Chapter 1
General introduction

1.1 Biological invasions

Anthropogenic loss of biodiversity is occurring at an unprecedented rate. Invasive species, by altering ecosystem composition, structure and function, are thought to be one of the main causes of this decline (Vitousek et al. 1997). In Australia's Murray Darling Basin, invasive species, including *Phyla canescens*, are now considered to be the main threat to its sustainability (Wong et al. 2007). *Phyla canescens* is also one of the 160 invasive plant taxa considered to be threatening biodiversity in Australian rangelands (Martin et al. 2006), and is identified as threatening the Endangered Ecological Community, Coolibah-Blackbox Woodland in NSW (Coutts-Smith and Downey 2006).

Biological invasions, like extinctions, are inevitable consequences of life in a changing world. Past invasions, resulting from events such as continental collisions, sea level changes and long-distance dispersal events, have led to the current distribution of organisms around the world. Human-mediated transport of organisms has simply increased the rate of such events, but the rate of transportation is now so high that we risk homogenising and impoverishing the biological systems upon which we rely (Mack et al. 2000). This homogenisation and impoverishment implies reduced potential to adapt to future change.

Presumably any species that can reproduce (i.e. all species) has the potential to become invasive. Even if we consider that all species are potentially invasive, and all habitats potentially invasible, there needs to be a match between the requirements of the invader and the conditions of the recipient environment.

A distinction, however, must be made between invaders, colonisers and weeds, three related concepts which have been used ambiguously and inconsistently (Colautti and MacIsaac 2004). Invaders are alien (introduced) species successfully recruiting, a

biogeographic/demographic phenomenon (Richardson et al. 2000); colonisers are successional pioneers (an ecological concept); and weeds are any plant growing where it is not desired (an artefact of human perception). While there is clearly much overlap among these ideas, particularly where introduced species colonise agricultural areas to the detriment of crops, they are not identical (Williamson 1996). Even within the concept of invasion, there is discordance, with some authors equating invasive with alien (e.g. Lonsdale 1999; Richardson et al. 2000), while others reserve the term invader for alien species causing measurable damage (the intersection of biogeography and anthropocentrism, e.g. Mack 1996; Lodge and Shrader-Frechette 2003).

A number of models have been proposed to describe this invasion process (Williamson and Fitter 1996; Richardson et al. 2000; Sakai et al. 2001; Colautti and MacIsaac 2004; Theoharides and Dukes 2007). These models differ in the number and definition of states (stages), but there is general agreement that only a small minority of species successfully transition from each state to the next (cross barriers, pass through filters); most biological introductions, whether deliberate or accidental, fail. 'The tens rule' has been proposed to approximate such rates of transition (Williamson and Fitter 1996). It suggests that 10% of imported species escape in the new range, 10% of which establish self-sustaining populations, with 10% of these become pests causing economic damage. One problem with such estimates is that the denominator is unknown, i.e. many failed introduction events are unrecorded (Simberloff 1989). Even deliberate introductions are 'apt to pass unnoticed except when successful' (Cook and Dias 2006, p. 610).

Some other sources of variation in rates of transition include:

1. differences in propagule pressure (Williamson 1996),
2. differential invasibility of the recipient environment (Williamson 1996),
3. specific traits of non-randomly selected imported species (Lonsdale 1994), and
4. unknown numerator, due to lag from introduction to invasion (Cadotte et al. 2006).

These sources of variation represent biologically meaningful phenomena.

1.1.1 Propagule pressure

The globalisation of trade has led to unprecedented long-distance movement of organisms around the world (di Castri 1989). This increased movement of organisms increases the number of collisions between the set of potential invaders and the set of the potentially invaded. Propagule pressure, which includes the number of introduction events and the number of individuals per introduction, is a universally accepted determinant of invasion success (Williamson 1996; Kolar and Lodge 2001; Rouget and Richardson 2003; Leung et al. 2004; Lockwood et al. 2005; Von Holle and Simberloff 2005; Colautti et al. 2006; Drake and Lodge 2006), a rare commodity in invasion ecology.

Propagule pressure varies among species. Primarily there is a bias toward species which have utilitarian or aesthetic appeal to people (Pysek and Richardson 2007), although vagrants, with historically close associations with human cultures, and common species, with large native ranges, are also represented (Carlton 1996; Cadotte et al. 2006).

Of 26 242 known plant species introduced into Australia, 25 448 (96.9%) are currently cultivated (Randall 2007). An estimated 8298 species were deliberately introduced for utilitarian, mostly agricultural, purposes between 1924 and 2000 (Cook and Dias 2006), which represents between 3 and 4% of global angiosperm diversity (assuming ~ 250 000 species, Heywood 1989). The species introduced into Australia, however, represent over 22% of the global species of Poaceae (2250 species introduced) and about 18% of Fabaceae *sensu stricto* (2691 species).

