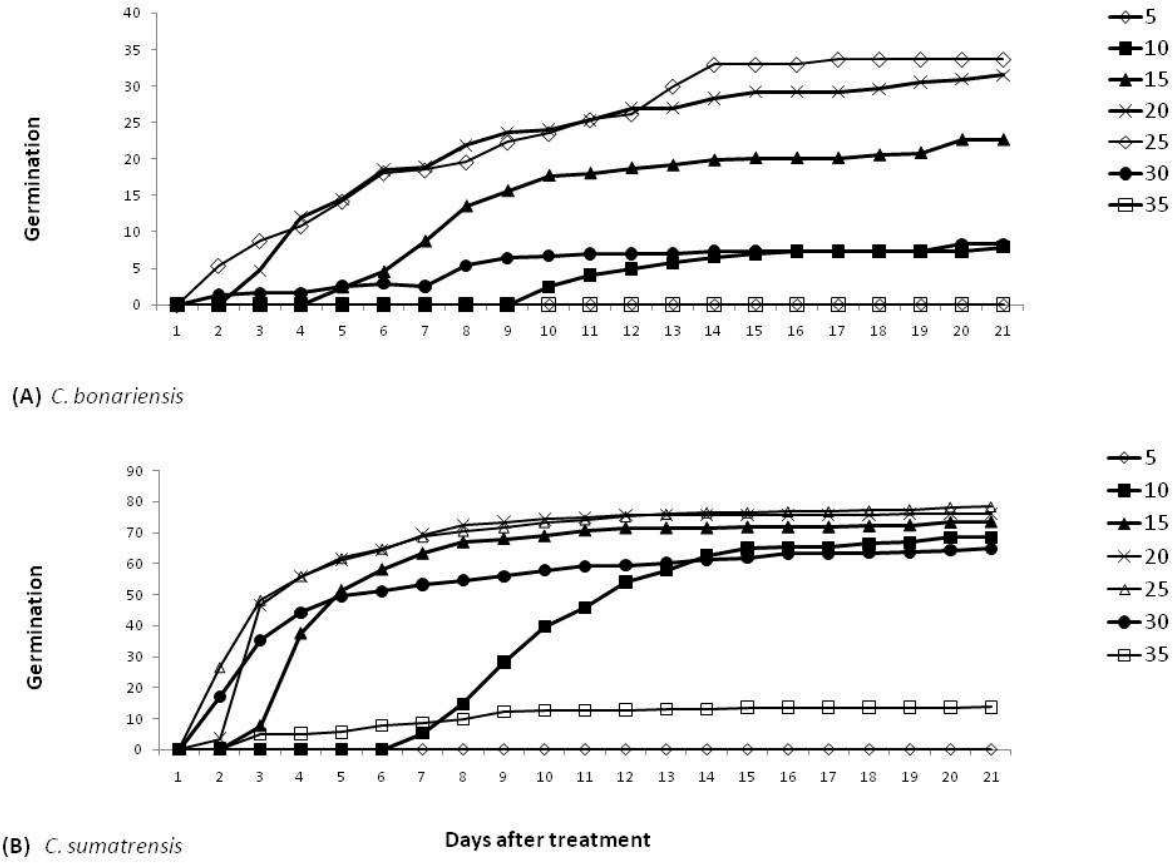

Figure 3.2 Cumulative germination under varying constant temperatures, in degrees celcius, for (A) *C. bonariensis* and (B) *C. sumatrensis* over 21 day treatment period.

Shading effects on germination

Analysis of variance returned significant species and shading main effects (Table 3.2). Dunnett multiple comparison, using 0% shade as the control, showed that shading up to 70% had little or no impact on germination of either species, whereas at 90% shade germination means for both species were significantly reduced compared with the control (Figure 3.3). The lack of germination under full shading (dark) for either species contrasts to the dominant *Conyza* species in the United States of America, *C. canadensis*, which had 15% germination in darkness with a day/night temperature regime of 24/20^{o}C (Nandula *et al.* 2006). Overall, shade levels up to 90% reduced the germination of *C. bonariensis* more than *C. sumatrensis*.

These findings may help explain field observations of *C. bonariensis* in uncultivated cropping fallows and *C. sumatrensis* on roadsides competing with grasses and other plants. However, these results do not fully explain the relative lack of *C. sumatrensis* in fallow situations given that its germination was high also in full light. Other ecological factors, such as its lack of dormancy in fresh seed and its longer time to flowering (Thebaud and Abbott 1995), may disadvantage it in an annual cropping system. The former will mean that seedlings may all germinate synchronously and thereby be easily controlled, while the latter may be a disadvantage for *C. sumatrensis* because of failure to complete its life cycle before a crop is sown. It is possible that the cooling effect of shading may also suppress germination of *C. bonariensis* more than *C. sumatrensis* (Figure 3.1). While low temperatures (10 to 15^{o}C) delayed the germination of seeds of both *Conyza* species (Figure 3.2) as well as reducing the total germination percentage, shading had little impact on the speed with which germination occurred (Figure 3.4), just the overall germination amount.

These results on shading support its use as a control method to assist with the integrated management of *C. bonariensis*. Agronomic practices to utilise shade could include tillage to bury seed, as well as stubble retention, covering and competing crops. Compared with full light, under a 90% shade coverage, the germination rate of *C. bonariensis* seeds was reduced from 57.3% (±7.4%) to 10.5% (±3.6%) and to zero germination under full shade. Donald (1963) reported that almost 100% light interception can be obtain under pastures and crops and Sindel (1989) reported 97.2% light intercepted under forage crop of *Lolium multiflorum* cv. Concord at the density of 280 plants m^{-2} and 30 cm tall.

Table 3.2 Analysis of variance results for shading (r^2=0.622).

Source	df	MS	F	p
Corrected Model	9	0.550	12.791	<0.05
Intercept	1	12.272	285.414	<0.05
Species	1	0.399	9.288	<0.05
Shading	4	1.090	25.340	<0.05
Species*Shading	4	0.048	1.118	0.355
Error	70	0.043		
Total	80			
Corrected Total	79			

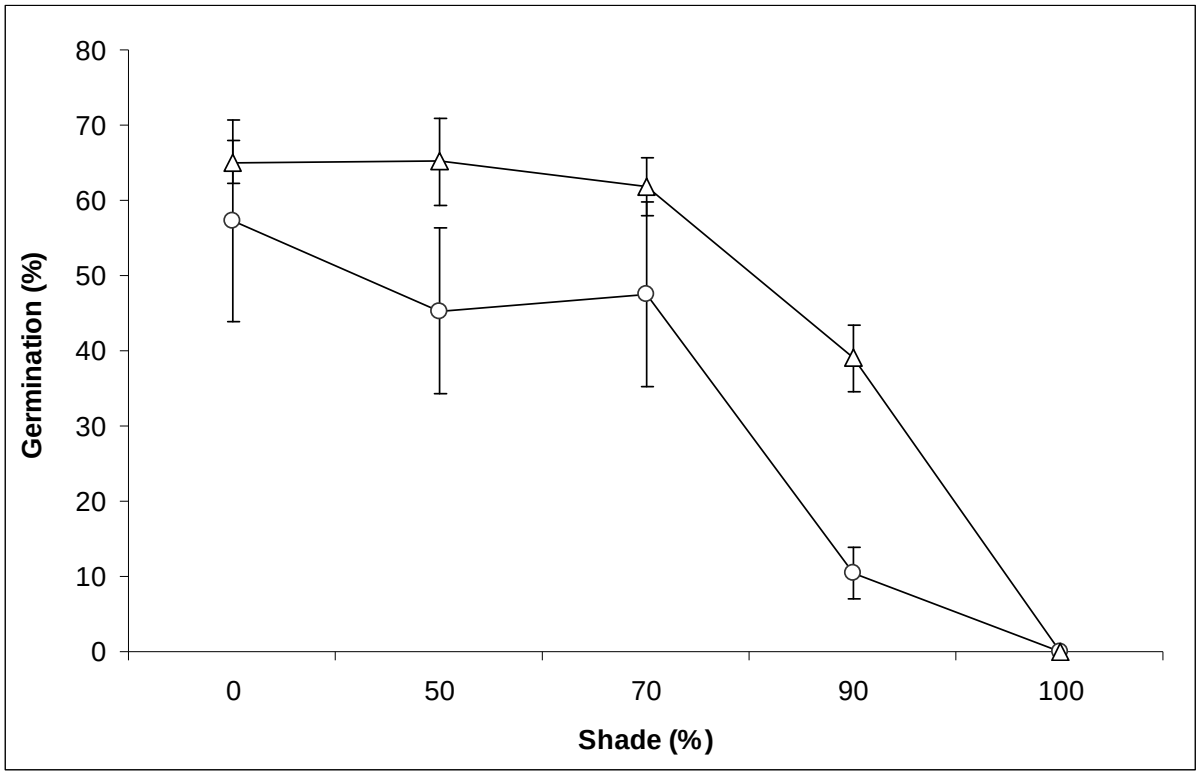

Figure 3.3 Effect of shade on germination after a 21 day treatment period for *C. bonariensis* (○) and *C. sumatrensis* (Δ) with standard error bars (⌶) at a constant 25°C.

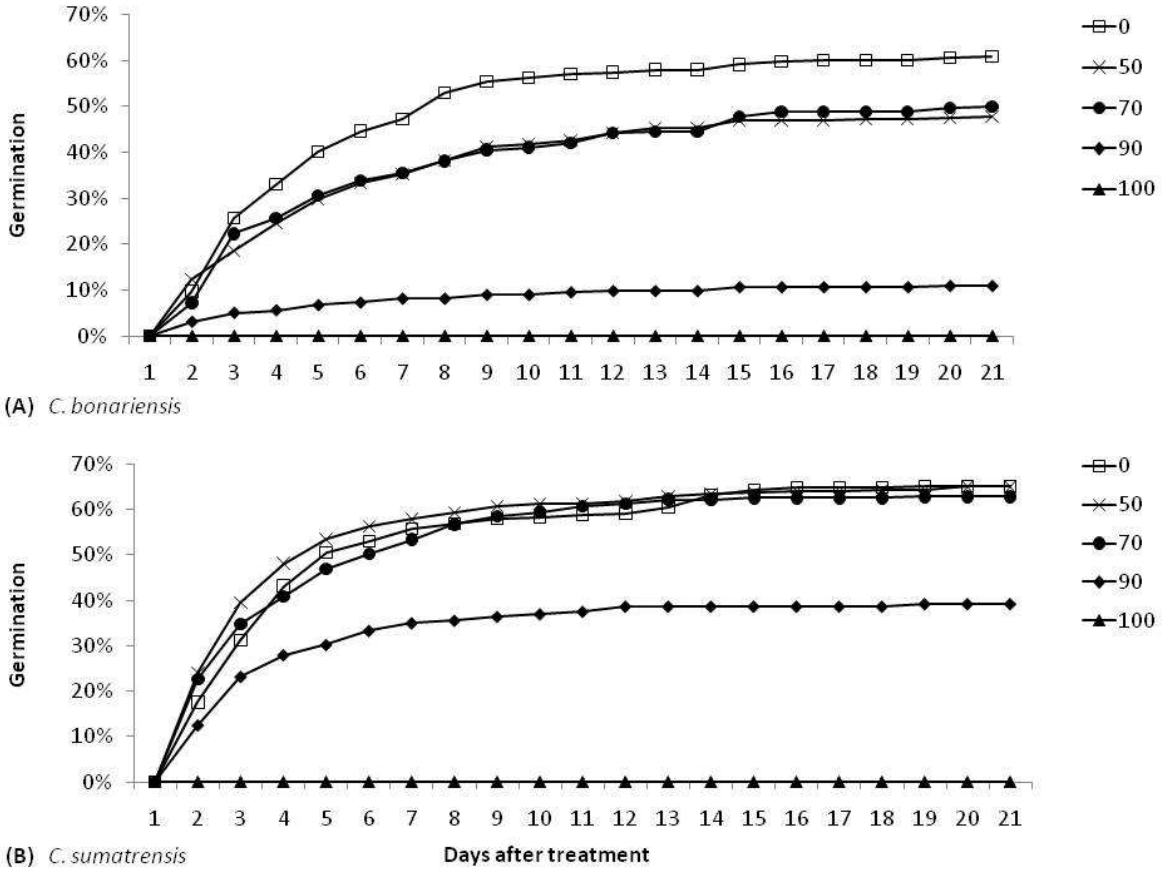

Figure 3.4 Cumulative germination under varying levels of shade of (A) *C. bonariensis* and (B) *C. sumatrensis* over 21 day treatment period.

Moisture effects on germination

Analysis of variance returned significance for species, moisture level and the interaction of the two (Table 3.3). Tukey multiple comparison showed that germination means of all treatment combinations comparing the two species were significantly different except *C. bonariensis* at -0.6 MPa with *C. sumatrensis* at -0.2, -0.4 and -0.6 MPa, and *C. bonariensis* at -0.8 MPa with *C. sumatrensis* at -0.8 MPa. Germination decreased from 77.6% (±3.0%) to 11.0% (±2.3%) and 51.1% (±4.0%) to 16.0% (±1.9%) for *C. bonariensis* and *C. sumatrensis* respectively, as osmotic potential decreased from -0.2 to -0.8 MPa (Figure 3.5). The most rapid decline in germination for *C. sumatrensis* occurred at moisture potentials below -0.6 MPa while for *C. bonariensis* the decline occurred below -0.4 MPa suggesting that germination of *C. bonariensis* is more sensitive to declining moisture levels than

C. sumatrensis, again indicating that *C. bonariensis* may be more seasonally restricted to wetter periods than *C. sumatrensis*. Germination was completely stopped at osmotic potentials of -1.0 MPa or less for both species. Nandula *et al.* (2006) reported only 2% germination of *C. canadensis* at -0.8 MPa compared with 25% at 0 MPa. Germination of all these *Conyza* species at -0.8 MPa indicates a degree of water stress tolerance – adding to their invasive abilities.

Table 3.3 Analysis of variance results for moisture (r^2=0.953).

Source	df	MS	F	p
Corrected Model	15	0.635	152.137	<0.05
Intercept	1	6.370	1525.329	<0.05
Species	1	0.132	31.684	<0.05
Moisture	7	1.277	305.660	<0.05
Species*Moisture	7	0.066	15.822	<0.05
Error	112	0.004		
Total	128			
Corrected Total	127			

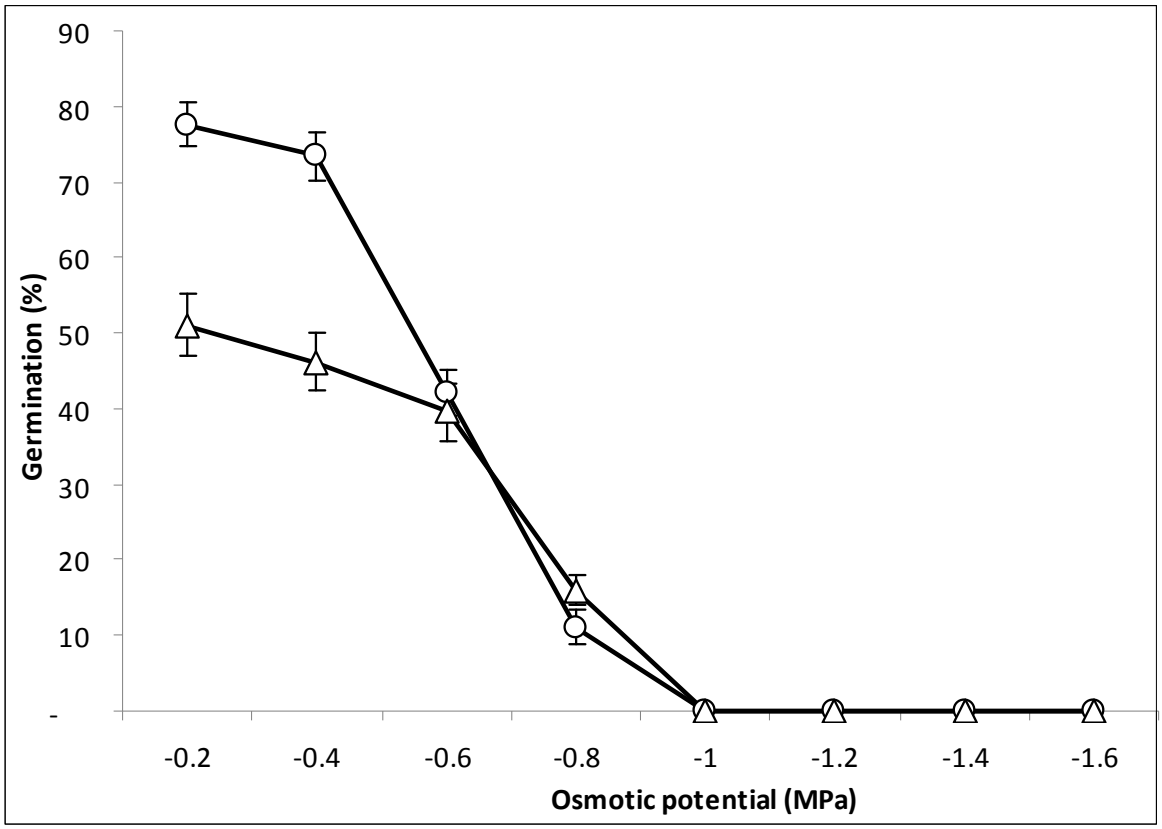

Figure 3.5 Effect of osmotic potential on germination of *C. bonariensis* (○) and *C. sumatrensis* (Δ) with standard error bars (⌶) at 25°C constant temperature and light.

General discussion

Although *C. bonariensis* and *C. sumatrensis* are 90% similar according to isozyme analysis (Thebaud and Abbott 1995), there are considerable differences in the germination response of the two species to environmental factors. *Conyza sumatrensis* may not currently be as important in cropping systems in Australia due to several ecological factors, such as lack of fresh seed dormancy and, compared with *C. bonariensis*, a relative susceptibility to glyphosate (Walker and Robinson 2008), which is the most commonly used herbicide in cropping fallows.

Further investigations are needed on the effect of crop stubble and soil types on the emergence of *Conyza* species to better understand the shift of *C. bonariensis* into minimum tillage systems in Australia. The effect of growth and fecundity, based on the season of

emergence, also remains a research gap and would assist with more targeted control measures.

CONCLUSIONS

These experiments showed that:

- Germination peaked at 25^{o}C for both species;
- Light was found to be essential for germination in both species;
- There was a c. 80% reduction in *C. bonariensis* germination with 90% shade compared with full light; and
- Both species were capable of germination in osmotic potentials of up to -0.8 MPa.

Chapter Four: Emergence

CHAPTER FOUR

EMERGENCE

INTRODUCTION

Conyza bonariensis (L.) Cronquist has been reported to occur on most soil types (Cunningham *et al.* 1981). There is limited information however, on the effects of different soil types and the influences of stubble on *C. bonariensis* emergence. This chapter reports on the effect of different soil types and different stubble levels on the emergence of *C. bonariensis* and *C. sumatrensis* (Retz.) E. Walker, which could assist in better understanding their habitat preferences.

Seedling recruitment, a crucial step in establishing a plant into a community, is the establishment of a seedling from a seed through germination and emergence (Harper 1977). This process is limited by two key factors: the availability of seed and the availability of a favourable microsite (soil conditions surrounding the seed). Each species has specific microsite conditions which contain a stimulus to break dormancy (if applicable), conditions necessary for emergence to occur and ongoing resources and protection from pests and diseases. Having a greater understanding of microsite requirements for weed species can assist with population prediction and possible control strategies.

Cropping systems which eliminate pre-planting tillage can experience increases in winter annual weed species which were not previously a problem (Buhler 1995). Winter annuals, like *C. bonariensis*, emerge in late summer or autumn, survive the winter, and produce seed the following spring or summer. Rapid growth early in spring can make them difficult to control with herbicides before planting summer annual crops in no tillage systems (Triplett 1985). Generally, wind dispersed species, annual and perennial grasses, perennial dicotyledonous species and volunteer crops increase and annual dicotyledonous weeds decrease in reduced tillage systems (Froud-Williams 1988; Derksen *et al.* 1994).

Tillage systems influence the periodicity of weed emergence (Bullied *et al.* 2003). Tillage affects both vertical seed distribution (Cousens and Moss 1990) and the soil conditions surrounding the seed (microsite) and there can be interactions between these. Under minimum tillage, light quality reaching the soil is altered under crop residue, and water evaporation and temperature amplitude is reduced (Oryokot *et al.* 1997).

Soil type can influence microsite conditions in a number of ways, including water holding capacity and availability, pH, nutrient availability, aggregate size and the vertical distribution of seed. Sodosols, chromosols, ferrosols and vertosols all occur within cropping areas of the northern cropping region (McKenzie 1998; Dalal and Chan 2001), although cracking clay soils, or vertosols, are the most common soil types of the cotton growing areas within the northern cropping region (McKenzie 1998).

In Australia, *C. bonariensis* is the most prevalent *Conyza* species within dry-land cropping systems and the increased incidence of this weed has increased fallow weed control costs (Wu *et al.* 2007). Limited results are available on the effect of soil type and stubble on emergence for *C. bonariensis* and *C. sumatrensis*. This chapter explores the effect of different soil types and stubble levels on the emergence of *C. bonariensis*, compared with *C. sumatrensis,* which is predominantly a weed of roadside and grazing systems in Australia and not generally a problem in fallows and crops. The study will provide a greater understanding of the microsite conditions required for *Conyza* species seeds to emerge and demonstrate any differences in responses between the two species which might explain their distribution and occurrence in Australia.

METHODS

The experiment was a randomised complete factorial comprising of two species (*C. bonariensis* and *C. sumatrensis*), four soil types (dark vertosol, grey vertosol, red vertosol and sandy loam) and three stubble levels (0, 1.8 t ha^{-1}, 3.6 t ha^{-1}). Each treatment was replicated four times, using 50 seeds per treatment replicate.

Seed and soil collection and analysis

Conyza bonariensis and *C. sumatrensis* seeds were collected from the same roadside site 50km east from Moree in northern New South Wales (29°32' S, 150°14' E) in January 2008. The capitula of 50 sampled plants, for each species, were placed into a paper bag and gently shaken to remove mature seeds. Seeds were air dried and stored at room temperature in the dark prior to experimentation (February 2009). The red vertosol was collected from Dorrigo, and all other soils from Armidale, New South Wales. The soils were sampled from the 0 to 20 cm layer, air dried and sieved to 2 mm. Soils were analysed for pH (1:5 water), Cation Exchange Capacity (CEC) (sum of the exchangeable magnesium (Mg), calcium (Ca), sodium (Na), potassium (K), hydrogen (H) and aluminium (Al)), total carbon (C) and nitrogen (N), organic matter (calculated as total carbon (C)% x 1.75), phosphorus (Colwell) and soil texture (clay/silt/sand composition) at the Environmental Analysis Laboratory (Lismore, Australia) using Albrecht methods.

Soil analysis results are outlined in Table 4.3. Lucerne (*Medicago sativa* L.) hay was used for the stubble treatment. The stubble was dried at 60°C for 24 hrs prior to fine grinding and analysed for nutrients and pH (1:5 water). The stubble analysis showed nutrient composition of nitrogen (2.41%), phosphorus (0.24%), potassium (1.80%), carbon (45.40%), a pH of 6.6 (1:5 water) and a CEC of 8.1 dS m^{-1}. Seed viability was assessed using tetrazolium, 0.5% 2,3-5-triphenyltetrazolium chloride (TTC) (Freeland 1976). To confirm viability using the TTC test, the solution was poured into Petri-dishes with seeds (four replicates, each of 100 seeds) and left for five hours at room temperature. Seeds which turned red in colour were classed as viable. Initial seed viability results for *C. bonariensis* and *C. sumatrensis* were 78.9% (±6.7%) and 83.1% (±5.3%) respectively.

Experimentation

Soil was placed into polyethylene pots of 15 cm diameter, up to a level of 2 cm below the top of each pot and subsequently watered fully to prevent run-off. Fifty seeds of the relevant *Conyza* species were sown on the soil surface of each pot. The stubble treatments were achieved by placing chopped stubble (c. 4 cm) at the rate of 1.8 t ha^{-1} and 3.6 t ha^{-1} on

top of the seeds. The weight of stubble for each respective treatment was equal; however, the stubble was chopped to allow improved consistency in the layering and arrangement of the stubble in the pot. The pots were randomly distributed in a glasshouse at the University of New England, Armidale, Australia and watered daily, from the surface, throughout the 21 day treatment period.

At the end of the treatment period, the stubble was carefully removed and emergence was counted. Emerged seeds were defined as those with visible cotyledons. The glasshouse temperature was maintained between 20 and 25^{o}C. To determine the shade level created in the microsite below the different stubble levels, clear plastic cling wrap was placed 2 cm from the top of pots, then the appropriate stubble levels were placed on top of the cling wrap and the bottom of the pot was removed to allow access of the photometer. Four replicates for each of the three stubble levels were used to calculate the shading levels and the results of the 1.8 t ha^{-1} and 3.6 t ha^{-1} stubble levels were expressed as a proportion of the cling wrap with no stubble results. The shading results were 42.25% (±2.13%) shade under the 1.8 t ha^{-1} stubble and 86.31% (±1.74%) under 3.6 t ha^{-1}.

Statistical analysis

Emergence was calculated as the percentage of seeds emerged during the treatment period in each treatment. All analysis was performed using SPSS v 17.0. The data set was tested for homogeneity of variance (Levene's test) with no transformation required; however, two observations were discarded as outliers (Box Plot test). A three-factor fixed effect ANOVA (2*4*3) was performed and separate two-way ANOVAs were performed for each species. All ANOVAs were performed to a confidence level of α=0.05. Where significance was returned, a Fisher's Least Significant Difference (LSD) test was performed (α=0.05). A factor analysis, using Principal Component Analysis (PCA) extraction methods, was performed to test significance of soil properties on emergence levels. All significant differences referred to are $p<0.05$, unless stated otherwise, and all means are stated with standard errors (±S.E.).

RESULTS

Generally, for both species, emergence was lowest under heavy stubble (3.6 t ha^{-1}), although there was either no significant difference in emergence between zero and light stubble (1.8 t ha^{-1}), or light stubble (1.8 t ha^{-1}) was more favourable for emergence (Figure 4.1). Emergence levels of *C. bonariensis* were similar with zero stubble and 3.6 t ha^{-1} of stubble (Figure 4.1).

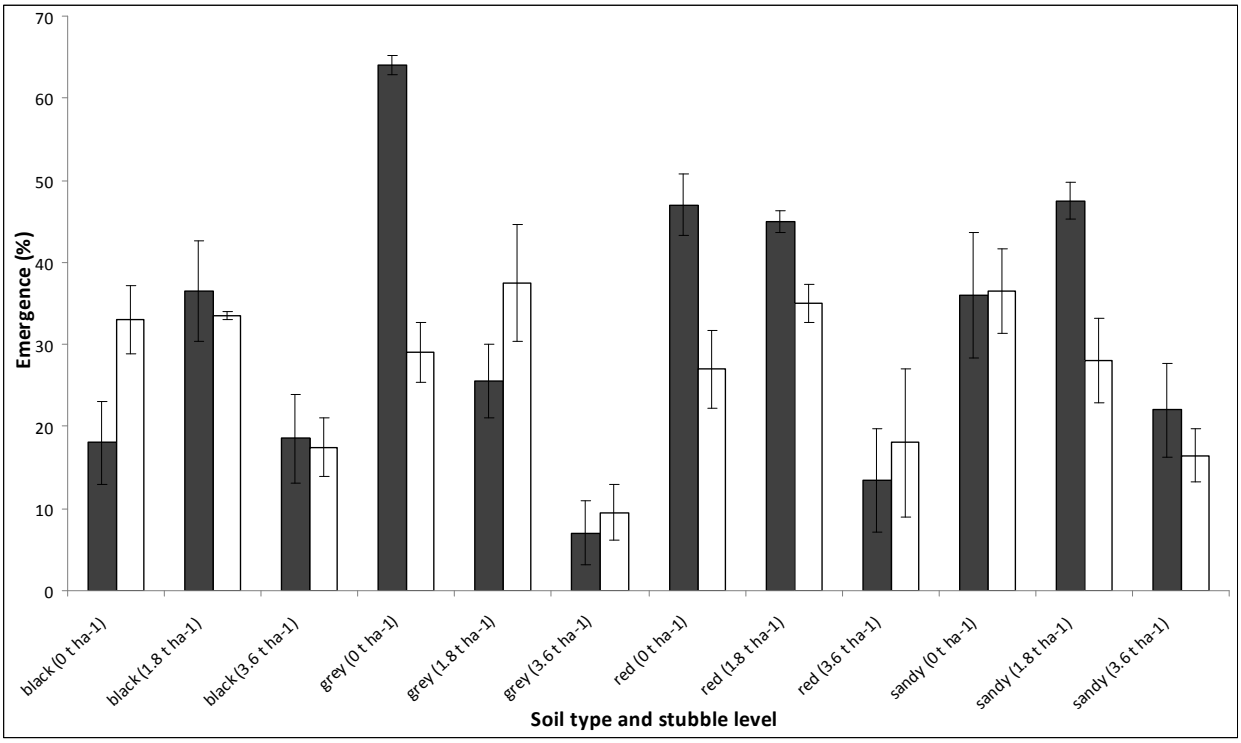

Figure 4.1 Emergence levels for *C. bonariensis* (■) and *C. sumatrensis* (□) in four soil types and three stubble levels at the end of 21 day treatment period. Values are means (n=4) with standard error (⌶).

The three-way ANOVA returned significant differences in stubble and species main effects, and the interactions soil*stubble and soil*stubble*species (Table 4.1). Through analysis of the two-way ANOVAs for each species (Table 4.2), the three-way significant interaction of soil and stubble was found to be due to the soil*stubble interaction varying between the

two species. The soil and stubble interaction was significant in *C. bonariensis* and not significant in *C. sumatrensis*. In other words, the effect of stubble for *C. sumatrensis* was quite consistent across the four soil types, whereas for *C. bonariensis* the effect of stubble varied across soil types. Soil type was significant when interacting with stubble and species*stubble. *Conyza bonariensis* emerged at higher levels than *C. sumatrensis* (31.30% ±2.66% and 26.75% ±1.78% respectively) overall, but the specifics depended on interactions with soil and stubble levels.

Table 4.1 Results of three-way analysis of variance for emergence levels (r^2=0.764).

Source	df	MS	F	p
Corrected Model	23	0.068	7.293	<0.05
Intercept	1	7.980	851.918	<0.05
Soil	3	0.012	1.313	0.277
Stubble	2	0.459	48.951	<0.05
Species	1	0.057	6.129	<0.05
Soil*Stubble	6	0.035	3.708	<0.05
Soil*Species	3	0.019	2.063	0.113
Stubble*Species	2	0.019	2.055	0.136
Soil*Stubble*Species	6	0.054	5.775	<0.05
Error	70	0.009		
Total	94			
Corrected Total	93			

A two-way ANOVA performed for each species showed *C. bonariensis* to have the main effects, soil and stubble, and the interaction to be significant (Table 4.2). The comparison of treatments using the LSD test showed the differences within *C. bonariensis* were due to the black vertosol emergence levels being significantly less than the red vertosol and sandy loam. In regards to the effect of stubble in *C. bonariensis*, emergence was lower under the high rate (3.6 t ha^{-1}) compared with the 0 and 1.8 t ha^{-1} rates. There was a higher emergence with 1.8 t ha^{-1} of stubble, compared with 0 stubble, for *C. bonariensis* in the black vertosol and sandy loam substrates – accounting for the significant soil*stubble interaction. *Conyza sumatrensis* significance within the stubble treatments (Table 4.2) was due to lower emergence in the 3.6 t ha^{-1} rate compared with the 0 and 1.8 t ha^{-1} rates. There was no significant effect of soil type or soil*stubble interaction in *C. sumatrensis* emergence (Table 4.2).

Table 4.2 Results of two-way analysis of variance for (A) *C. bonariensis* (r^2=0.799) and (B) *C. sumatrensis* (r^2=0.526).

(A) *C. bonariensis*

Source	SS	df	MS	F	p
Corrected Model	1.137	11	0.103	11.898	<0.05
Intercept	4.335	1	4.335	498.985	<0.05
Soil	0.110	3	0.037	4.228	<0.05
Stubble	0.600	2	0.300	34.507	<0.05
Soil*Stubble	0.431	6	0.072	8.260	<0.05
Error	0.287	33	0.009		
Total	5.705	45			
Corrected Total	1.424	44			

(B) *C. sumatrensis*

Source	SS	df	MS	F	p
Corrected Model	0.374	11	0.034	3.631	<0.05
Intercept	3.435	1	3.435	366.912	<0.05
Soil	0.004	3	0.001	0.155	0.925
Stubble	0.314	2	0.157	16.780	<0.05
Soil*Stubble	0.055	6	0.009	0.986	0.449
Error	0.337	36			
Total	4.146	48			
Corrected Total	0.711	47			

Conyza seedlings emerged in all treatments. The highest emergence recorded for *C. bonariensis* was 64.0% (±1.0%) with zero stubble on a grey vertosol substrate, and the lowest, 7.0% (±3.9%), under stubble (3.6 t ha^{-1}) with grey vertosol substrate (Figure 4.1). *Conyza sumatrensis* reached the highest emergence levels of 37.5% (±7.1%) with stubble (1.8 t ha^{-1}) on a grey vertosol and the lowest of 9.5% (±3.4%) with stubble (3.6 t ha^{-1}) on a grey vertosol (Figure 4.1).

Table 4.3 Soil analysis results of the four soil types.

Feature	Black vertosol	Grey vertosol	Red vertosol	Sandy loam
pH (1:5 water)	5.05	6.24	4.74	5.44
Organic matter (%)	3.47	1.03	9.0	1.13
Nitrate (ppm)	102.5	1.0	53.1	30.5
Phosphorus (ppm)	96	4	25	10
N:P	1.07	0.25	2.12	3.05
Ammonium (ppm)	6.5	3.9	42.0	5.6
Total C (%)	1.98	0.59	5.14	0.65
Total N (%)	0.20	0.05	0.44	0.06
C:N	10.1	11.4	11.7	10.6
Calcium (%)*	49.8	64.6	47.7	49.8
Potassium (%)*	1.9	4.8	6.0	6.5
Magnesium (%)*	46.1	25.9	8.1	27.8
Sodium (%)*	1.1	3.2	2.7	3.9
Aluminium (%)*	1.1	1.5	35.3	6.5
Hydrogen (%)*	0.0	0.0	0.1	5.5
CEC (cmol kg^{-1})	35.7	3.0	4.7	2.9
Ca:Mg	1.1	2.5	5.9	1.8
Clay (%)	48.3	51.6	43.7	12.4
Silt (%)	23.6	21.4	25.8	29.6
Sand (%)	28.1	27.0	30.5	58.0

*Figures are percent base saturation

The factor analysis to investigate any effects of soil characteristics on emergence showed that N:P, CEC, K and Mg were significantly correlated to emergence levels. The red vertosol and sandy loam had a N:P of more than two and three times, respectively, to that of the

black vertosol and they both had higher emergence levels. Furthermore, the substrate with the lowest emergence levels (black vertosol) had the highest cation exchange capacity and magnesium levels and the lowest potassium levels.

DISCUSSION

This chapter set out to better understand the effect of different soil types and stubble loads on the emergence of *C. bonariensis* and *C. sumatrensis*. Furthermore, it set out to better understand the ecological reasons for the success of *C. bonariensis* in Australia's northern cropping region, particularly minimum tillage systems. The results showed that for *C. bonariensis*, soil type and stubble main effects and the interaction was significant. This was not the case for *C. sumatrensis,* with only stubble significant.

The amount of light reaching the microsite, as affected by stubble, will influence emergence levels. Differing levels of plant residues alter light transmission for microsites, with crop residue reducing shortwave radiation transmission to the soil. There was a 63% reduction in *C. bonariensis* emergence at 3.6 t ha^{-1} of stubble, when compared with no stubble. This stubble rate provided a shade environment of 86%. Decreased emergence under the 3.6 t ha^{-1} of stubble could also be attributed to allelopathic compounds from the lucerne, namely saponins (Shany *et al.* 1970). However, *C. bonariensis* emergence on the black vertosol and sandy loam substrates was increased with 1.8 t ha^{-1} of stubble compared with no stubble. This was likely due to an increase in soil moisture, as crop residue can reduce water evaporation and increase infiltration (Bond and Willis 1969).

Differences in soil temperature, as affected by stubble, will also influence emergence levels. The soil maximum temperature and daily soil temperature amplitude of the soil is reduced by the presence of stubble (Nyborg and Malhi 1989; Blevins and Frye 1993; Oryokot *et al.* 1997). Blevins and Frye (1993) reported a reduction in soil temperature of 3.2 to 3.8^{o}C under crop residue compared with no residue. With *C. bonariensis* being a temperate climate plant, the microsite beneath stubble permits emergence during warmer periods. The reduction in soil temperature by stubble may help explain the increased emergence with stubble (1.8 t ha^{-1}) on the sandy loam substrate, as sandy soils warm up quicker than clay

soils and the soil temperatures without stubble could have exceeded the optimal germination temperature.

Humidity conditions in a microsite below crop residue will also influence emergence of *Conyza* species. The greater humidity under stubble environment (Bond and Willis 1969; Blevins and Frye 1993) will flatten the pappus bristles of *C. bonariensis* and *C. sumatrensis* seeds (Chapter 6) and therefore potentially provide a greater soil/seed contact area to promote germination.

Once emerged in a stubble environment, the survival of *Conyza* species is positively influenced by the provision of protection during dry spring conditions (Prieur-Richard *et al.* 2002), and also cold winter conditions (Regehr and Bazzaz 1979). A higher emergence rate under litter cover compared with full light has been shown in *C. bonariensis* (Prieur-Richard *et al.* 2002); this could be due to more favourable temperature or moisture conditions of the microsite.

Differences in the species response to soil type and stubble were found. *Conyza sumatrensis* emergence was less affected by soil type compared with *C. bonariensis* and had no difference in emergence between the 0 and 1.8 t ha^{-1} stubble, whereas *C. bonariensis* achieved highest emergence under zero stubble in the grey vertosol soil. Although emergence levels of the two *Conyza* species were low under the 3.6 t ha^{-1} stubble, given the prolific seed production of the species (Chapter 5), they have the capacity to build up seed banks in a short time. Overall, *C. sumatrensis* is less affected by the shaded microsite at the 3.6 t ha^{-1} stubble rate when contrasted to *C. bonariensis*. This result is supported by the germination results (Chapter 3), which showed *C. sumatrensis* to be more shade tolerant. The congeneric *C. canadensis* has been reported to have emergence rates reduced by 77% with a corn or cotton crop residue compared with no prior crop (Main *et al.* 2006).

Conyza species occupy disturbed habitats (Everett 1990; Thebaud and Abbott 1995) and both species experienced the highest emergence levels on a substrate (grey vertosol) with low nitrogen, low phosphorus, low nitrogen to phosphorus ratio and low organic matter levels (Table 4.3). Factor analysis on *C. bonariensis* showed a preference for a lower N:P environment. The N:P ratio is an important explanatory variable for determining a gradient of ruderality (a plants ability to survive in disturbed conditions) based on soil characteristics (Fanelli *et al.* 2008).

An unirrigated, field based study found that *C. bonariensis* had no emergence on a heavy black vertosol soil (Wu *et al.* 2007). The regular watering of the treatments described in this thesis would have reduced the cracking incidence of the vertosols and hence reduced the chance of the seeds moving below the soil surface through cracks. *Conyza bonariensis* is photoblastic (Zinzolker *et al.* 1985; Wu *et al.* 2007; Chapter 3), and therefore if the seeds are moved below the surface, germination is reduced due to lack of light.

Stubble treatment differences support shade as a control to assist in an integrated weed management approach with *C. bonariensis*. Agronomic practices involving shade could include tillage to bury seed. Discing in spring or autumn has been successful in controlling *C. canadensis* (L.) Cronquist (Brown and Whitwell 1988), cover and competing crops can also be used.

Although *C. bonariensis* emerged from the surface of all soil types, the black vertosol emergence rates were significantly less than the red vertosol and sandy loam, in particular when there was no stubble cover (Figure 4.1). The increase in emergence of *C. bonariensis* on the sandy loam under light stubble could be due to the reduction of water evaporation.

CONCLUSIONS

This experiment showed that:

- The response of soil type and stubble on emergence of *C. bonariensis* and *C. sumatrensis* differed between the two species;
- Soil type influenced emergence in *C. bonariensis*, with the black vertosol emergence levels significantly less that the red vertosol and sandy loam; and
- Soil characteristics found to affect *C. bonariensis* emergence were N:P, CEC, K and Mg.

Chapter Five: Growth and Development

CHAPTER FIVE

GROWTH AND DEVELOPMENT

INTRODUCTION

Studies on weed life cycles have been reported by numerous authors as important for effective long-term weed control (Finnerty and Klingman 1962; Ghersa and Holt 1995; Bhowmik 1997; Liebman and Gallandt 1997; Mortensen *et al.* 2000; Mohler 2001). Increasing ecological knowledge of weeds provides a greater understanding of the interference mechanisms, expands crop loss prevention techniques and leads to more effective long-term management strategies (Uscanga-Mortera *et al.* 2007). Simulation of weed phenological development is fundamental in the development of mechanistic weed-crop models (Deen *et al.* 1998). Knowing the potential of seed production, for example, provides an opportunity for predicting forthcoming weed populations (Uscanga-Mortera *et al.* 2007). Accurate predictions of shoot biomass and fecundity are critical in understanding weed population dynamics (Swanton and Murphy 1996). Weed management strategies which include herbicide use, depend on an understanding of weed seedling growth rates for effective timing of herbicide control (Horak and Loughin 2000).