1.1.2 Habitat invasibility

Not all habitats appear to be equally vulnerable to invasion. Invasive species benefit from disturbance, particularly anthropogenic disturbance (Dietz and Steinlein 1998; Mack et al. 2000; Lake and Leishman 2004; Cadotte et al. 2006). Since invasion, by definition, is dependent on recruitment, and disturbances represent recruitment opportunities (Bullock 2000), it is not surprising that increased disturbance leads to increased invasion. Disturbance is to the invaded habitat as propagule pressure is to the invading species, simply a measure of opportunity.

An ecological disturbance is any biotic or abiotic agent which causes a detectable change in an ecological system and either can be anthropogenic (Rykiel 1985). A disturbance is generally thought of as a discrete event in time (at least at the scale of the individual), which can have transient or permanent effects at this and other scales, such as the community (Rykiel 1985). As the ecological community is generally considered to be a function of the type, intensity, duration and periodicity of disturbance, collectively known as disturbance regime, to which it has been subject, changes in disturbance regime can alter structure and composition at community and landscape scales (Pickett et al. 1989). Grazing by introduced livestock (Jansen and Robertson 2001) and harvesting water for irrigation (Kingsford 2000) are ubiquitous and ongoing changes to the disturbance regime on the floodplains of the Murray Darling Basin.

A general theory of invasibility in plant communities, which incorporates the accepted role of disturbance in facilitating invasion, has been proposed based on the temporal fluctuation of resources (Sher and Hyatt 1999; Davis et al. 2000). Disturbance can either increase resource supply (e.g. flood), decrease resource demand (through mortality of adult plants), or both (e.g. fire). Invasive species may exploit this (temporary) resource surplus to become established.

Extricating broader patterns of invasibility from the effects of propagule pressure and disturbance using species richness data is difficult (Lonsdale 1999), due to the confounding of exotic species richness with native species richness, and the function of area, habitat diversity and latitude. For example, it has often been stated that the more species-rich habitats are more resistant to invasion, but Lonsdale (1999) found the global trend was that species-rich habitats tended to have more invasive species too. The explanation is that species richness is a function of habitat diversity and area, and we should expect large, diverse areas to contain more invasive species. However, it has been argued that at local scales there is a negative relationship between native species richness and invasive species richness (Shea and Chesson 2002). It seems intuitive to think that communities with very few (say, one) species present more invasion opportunities than species-rich communities (except that those additional species may themselves provide

new niches). Should we therefore expect monospecific stands of invasive species to be highly invasible? It remains unclear if high species richness *per se* prevents invasion or whether disturbance leads to greater invasion at the expense of native species. In either case, the problem with invasive species may be as much about biomass – resource utilisation – than species richness.

Even so, disturbance and the presence of propagules are not sufficient for invasion, as an invader must still have some advantage over the resident species (Shea and Chesson 2002). Such advantage need only occur at some times or some places, or can be simply due to better dispersal, i.e. the ability to find sites your competitors cannot. Specific traits of invaders, therefore, are just as important in invasion success as prevailing conditions.

1.1.3 Invasive plants

Of the 2739 alien plant species forming wild, self-sustaining populations in Australia (Randall 2007), 798 are considered to be causing major problems (Groves et al. 2003), directly costing the Australian economy between $A3.5 billion and $A4.5 billion per year (Sinden et al. 2004).

In the Murray Darling Basin alone, *Phyla canescens* is estimated to have invaded in excess of 5.3 million ha and cost the grazing industry at least $A38 million per annum (Earl 2003). The same report claims to calculate the monetary value of the environmental cost (in lost ecosystem services) of *P. canescens* invasions in the Murray Darling Basin. However, a closer examination of the procedure used (Earl 2003, p. 40) suggests that the $A1800 million per annum could be more accurately described as the cost of environmental services lost as a result of the loss of major floodplain wetlands of the Murray Darling Basin, not just the impact of *P. canescens*. The economic costing of ecosystem services remains an active area of research and beyond the scope of this thesis. Because invaders can cause such damage, a central aim of invasion ecology has been to predict which species are likely to become invasive next, so that their immigration can be prevented (e.g. Pheloung et al. 1999), or if already present if current populations are sufficiently small to be able to be eradicated (Simberloff 2003a).

A good predictor of invasiveness for a given species is a history of invasion elsewhere (Williamson 1999; Kolar and Lodge 2001). In addition, common and widespread species, particularly those of large native latitudinal range (Rejmanek 1995), and therefore with broad environmental tolerances, are more likely to become common and widespread (invasive) in new environments (Goodwin et al. 1999). Then in turn, they are more likely to be transported further (Cadotte et al. 2006). Invasion begets invasion. But is there something inherent in these species that makes them more invasive?