Conyza bonariensis (L.) Cronquist is reported to be capable of emerging all-year-round and follows a winter or summer annual life cycle (Wu 2007; Wu *et al.* 2007). It has also been reported as a biennial weed (Prieur-Richard *et al.* 2000). In northern New South Wales and southern Queensland, emergence is predominantly in autumn and early winter, forming a basal rosette stage over winter and producing seeds in the following spring or summer. A small fraction of *C. bonariensis* seedlings also emerge in spring and bolt without an overwintering growth stage (Wu *et al.* 2007). In the northern grain region of Australia, the peak growth periods of *Conyza* species are reported to occur in spring and summer (Wu *et al.* 2007). *Conyza bonariensis* is reported to bolt and flower earlier under long-day length (16 hrs) than under short-day (8 hrs) conditions (Zinzolker *et al.* 1985). There is currently no published information on the emergence cohort effect on growth and fecundity for *Conyza* species.

This chapter reports on the impact of emergence cohorts (late-autumn and spring) on growth and fecundity of *C. bonariensis*, to provide a better understanding of its population dynamics. Overwintering *C. bonariensis* plants of the late-autumn cohort seem to have certain ecological advantages. Plant growth requirements and characteristics affect a species' ability to spread, survive and increase in a population (Horak and Loughin 2000). A better understanding of *C. bonariensis* growth may assist in elucidating its success in northern New South Wales and southern Queensland cropping systems, especially minimum tillage systems.

The objectives of this chapter are to (i) determine the effect of emergence cohorts (late-autumn and spring) on the fecundity of *C. bonariensis* and *C. sumatrensis* (Retz.) E. Walker, (ii) quantify and compare the life stages for the two emergence cohorts, including growing degree days, (iii) quantify the differences in growth of overwintered and non-overwintered individuals, and (iv) compare the results of *C. bonariensis* with *C. sumatrensis*, a less important *Conyza* species in cropping systems. In the discussion I will explore possible ecological reasons for the success of *C. bonariensis* in the northern cropping region of Australia and propose possible management practices to assist with the control of this weed.

METHODS

Seed collection

To ensure similar maturation conditions, *C. bonariensis* and *C. sumatrensis* seeds were collected from the same roadside site 60 km east of Moree in Northern New South Wales, Australia in February 2009. The capitula of 30 sampled plants of each species were placed into paper bags and gently shaken to remove mature seeds, air dried and stored in closed paper bags at room temperature prior to experimentation (September 2009).

Experiment

The two *Conyza* species were grown under controlled conditions simulating both autumn and spring germinations with multiple harvests. The experimental design was a 2 x 6 x 2 mixed-design or split-plot with four replicates. The between-subject variables were cohort (with two levels - late-autumn and spring) and harvest (with six levels). The within subject variable was species, with two levels (*C. bonariensis* and *C. sumatrensis*).

The experiment was conducted in a growth chamber at the University of New England, Armidale, using 21 cm pots and a potting medium of sand:peat (3:1). Pots were filled with a sand:peat (3:1) mix, watered fully to prevent run-off and seeds were sown by scattering them onto the soil surface. Ten grams of slow release Osmocote® fertiliser (18% nitrogen, 5% phosphorus, 10% potassium and 5% sulphur) was added to each pot. Additional pots were sown for each species as backups in case of poor establishment. All treatments were initially established at 25^{o}C and constant light for a period of 28 days. After establishment, the temperature and lighting was adjusted to simulate the two different emergence cohort treatments (late-autumn and spring).

Figure 5.1 Photograph of experiment setup in growth chamber with seeds under pre-treatment germination conditions.

The simulated late-autumn emergence was achieved by three months of 18^{o}C/5^{o}C and 10 hours light, followed by three months of spring-like conditions (25^{o}C/12^{o}C and 12 hours light). The temperatures used are similar to that experienced at Moree, New South Wales – part of the northern cropping region. The simulated spring cohort was achieved by six months of 25^{o}C/12^{o}C and 12 hours light. The experiment ended when treatments had completed seed set. Throughout the treatment period, plants were watered fully to prevent run-off and observed regularly. The position of the pots within the growth chamber was changed weekly. Seedlings in each pot were thinned to one plant per pot after establishment, on a selective basis to ensure consistency of growth stage between pots.

Destructive and non-destructive measurements were made during the experiment and the timing for these are detailed in Table 5.1, with the details of measurements outlined in Table 5.2. During the destructive harvests, pots were squeezed around the sides to loosen the potting mix and roots. The plant was then removed and any soil adhering to the roots was removed by careful washing with gently running water. The plant biomass was divided into root, shoot, leaf and flower components and wet weights obtained for all using an electronic balance. The plant components were then dried to a constant weight at 80^{o}C for 48 hrs and weighed.

Table 5.1 Days after treatment (DAT) when measurements were recorded through non-destructive and destructive harvests for each emergence cohort.

Cohort	non-destructive	destructive harvest
Late-autumn	14, 42, 70, 98, 119, 133	28, 56, 84, 112, 126, 151
Spring	14, 42, 70, 102	28, 56, 84, 120

Table 5.2 A list of the morphological measurements recorded.

Measurement type	Measurements recorded
Non-destructive	plant height, number of rosette leaves, number of non-rosette leaves, rosette diameter, number of branches, number of capitula.
Destructive	as for non-destructive harvest, and taproot length, root dry weight, leaf dry weight, stem dry weight, flowers dry weight. The final destructive harvest also measured the number of seeds per capitulum.
Life stages	number of days to bolting, flowering and seed set.

Morphology measurements

The measurements taken were plant height (measured from the base of the plant to the terminal point of the main stem), rosette diameter, number of rosette leaves, number of non-rosette leaves, number of branches, number of capitula (at all stages of capitulum development), number of seeds per capitulum, root/leaf/stem/flower dry weight, taproot length, and number of days to bolting, flowering and seed set. Bolting was defined as the visible elongation of the central axis. Flowering was defined as the opening of the first capitulum. Seed maturity was when the first capitulum had completely opened and set seed.

Seeds per capitulum

The first five capitula to set seed on each plant were removed. The seeds were then removed from the capitula and the total number of seeds per capitulum were determined by counting the number of seed attachment points on the receptacle under a stereoscopic microscope. The 1 000 seed weight was also obtained for each species and cohort for use in calculations of reproductive effort, using four replicates, one from each replicate pot.

Calculations and statistical analysis

The following calculations were made in the experiment.

Growing degree days (GDD) were calculated as:

$$GDD = \sum [(T_{max} + T_{min})/2] - T_{base} \qquad [5.1]$$

Where T_{max} is the maximum daily temperature, T_{min} the minimum daily temperature and T_{base} the base temperature at which growth occurs (Forcella and Banken 1996). The base temperature calculated for each species was less than the minimum temperature used; *C. bonariensis* 4^{o}C and *C. sumatrensis* 5^{o}C (Chapter 3), and therefore did not impact on the GDD calculations. GDDs for each day were added together to obtain an accumulated GDD.

Relative growth rate (RGR) was calculated as:

$$RGR = (lnW_2 - lnW_1)(t_2 - t_1)^{-1} \quad [5.2]$$

Where lnW_2 is the natural logarithm of the final weight at time t_2 and lnW_1 is the natural logarithm of the initial weight at time t_1 (Ballard *et al.* 1996) measured in g g^{-1} d^{-1}.

The root:shoot (R:S) ratio was calculated as:

R:S = (root dry weight / above ground dry weight) [5.3]

(Grantz *et al.* 2008).

The reproductive effort was calculated as:

(Total seed weight produced / Total plant biomass)*100 [5.4]

(Harper and Ogden 1970). Total seed weight was estimated by multiplying the average seed weight by the average number of seeds per capitulum by the number of capitula per plant.

Total seed production was estimated for each plant sample by multiplying the average number of seeds per capitulum (from five measurements) by the total number of capitula on each plant.

All statistical analyses were performed using SPSS v. 18. Data were tested for homogeneity of variance using Levene's test of equality of error variances and as a result, seed production data were log-transformed. A mixed-design ANOVA was used to analyse total seed production. Reproductive effort results were analysed using ANOVA. The root:shoot ratio data were analysed using repeated measures ANOVA, with the life stages (bolting, flowering and seed set) used as the time factors. Root:shoot ratio data were tested for sphericity using Mauchly's test. The Mauchly's test statistic was not significant, therefore the condition of sphericity was assumed. A three-way ANOVA was used to analyse key growth and development features (rosette diameter, plant height, taproot length, number of branches, relative growth rate and total biomass). All significant differences referred to are $p<0.05$ and all means are presented with standard errors in parentheses (±S.E.).

RESULTS

Fecundity

Fecundity for both species was significantly higher in the late-autumn cohort than in the spring cohort, with seed production of 85 074 (±2 086) and 21 488 (±1 139) for *C. bonariensis* and *C. sumatrensis* respectively (Table 5.3). Seed production in the spring cohort was 70.3% and 63.8% of that for the autumn cohort in *C. bonariensis* and *C. sumatrensis* respectively. Both the total number of capitula and seed per capitulum were reduced for both species in the spring cohort when compared with the late-autumn cohort. Compared with *C. sumatrensis, C. bonariensis* produced more seeds from both emergence dates and had a greater number of capitula and seed per capitulum (Table 5.3). The ANOVA for seed production showed significance in the main effect of species and cohort and the interaction between the two (Table 5.4).

Table 5.3 Total fecundity in *C. bonariensis* and *C. sumatrensis* for different emergence cohorts. Values are means with standard errors in parentheses.

Cohort	No. of capitula	Seed/capitulum	Total seed
C. bonariensis			
Late-autumn	232.0 (±11.9)	366.5 (±4.4)	85 074.8 (±2 086.4)
Spring	190.0 (±10.9)	315.0 (±4.5)	59 847.5 (±1 598.7)
C. sumatrensis			
Late-autumn	166.0 (±7.7)	128.8 (±5.5)	21 488.0 (±1 138.9)
Spring	126.2 (±7.8)	109.0 (±3.4)	13 712.5 (±475.1)

Table 5.4 Results of two-way analysis of variance for seed production (r^2=0.962).

Source	df	MS	F	p
Corrected Model	3	134416.2	650.2	<0.05
Intercept	1	3183494.7	15398.2	<0.05
Species	1	372763.4	1803.0	<0.05
Cohort	1	28843.4	139.5	<0.05
Species*Cohort	1	1641.8	7.9	<0.05
Error	76	206.7		
Total	80			
Corrected Total	79			

In addition to fecundity levels, the proportion of plant biomass attributed to seeds out of the total plant biomass (reproductive effort) was determined. Reproductive effort is defined as the total amount of resources allocated to reproduction and therefore diverted from vegetative activity (Reekie and Bazzaz 1987). The highest reproductive effort was observed in overwintered *C. bonariensis* plants, with 11.8% (±0.92) of the final biomass represented by seeds (Figure 5.2). In both species, the spring cohort had significantly lower energy inputs diverted into seed production when compared with the late-autumn cohort. The ANOVA for reproductive effort showed that there was a main effect of species and cohort, with no significant interaction between the two (Table 5.5).

Table 5.5 Results of two-way analysis of variance for reproductive effort (r^2=0.947).

Source	df	MS	F	p
Corrected Model	3	0.01	71.76	<0.05
Intercept	1	0.07	620.64	<0.05
Species	1	0.02	193.79	<0.05
Cohort	1	0.00	19.06	<0.05
Species*Cohort	1	0.00	2.43	0.145
Error	12	0.00		
Total	16			
Corrected Total	15			

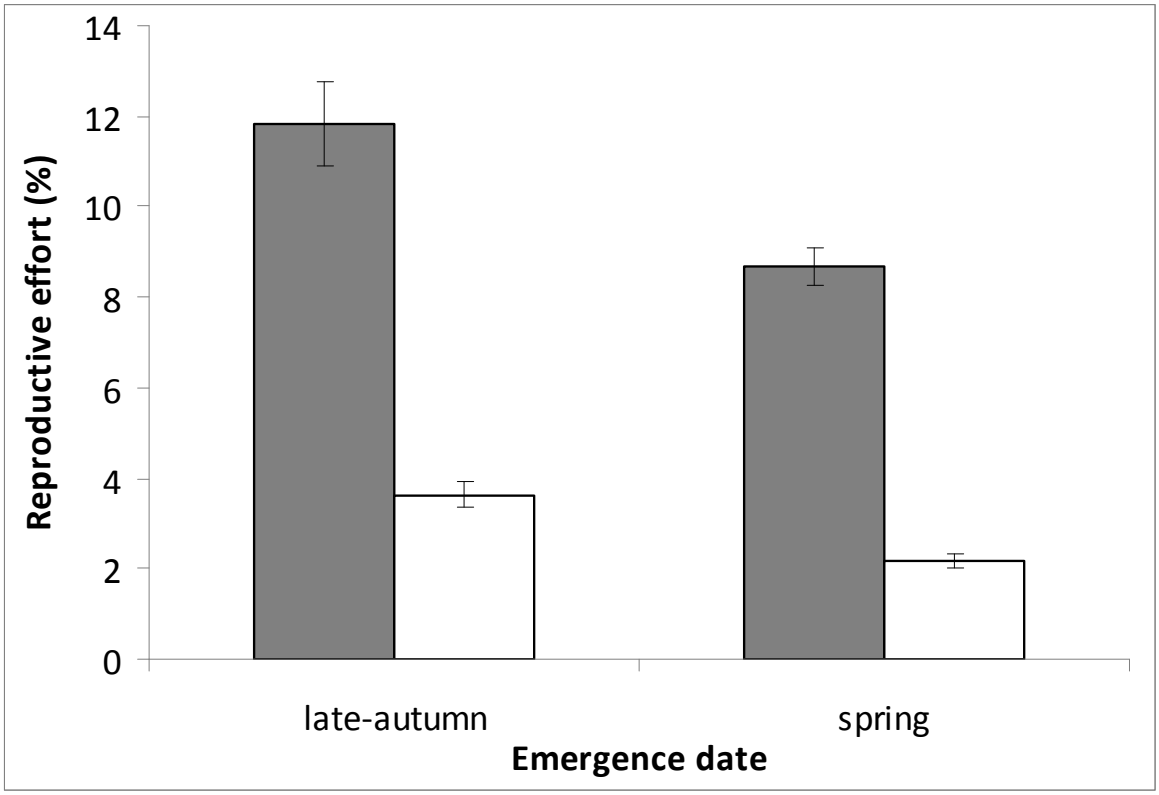

Figure 5.2 Mean reproductive effort, measured by seed dry weight as a percentage of total plant dry weight, in *C. bonariensis* (■) and *C. sumatrensis* (□) for the two emergence cohorts. Vertical bars are standard errors (⌶).

Growth and development

In addition to differences in fecundity between cohorts and species, there were also differences in growth characteristics between the two species over the different emergence times. The late-autumn emerged *C. bonariensis* plants were almost always taller, had a larger rosette diameter, a deeper taproot, a higher root:shoot ratio and a higher number of branches per plant compared with the spring emerged cohort (Table 5.7). This was the case for *C. sumatrensis* as well, except that the taproot length was not significantly different at the seed maturity stage (Table 5.8). The rosette leaves of *C. bonariensis* were all dead by the time the plant commenced setting seed. This was not the case in *C. sumatrensis*. The taproot was longer for both species in the late-autumn cohort. The maximum taproot length recorded for *C. bonariensis* was 21.3 cm and 18.2 cm for *C. sumatrensis*. Season-long growth rates for *C. bonariensis* were 0.052 (±0.001) for both cohorts and *C. sumatrensis*

0.065 (±0.001) for spring emerged and 0.067 (±0.001) for the late-autumn cohort. The three-way ANOVA results for growth and development features showed that the main effects of species, emergence cohort and life stages (bolting, flowering and seeding) were all significant (Table 5.6).

Root to shoot ratios were calculated to determine the effect in allocation to above ground and below ground biomass for overwintered plants and those emerging in spring. Late-autumn emerging *C. bonariensis* plants had a root:shoot ratio which was more than double that of the spring cohort at the flowering and seeding stages. The greatest variability in root:shoot ratio occurred in the late-autumn cohort for both species. The late-autumn cohort root:shoot ratio in both species increased until 112 DAT and then decreased (Figure 5.3). The largest change in the root:shoot ratio occurred in the late-autumn cohort between 84 and 112 DAT for both species (Figure 5.3), corresponding with bolting in each species and increases in the temperature and day light hours. In the late-autumn cohort, *C. bonariensis* root:shoot ratio increased from 0.47 (±0.02) to 0.77 (±0.03) between the 84 and 112 DAT harvest times and *C. sumatrensis* 0.56 (±0.03) to 0.87 (±0.03). The spring cohort results showed that both species had similar ratios at the initial harvest and the proportion of biomass allocated to below ground increased gradually over time (Figure 5.4). This increase in root biomass proportion was greater in *C. sumatrensis* compared with *C. bonariensis* (Figure 5.4).

Table 5.6 Summary three-way ANOVA results for growth and development features. Values are p-values, *=p<0.05 and **=p<0.01.

Source	Rosette diameter	Plant height	Taproot length	No. of branches	RGR	Biomass
Species	**	**	*	**	**	**
Cohort	**	**	**	**	**	**
Lifestage	**	**	**	**	**	**
Species*Cohort	0.74	0.06	**	0.51	**	**
Species*Lifestage	*	**	*	**	**	**
Cohort*Lifestage	0.23	0.23	0.62	*	**	**
Species*Cohort*Lifestage	*	0.16	0.75	0.51	**	*

Table 5.7 Morphology and growth measurements of *C. bonariensis* for late-autumn (LA) and spring (Sp) emerged plants. Values are means with standard errors in parentheses.

Features		**Bolting stage**	**Flowering stage**	**Seed maturity**
Rosette diameter	(LA)	18.90 (±1.63)	20.18 (±0.65)	-
(cm)	(Sp)	16.03 (±0.18)*	15.50 (±0.41)*	-
Taproot length	(LA)	16.43 (±0.72)	17.85 (±0.74)	20.15 (±0.47)
(cm)	(Sp)	13.13 (±0.36)*	15.45 (±0.35)*	17.63 (±0.44)*
No. of branches	(LA)	-	6.75 (±0.25)	10.00 (±0.41)
	(Sp)	-	5.50 (±0.65)*	7.25 (±0.48)*
Root:shoot ratio	(LA)	0.47 (±0.02)	0.79 (±0.03)	0.69 (±0.02)
	(Sp)	0.29 (±0.02)*	0.33 (±0.02)*	0.32 (±0.02)*
RGR^	(LA)	0.003 (±0.002)	0.011 (±0.001)	0.007 (±0.002)
($g\ g^{-1}\ d^{-1}$)	(Sp)	0.095 (±0.002)*	0.017 (±0.001)*	0.004 (±0.001)
Total biomass	(LA)	13.50 (±0.74)	18.28 (±0.62)	25.76 (±0.59)
(g)	(Sp)	13.37 (±0.88)	21.77 (±0.64)*	25.072 (±0.93)
Height	(LA)	10.38 (±0.95)	36.45 (±4.69)	43.62 (±3.16)
(cm)	(Sp)	12.02 (±0.52)*	31.03 (±0.54)*	36.80 (±0.56)*

^RGRs quoted represent growth between the life stages, i.e. from emergence to bolting, bolting to flowering and flowering to seed maturity.

*****represents a significant difference between cohorts for each life stage and feature.

Table 5.8 Morphology and growth measurements of *C. sumatrensis* for late-autumn (LA) and spring (Sp) emerged plants. Values are means with standard errors in parentheses.

Features		**Bolting stage**	**Flowering stage**	**Seed maturity**
Rosette diameter	(LA)	23.05 (±0.73)	28.05 (±0.60)	25.80 (±0.36)
(cm)	(Sp)	21.98 (±0.86)	25.78 (±1.18)*	22.50 (±0.96)*
Taproot length	(LA)	15.15 (±0.40)	16.93 (±0.18)	17.45 (±0.26)
(cm)	(Sp)	14.30 (±0.37)*	16.03 (±0.22)*	17.05 (±0.52)
No. of branches	(LA)	-	21.00 (±1.30)	23.50 (±0.50)
	(Sp)	-	18.00 (±0.82)*	21.00 (±1.29)*
Root:shoot ratio	(LA)	0.87 (±0.03)	0.86 (±0.03)	0.77 (±0.02)
	(Sp)	0.43 (±0.02)*	0.51 (±0.02)*	0.52 (±0.03)*
RGR^	(LA)	0.007 (±0.003)	0.011 (±0.002)	0.008 (±0.001)
($g\ g^{-1}\ d^{-1}$)	(Sp)	0.082 (±0.001)*	0.011 (±0.001)	0.011 (±0.001)*
Total biomass	(LA)	14.81 (±1.07)	22.35 (±0.54)	27.45 (±0.71)
(g)	(Sp)	15.04 (±0.34)	20.48 (±0.53)*	29.99 (±0.88)*
Height	(LA)	13.93 (±1.99)	91.28 (±1.21)	122.68 (±2.13)
(cm)	(Sp)	13.50 (±0.30)	77.53 (±2.96)*	104.18 (±4.84)*

^RGRs quoted represent growth between the life stages, i.e. from emergence to bolting, bolting to flowering and flowering to seed maturity.

*****represents a significant difference between cohorts for each life stage and feature.

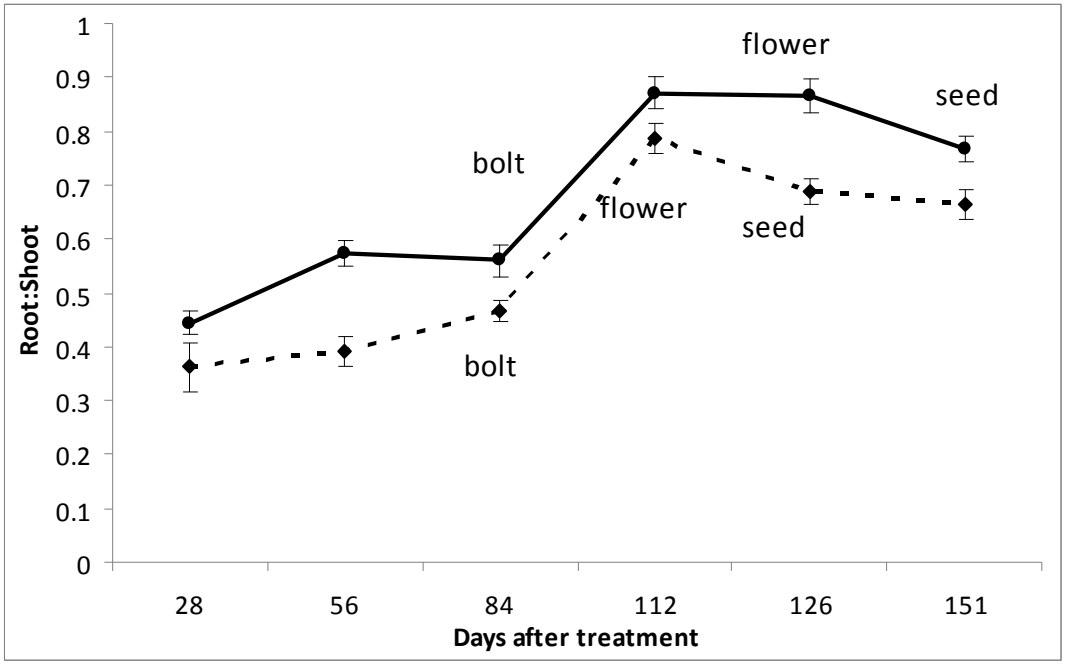

Figure 5.3 Late-autumn cohort root:shoot ratio for *C. bonariensis* (- -) and *C. sumatrensis* (__) with standard error (⌶).

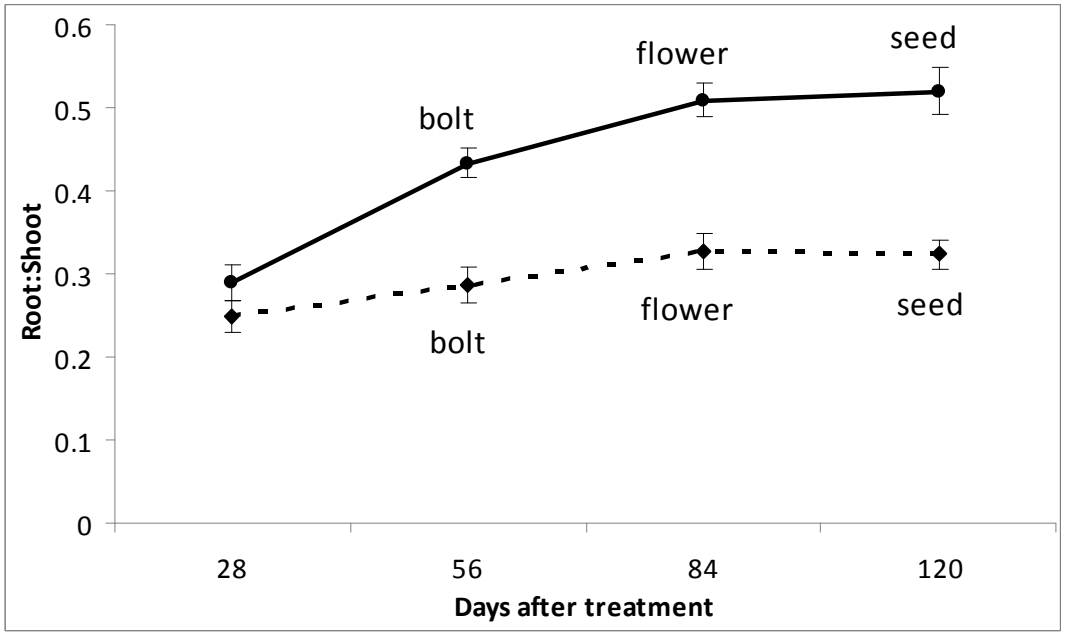

Figure 5.4 Spring cohort root:shoot ratio for *C. bonariensis* (- -) and *C. sumatrensis* (__) with standard error (⌶).

Repeated-measures ANOVA results for root:shoot ratio returned significance in the following main effects and interactions: species, cohort, time, species*cohort, and cohort*time (Table 5.9).

Table 5.9 Results of repeated-measures analysis of variance for root:shoot ratio.

Source	df	MS	F	p
Species	1	0.20	141.82	<0.05
Cohort	1	1.00	1434.65	<0.05
Time	2	0.15	67.62	<0.05
Species*Cohort	1	0.03	38.84	<0.05
Species*Time	2	0.00	0.25	0.789
Cohort*Time	2	0.06	19.20	<0.05
Species*Cohort*Time	2	0.00	0.49	0.637

The time to bolting was fastest in *C. bonariensis,* taking 8.08 (±0.06) weeks in the spring cohort (Table 5.10). *Conyza bonariensis* plants also had a shorter time between bolting and flowering, 3.92 and 3.09 weeks for the late-autumn and spring cohorts respectively. This time contrasts with 5.92 and 4.65 weeks for late-autumn and spring cohort respectively for *C. sumatrensis* (Table 5.10). The time between flowering and seed set was similar for both species and cohorts; however, *C. bonariensis* set seed earlier overall than *C. sumatrensis* (Figure 5.5). The late-autumn cohort of *C. bonariensis* set seed 3.85 weeks ahead of *C. sumatrensis* and 3.29 weeks ahead in the spring cohort. The GDDs required to reach seed maturity between the two species was significantly different. *Conyza bonariensis* required 1 636.0 (±17.7) and 1 781.7 (±16.2) GDDs for late-autumn and spring cohort respectively compared with 2 134.3 (±11.9) and 2 208.3 (±20.7) in *C. sumatrensis* (Table 5.10). The stated GDDs do not include the initial 700 GDDs (28 days at 25^{o}C) for seedling establishment.

Figure 5.5 Photograph of *C. sumatrensis* and *C. bonariensis* plants showing the faster time to reach seed maturity in *C. bonariensis*. *Conyza sumatrensis* is still developing vegetatively while *C. bonariensis* had already commenced seed set.

Table 5.10 Life stage development in weeks and growing degree days for *C. bonariensis* and *C. sumatrensis* for different emergence cohorts.

Cohort	Life stage	Time (weeks)	Growing degree days
C. bonariensis			
Late-autumn	bolting	11.39 (±0.12)	916.9 (±9.4)
	flowering	15.31 (±0.18)	1 345.5 (±23.3)
	seed maturity	17.55 (±0.14)	1 636.0 (±17.7)
Spring	bolting	8.08 (±0.06)	1 046.8 (±7.9)
	flowering	11.17 (±0.07)	1 446.3 (±8.8)
	seed maturity	13.76 (±0.12)	1 781.7 (±16.2)
C. sumatrensis			
Late-autumn	bolting	13.13 (±0.20)	1 074.3 (±22.0)
	flowering	19.05 (±0.16)	1 830.1 (±21.0)
	seed maturity	21.40 (±0.09)	2 134.3 (±11.9)
Spring	bolting	9.84 (±0.10)	1 274.1 (±13.3)
	flowering	14.49 (±0.11)	1 875.9 (±14.7)
	seed maturity	17.05 (±0.16)	2 208.3 (±20.7)

DISCUSSION

The aim in this chapter was to better understand the effect of *Conyza* species emergence time on the overall fecundity, growth and development of the species, particularly in regard to the ecological reasons for the success of *C. bonariensis* in Australia's northern cropping region and minimum tillage systems in comparison with *C. sumatrensis*.

A cohort effect on fecundity was observed in this study, with a higher fecundity reported in the late-autumn cohort for both species. To reduce *C. bonariensis* seed rain, rosettes present during winter must be effectively controlled, as overwintered *C. bonariensis* plants produce more than 42% more seeds compared with spring emerged plants. It is already known from studies of different populations of *C. bonariensis* that it has a high level of seed production (Kempen and Graf 1981; Wu *et al.* 2007) and the results from this study show that fecundity of northern New South Wales populations are similar to southern Queensland populations, with 367 seeds/capitulum in this study (northern NSW) and 400 seeds/capitulum in southern QLD samples (Wu *et al.* 2007). *Conyza bonariensis* has no dormancy requirement and so is well adapted to the mild winter of the northern cropping region. Mature seeds dispersed in summer can therefore successfully germinate in autumn/winter with adequate light and moisture. As a result, a large proportion of the *C. bonariensis* population in this region may overwinter, thereby adding more seeds into the system for future generations and adding to the success of the weed in this region. A morphological feature of *C. bonariensis* which is likely to add to its invasiveness is the high relative reproductive effort, with 11.8% of the total biomass allocated to seeds in overwintered plants. Norris (2007) reports that reproductive effort estimates expressed as seed production per plant biomass appears to offer the greatest potential for providing data that are transportable to differing situations, when used for modelling purposes. *Conyza bonariensis* diverted a higher proportion of biomass into reproductive effort, as might be expected of a fast growing cropping weed, compared with a more ruderal species, such as *C. sumatrensis*. When *C. bonariensis* was compared with *C. sumatrensis,* it had a significantly higher seed production and reproductive effort in both cohorts tested.

Generally, plant fecundity decreases when plants emerge late in the growing season (Clay *et al.* 2005); although a smaller number of viable seeds can still be enough to reinfest an area or further spread an infestation. This study reports reductions in both the number of capitula per plant and seed number per capitulum in the spring cohort compared with the late-autumn. Total seed production was reduced by 29.6% in spring emerging *C. bonariensis* plants compared with overwintered plants and a 36.2% seed reduction in *C. sumatrensis*. Regehr and Bazzaz (1979) reported reduced seed production in spring emerged *C. canadensis* (L.) Cronquist compared with overwintered individuals. There are additional survival pressures on *Conyza* species over winter, and *C. canadensis* mortality due to frost-heaving has been reported (Regehr and Bazzaz 1979). Late-autumn emerging *C. bonariensis* rosettes can also be protected by crop residues in minimum tillage systems (Regehr and Bazzaz 1979) – adding to its success in minimum tillage systems within the northern cropping region.

The need for effective control of winter *C. bonariensis* rosettes is further supported by the root:shoot ratio results. Overwintered *C. bonariensis* had a high root:shoot ratio, and at flowering the root biomass represented 44.0% (±1.0%) of total biomass. This morphological feature increases the competitive ability of *C. bonariensis* for below ground resources including moisture and nutrients, thereby, adding to its invasiveness. The root:shoot ratio at the time of stem elongation in overwintered *C. bonariensis* plants is 60% higher than spring emerged plants and therefore supports why the late-autumn cohort is more difficult to control. In both cohorts and species, there was an increased root:shoot ratio at the time of flowering, which could relate to additional nutrient requirements at this life stage. Although the highest value recorded for root:shoot in all treatments occurred in *C. sumatrensis*, *C. bonariensis* had the largest differences between the two emergence cohorts. A change in root:shoot ratio due to temperature changes has been reported for several grasses. Davidson (1969) reported that root:shoot ratio is lowest at optimum soil temperature and is higher at soil temperatures above and below the optimum for several pasture grasses. *Conyza canadensis* has been reported to have significantly different root:shoot ratio under different treatment conditions including nitrogen availability and flooded conditions. Levang-Brilz and Biondini (2002) reported root:shoot ratio of 0.59 and 1.04 in *C. canadensis* in a high and low nitrogen environment respectively, 56 days after treatment, and Stoecker *et al.* (1995) reported root dry weights of *C. canadensis* seedlings growing for 8 weeks in

flooded conditions were only 4.3% of the dry weight of the control seedlings. Cyr and Bewley (1989) described increases in overwintering plant tissues as an important storage reserve for greater spring growth capacity.

Furthering the success of *C. bonariensis* is the short time between bolting and seed production. The total time from bolting to producing seed was 6 weeks or 719 GDDs from the simulated late-autumn cohort. To illustrate this time period, a cumulative GDD graph based on the temperatures at Narrabri, NSW is provided for *C. bonariensis* (Figure 5.6) and *C. sumatrensis* (Figure 5.7). In addition to the short time between bolting and seeding, *C. bonariensis* reaches the bolting stage in 8 weeks for spring emerged plants (917 GDDs) and there is a 3 to 4 week period between bolting and flowering. *Conyza bonariensis* is reported to flower earlier in longer day light conditions (Zinzolker *et al.* 1985). However, Thebaud *et al.* (1996) report the cue for *C. bonariensis* to initiate bolting is more related to resource availability than to light. In winter annuals, their vegetative rosettes are capable of substantial photosynthesis and energy storage during winter. As a result, these plants grow rapidly in the spring and are able to pre-empt the environmental resources of the habitat (light, water, and nutrients), thereby suppressing the spring-emerging plants (Regehr and Bazzaz 1979).

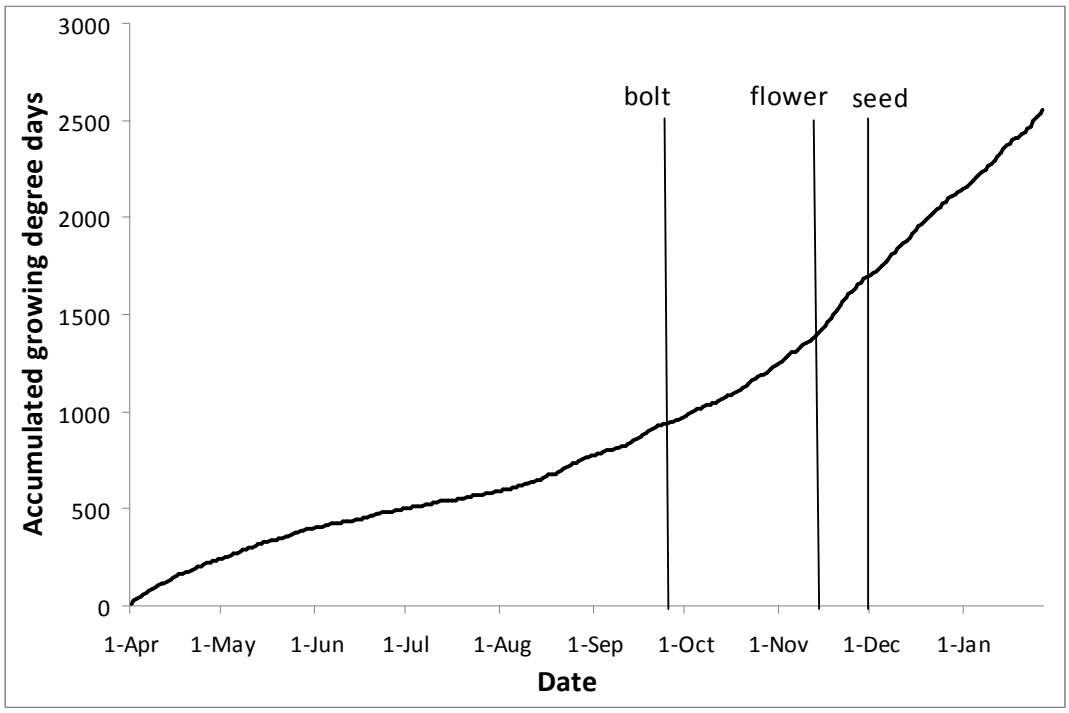

Figure 5.6 Accumulated growing degree days for Narrabri, New South Wales, from 1/04/2009 to 27/01/2010 with *C. bonariensis* bolting, flowering and seeding time based on seedlings established in late-autumn.

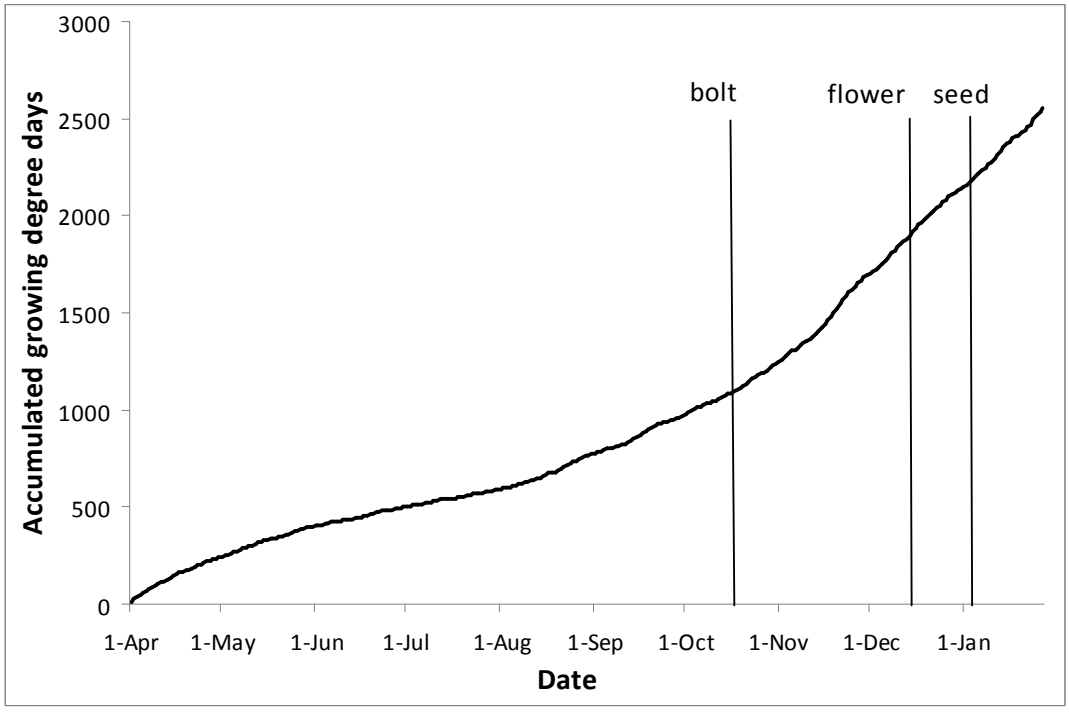

Figure 5.7 Accumulated growing degree days for Narrabri, New South Wales, from 1/04/2009 to 27/01/2010 with *C. sumatrensis* bolting, flowering and seeding time based on seedlings established in late-autumn.

Conservation tillage systems in the northern cropping region provide favourable conditions for the establishment and survival of *C. bonariensis* during winter. Overwintering *C. bonariensis* plants have larger rosettes, a greater number of branches, a higher root:shoot ratio and a deeper taproot to compete for below ground resources and a significantly higher level of seed production compared with spring emerged plants. Overwintered *C. bonariensis* are therefore more difficult to control and if left to seed will produce much higher seed rain levels than those plants emerging in spring.

Conyza bonariensis appears to avoid a trade-off between energy allocation on reproduction and growth. Blossey and Notzold (1995) hypothesise this is achieved in invasive plants by allocating fewer resources to anti-herbivore defence. *Conyza bonariensis* is not toxic to stock (Andrade and Holzhacker 1959) and although it has the ability to regrow after herbivory (Davies 1999; Wu 2007), continued grazing throughout the peak emergence time and leading into summer crop planting could reduce its incidence. The use of cover crops grown during the winter fallow could also suppress *C. bonariensis* emergence. Such crops could out compete *C. bonariensis*. In addition to weed suppression, cover crops also reduce soil erosion, reduce water runoff, reduce surface water pollution, add organic matter and structure to the soil (Hartwig and Ammon 2002).

Ecological differences between the two *Conyza* species which support why *C. bonariensis* is more prevalent than *C. sumatrensis* in crops are the production of more seeds, a higher relative reproductive effort and more rapid development in *C. bonariensis*. *Conyza sumatrensis* grows much taller than *C. bonariensis,* which is likely to be an advantage in more competitive ruderal environments, e.g. roadsides.

CONCLUSION

These experiments showed that:

- The total fecundity of *C. bonariensis* and *C. sumatrensis* was affected by season of emergence, with less seed produced in the spring emerging cohorts;
- *C. bonariensis* has a higher reproductive effort compared with *C. sumatrensis;*

- The root:shoot ratio was higher for both species in the late-autumn cohort. Therefore overwintered plants are more competitive for below ground resources and potentially more difficult to control;
- *C. bonariensis* can reach seed maturity faster than *C. sumatrensis* – 1 636 and 2 134 growing degree days respectively; and
- Overwintered *C. bonariensis* plants are taller, have a larger rosette, deeper taproot, more branches, more capitula and more seed/capitulum compared with plants emerging in spring.

Chapter Six: Seed Dispersal

CHAPTER SIX

SEED DISPERSAL

INTRODUCTION

To assist in the understanding of the success of *Conyza bonariensis* (L.) Cronquist in minimum tillage systems, this chapter reports on seed settling velocities and the change in pappus geometry due to humidity. The results for *C. bonariensis* are compared with the less prominent cropping system *Conyza* species, *C. sumatrensis* (Retz.) E. Walker. Determining seed settling velocities, the velocity reached by a seed as it falls, enables dispersal distances to be calculated and changes in the pappus geometry due to different humidities may provide additional reasons for the success of *C. bonariensis* in a minimum tillage system.