Baker (1974) suggested a list of characters for the 'ideal weed' (Table 1.1), but these characters have been criticised for their lack of predictive utility (Williamson 1993). More recently, a more statistical approach has been applied to the problem of identifying traits which may proffer invasiveness to plant species (see reviews by Kolar and Lodge 2001; Cadotte et al. 2006; Pysek and Richardson 2007). While these traits are more explanatory than predictive, they do mirror a number of Baker's earlier ideas (Table 1.1). Given that propagule pressure is of such importance in invasions, it is not surprising that there is also support for high fecundity being associated with invasiveness. However, while some of these traits are consistent, for example both seed longevity (Bekker et al. 1998) and fecundity (Henery and Westoby 2001) are correlated with seed size, other traits appear contradictory, such as ready germination and seedbank longevity (Baskin and Baskin 1989). Clearly a species does not require all such traits to be a successful invader (Williamson 1996).

Many of these traits are typical of *r*-selected species, i.e. coloniser species of early successional habitats, something which is perhaps not surprising given that the majority of plant invasions occur in disturbed habitats (Rejmanek and Richardson 1996), and that there is substantial overlap of colonisers and invaders (Williamson 1993). But are *r*-selected species inherently better invaders? Will future ecologists (say, in 1000 years), when the *K*-selected species have had time to establish, think *r*-selected species were more invasive, or just that they were faster at invading disturbed habitats?

Table 1.1 Comparison among 'ideal weed' characters (Baker 1974) and more recently recognised 'invasive' traits from: [1] Kolar and Lodge (2001), [2] Cadotte *et al.* (2006) and [3] Pysek and Richardson (2007).

Baker character	Invasive trait
1. Germination requirements fulfilled in many environments	Easy germination[3]
2. Discontinuous germination (internally controlled) and great longevity	Seed dormancy, seedbank and longevity[3]
3. Rapid growth through vegetative phase to flowering	High growth rate[3]
4. Continuous seed production for as long as growing conditions permit	Early and longer flowering period[3]
5. Self-compatible but not completely autogamous or apomictic	
6. When cross-pollinated, unspecialised visitors or wind utilised	
7. Very high seed output in favourable environmental conditions	High fecundity[3]
8. Produces some seed in wide range of environmental conditions; tolerant and plastic	
9. Has adaptations for short- and long-distance dispersal	
10. If a perennial, has vigorous vegetative reproduction or regeneration from fragments	Vegetative reproduction[1,2]
11. If a perennial, has brittleness, so not easily drawn from ground	Defoliation tolerance[3]
12. Has ability to compete interspecifically by special means (rosette, choking growth, allelochemicals)	

The lack of robust generalities in the search for 'invasive traits' may be because particular traits are only advantageous under particular conditions (e.g. Chapin et al. 1993). The prospect of finding a trait (or set of traits) to be universally invasive is clearly unrealistic.

Many studies have found traits correlated with invasiveness at local or regional scales (see list in Pysek and Richardson 2007). For example, in bushland around Sydney, Australia, invasive aliens were found to have larger specific leaf area than non-invasive aliens or resident native species (Lake and Leishman 2004). However, this may be symptomatic of the transition of previously sclerophyllous plant communities to rainforest, due to anthropogenic environmental change, i.e. decreased fire frequency, increased soil disturbance and water and nutrient enrichment, at such sites, rather than invasiveness *per se*; without these coincident environmental changes, would these same species be invasive here?

There also seems to be some taxonomic basis to invasiveness. This can be interpreted in a variety of ways. Related taxa are more likely to share traits, including traits which may promote invasion (above) or traits which may endear them to humans, and therefore led to increased propagule pressure (Heywood 1989; Kolar and Lodge 2001). Alternatively, if a taxon is absent from a locality, and subsequently invades that locality, there may be few natural predators preadapted to recognise or utilise it (in this sense, enemy release = novel weapons = inherent superiority).

1.1.4 Time since introduction

Time since introduction is also an important determinant of invasiveness (Cadotte et al. 2006). Short-lived species, such as annuals, will become locally extinct if they do not reproduce quickly. However, longer lived species, e.g. trees, may only need to reproduce once per century, so that the temporary absence of conditions suitable for recruitment, including mutualists, which may arrive later, does not preclude invasion, just defers it.

Of the 26 242 plant species known to have been introduced into Australia, 2739 (10.4%) have become naturalised, although there are a further 5907 species present in Australia, recognised as weeds elsewhere in the world, that are yet to become naturalised in Australia (Randall 2007). We cannot be certain that these 'sleeper' weeds will not awaken in the future, particularly in light of global climate change.

1.1.5 Stages of invasion

The process of invasion can be broken into stages, and different traits can be more or less important for the successful transition between particular stages (Theoharides and Dukes 2007). For higher plants, some appeal to humans is clearly the most important attribute in overcoming the barriers of the native range (e.g. Randall 2007). Once arrived at the new destination, preadaptation to abiotic conditions and anthropogenic disturbance appears most advantageous for becoming established (e.g. Cadotte et al. 2006). Biotic interactions may be the most significant barriers to becoming invasive (Theoharides and Dukes 2007), for example by being evolutionarily adaptable (Blossey and Notzold 1995). A further set of characters are advantageous in resisting deliberate control efforts, such as being difficult to detect (Cacho et al. 2006), being able to reproduce vegetatively, having a short pre-reproductive period, developing a persistent seedbank, and being difficult to kill (Panetta and Timmins 2004).

Such a high rate of failure among biological importations is perhaps not surprising, given the obstacles, such as:

1. hazards inherent in small population size, e.g. Allee effects, demographic, environmental and genetic stochasticity
2. potentially unsuitable abiotic conditions, e.g. climate
3. biotic or ecological resistance, i.e. resident species are better adapted to local conditions than the introduced species.

The risk of extinction for small populations has been studied intensively in the context of endangered species (e.g. Lande 1999). Captive breeding and reintroduction programs can be seen as deliberate attempts to overcome these risks by increasing the propagule

pressure of rare species. The same principles apply to the extinction or expansion of initially small populations of invading species. The risk of extinction of these initial small populations can apparently be overcome with more introduction events with larger inocula, thus emphasising the importance of propagule pressure (Leung et al. 2004; Drake and Lodge 2006).

Suitable abiotic (climatic) conditions are clearly a prerequisite for invasion (e.g. Scott and Panetta 1993). Cases such as the European rabbit, which upon introduction to Australia expanded into areas more arid than anywhere in its native range (Williamson 1996), may simply reflect that factors other than climate may be limiting a species' native range.

The biotic resistance hypothesis is invoked to explain everything else, i.e. the failure of an introduction despite apparent climatic suitability and sufficient propagule pressure. The set of exceptions to the biotic resistance hypothesis (i.e. successful invaders) has itself become suitable habitat for a number of competing hypotheses (see list in Hufbauer and Torchin 2007). However, many of these hypotheses, such as the biotic resistance hypothesis itself, are used as retrospective explanations rather than predictive models.

Sometimes the introduced species can be at a particular advantage when they are introduced without the burden of predatory, parasitic or pathogenic organisms from their home range (Torchin and Mitchell 2004). This release from natural predators is thought to be a major driver in the success of invasive species. It is the fundamental premise behind the use of biological control agents; invasive populations can be modulated by the introduction of predators and pests which selectively attack the invasive organism.

1.2 Management of invasive species

The management of invasive species is therefore of major importance in both primary production and biodiversity conservation (Hobbs and Humphries 1995). Management interventions fall into two categories. Intensive management targets the invasive species itself, and includes standard weed management interventions, such as herbicide application, physical removal, and solarisation. Extensive management involves

modifying the habitat such that it is less favourable for the invasive species and more favourable for desirable species. Such approaches include the use of grazing, fire, fertiliser, irrigation or flooding. The use of the terms intensive and extensive here is deliberate, to align these management interventions with land use types.

Intensive management options are particularly suited to, and indeed predominantly used in, intensive land use types, such as annual cropping systems (Powles and Bowran 2000). They are also appropriate for small and isolated populations of invasive species (Simberloff 2003b), where some specific value, such as an endangered species, is threatened, or in preparation for the establishment of more or less permanent stands of desirable vegetation (e.g. forestry, Hall 2000).

In extensive, low-input primary production systems (e.g. rangelands) and biodiversity conservation areas, where invasive species may already be widespread and abundant and beyond any reasonable (i.e. economically feasible) hope of extirpation, extensive management approaches may be the only sustainable options. However, to be effective, such extensive management systems must rely not only on robust knowledge of the invasive species but also other species of the attendant community, particularly how they will respond to proposed management regimes, and the reasons behind the vulnerability to invasion in the first place (Mack et al. 2000).

1.3 *Phyla canescens*

In much of the Murray Darling Basin, *P. canescens* has clearly become widespread and dominant, forming 'stage V' populations, according to the 'neutral terminology' of Colautti and MacIsaac (2004), apparently due to repeated introductions to ideal habitats. While it may be appealing to consider targeting the weak-point in the life-cycle of such invasive species, it is unlikely that management that concentrates on a single point in the life-cycle will be successful. If only a single intervention were required, the species is perhaps more likely to be endangered than invasive! More realistically, successful management of dominant invasive species is likely to derive from a strategy of coordinated targeting of multiple points in the life-cycle, including increasing

competition from desirable species, consistent with the principles of 'integrated weed management' (e.g. Sindel 2000).

The lack of information on the fundamental life-history of *P. canescens* is recognised as a substantial limitation to its effective management (e.g. McCosker 1994b; Lucy et al. 1995; Earl 2003; Leigh and Walton 2004). The experiments reported in this thesis quantify, for the first time, aspects of the seed and recruitment ecology of *P. canescens*. Although *P. canescens* can reproduce both vegetatively and from seed (McCosker 1994a), as illustrated in Figure 1.1, this thesis is primarily concerned with reproduction from seed. The general rationale for focusing on seed biology rather than vegetative reproduction is simply that seeds are smaller, more abundant, longer lived and more mobile than vegetative fragments. Strategies effective for managing seed reproduction will substantially encompass vegetative recruitment, whereas management approaches that capture fragments may 'leak' seeds.