Seed dispersal is the link between seed production and seedling establishment. Primary seed dispersal, the transit of seeds from parent plant to soil surface, in *Conyza* species is via wind. Secondary dispersal, the subsequent horizontal or vertical movements of seeds, is via water (e.g. movement of water through irrigation channels and run-off) and wind. *Conyza* species seeds are dispersed within 1 to 2 days from mature capitula, dependent on climate (Thebaud *et al.* 1996), and are dispersed with a fully developed embryo that can easily absorb water (Karlsson and Milberg 2007).

Structural features of a seed which reduces the speed at which it falls, for example, a pappus of a high surface area to volume ratio, increases the likelihood of lateral transportation by air currents (Chambers and MacMahon 1994; Cousens and Mortimer 1995), although most seeds remain close to the parent plant after dispersal (Cousens and Mortimer 1995). The pappus attached to *Conyza* species achenes, acts as a drag-enhancing parachute, a common feature for members of the Asteraceae (Andersen 1993). With a slower rate of diaspore fall, there is a greater effect of upward currents of air on the seed trajectory and therefore a greater chance of long distance dispersal (Sheldon and Burrows 1973).

Morphological traits are considered the major determinant of dispersal distance, and the settling velocity is regarded as the most important aerodynamic property (Matlack 1987; Nathan *et al.* 2001; Davies and Sheley 2007). Topography of the seed release site and the structure of surrounding vegetation also influences seed dispersal (Soons *et al.* 2004). The use of settling velocities as a means of determining dispersal distance assumes that diaspores attain terminal velocity (constant maximum velocity) practically instantaneously, which Burrows (1973) reported is valid for seeds with drag-enhancing pappi, such as *Conyza* species.

Seed dispersal contributes to the spread of glyphosate resistant populations of weeds (Dauer *et al.* 2007) and wind-based dispersal (anemochory) increases the scale by which resistant genes can travel (Marvier and Van Acker 2005). Glyphosate resistant *C. bonariensis* was first reported in South Africa in 2003 (Heap 2010). With predominantly self-pollination in *Conyza* species, the movement of seed is the main source of resistance spread (Smisek *et al.* 1998), therefore a greater understanding of dispersal ecology is important for effective long-term management of this weed.

There are no reported measurements of settling velocities for *C. bonariensis* or *C. sumatrensis* using samples from Australian populations. Furthermore, the effect of humidity environments on the pappus geometry and settling velocities of *C. bonariensis* and *C. sumatrensis* has not been reported. However, Sheldon (1974) has identified several species in the Asteraceae that change pappus geometry under different humidity environments. Pappus geometry responses to humidity could assist with the success of *C. bonariensis* within conservation tillage systems, where crop residue can provide higher humidity microsites (Bond and Willis 1969; Blevins and Frye 1993). The objectives of this chapter are to determine if changes in humidity have any impact on pappus geometry or diaspore settling velocity, and to contrast any response in pappus geometry or settling velocity due to humidity between *C. bonariensis* and *C. sumatrensis*. This will help in determining if seed dispersal behaviour is likely to be responsible for the invasion of *C. bonariensis* into reduced tillage farming systems in the northern cropping region.

METHODS

Collection of seeds

Conyza bonariensis and *C. sumatrensis* seeds were collected from the same roadside site 60 km east of Moree in northern New South Wales, Australia in February 2009. The capitula of 30 sampled plants of each species were placed into paper bags and gently shaken to remove mature seeds, air dried and stored in closed paper bags at room temperature prior to experimentation (November 2009).

Morphology measurements

Morphology measurements were taken prior to the application of humidity treatments. With the aid of a stereoscopic microscope, the pappus number of bristles, pappus length, achene length and width were determined by recording measurements of 40 randomly selected seeds of each species. The anatomy of the *C. bonariensis* diaspore is shown in Figure 6.1. Achene lengths were established by measuring from the pointed end to the summit of the achene. Widths were measured as the diameter of the achene at the summit. Measurements were performed in laboratory conditions of 21^{o}C and 38% humidity, as determined by thermometer and hygrometer. Seed weight, which included pappus, was determined by averaging the 1 000 seed weight of four replicates for each species. Wing loading was calculated as the seed mass divided by the pappus area, with pappus area determined using the surface area of a cone (surface area = $\pi rs + \pi r^2$) for each pappus bristle (Meyer and Carlson 2001).

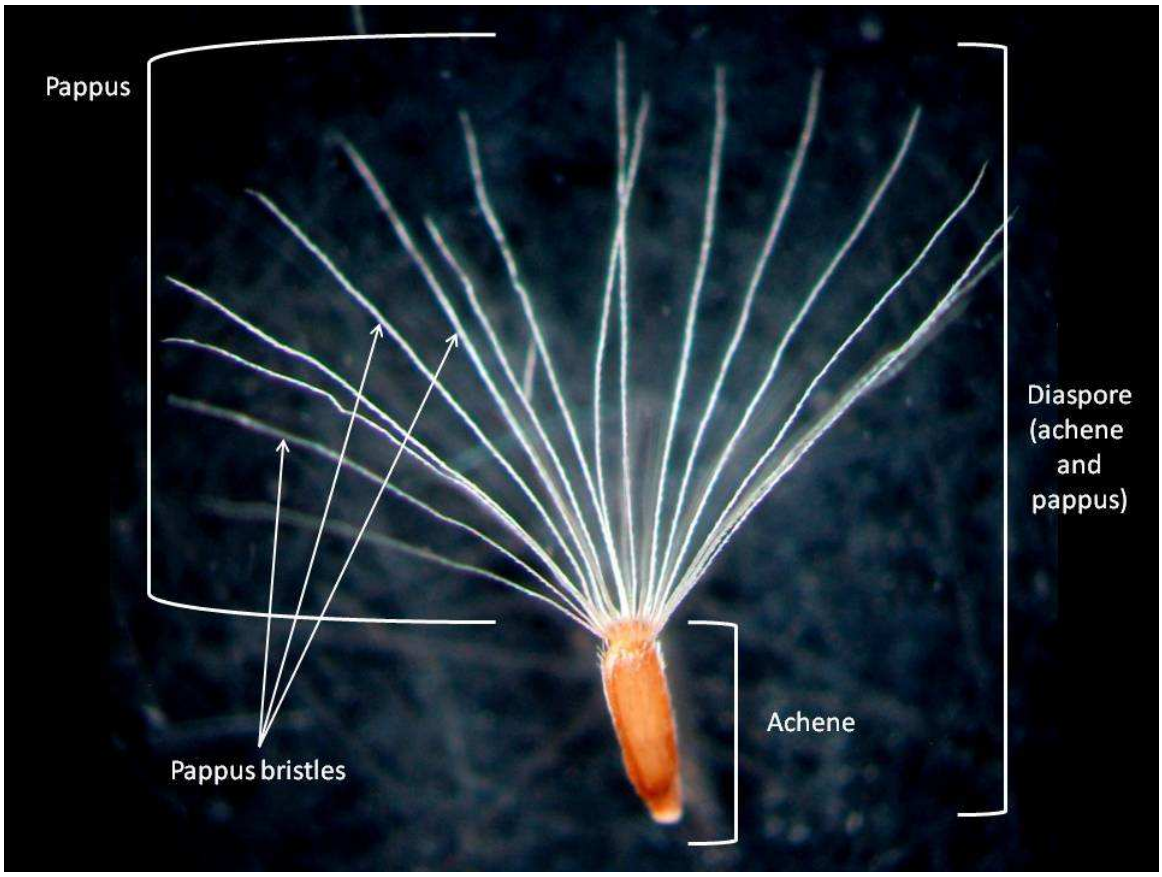

Figure 6.1 Photograph of *C. bonariensis* seed with components labelled.

Creating humidity environments

To create microsites of predetermined relative humidities, saturated solutions of hydrated calcium chloride ($CaCl_2.6H_2O$), sodium nitrite ($NaNO_2$) and hydrated zinc sulphate ($ZnSO_4.7H_2O$) were placed in three separate desiccators at 20^{o}C (Weast 1972). The respective humidities for each of the saturated solutions were 30, 75 and 90%. The saturated solutions were left in the desiccators for 24 hrs and the relative humidity was confirmed using a hygrometer. Forty seeds of each species were placed into separate glass Petri-dishes, with lids off, within each of the three relevant desiccators. The Petri-dishes were treated with anti-static wipes (Dick Smith Electronics Australia) prior to use to eliminate static interference. Seeds were handled with care and when forceps were used, the achene was held to avoid damage to the pappus bristles. Seeds remained in the desiccators for 24 hours prior to experimentation.

Pappus geometry

Pappus geometry response to humidity was tested using a stereoscopic microscope and protractor. The pappus bristle forming the greatest angle from the achene summit was measured to the nearest degree (Figure 6.2). The experiment comprised two species (*C. bonariensis* and *C. sumatrensis*) and three humidity levels (30, 75 and 90%), with 40 seeds measured in each treatment combination.

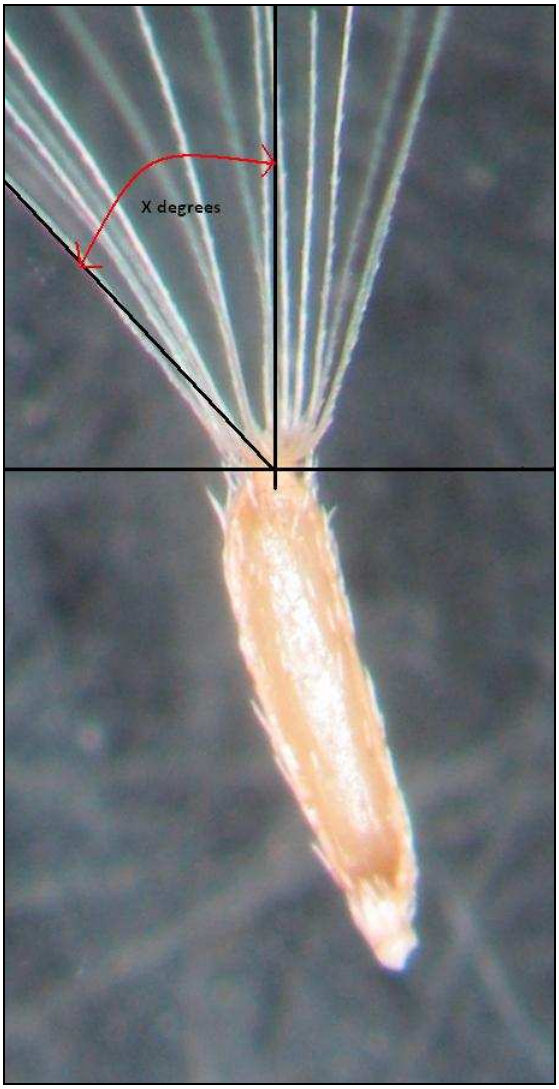

Figure 6.2 Photograph of *C. bonariensis* diaspore highlighting the angle measured.

Measuring settling velocities

Settling velocities were measured by dropping, pappus-up, individual *C. bonariensis* and *C. sumatrensis* diaspores down a vertical glass tube, with its base on the floor, measuring 1.45 m in length and 0.15 m inside diameter. A round plastic container with a small hole in the centre was placed at the top of the glass tube to minimise the impact of room air currents. To assist in locating the seed during descent, black cardboard was placed around part of the bottom 40 cm of the glass tube and a 40 W fluorescent light illuminated the lower part of the tube. The glass tube was treated inside with anti-static wipes (Dick Smith Electronics Australia) prior to use to eliminate static interference. The descent of the seed was timed using a digital stop-watch. This methodology follows that of Andersen (1992). The experiment involved two species (*C. bonariensis* and *C. sumatrensis*), and three humidity levels (30, 75 and 90%), with 40 replicate seeds for each treatment combination. Individual seeds remained in desiccators, at the required humidity, immediately prior to their descent down the glass tube, thereby reducing the time elapsed from the seeds being removed from the humidity environment.

Dispersal distance calculation

Dispersal distance for a seed falling at a constant velocity is defined as;

$$D = \frac{H \times U}{F}$$; where [6.1]

D = distance (m)

H = release height (m)

U = constant horizontal wind speed (m s^{-1})

F = the seed's settling velocity (m s^{-1}) (Nathan *et al.* 2001).

Calculations were made for both the species under low and high humidity environments (30 and 90% humidity) with different horizontal wind speeds and seed release heights using the respective mean settling velocity.

Statistical analysis

Settling velocities (m s^{-1}) were calculated by dividing the height of release (1.45 m) by the time of fall in seconds. All settling velocity data were log-transformed prior to analysis. A two-way ANOVA was used to compare the pappus geometry response to humidity for the two species and three humidity levels to a confidence level of α=0.05. The effect of species and humidity on settling velocities was analysed using a two-way ANOVA to a confidence level of α=0.05, with a Tukey multiple comparison performed on significant factors. Regression analysis was performed to explore the relationship between humidity level and settling velocity for the two species. All references to significant differences are $p<0.05$ and all means stated include their standard errors (±S.E.).

RESULTS

Morphology

There were small differences in the morphology measurements between the two species. *Conyza bonariensis* diaspores were lighter, had shorter and fewer pappus bristles and a larger achene length compared with *C. sumatrensis* (Table 6.1). Furthermore, *C. sumatrensis* had a higher wing loading.

Table 6.1 Diaspore measurements for *C. bonariensis* and *C. sumatrensis*. Values are means (n=40) with standard error in parentheses.

Measurement	*C. bonariensis*	*C. sumatrensis*
Pappus no. of bristles (#)	14.28 (± 0.24)	15.08 (± 0.24)
Pappus length (mm)	3.19 (± 0.05)	3.38 (± 0.07)
Pappus area (mm^2)	7.27 (± 0.17)	7.80 (± 0.22)
Achene length (mm)	1.26 (± 0.02)	1.09 (± 0.02)
Achene width (mm)	0.54 (± 0.01)	0.56 (± 0.02)
1 000 seed weight (g)	0.03745 (± 0.00110)	0.04693 (± 0.00167)
Wing loading (g $mm^{-½}$)	0.00229 (± 0.00003)	0.00248 (± 0.00004)

Pappus geometry

There was a significant change in pappus geometry as a result of different levels of humidity in both species. *Conyza bonariensis* and *C. sumatrensis* pappus bristles spread out in lower humidity conditions: 49.5^o (±1.1) and 47.5^o (±1.4) respectively (Figure 6.3 and Table 6.2) at 30% humidity levels. Pappus bristles became closer together at higher levels of humidity (Figure 6.3 and Table 6.2); at 90% relative humidity *C. bonariensis* pappus bristle spread was 13.0^o (±0.7) and *C. sumatrensis* 10.2^o (±0.8). The two-way ANOVA for species and humidity level found the main effect of humidity was significant (Table 6.3).

Figure 6.3 Microscope photographs of *C. bonariensis* and *C. sumatrensis* diaspores under 30 and 90% relative humidity environments.

Table 6.2 Pappus bristle angles of *C. bonariensis* and *C. sumatrensis* after diaspores stored in different humidity environments. Values are means (n=40) and in degrees with standard error in parentheses.

	Humidity (%)		
	30	75	90
C. bonariensis	49.5 (±1.14)	17.5 (±0.78)	13.0 (±0.74)
C. sumatrensis	47.5 (±1.38)	18.0 (±0.90)	10.2 (±0.79)

Table 6.3 Two-way analysis of variance results for pappus geometry (r^2=0.874).

Source	df	MS	F	p
Corrected Model	5	12 544.22	324.18	<0.05
Intercept	1	161 928.15	4 184.67	<0.05
Species	1	120.42	3.11	0.08
Humidity	2	31 242.04	807.38	<0.05
Species*Humidity	2	58.30	1.51	0.22
Error	234	38.70		
Total	240			
Corrected Total	239			

Settling velocities

Conyza bonariensis diaspores had a faster settling velocity than *C. sumatrensis* in all humidity treatments. When comparing the 30 and 90% humidity results and the 30 and 75%, both species experienced an increase in settling velocities with an increase in humidity (Figure 6.4). The settling velocities in 30% humidity for *C. bonariensis* and *C. sumatrensis* were 0.281 m s^{-1} (±0.008) and 0.242 m s^{-1} (±0.010) respectively and in 90% humidity 0.329 m s^{-1} (±0.010) and 0.282 m s^{-1} (±0.011) respectively. When contrasted to *C. sumatrensis*, *C. bonariensis* had a greater range in mean settling velocities between the low 30% humidity and the high 90% humidity (Figure 6.4).

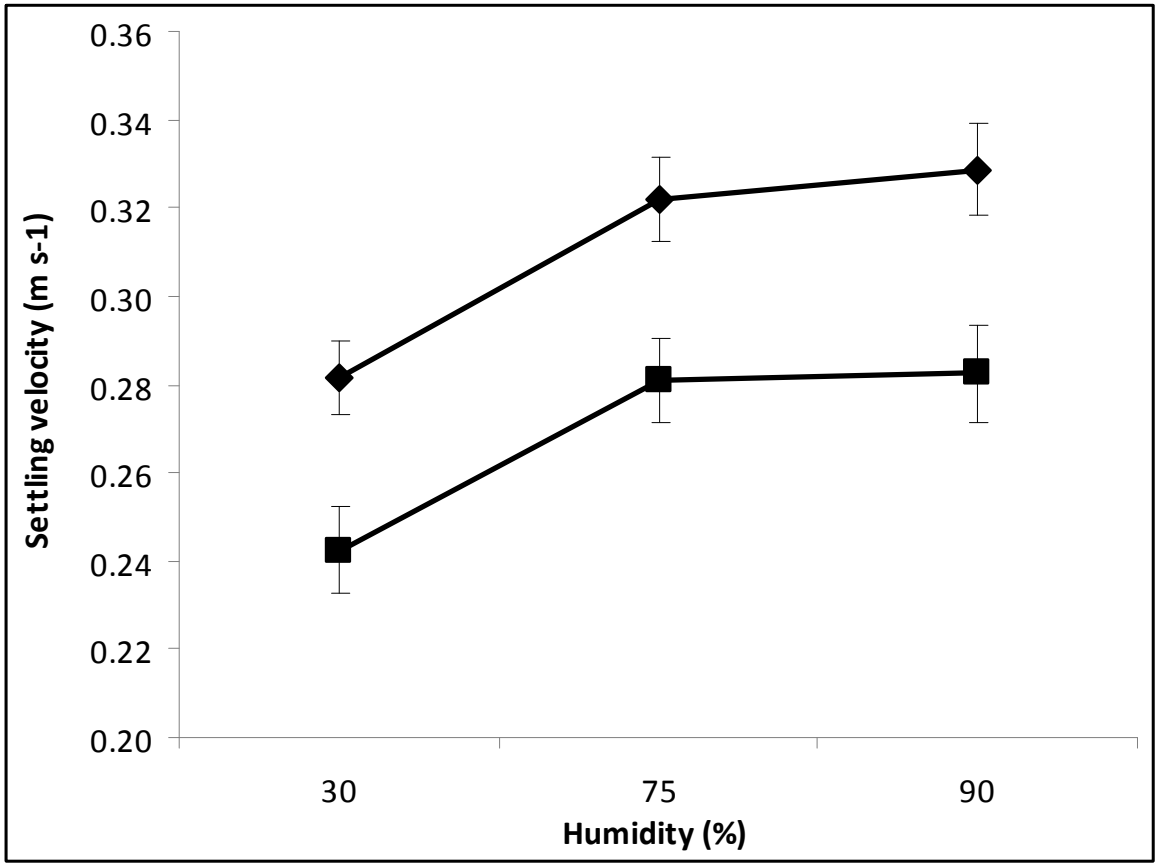

Figure 6.4 Mean settling velocities for *C. bonariensis* (◆) and *C. sumatrensis* (■) under three different humidity levels with standard errors (⌶).

The two-way ANOVA for settling velocity returned significance for the species and humidity main effects (Table 6.4). Tukey multiple comparisons showed that the 75 and 90% treatments were not significantly different. Regression analysis showed a significant relationship ($p<0.05$) between humidity level and settling velocity in each of the two species, however with weak coefficient of determination values. *Conyza bonariensis* regression equation was $\log_{10}(\text{settling velocity}) = 0.00113(\text{Humidity}) - 0.590$ ($r^2=0.11$, $p=0.0002$) and *C. sumatrensis,* $\log_{10}(\text{settling velocity}) = 0.00129(\text{Humidity}) - 0.665$ ($r^2=0.10$, $p=0.0004$).

Table 6.4 Two-way analysis of variance results for settling velocities (r^2=0.218).

Source	df	MS	F	p
Corrected Model	5	0.04	9.70	<0.05
Intercept	1	50.86	12 964.13	<0.05
Species	1	0.13	33.48	<0.05
Humidity	2	0.03	7.32	<0.05
Species*Humidity	2	0.01	0.20	0.82
Error	174	0.01		
Total	180			
Corrected Total	179			

Dispersal distance

Conyza sumatrensis seed has the potential to disperse greater distances than *C. bonariensis* due to a slower settling velocity. The dispersal capacity is further enhanced in *C. sumatrensis* with this species growing, on average, taller than *C. bonariensis*, with maximum heights of 2 m and 1 m respectively (Everett 1990), and therefore having a higher seed release height. Dispersal distance calculations are given in Table 6.5.

Table 6.5 Dispersal distances (m) calculated for *C. bonariensis* and *C. sumatrensis* at different humidity, wind speed and release heights.

	Humidity level (%)					
	30			90		
	Wind speed (km hr^{-1})					
	15	25	35	15	25	35
Release height (m)						
C. bonariensis						
0.2	3.0	4.9	6.9	2.5	4.2	5.9
0.4	5.9	9.9	13.8	5.1	8.5	11.8
0.6	8.9	14.8	20.7	7.6	12.7	17.7
0.8	11.8	19.7	27.6	10.1	16.9	23.7
1.0	14.8	24.7	34.5	12.7	21.1	29.6
C. sumatrensis						
0.2	3.4	5.7	8.0	3.0	4.9	6.9
0.4	6.9	11.5	16.0	5.9	9.8	13.8
0.6	10.3	17.2	24.1	8.9	14.7	20.6
0.8	13.8	22.9	32.1	11.8	19.7	27.5
1.0	17.2	28.6	40.1	14.8	24.6	34.4
1.2	20.7	34.5	48.2	17.7	29.5	41.3
1.5	25.8	43.1	60.3	22.1	36.9	51.6
2.0	34.4	57.3	80.2	29.5	49.2	68.8

DISCUSSION

The morphological measurements reported here for *C. bonariensis* are in line with those reported by Clarke (1999): achenes measuring c. 1 to 1.4 mm long, c. 0.5 mm wide with c. 3 to 4 mm long pappus bristles. The pappus attached to *C. bonariensis* and *C. sumatrensis* seeds make it difficult for the seed to passively move down cracks in soil (Bekker *et al.* 1998) or be buried by earth-worms (Van der Reest and Rogaar 1988). This feature assists the seed to remain on or near the soil surface – the preferred germination site for *Conyza* species (Chapter 7). Features of seed morphology could be a result of selection either for seed dispersal or for seedling survival (Andersen 1993). A higher reproductive effort of a species is associated with a shorter life span and a reduced competitive ability (Ehrlen and van Groenendael 1998). Small seeds, as in *Conyza* species, typically have a lower survival and competitive ability than larger seeds, albeit the dispersal ability and extent is greater (Harper *et al.* 1970).

A change in pappus geometry due to humidity was reported in this experiment for both *C. bonariensis* and *C. sumatrensis.* Examples of this response in other species include *Centaurea imperialis* Hausskn. ex Bornm., with the pappus becoming open and closed at different humidity levels (Small 1918). Sheldon (1974) reported responses in pappus geometry to high humidity soil surface environments; *Erigeron acer* L., *Senecio vulgaris* L. and *Sonchus oleraceus* L. all collapsed, *Leontodon autumnalis* L. became fully open and several other Asteraceae have hygroscopic closure (*Senecio jacobaeae* L., *Senecio viscosus* L., *Taraxacum officinale* Weber and *Tragopogon porrifolius* L.). With the pappus closed, there is a reduction in the area exposed to the wind and therefore dispersal is affected (Sheldon and Burrows 1973). In addition, diaspores with flattened pappus geometry in areas of high humidity, for example *C. bonariensis* and *C. sumatrensis,* provide a greater soil/seed contact area and therefore increases the probability of germination. This feature adds to the success of *C. bonariensis* in a conservation tillage system due to the increase soil surface humidity (Bond and Willis 1969; Blevins and Frye 1993), but does not explain why *C. sumatrensis* is less successful in invading such cropping systems.

Preventing *C. bonariensis* from setting seed is an important management strategy. If left to seed in fallows, there is the potential for a greater dispersal distance. Seeds landing on an area with no resident vegetation are more capable of being further transported via winds along the surface soil, whereas areas with vegetation restrict the horizontal wind dispersion (Zimdahl 1999). In a fallow setting, there is a higher surface soil temperature when compared with a vegetated area and this will give rise to increased updraft winds and hence increased potential dispersal distance (Tackenberg *et al.* 2003). Most seeds dispersed from a dense stand of a single species have a seed shadow within or very close to the source, whilst dispersal from an isolated individual places seed at further distances (Sheldon and Burrows 1973). Within dense stands, wind speed is reduced and there is obstruction by neighbouring plants which impact dispersal (Sheldon and Burrows 1973).

The dispersal distance calculations show that seeds can land close to the source and therefore if left to seed in cropping systems, there will be a considerable addition to the seed bank. With stronger wind conditions, seeds can travel greater distances. For example, seeds released at a height of 1 m from *C. bonariensis* in 35 km hr^{-1} winds can travel 35 m before landing on the ground. Infestations will, therefore, be able to move relatively quickly and this will need to be taken into account when searching for satellite infestations. *Conyza bonariensis* seeds can be caught on spider webs (Figure 6.5) (T. Green, pers. obs.), thereby reducing dispersal distance and potentially viability.

Figure 6.5 *Conyza bonariensis* seeds caught on a spiders web adjacent to a dense roadside stand of *C. bonariensis* and within 20 m of a cotton cropping system in Moree, New South Wales.

Secondary dispersal can significantly change the seed shadow created after primary dispersal (Harper 1977; Chambers and MacMahon 1994), and is more effective in conditions with a smooth surface, minimal obstacles and high wind velocities close to the ground (Monteith and Unsworth 1990). The secondary dispersal can continue until a seed germinates, it becomes permanently entrapped or until certain structures that enable dispersal deteriorate (Johnson and Fryer 1992), such as the pappus in *Conyza* species. Within conservation tillage systems, crop residue provides an obstruction to secondary seed dispersal when seed is beneath residue. The higher humidity environment in a suitable microsite will also flatten pappus bristles of *C. bonariensis* and *C. sumatrensis*, further reducing the likelihood of secondary wind dispersal and increasing germination probability through an increased soil/seed contact. During a rain event, the flattened pappus in this

increased humidity environment might allow for easier seed movement through crop stubble to a greater distance with surface runoff.

An increase in humidity resulted in a faster settling velocity for both species. This has also been reported in *S. vulgaris,* where dispersal distance was reduced by more than half in a 75% humidity environment compared with a 0% humidity environment (Sheldon and Burrows 1973). Although there were changes in the settling velocities under different humidities, the effect on dispersal distance was minimal. For example, *C. bonariensis* seeds with a release height of 80 cm in 25 km h^{-1} wind, were calculated to be able to travel 19.7 m at 30% humidity and 16.9 m at 90% humidity. *Conyza canadensis* (L.) Cronquist is reported to have a settling velocity of 0.323 m s^{-1} (Dauer *et al.* 2007), and 99% of *C. canadensis* seeds were reported to be found within 100 m of the source in field based seed trap trials (Dauer *et al.* 2007). The *C. canadensis* settling velocities reported are almost identical to those for *C. bonariensis* reported here at the 75 and 90% humidity levels.

The small differences in seed morphology, geometry and dispersal characteristics between the two species did not explain why *C. bonariensis* is more successful in conservation tillage than *C. sumatrensis*. Despite having heavier seeds and higher wing loading, *C. sumatrensis* had a lower settling velocity, which when combined with a higher release height which gives rise to a greater potential seed dispersal distance. There were no significant differences in the settling velocity responses between the two species due to changes in humidity. However, the response in pappus geometry to humidity can assist the success of *Conyza* species generally in a conservation tillage system.

CONCLUSIONS

These experiments showed that:

- *Conyza bonariensis* and *C. sumatrensis* pappus bristles alter their geometry in response to humidity, with bristles closer together in higher humidity levels; and
- The settling velocities of *C. bonariensis* and *C. sumatrensis* were affected by different humidity, with slower settling velocities in lower humidity levels.

Chapter Seven: Seed Longevity and Emergence from Depth

CHAPTER SEVEN

SEED LONGEVITY AND EMERGENCE FROM DEPTH

INTRODUCTION

To further understand the success of *Conyza bonariensis* (L.) Cronquist in minimum tillage systems, the influence of seed burial depth and duration on seed longevity for *C. bonariensis* and the less prominent cropping system *Conyza* species, *C. sumatrensis* (Retz.) E. Walker is reported. Determining the effect of seed burial will assist in understanding the effect of different tillage practices on *C. bonariensis* seed longevity, possible reasons for the success of *C. bonariensis* in a minimum tillage system and potential weed management options.

The composition of species within the seed bank is the combined result of seed production, germination and mortality (Hoffman *et al.* 1998). This is extended in agronomic settings to include crop management practices (Hoffman *et al.* 1998), including tillage and pesticide use. Agricultural practices can influence the emergence, persistence and dormancy of a seed bank and therefore change the weed density and composition (Derksen *et al.* 1993). Seed longevity in soil depends on numerous interactions, including the intrinsic dormancy of seed, environmental conditions (e.g. temperature, light, water and gases) and biotic activity (e.g. bacteria, fungi, predation and allelopathy) (Chambers and MacMahon 1994). Although *C. bonariensis* has been reported to have no dormancy (Thebaud *et al.* 1996; Wu *et al.* 2007), Karlsson and Milberg (2007) reported that *C. bonariensis* has a weak dormancy, and using the dormancy classification of Baskin and Baskin (2004), it has non-deep physiological dormancy.

Understanding the seed bank dynamics of annual plants, such as *Conyza* species, is especially important in understanding population dynamics. Walters *et al.* (2005) reported that species originating from temperate climates, like *C. bonariensis*, tended to produce seeds with short life-spans. Where seed production is prevented or eliminated, the seed bank will be the source for recruitment in later years. Tillage systems change the composition,

vertical distribution and density of weed seed banks (Buhler *et al.* 1997), and influence the periodicity of weed emergence (Cousens and Moss 1990).

There is limited information on the seed longevity of *Conyza* species. The seed of the congeneric species, *C. canadensis* (L.) Cronquist*,* remain viable for at least 1 to 2 years after shedding (Weaver 2001) and longevity within a laboratory setting has been measured as 2 to 3 years for *C. sumatrensis* and *C. canadensis* (Hayashi 1979). An investigation into burial depth and seed longevity can assist to understand the effects of different tillage practices on seed longevity. The objectives of this experiment were to: (i) compare the ability of the two species to emerge from different depths in the soil; and (ii) compare the effect of seed burial depth and duration on seed longevity in *C. bonariensis* and *C. sumatrensis.* Such information could help to explain the success of *C. bonariensis* within conservation tillage systems and provide possible management options for *C. bonariensis*.

METHODS

Seed collection and viability testing

Conyza bonariensis and *C. sumatrensis* seeds were collected from the same roadside site 50 km east of Moree in Northern New South Wales, Australia (29^{o}32' S, 150^{o}14' E) on the same day in January 2008. The capitula of 50 sampled plants of each species were placed into paper bags and gently shaken to remove mature seeds, air dried and stored in closed paper bags at room temperature prior to experimentation. Seed viability was assessed using tetrazolium, 0.5% 2,3-5-triphenyltetrazolium chloride (TTC) (Freeland 1976), in June 2008. To confirm viability using the TTC test, the solution was poured into Petri-dishes with seeds (four replicates, each of 100 seeds) and left for five hours at room temperature. Seeds which turned red in colour were classed as viable. Seed viability results for *C. bonariensis* and *C. sumatrensis* were 62.4% (±4.8%) and 66.1% (±6.3%) respectively.

Emergence from depth

Prior to the field based investigation of seed longevity, a controlled environment experiment was performed in July 2008, to assess the ability of *C. bonariensis* and *C. sumatrensis* to emerge from different depths. The experiment included the two species of *Conyza*, six burial depths (0, 0.5, 1, 2, 5 and 7 cm) and four replicates (each of 100 seeds). A three part sand and one part peat substrate was mixed and a 2 cm layer was placed into aluminium trays measuring 10 cm wide, 20 cm long and 10 cm deep. Seeds were then distributed onto the soil and more soil was added to cover the seeds to the appropriate treatment depths. Treatments were placed in a growth chamber in a randomised block design at 25^{o}C with constant light, a favourable germination environment for both species (Chapter 3). Seeds were watered daily using a mist spray to avoid soil and seed movement and the locations of the aluminium trays were changed every three days during the 30 day treatment period. Germinated seeds were counted at the end of the treatment period. Seeds were defined as germinated when the radicle or shoot extended further than 1 mm beyond the seed coat (Steinmaus *et al.* 2000).

Seed longevity over time and at different depths

To investigate the effects of depth on seed longevity over time, seeds were buried in bags, made of cotton fibre, in a field site at 'Trevanna' on the grounds of the University of New England, Armidale, Australia. A factorial experiment design of two species (*C. bonariensis* and *C. sumatrensis*), four burial depths (1, 2, 5 and 10 cm) and six exhumation intervals (0, 3, 6, 9, 12 and 15 months), was employed with four replications. Grey vertosol soil was collected for use within the bags, but before use was sieved to 2 mm and autoclaved at 121^{o}C for 2 hrs to kill any seed and pathogens. Bags measuring 10 cm x 7 cm with a fine pore size of 0.5 mm were each filled with 50 cm^{3} of soil and 300 seeds.

Four 13 m long trenches 1 m apart measuring 45 cm wide and 30 cm deep were dug at 'Trevanna' to house pots of soil containing the buried seeds. The area of the in-ground experiment and immediate surrounding were sprayed with glyphosate (a.i. 360 g L^{-1}) at the rate of 1.6 L ha^{-1} prior to commencement. Polyethylene pots measuring 30 cm diameter and

35 cm deep were filled with grey vertosol soil, placed into the trenches and soil was backfilled around each pot. Two bags, one of each species, was then buried to the appropriate depth and secured by a loop of wire in each pot. The soil above the bag was padded down and smoothed over by hand to minimise movement of soil (e.g. via heavy rain) which could alter the burial depth. The field site was maintained with manual weeding.

After exhumation of seeds for each of the six intervals (0, 3, 6, 9, 12 and 15 months), seeds were tested for ability to germinate. The contents of each bag was spread over two 9 cm Petri-dishes with two layers of Whatman's No. 1 filter paper. Soil was spread over two dishes to prevent any seed from being buried beneath the soil surface. Petri-dishes were placed in an incubator at 25^{o}C with constant light and watered as required. Germinated seeds were counted after a 21 day treatment period and seeds were defined as germinated when the radicle or shoot extended greater than 1 mm beyond the seed coat (Steinmaus *et al.* 2000). The persistence of *C. bonariensis* and *C. sumatrensis* seeds was calculated as (no. of germinated seeds/300 seed buried) x 100.

The zero month exhumation, performed at the commencement of the burial experiment, was performed by mixing 300 seeds of each species, using four replicates, with the grey vertosol soil and employing the same methods described above for the germination test of buried seeds post-exhumation.

Statistical analysis

All analysis was performed using SPSS v 17.0. Data were tested for homogeneity using Levene's equality of variance test and as a result seed longevity over time results were log transformed prior to analysis. A univariate analysis was performed on emergence from depth results. A three-way ANOVA was used to analyse the seed longevity results over time at different burial depths for the two species. Where significance was returned, a LSD (α=0.05) was performed. A univariate analysis of the variance was performed on longevity results for the two species separately and a LSD (α=0.05) performed where significance was returned. Exponential decay curves ($Y = Ae^{-kx}$) for loss of seed persistence were calculated for both species and each depth treatment using SPSS regression curve fitting to determine k

(slope), R^2 (variance accounted for) and A (y intercept). All references to significant differences are $p<0.05$ and all means stated include their standard errors (±S.E.).

RESULTS

Emergence from depth

Neither *C. bonariensis* nor *C. sumatrensis* were able to germinate below the soil surface. Depth was the only significant main effect – there was no significant difference in species response. The 0 cm burial depth had germination levels of 54.2% (±3.9%) and 58.5% (±3.1%) for *C. bonariensis* and *C. sumatrensis* respectively.

Seed longevity over time and at different depths

Viability of buried seeds in both species decreased with time and the depth of burial influenced this process (Figure 7.1 and 7.2). Seeds buried closer to the surface lost viability more rapidly than those buried deeper. After 15 months of burial, the 1 cm depth had seed persistence of 3.9% (±1.3%) and 3.4% (±1.0%) for *C. bonariensis* and *C. sumatrensis* respectively. This contrasts with the deeper burial of 10 cm, where seed persistence was 13.7% (±1.8%) in *C. bonariensis* and 11.6% (±2.4%) in *C. sumatrensis*.

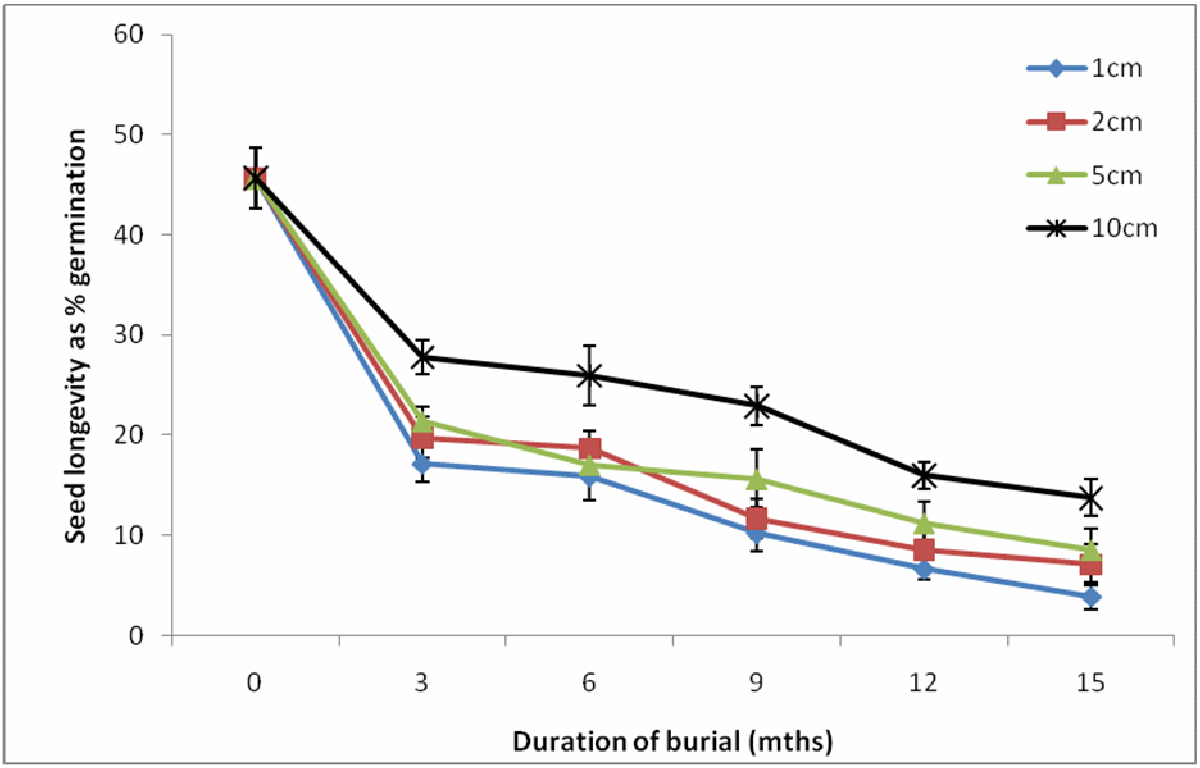

Figure 7.1 Effect of burial depths over time on the seed longevity of *C. bonariensis* expressed as percentage germination from the original 300 buried seeds. Data points are mean values and include standard errors (⌶).

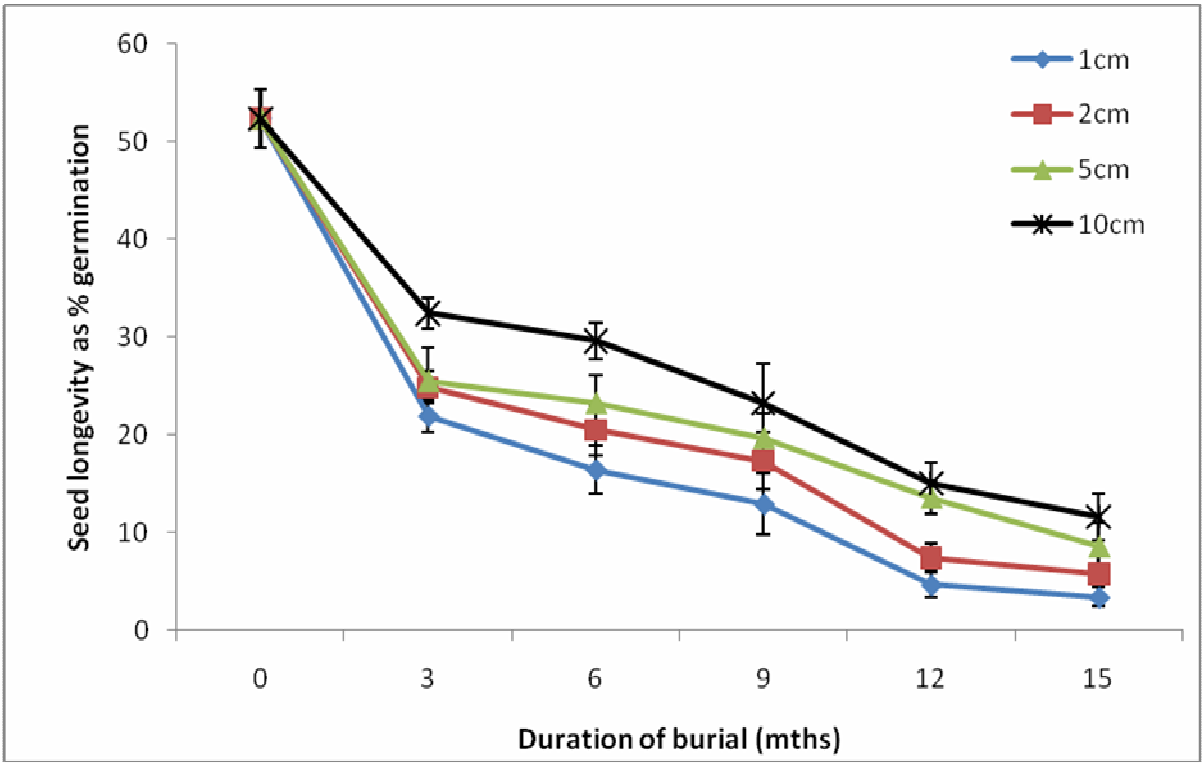

Figure 7.2 Effect of burial depths over time on the seed longevity of *C. sumatrensis* expressed as percentage germination from the original 300 buried seeds. Data points are mean values and include standard errors (⌶).