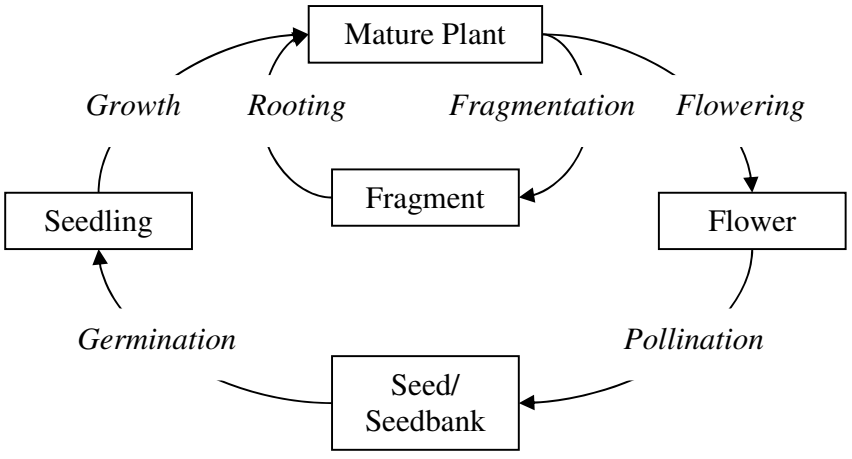


Figure 1.1 Generalised life-cycle of *Phyla canescens* showing reproduction from both seed and vegetative fragments.

1.4 Thesis structure

While there are two recent reviews of the Australian literature concerning *P. canescens* (Earl 2003; Leigh and Walton 2004), both omit a substantial proportion of the native range literature (mostly from Argentina). Chapter 2 integrates these disparate but complementary sources of information.

A substantial source of uncertainty encountered during this literature review was due to the complicated taxonomic history of *P. canescens*. Cognisant of this uncertainty, and the frequent and ongoing misidentification within the genus (Hosking et al. 1996), a review of *Phyla* specimens held at all Australian state and territory herbaria was undertaken. The principal objective was to become familiar with the phenotypic variation and the currently accepted treatment (Munir 1993) of the genus in Australia, but this study also revealed some historical, geographical and ecological insights (Chapter 3).

The bulk of the thesis is thereafter concerned with laboratory and field experiments, with the aim of better understanding the recruitment biology of *P. canescens*. The field sites were situated in two adjacent catchments of the northern New South Wales (NSW) sector of the Murray Darling Basin (described in detail in Chapter 4). Chapter 5 provides information on the germination requirements of *P. canescens* seed, with the objective of determining suitable conditions for subsequent fecundity and seedbank experiments. An ecological interpretation of these germination requirements is also presented. Chapter 6 reports on the variation in seed production with season and site conditions. Chapter 7 looks at the longevity of the soil-stored seedbank, and Chapter 8 examines the response of *P. canescens* (and associated species) to soil disturbance in different seasons, and the opportunistic survey of recruitment following a winter flood.

The final chapter (Chapter 9) synthesises these findings with previous studies on *P. canescens* and broader invasion ecology theory. Management options are explored in the context of this new information and ongoing research into *P. canescens*, including the search for biocontrol agents (Julien et al. 2004).

Chapter 2

Taxonomy, distribution and biology of *Phyla canescens*

Literature relevant to *Phyla canescens* (Kunth) Greene is reviewed. The taxonomic and nomenclatural history of the species is necessary to define the subject adequately. A description of the current known world distribution and native range illustrates the broad relevance of this study. The habitat and ecology of *P. canescens* in Australia and in its native range in South America, and the phytochemistry and potential allelopathy of *P. canescens* and related species, is also discussed.

2.1 Taxonomy

There is considerable confusion among the species of the genus *Phyla* and with other genera of Verbenaceae. Species are placed in *Phyla* by some authors and *Lippia* by others. This situation is not helped by the use of 'lippia' as a common name for species which are no longer considered to belong to genus *Lippia*. Such confusion casts doubt over the identity of species in previous studies.