The zero month exhumation germination results for *C. bonariensis* and *C. sumatrensis* were 45.7% (±3.0%) and 52.3% (±2.9%) respectively. All treatments experienced the largest decline in seed longevity between the 0 and 3 month exhumations. Climate data for the period of experimentation are given in Figure 7.3.

The three-way ANOVA showed the main effects depth and duration as significant (Table 7.1). Post-hoc analysis (LSD) showed all depths were significantly different and the 3 and 6 month exhumations were the only exhumations which were not significantly different. There was no significant difference in response to burial depth between the two species.

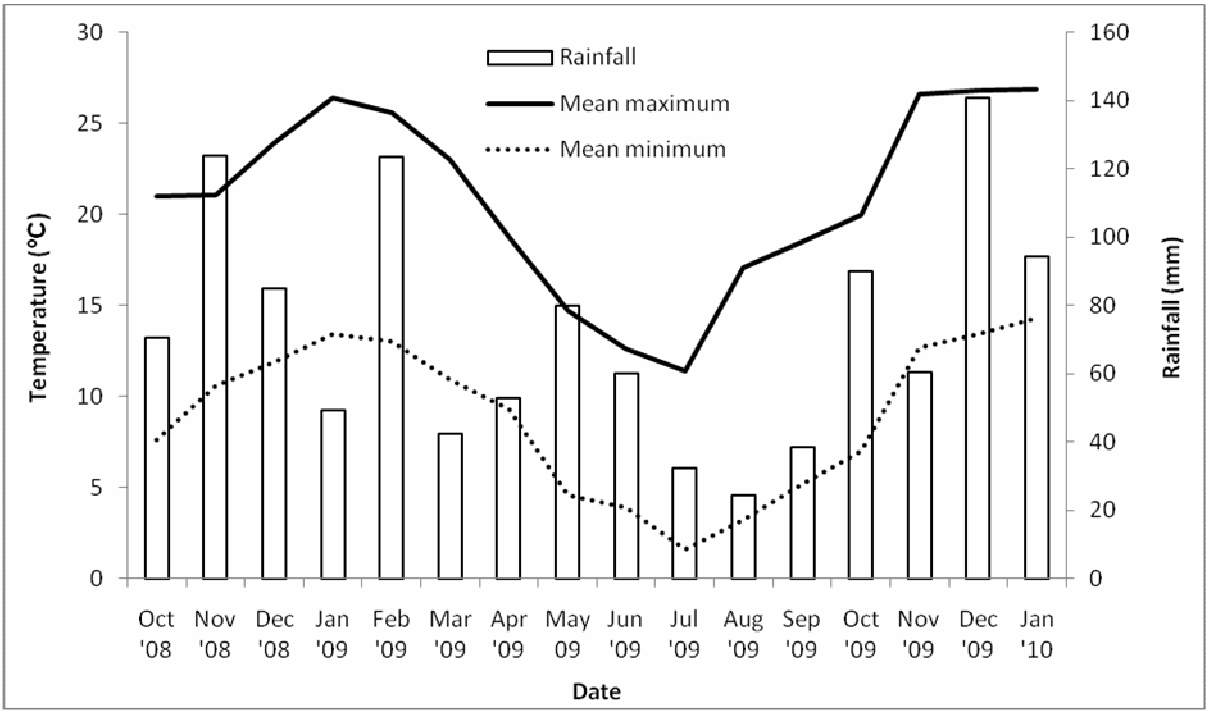

Figure 7.3 The mean monthly rainfall and mean maximum and minimum temperatures for Armidale during the field experiment (October 2008 to January 2010).

Table 7.1 Results of three-way analysis of variance for seed longevity (r^2=0.793).

Source	df	MS	F	p
Corrected Model	41	0.332	11.801	<0.05
Intercept	1	89.377	3178.240	<0.05
Species	1	0.31	1.116	0.293
Depth	3	0.947	33.679	<0.05
Duration	4	1.847	65.679	<0.05
Species*Depth	3	0.014	0.494	0.687
Species*Duration	4	0.044	1.563	0.188
Depth*Duration	12	0.048	1.693	0.076
Depth*Duration*Species	12	0.009	0.324	0.984
Error	126	0.028		
Total	166			

The univariate ANOVA on the species separately showed that for both species, depth and duration were significant factors, with no significant interaction between these factors (Table 7.2 and 7.3). Least squares of difference test in *C. bonariensis* showed the 2 cm and 5 cm burial depths and the 3 month and 6 month exhumations as not significant. For *C. sumatrensis*, the LSD results showed the 5 cm and 10 cm burial depth to not be significantly different, and the 3 month compared with the 6 month and the 6 month compared with the 9 month exhumation times were not significantly different.

Table 7.2 Univariate analysis of variance results for *C. bonariensis* seed longevity (r^2=0.771).

Source	df	MS	F	p
Corrected Model	20	0.278	10.5777	<0.05
Intercept	1	46.379	1764.754	<0.05
Depth	3	0.467	17.782	<0.05
Duration	4	0.680	25.856	<0.05
Depth*Duration	12	0.024	0.921	0.532
Error	63	0.026		
Total	83			

Table 7.3 Univariate analysis of variance results for *C. sumatrensis* seed longevity (r^2=0.809).

Source	df	MS	F	p
Corrected Model	20	0.401	13.379	<0.05
Intercept	1	43.029	1436.113	<0.05
Depth	3	0.494	16.475	<0.05
Duration	4	1.211	40.431	<0.05
Depth*Duration	12	0.033	1.086	0.388
Error	63	0.03		
Total	83			

The decline in the number of viable seeds with time for both species was well accounted for by the fitted exponential curves with R^2 values ranging between 0.73 and 0.85 (Table 7.4). The increased rate of loss of viability at shallower depths is supported by the increase in the steepness of the slope (k) of the fitted exponential curves where, for example, *C. bonariensis* k = -0.1599 at a depth of 1 cm compared with -0.0752 at 10 cm (Table 7.4). The fitted exponential curves were used to calculate the length of time for 95, 99 and 99.9% viability loss in seeds (Table 7.5).

Table 7.4 Parameters from fitted exponential decay curves of loss of seed viability ($Y = Ae^{-kx}$) in *C. bonariensis* and *C. sumatrensis* at burial depths of 1, 2, 5 and 10 cm. A = y intercept, k = slope and R^2 = variance accounted for.

Depth (cm)	A	k	R^2
C. bonariensis			
1	0.3798	-0.1599	0.79
2	0.3682	-0.1252	0.76
5	0.3634	-0.1058	0.73
10	0.4061	-0.0752	0.80
C. sumatrensis			
1	0.4742	-0.1860	0.85
2	0.4914	-0.1552	0.78
5	0.4512	-0.1114	0.75
10	0.5017	-0.1008	0.80

Table 7.5 Time (months) for 95, 99 and 99.9% of the original seed bank of *C. bonariensis* and *C. sumatrensis* to lose viability when buried at depths of 1, 2, 5 and 10 cm. Time was calculated using the respective exponential equations in Table 7.4.

Depth (cm)	Viability loss in seeds (%)		
	95	99	99.9
C. bonariensis			
1	12.7	22.7	37.1
2	15.9	28.8	47.2
5	18.7	34.0	55.7
10	27.8	49.3	79.9
C. sumatrensis			
1	12.1	20.7	33.1
2	14.7	25.1	39.9
5	19.7	34.2	54.9
10	22.9	38.8	61.7

DISCUSSION

The purpose of this study was to examine the effect of burial depth on emergence and burial depth and duration on seed longevity of *C. bonariensis* and *C. sumatrensis;* to determine if there were any differences in the response of the two species; and whether the results suggested possible management options for *C. bonariensis*.

Conyza bonariensis and *C. sumatrensis* emergence are both highly sensitive to seed burial. This study showed that neither species was able to emerge at depths of 5 mm or more

below the soil surface. This agrees with a similar study which reported that *C. canadensis* seedlings did not emerge from seeds placed at a depth of 5 mm or more (Nandula *et al.* 2006). The lack of ability of *C. bonariensis* and *C. sumatrensis* to germinate from below the soil surface might partly be due to the prevention of light penetrating to the seed – Chapter 3 reported no germination for either species in a completely dark environment. Furthermore, Woolley and Stoller (1978) found that less than 1% of incident light penetrated further than 2.2 mm into undisturbed soil. Watering the treatments with a gentle mist spray prevented soil and seed movement, while other watering methods may have moved the seed and/or soil and might allow light to reach shallow buried seeds. An integrated weed management approach for *C. bonariensis* which included cultivation to attempt to bury the seed deeper in the soil could reduce emergence. *Conyza canadensis* has been reported to be effectively controlled in minimum tillage cotton systems by discing in spring or autumn (Brown and Whitwell 1988).

While both *C. bonariensis* and *C. sumatrensis* seeds can remain viable in the soil for more than 15 months, the proportion of the seed bank remaining viable is determined by the depth at which the seed is buried, with deeper burial resulting in greater seed persistence. Seeds buried at 1 cm deep in the in-ground pot trial were quickly depleted, with the persistence at 6 months being approximately one-third (34.9%) of the zero month levels, whilst at the 10 cm depth, the persistence remained at 50% of the zero month levels. One reason for the rapid decline in viability at shallower depths is that seeds near or at the soil surface are exposed to the most variable fluctuations in environmental conditions, which could promote metabolic failure (Stoller and Wax 1974; Wu *et al.* 2007).

The large decline in longevity for both species reported between the 0 and 3 months time is most likely due to the seeds being buried in the field and experiencing changes in environmental conditions. An increase in moisture and temperature will result in a decrease in viability (Probert *et al.* 2009) and climate results for the first three months of the field trial were 279 mm of rainfall, with a mean maximum temperature of 22^{o}C. These conditions could have added to the accelerated decline in persistence of the seeds during this initial burial period.

The difference in the rate of *C. bonariensis* seed viability loss at different soil depths has consequences for the long-term management of the seed bank in cropping systems. For example, with *C. bonariensis*, it will take approximately 12.7 months for the seed bank to decline to the point where only 5% of seeds remain viable at a depth of 1 cm in contrast to 27.8 months at a depth of 10 cm (Table 7.5). Tillage practices that allow a large proportion of seed to remain on the soil surface will promote quicker depletion of the seed bank in the absence of seed replenishment. In contrast, agricultural practices that bury seeds will promote persistence of the seed bank though not emergence. Although seed persistence in the two *Conyza* species were below 4% at 1 cm depth after 15 months of burial, given the prolific seed production of the species (Chapter 5), they have the capacity to build up seed banks in a short period of time. Wu (*et al.* 2007) reported 1.3% viable seeds at a burial depth of 0 – 2 cm in *C. bonariensis* after three years and 7.5% viability at 10 cm depth.

Conyza bonariensis emergence is favoured under zero tillage systems and is reduced when seed is buried through tillage, however, buried seeds are able to persist for a longer time period and there is opportunity for these seeds to emerge once they are brought back to the soil surface by subsequent tillage. In managing *C. bonariensis,* it is therefore advisable to allow the seed bank on the surface soil to be depleted, largely through controlling emerged seedlings, and not to bury seeds through tillage. Seed burial could be an option in dense infestations, however once the seed has been buried it should remain buried for a number of years. For this management practice to be effective, no new *C. bonariensis* seed should enter the system. To successfully deplete the seed bank it is important to manage *C. bonariensis* in nearby non-cropping areas. If this weed can be effectively managed over a one year period in a zero tillage system, with no seed replenishment, the weed population in the following year will be significantly reduced. There is further importance for meticulous weed management for *C. bonariensis* given it has the ability to emerge all-year-round (Chapter 5). In summer cropping systems, *C. bonariensis* is problematic in fallows: the success of *C. bonariensis* to emerge in the drier fallow environment is supported by the ability to germinate at moisture levels of -0.8 MPa (Chapter 3).

It is possible that the seeds in this study underwent some change in dormancy during the dry storage for 7 months prior to the establishment of the experiment, which unfortunately was not assessed. In addition to a possible change in dormancy during storage, seeds may have

undergone a reduction in viability. The initial seed viability for *C. bonariensis* was c. 65%, while the zero month germination test (conducted 7 months later) had rates of germination of c. 45%. Soil seed banks are also reduced through predation. Although no measurements were taken in this research due to the difficulty in successfully separating all seeds when mixed with soil, seed predation in *C. canadensis* and *C. sumatrensis* has been reported as negligible (Escarre *et al.* 1998).

Although species was not found to be a significant factor in this study, the decay curves suggest that *C. bonariensis* has a longer persistence in the seed bank compared with *C. sumatrensis*. At a burial depth of 10 cm, *C. bonariensis* has a seed persistence of 49.3 months and *C. sumatrensis* 38.8 months. The ability of *C. bonariensis* to persist longer in the seed bank than *C. sumatrensis* supports the observations of *C. bonariensis* being more prominent in cropping systems compared with *C. sumatrensis*.

CONCLUSIONS

These experiments showed that:

- *Conyza bonariensis* and *C. sumatrensis* are not able to germinate when buried beneath the soil surface;
- *Conyza bonariensis* and *C. sumatrensis* seed longevity is increased as the burial depth increases;
- Emergence is favoured under zero tillage systems, as this agricultural practice leaves a large proportion of seed on the soil surface; and
- There was no significant difference in seed longevity response to burial depth and duration between the two species, however exponential decay curves show *C. bonariensis* to have a longer persistence in the seed bank.

Chapter Eight: General Conclusions

CHAPTER EIGHT

GENERAL CONCLUSIONS

INTRODUCTION

This thesis set out to expand the ecological knowledge of *Conyza bonariensis* (L.) Cronquist in order to better understand the ecological niche this plant occupies. This knowledge will assist in understanding the ecological reasons for the success of *C. bonariensis* in minimum tillage systems of the northern cropping region of Australia. A series of experiments was conducted targeting each life stage of *C. bonariensis* and all results were compared with a congeneric species, *C. sumatrensis* (Retz.) E. Walker, which is present but currently less important in cropping systems than *C. bonariensis*. This chapter revisits the findings to elucidate ecological reasons for the success of *C. bonariensis*, compare the ecology of the two species, provide management principles for effective control and describe future research priorities.

RESEARCH FINDINGS

There are several ecological characteristics of *C. bonariensis* which contribute to its increased importance in the northern cropping region of Australia. Furthermore, changes in agronomic practices of cropping systems, including the shift towards minimum tillage, have contributed to its prevalence by favouring its ecology. A lifecycle schematic drawing (Figure 8.1) summarises the ecological characteristics of *C. bonariensis* as identified by this research. Each experimental objective is restated below, with commentary on findings and limitations of the results.

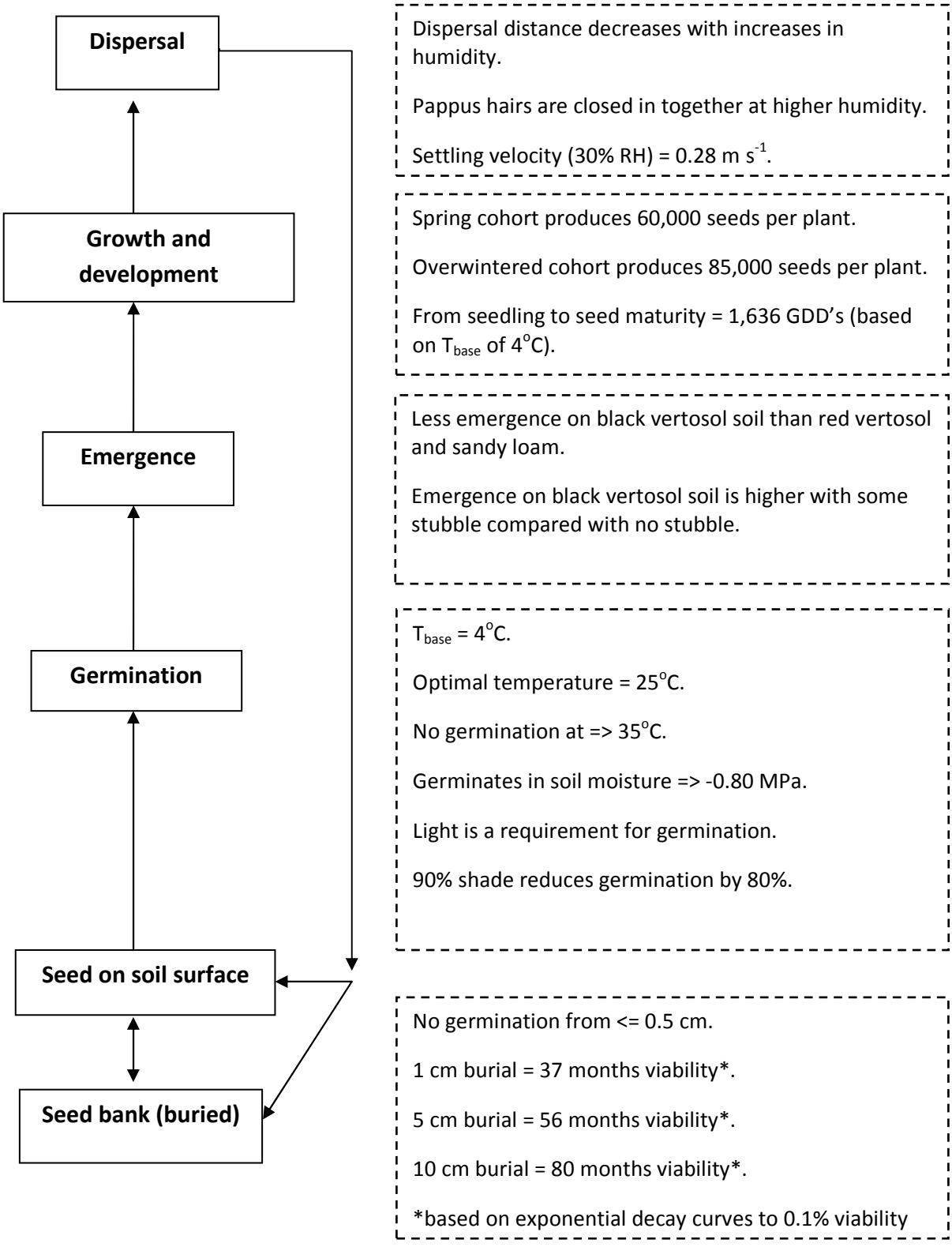

Figure 8.1 Lifecycle of *C. bonariensis* including summary of ecological information obtained from this research.

(1) Determine the germination requirements (temperature, moisture and light) of* C. bonariensis *and determine if its prevalence in the northern cropping region of Australia, particularly minimum tillage systems, is related to its germination requirements.

Temperature requirements for germination of *C. bonariensis* demonstrated the ecological characteristic of potential all-year-round germination within northern NSW and southern QLD. The base temperature (T_{base}) for *C. bonariensis* was calculated as 4^{o}C and germination occurred between 10 and 30^{o}C (Chapter 3). The temperatures in the northern cropping region of Australia are suited to this range. During hotter conditions in this region, a microsite under crop residues within a minimum tillage system will have a reduced temperature (Nyborg and Malhi 1989; Oryokot *et al.* 1997), thereby increasing the probability of germination. Blevins and Frye (1993) reported soil temperature reductions of up to 3.8^{o}C with the presence of crop residue compared with no residue. *Conyza bonariensis* has no innate dormancy; therefore seeds are able to germinate any time after seed maturity and dispersal. In the agroecosytem setting, seeds set by one generation of *C. bonariensis* in a crop/fallow are able to germinate in the following crop/fallow. With a base germination temperature of 4^{o}C seedlings are theoretically capable of growth and development during winter. In this study, however, germination only occurred when the temperature was 10^{o}C or above (Chapter 3). Average temperatures only drop below 10^{o}C in the middle of winter in the northern cropping region. This may explain why emergences in the field rarely occur at this time. The germination temperature range of *C. bonariensis* and the protection from high temperatures in minimum tillage systems add to its success in the northern cropping region of Australia.