2.1.1 Verbenaceae

The Verbenaceae has recently undergone substantial revision, with many genera transferred to Lamiaceae (Cantino 1992a; Cantino 1992b). This narrower concept of the family includes: 6 tribes, 34 genera and 1100–1200 species (Atkins 2004, Table 2.1). Stevens (Stevens, P. F. 2001) included 35 genera in the family (adding *Stylodon*, and replacing *Pitraea* with *Castelia*), without any mention of infrafamilial taxa or total number of species. The vast majority of genera and species are restricted in their distribution to the Americas. The genera with the largest number of species are: *Verbena*, 200–250 spp.; *Lippia*, *c.* 200 spp. and *Lantana*, *c.* 150 spp. (Stevens, P. F. 2001; Atkins 2004). There are 130 taxa in the Verbenaceae recorded as invasive (Randall 2002), including some of the world's most abundant and widespread weeds, such as *Lantana camara* L. and *Citharexylum spinosum* L. (Global Invasive Species Database 2006) and several widespread *Verbena* spp.

Table 2.1 Tribes, genera and species richness within Verbenaceae (Atkins 2004), number of invasive taxa recorded globally (Randall 2002), geographic origin of each genus (Atkins 2004), and number of species in Australia (Australian Plant Census 2006; Randall 2007).

Tribe	Genus	Species	Invasive taxa	Origin	Taxa in Australia
Casselieae	*Casselia*	11	–	South America	–
	Parodianthus	2	–	South America	–
	Tamonea	6–7	1	Americas	–
Citharexyleae	*Citharexylum*	~130	4	Americas	7
	Rehdera	3	–	Central America	–
	Verbenoxylum	1	–	South America	–
	Rhaphithamnus	2	–	South America	2
	Baillonia	1	–	South America	–
	Recordia	1	–	South America	–
	Duranta	~20	2	Americas	4
Lantaneae	*Acantholippia*	~6	–	South America	–
	Aloysia	~30	4	Americas	2
	Bouchea	~9	3	Americas	–
	Chascanum	~27	–	Africa & Asia	–
	Diostea	1	–	South America	1
	Lampaya	2–3	–	South America	–
	Lantana	~150	17	Pantropical	4
	Lippia	~200	14	Americas & Africa	3
	Nashia	7	–	Central America	1
	Neosparton	4	–	South America	–
	Phyla	~15	10	Mostly Americas	3
	Stachytarpheta	~90	16	Americas	4
	Xeroaloysia	1	–	South America	–
Petreeae	*Petrea*	~11	2	Americas	4
	Xolocotzia	1	–	Central America	–
Priveae	*Priva*	~20	7	Asia, Africa & America	—
	Pitraea	1	1	South America	–
	Dipyrena	1	–	South America	–
Verbeneae	*Glandularia*	~100	9	Americas	7
	Hierobotana	1	–	South America	–
	Junellia	~50	1	South America	–
	Urbania	1	–	South America	–
	Verbena	200–250	39	Cosmopolitan	19
Incertae sedis	*Coelocarpum*	5	–	Africa	–
Total	34	1100-1200	130	Mostly Americas	63

There are approximately 65 taxa of Verbenaceae recorded for Australia, with representatives from 13 genera (Table 2.2). Three of these taxa are considered native: *Verbena gaudichaudii* (Briq.) P.W.Michael; *V. macrostachya* F.Muell. (both described in Michael 1997); and *V. officinalis* L. var. *monticola* Munir, which is 'endemic in Victoria' (Munir 2002). A further two species are cryptogenic, their origin uncertain, but probably including both indigenous and introduced elements. These two species are *Verbena africana* (R.Fern. & Verdc.) P.W.Michael, which Michael (1997) states: 'I think, is native in Australia'; and *Phyla nodiflora* (L.) Greene, which is 'probably introduced' (Munir 1993). The remaining 60 taxa are all known to have been introduced; of these 25 have naturalised, and 35 are not known to form self-sustaining populations in Australia. A further 17 taxa are recorded as weeds elsewhere in the world (Randall 2007).

Most plant species that have become naturalised in Australia have been deliberately introduced for use as ornamental garden plants. Sixty-five percent of recorded new incursions in Australia for the period 1971–1995 were introduced for horticultural purposes (Groves 1997). This is likely to have been the route of introduction for *P. canescens*. Plants of *Phyla* were advertised for sale in nursery catalogues in Melbourne in 1886 (Brookes and Barley 1992) and *P. canescens* continues to be sold at nurseries and garden retailers, invariably labelled '*Phyla nodiflora*' (Figure 2.1).

Figure 2.1 *Phyla canescens* sold as '*Phyla nodiflora*' in a commercial hardware and garden centre, Bendigo, Victoria, 3 January 2008.

Table 2.2 Verbenaceae in Australia, with weed status (recorded as a weed somewhere in the world) and whether naturalised in Australia (Randall 2007). Taxa with * are introduced, those with ? are cryptogenic. Nomenclature follows the International Plant Names Index (International Plant Names Index 2006) where it differs from Randall (2007).

	Taxon	Weed?	Naturalised?
*	*Aloysia citriodora* Paláu	✓	–
*	*Aloysia triphylla* Britton	✓	–
*	*Citharexylum berlandieri* B.L.Rob.	–	–
*	*Citharexylum caudatum* L.	✓	–
*	*Citharexylum cinereum* L.	–	–
*	*Citharexylum hidalgense* Moldenke	–	–
*	*Citharexylum montevidense* Moldenke	–	–
*	*Citharexylum myrianthum* Cham.	–	–
*	*Citharexylum spinosum* L.	✓	✓
*	*Diostea juncea* Miers	–	–
*	*Duranta erecta* L.	✓	✓
*	*Duranta lorentzii* Griseb.	–	–
*	*Duranta mutisii* L.f.	–	–
*	*Duranta stenostachya* Tod.	–	–
*	*Glandularia aristigera* (S.Moore) Tronc.	✓	–
*	*Glandularia* X *hybrida* (Groenl. & Rumpler) G.L.Nesom & Pruski	✓	–
*	*Glandularia laciniata* (L.) Schnack & Covas	✓	–
*	*Glandularia peruviana* (L.) Small	✓	–
*	*Glandularia pulchella* (Sweet) Tronc.	✓	–
*	*Glandularia tenera* (Spreng.) Cabrera	✓	–
*	*Lantana camara* L. var. *camara*	✓	✓
*	*Lantana crocea* Jacq.	✓	–
*	*Lantana montevidensis* (Spreng.) Briq.	✓	✓
*	*Lantana trifolia* L.	✓	–
*	*Lippia alba* (Mill.) N.E.Br. ex Britton & P.Wilson	✓	✓
*	*Lippia chamaedrifolia* Steud.	–	–
*	*Lippia graveolens* Kunth	–	–
*	*Nashia inaguensis* Millsp.	–	–
*	*Petrea arborea* Kunth	–	–
*	*Petrea glandulosa* Pittier	–	–
*	*Petrea rugosa* Kunth	–	–
*	*Petrea volubilis* L.	✓	–
*	*Phyla canescens* (Kunth) Greene	✓	✓
?	*Phyla nodiflora* (L.) Greene var. *nodiflora*	✓	✓
*	*Phyla dulcis* (Trevir.) Moldenke	✓	–
*	*Rhaphithamnus cyanocarpus* Miers	–	–
*	*Rhaphithamnus spinosus* (Juss.) Moldenke	–	–
*	*Stachytarpheta* X *adulterina* Urb. & E.Ekman	✓	✓
*	*Stachytarpheta cayennensis* (Rich.) Vahl	✓	✓
*	*Stachytarpheta jamaicensis* (L.) Vahl	✓	✓
*	*Stachytarpheta mutabilis* (Jacq.) Vahl	✓	✓
*	*Stachytarpheta* X *trimenii* Rech.	✓	✓

Table 2.2 (continued)

	Taxon	Weed?	Naturalised?
?	*Verbena africana* (R.Fern. & Verdc.) P.W.Michael		
*	*Verbena aristigera* S.Moore	✓	✓
*	*Verbena bonariensis* L.	✓	✓
*	*Verbena brasiliensis* Vell.	✓	✓
*	*Verbena caracasana* Kunth	✓	✓
*	*Verbena chamaedrifolia* Juss.	✓	
	Verbena gaudichaudii (Briq.) P.W.Michael		Indigenous
*	*Verbena hastata* L.	✓	
*	*Verbena hispida* Ruiz & Pavón	✓	
*	*Verbena* X *hybrida* Groenland & Rümpler	✓	
*	*Verbena incompta* P.W.Michael	✓	✓
*	*Verbena incompta* P.W.Michael X *Verbena litoralis* Kunth	✓	✓
*	*Verbena laciniata* (L.) Briq.		
*	*Verbena litoralis* Kunth	✓	✓
	Verbena macrostachya F. Muell.		Indigenous
*	*Verbena officinalis* L. var. *officinalis*	✓	✓
	Verbena officinalis L. var. *monticola* Munir		Indigenous
*	*Verbena patagonica* Spreg.		
*	*Verbena quadrangularis* Vell.	✓	✓
*	*Verbena rigida* Spreng. var. *rigida*	✓	✓
*	*Verbena supina* L.	✓	✓
*	*Verbena urticifolia* L.	✓	✓
*	*Verbena venosa* Gillies & Hook.	✓	

2.1.2 *Phyla* Lour.

Loureiro (1790) proposed the genus *Phyla* when he described *Phyla chinensis* Lour. Linnaeus (1753) had previously described *Verbena nodiflora* L., referring to earlier work, and *Lippia americana* L., which he described for the first time. *Phyla chinensis* is now considered synonymous with *V. nodiflora*, therefore Loreiro's circumscription of *Phyla* is based on the lectotype of *V. nodiflora*. Michaux (1803) proposed that *V. nodiflora* and *L. americana* belonged to the same genus. Linnaeus' broad circumscription of *Verbena* was not maintained and the species of *Verbena* described before *V. nodiflora* had precedence to the generic name *Verbena*. Michaux (1803), therefore, transferred *V. nodiflora* to *Lippia*, apparently ignorant of Loureiro's (1790) description of the genus *Phyla.* When Kunth (1818) described *Lippia canescens* Kunth, he was either unaware of the distinction between *Phyla* and *Lippia*, or considered them synonymous. The current taxon concepts were established when Greene (1899) formalised the distinction between the genera,

noting that species of *Phyla* are 'creeping perennial herbs', whereas '*Lantana* and *Lippia* are coarse rough-leaved shrubs'. He transferred *L. canescens* and *L. nodiflora* to the genus *Phyla*.