Light was found to be essential for germination of *C. bonariensis.* However, there was no significant difference in either total germination or rate of germination, between the 0, 50 and 70% shade levels. Furthermore, *C. bonariensis* was capable of 10.5% germination under a 90% shade environment. Crop residues in minimum tillage systems create a shaded microsite, however, as these results indicate, a level of stubble providing 90% shade to the seed still permits some germination when moisture and temperature requirements are met. Because of the lack of surface soil disturbance in a minimum tillage system, areas adjacent to stubble but without crop residue, have the benefits of additional moisture for

germination, without the reduction of light. Adding to the success of *C. bonariensis* in minimum tillage systems is the lack of reduction in germination of seeds up to 70% shade and the increase in moisture in the stubble microsite providing favourable germination conditions.

Conyza bonariensis is capable of germinating at osmotic potentials of -0.8 MPa or higher, with optimal germination at -0.4 MPa and above (Chapter 3). The distribution of both summer and winter rain in the northern cropping region favours the incidence of this weed. When rainfall supplies soil water at levels greater than or equal to -0.8 MPa for a short interval, combined with favourable temperature and light, the weed is able to germinate within 2 to 3 days. In addition to the climate of the region and the ability of *C. bonariensis* to germinate under relatively dry conditions, the additional surface soil moisture provided in a minimum tillage system promotes its occurrence (Bond and Willis 1969; Unger and Parker 1976; Smika and Unger 1986; Nyborg and Malhi 1989; Blevins and Frye 1993; Oryokot *et al.* 1997; Singh *et al.* 1998).

***(2) Determine the effect of different soil types and stubble loads on the emergence of* C. bonariensis.**

Emergence was recorded for all treatments, including the four soil types (black/grey/red vertosol, sandy loam) and three stubble loads (0, 1.8, and 3.6 t ha^{-1}). A higher emergence in the black vertosol occurred with a stubble load of 1.8 t ha^{-1} compared with no stubble (Chapter 4). This result is most likely due to the additional moisture provided to the microsite under stubble. Smika and Unger (1986) reported 54% of precipitation was stored in soil with wheat (*Triticum aestivum* L.) straw on the soil surface compared with 21% storage of precipitation in ploughed soil with no straw. Although black vertosols are common in the northern cropping region, the presence of higher moisture levels under stubble will assist with the establishment of *C. bonariensis* which only germinates on the soil surface where there is often rapid drying.

The limitations of the investigation into *C. bonariensis* emergence under stubble relates to what reduction of emergence at higher stubble loads may have been due to allelopathy – if any. Lucerne (*Medicago sativa* L.) was the only material used for the stubble and therefore there was no comparison for the same stubble loads using different plant material.

(3) Determine the emergence cohort effect on growth and fecundity of C. bonariensis *and whether this adds to its success in the northern cropping region.*

There are differences in *C. bonariensis* growth and seed production levels between emergence cohorts. *Conyza bonariensis* plants which germinate in autumn and overwinter were shown to produce more seeds compared with those plants emerging in spring – c. 85 000 compared with c. 60 000 per plant respectively (Chapter 5). The climate of the northern cropping region consists of a mild winter and with no dormancy requirement in *C. bonariensis*, mature seeds dispersed in summer can successfully germinate in autumn or winter with adequate light and moisture provisions. Wu *et al.* (2007) reported that 99% of *C. bonariensis* emergence occurred in late-autumn or early winter. Therefore, a large proportion of the *C. bonariensis* population overwinters in this region, adding to the seed bank for future generations, thereby aiding its proliferation. Adding to the success of *C. bonariensis* in minimum tillage systems are the winter emerging rosettes that can be protected by crop residues during the short period of cold conditions in this region. The short time between stem elongation and seed production, c. 6 weeks or c. 720 growing degree days, further adds to the success of *C. bonariensis* (Chapter 5).

With the majority of *C. bonariensis* emergence in the northern cropping region occurring in late-autumn or winter (Wu *et al.* 2007), the results on growth and development showed the weeds competitiveness for below ground resources in winter crops and fallows to be strong. At the stage of stem elongation, the overwintered *C. bonariensis* rosettes were, on average, 10.4 cm tall with a 16.4 cm long taproot (Chapter 5), with below ground biomass representing 32% of total biomass. These growth characteristics, going into summer, are likely to give *C. bonariensis* an advantage over summer annual weeds. The growth characteristics, combined with a slow response to herbicides, also make overwintered *C. bonariensis* plants more difficult to control.

(4) Determine the effect of humidity on C. bonariensis *seed and seed dispersal and whether this adds to its success in the northern cropping region.*

Humidity was found to affect both the pappus bristle geometry and settling velocities in *C. bonariensis*. Higher humidity environments caused the pappus bristles to flatten, whilst in low humidity environments, pappus bristles were at a greater angle to the achene (Chapter 6). The prevalence of *C. bonariensis* in minimum tillage systems could be associated by the

increased humidity in these systems (Bond and Willis 1969; Blevins and Frye 1993). By flattening the pappus bristles, higher humidity may encourage a higher soil/seed contact, increasing the likelihood of germination, while at the same time reduce secondary dispersal.

A lower humidity environment reduced the seed settling velocity, thereby increasing the potential dispersal distance. Settling velocities were measured as 0.28 m s^{-1} in 30% humidity and 0.24 m s^{-1} in 90% humidity. In the absence of any updraft, *C. bonariensis* seeds in 30% humidity released from a height of 1 m in a 35 km hr^{-1} wind can travel c. 35 m (Chapter 6). This dispersal potential supports the need for control of *C. bonariensis* beyond the edges of the cropping system to reduce additional seed input. In minimum tillage systems, seed entering the system remain on the soil surface, which is favourable for germination (Chapter 7). The increased humidity of the microsite reduces the likelihood of secondary dispersal, adding to the success of *C. bonariensis* in these systems.

(5) Determine the effect of seed burial depth on seed longevity of* C. bonariensis *and whether this adds to its success in the northern cropping region.

Conyza bonariensis was shown to germinate on the soil surface only (Chapter 7); therefore the prevalence of this weed is favoured by minimum tillage systems. Germination on the soil surface offers *C. bonariensis* an ecological advantage in minimum tillage systems, in which the lack of cultivation practices leaves the majority of seeds on the soil surface. The results showed that *C. bonariensis* seed longevity is increased at greater burial depths, therefore, although cultivation will reduce emergence in the short term, the seeds are viable for a longer period. The persistence of *C. bonariensis* in minimum tillage cotton systems could be increased through the tillage involved to control insects (pupae busting) and through planting crops.

COMPARATIVE ECOLOGY

All experiments were designed to compare the results of *C. bonariensis* with the congeneric species, *C. sumatrensis* to better understand the former's increasing occurrence in the northern cropping region. In this way, we have a reference point to gauge the relative benefits of the ecological characteristics of *C. bonariensis* to its success in these cropping systems, allowing identification of characteristics of other species that may enable them to emerge as weed problems in the future. This section summarises the differences found between the ecology of the two species which could further account for their different habitat preferences.

Results on germination showed that *C. sumatrensis* can germinate at warmer temperatures compared with *C. bonariensis* (Chapter 3). Although the northern cropping region can experience hot summers, there is a reduction in soil temperature provided by crop residue in minimum tillage systems (Nyborg and Malhi 1989; Oryokot *et al.* 1997) of up to 3.8^{o}C (Blevins and Frye 1993), which adds to the success of *C. bonariensis* over *C. sumatrensis* in these systems. *Conyza sumatrensis* has a greater tolerance to shading (Chapter 3) which helps to explain its more common occurrence in the roadside environment where it can successfully compete with perennial vegetation.

An impediment to the success of *C. sumatrensis* in the agroecosystem setting is the longer time for stem elongation, flowering and seed production for this species. The lifecycle of *C. sumatrensis* extends beyond the growing season of an annual cropping system. *Conyza bonariensis* sets seed in c. 500 growing degree days less than *C. sumatrensis*. An additional advantage of *C. bonariensis* over *C. sumatrensis* for an annual cropping environment, is in total seed production. *Conyza sumatrensis* produced fewer capitula, fewer seed per capitulum and therefore fewer total seed compared with *C. bonariensis*. Overwintered *C. bonariensis* and *C. sumatrensis,* grown in climatic conditions of the northern cropping region, produced 85 075 and 21 488 seeds respectively, i.e. *C. bonariensis* seed production was close to four times that of *C. sumatrensis* (Chapter 5).

Conyza sumatrensis has the potential for greater dispersal distances due to its taller average height (Chapter 5) and a slower settling velocity compared with *C. bonariensis* (Chapter 6),

but produced fewer seed than *C. bonariensis* to disperse. The examination of seed longevity at different burial depths showed that *C. bonariensis* seed remain viable for a longer period than *C. sumatrensis* (Chapter 7). For example, at a 2 cm burial depth, *C. bonariensis* seed had an additional 7.3 months longevity (to 0.1% viability) compared with *C.* sumatrensis. At a 10 cm depth this was increased to an additional 18.2 months. This additional seed persistence adds to the success of *C. bonariensis* in the cropping environment over *C. sumatrensis*.

An additional factor favouring *C. bonariensis* over *C. sumatrensis* in cropping systems is herbicide tolerance. There have been differential responses to glyphosate reported in *C. bonariensis* populations in southern Queensland, with populations from cropping paddocks more tolerant than populations from non-agricultural situations (Walker and Robinson 2008).

MANAGEMENT PRINCIPLES FOR *C. BONARIENSIS* BASED ON ITS ECOLOGY

Conyza bonariensis is an annual weed and therefore, effective long-term management needs to target the seed bank. This involves promoting a reduction in the seed bank and minimising future seed bank inputs. Reducing the seed bank is promoted in a minimum tillage system where seeds remain on or near the soil surface, thereby promoting seedling emergence and increasing decay rates. Reducing the seed bank through seedling emergence is reliant on the effective control of seedlings to avoid high plant numbers, competition and further seed bank replenishment. With the ability of *C. bonariensis* to emerge all-year-round given light and soil moisture greater than or equal to -0.8 MPa, there is a requirement for all-year-round monitoring and control of this weed. Seed input is not just provided by plants within the cropping system. Seeds from outside the cropping area can be blown in and therefore the control of such plants is also important.

Cultivation can appear to be counter-productive to the ideals of a conservation tillage system; however, in the case of large infestations or difficult to control populations, cultivation could be useful. Rotating tillage practices reduces selection pressures on *C. bonariensis* and other weeds which are favoured by minimum tillage systems. The burial

of *C. bonariensis* seed, however, extends the period the seed remains viable, therefore, if seed burial was used as the primary means of control, there would need to be no additional deep cultivation which could return those buried seeds to the surface after several years, or further active control of seedlings would be required.

The effective long-term management of *C. bonariensis* requires an integrated approach to weed management, in which herbicide use is complemented with non-chemical control tactics. These tactics may include strategic cultivation, crop competition, grazing, burning and manual removal. The use of herbicides, even when used in conjunction with non-chemical options, needs to be practised in a way to minimise selection pressures for resistance to a single herbicide. This can be achieved by rotating the mode of action groups of the herbicides used.

Herbicide use is relied upon heavily in minimum tillage systems. Glyphosate resistant populations of *C. bonariensis* are present overseas (Heap 2010) and there are reports of increased tolerance to glyphosate in populations from a cropping and glyphosate use background in southern Queensland (Werth *et al.* 2010). Herbicide mode of action groups should be rotated to reduce selection pressures and thereby extend the useful life of currently used herbicides.

Farm hygiene is another important element in effectively managing this weed. With a very high fecundity and ability for long-distance seed dispersal, control measures need to be extended to non-cropping areas of the property.

FUTURE RESEARCH

Ecological influences on all key life stages of *C. bonariensis* were investigated in this study. To assist with population modelling of *C. bonariensis,* however, research is required to obtain information on the survival of *C. bonariensis* during each of the life stages. With the establishment of population models, different management scenarios could be investigated. Although some weed management principles have been discussed in this study, such options need to be tested and validated in the field.

Information on the germination ecology of *C. bonariensis* has been expanded through this study. Additional areas to explore, however, could include light quality, alternating high/low temperatures, pH and different nutrient regimes. This could add to the understanding of the ecological niche occupied by *C. bonariensis* in minimum tillage systems.

Another opportunity to expand the suite of options for an integrated weed management approach for *C. bonariensis* is biological control. Future research in the use of biological control agents, allelopathy and bioherbicides is important as no one single management option can successfully control *C. bonariensis* in the long-term.

The threat of glyphosate resistant biotypes of *C. bonariensis* in Australia needs to be managed. Werth *et al.* (2010) have recently reported on use of 'double knock' approaches to effectively control *C. bonariensis* and manage resistance. Research into managing chemical resistance, however, needs to be ongoing.

The extent of genetic diversity within *C. bonariensis* plants in Australia remains unknown. *Conyza* species have been reported to hybridise (Thebaud and Abbott 1995). An understanding of genetic diversity within this species will assist in explaining the distribution of *C. bonariensis* and better managing for future risks, including the potential spread of herbicide resistance.

CLOSING

Through this thesis the knowledge on the ecology of two *Conyza* species in Australia has been furthered, ecological reasons for the success of *C. bonariensis* within the northern cropping region of Australia – particularly minimum tillage systems has been presented, and weed management principles required for effective control have been outlined. The findings of this research can also be used to predict future problem weeds and species shifts within these cropping systems.

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Appendix

A review of the ecology of fleabane (*Conyza* spp.)

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Summary Fleabanes (*Conyza* spp.) are an increasing problem in annual summer crops in Australia. In this paper we review the available literature on the ecology of *Conyza* species in order to better understand the possible reasons for this recent increase. Aspects of germination, growth and development, seed dispersal, crop interaction and herbicide resistance are included. In addition we highlight research gaps in fleabane ecology for subsequent investigation of the species in Australia.

Keywords *Conyza*, germination ecology, weed ecology.

INTRODUCTION

Fleabanes (*Conyza* spp.) are annual, exotic, herbaceous, invasive weeds of the Asteraceae family. There are seven *Conyza* species naturalised in Australia, with infestations of one or more species in every state and territory and climatic zone (Everett 1990). These species most commonly invade disturbed sites including roadsides, wastelands and crop edges. *Conyza bonariensis* (L.) Cronquist (flaxleaf fleabane), has the widest geographic distribution in Australia, tolerates a wide range of climates and habitats (Everett 1990), and is an increasing problem in summer fallows and crops such as sorghum and cotton. The objective of this paper is to describe the current understanding and research gaps of fleabane ecology.

SEED PRODUCTION AND DISPERSAL

Conyza species are prolific seed producers. Flaxleaf fleabane has a range of reported total seed numbers per plant, up to 375,561 (Kempen and Graf 1981). *Conyza canadensis* (L.) Cronquist (Canadian fleabane) is reported to produce 200,000 seeds per plant (Weaver 2001). Seeds are dispersed within one or two days of capitula maturing, dependent on climate (Thebaud *et al*. 1996). Primary dispersal of fleabane seeds is via wind. There is no seed dormancy in *Conyza* with viability estimated as 1–2 years in the field (Weaver 2001).

GERMINATION AND EMERGENCE

The temperature preferences for germination are between 10 and 25°C (Zinzolker *et al*. 1985); optimal temperature for flaxleaf fleabane was estimated at 20°C with a 4.2°C base temperature (Wu *et al*. 2007). A study by Nandula *et al*. (2006) demonstrated that a 24°C day and 20°C night temperature achieved the highest germination result in Canadian fleabane of 61% after 10 days.

The findings of light requirements for germination are mixed. Nandula *et al*. (2006) report that Canadian fleabane does not require light. Others report an absolute requirement for light (Zinzolker *et al*. 1985) including for flaxleaf (Wu *et al*. 2007). The length of any requirement for light has been debated, with Milberg *et al*. (1996) finding that Canadian fleabane can germinate with a total light exposure of five seconds.

Under sustained flooding conditions (14 days), there was a 50% reduction in the survival of Canadian fleabane (Stoecker *et al*. 1995). Conversely, water stress experiments showed 25% germination at 0 MPa reducing to 2% at −0.8 MPa (Nandula *et al*. 2006). Observations in the Australian landscape indicate that significant rain events stimulate emergence of fleabane (Wu and Walker 2004).

A limited amount of documented experimentation is available on the effect of soil type on germination. Wu *et al*. (2007) investigated burial depth impact on flaxleaf fleabane in heavy black vertosol and light sodosol soils. They found that no emergence occurred in the heavy soil, and only the minimal burial depth (0–2 cm) in the light soil produced emergence. Canadian fleabane had a higher rate of germination under neutral-to-alkaline conditions (Nandula *et al*. 2006). Soil temperature showed only a weak correlation ($r^2 = 0.21$) with germination when tested with Canadian fleabane (Main *et al*. 2006).

Other ecological factors that affect fleabane germination include intraspecific competition and pesticides. Palmblad (1968) found the germination rate in Canadian fleabane was reduced with an increase

in intraspecific competition. The use of dimethoate, a phloem-feeding insect control, was also found to significantly reduce germination of Canadian fleabane (Gange *et al*. 1992).

The emergence of fleabane, favoured by mild conditions, is predominantly in autumn and early winter with limited emergence in spring. Within the northern grain region of Australia, *Conyza* species are reported to emerge all-year-round with active growth in spring and early summer.

FLOWERING

There is limited information available on flowering requirements. One molecular based study found that Canadian fleabane contained proteins similar to plants requiring vernalisation (Rudnoy *et al*. 2002). Flowering in flaxleaf fleabane is favoured by long photoperiods, such as 14 hours (Amsellem *et al.* 1993). Fleabane flowers sequentially within an individual plant and the flowering period can span 1–4 months (Thebaud *et al*. 1996). Flowers reproduce autogamously and are self-compatible. Documented effects of ecological factors on growth and development in fleabane are limited.

INTERFERENCE

Intraspecific and interspecific competition has been explored. Thebaud *et al*. (1996) reported that the ability to absorb and utilise both water and nutrient resources within a competitive environment was greater in *Conyza sumatrensis* (Retz.) E.Walker (tall fleabane) than Canadian fleabane. Furthermore, they found that tall fleabane established and persisted in previously cultivated fields (0–30 years) whilst Canadian fleabane was restricted to recently disturbed habitats (Thebaud *et al*. 1996).

Lavorel *et al*. (1999) showed that the impact of functional group composition (e.g. grasses, herbs or shrubs) of surrounding vegetation varied across life stages of flaxleaf fleabane and Canadian fleabane. Survival of fleabane increased with an increase in Asteraceae species richness. Biomass and reproduction decreased in the presence of higher annual grass species (e.g. *Avena sterilis*, *Bromus* spp. and *Lolium italicum*) richness but increased in the presence of annual legumes (Lavorel *et al*. 1999).

An investigation of the effect of cattle grazing on plant density in South East Queensland found that flaxleaf fleabane density increased with grazing whilst tall and Canadian had no significant increase or decrease (McIntyre *et al*. 2003). Neave and Tanton (1989) explored grazing effects of the grey kangaroo on grasslands in plots within the Australian Capital Territory, which showed that flaxleaf fleabane appeared only in plots that excluded kangaroos.

HERBICIDE RESISTANCE

Herbicide resistance has evolved within *Conyza* populations in several countries. The first recorded incidence of glyphosate resistance was in Canadian fleabane in Delaware in 1999 (VanGessel 2001). The mechanism of resistance in Canadian fleabane is believed to be that of reduced translocation (Feng *et al*. 2004), with glyphosate resistant populations estimated to be present on 44,000 ha in 12 states of the USA (Heap *et al.* 2005). Glyphosate resistance in flaxleaf fleabane was also reported in South Africa in 2003 (Heap *et al.* 2005). The development of resistance to glyphosate is of great concern to farmers, especially those that utilise glyphosate resistant crops and conservation tillage. Flaxleaf fleabane has also developed resistance to other herbicidal mode of action groups (L, C and B) in certain countries (Heap *et al.* 2005).

TILLAGE SYSTEM

Conyza is a relatively new and emerging weed of cotton systems, believed to have progressed as a result of a shift towards conservation tillage practices and reduced reliance on soil-applied residual herbicides. The viability and germination of *Conyza* species seed decreases with soil burial depth and therefore under minimal tillage, the fleabane seeds remain on or near the soil surface – the preferred germination site. In Australia, flaxleaf fleabane is the most prevalent *Conyza* species within dryland cropping systems and its increased incidence has increased the cost of fallow weed control (Wu *et al*. 2007).

In a reduced tillage system, crop residue remains on the soil. Canadian fleabane showed 77% less emergence after a cotton crop (with residue) compared with bare fallow (Burke *et al*. 2003).

CONCLUSION

It is evident from this review of literature that there have been no detailed comparisons of the ecology of the three main species of *Conyza* in Australia. This includes abiotic and biotic factors that affect the weed throughout its life stages. Such work is likely to reveal why flaxleaf fleabane is the most abundant in cropping in Australia, compared with the overseas experience where tall and Canadian fleabane are the most populous and problematic for agriculture, and help to identify weed characteristics that may be favoured by conservation farming systems in the future.

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