The genus *Zapania* Lamarck (1791) is a later synonym of *Phyla*. Lamarck (1791) proposed the genus as *Zapania nodiflora* Lam., with *Verbena nodiflora* L. as the type, just one year after Loureiro had published *Phyla* (Loureiro 1790).

Phyla is a relatively small genus. Different authors have reported different numbers of species for the genus: Kennedy (1992) lists nine, Munir (1993) 'about 11', Mulgura de Romero (2002) suggests 10 and Atkins (2004) 'about 15'. However, the latter three publications do not provide a full list of species, so the main source for this review is Kennedy (1992). The International Plant Names Index (International Plant Names Index 2006) lists 20 species combinations in the genus, including one hybrid. Kennedy (1992) accounted for all of these combinations (as synonyms of one or other of the nine species) except the hybrid *Phyla* x *intermedia* Moldenke, which is apparently a hybrid of *P. lanceolata* (Michx.) Greene and *P. nodiflora* (L.) Greene. (see Appendix 1 for complete list of *Phyla* species and synonyms). Kennedy also argued that specimens of *P. reptans* (Kunth) Greene are hybrids of *P. nodiflora* (L.) Greene and *P. fruticosa* (Miller) K.Kenn. ex Wunderlin & B.F.Hansen, being found only within the range of *P. fruticosa*, the more geographically restricted of the two parents (Kennedy 1992).

Three of the nine species of *Phyla* have been recorded naturalised outside the Americas (Table 2.3). *Phyla lanceolata* has apparently only been collected once in the eastern hemisphere (i.e. outside the Americas), from Mont Cenis, southern France in 1891 (Kennedy 1992). The two most widespread species, *P. nodiflora* and *P. canescens*, are found in Australia (Munir 1993). Randall (2007) also listed *P. scaberrima* (Juss. ex Pers.) Moldenke, a synonym of *P. dulcis* (Trevir.) Moldenke (Kennedy 1992), as present, but not yet naturalised in Australia (Table 2.2).

Table 2.3 Current world distribution of nine species of *Phyla* (from Kennedy 1992).

Species	Current Distribution
Phyla betulaefolia (Kunth) Greene	Central and South America, Cuba to Argentina
Phyla canescens (Kunth) Greene	All continents except Antarctica
Phyla cuneifolia (Torrey) Greene	Central and western USA
Phyla dulcis (Trevir.) Moldenke	Americas, southern USA to northern Argentina
Phyla fruticosa (Miller) K. Kenn. ex Wunderlin & B.F.Hansen	Americas, Florida to Colombia
Phyla lanceolata (Michx.) Greene	USA, Europe
Phyla linearis (Kunth) Troncoso & Lopez-Palacios	Venezuela
Phyla nodiflora (L.) Greene	All continents except Antarctica
Phyla stoechadifolia (L.) Small	Americas, Florida to Venezuela

2.1.3 *Phyla nodiflora* and *Phyla canescens*

Phyla nodiflora has long been a widespread and familiar species, even before being described (as *Verbena nodiflora*) in the seminal work of modern botany (Linnaeus 1753). *Phyla canescens* was first described (as *Lippia canescens*) from a collection by Bonpland from Truxillo (Trujillo), Peru (Kunth 1818). Both species acquired their currently accepted combinations through Greene's (1899) restoration of 'neglected generic types'.

The first Australian publication to use the specific epithet *canescens*, albeit as *Lippia canescens* Kunth, was 'Flora of South Australia' (Black 1929) in a list of 'alien but scarcely naturalised plants'. However, most major Australian botanical texts refer only to *P. nodiflora* (e.g. Bentham 1870; Cunningham et al. 1981; Beadle 1984; Munir 1986; Conn 1992) or *P. nodiflora* var. *nodiflora* (Stanley and Ross 1986), but some refer to *P. nodiflora* var. *canescens* (e.g. Willis 1972; Ross 1993). Since a taxonomic revision of

the genus by Munir (1993), the name *Phyla canescens* has come into widespread use (e.g. Conn 1999).

Therefore, it is often unclear in the literature to which species, *P. canescens* or *P. nodiflora* (as they are currently accepted), is being referred. This and related issues, including the morphological differences between *P. canescens* and *P. nodiflora*, are addressed in Chapter 3.

2.2 Distribution of *Phyla canescens*

2.2.1 Native range: South America

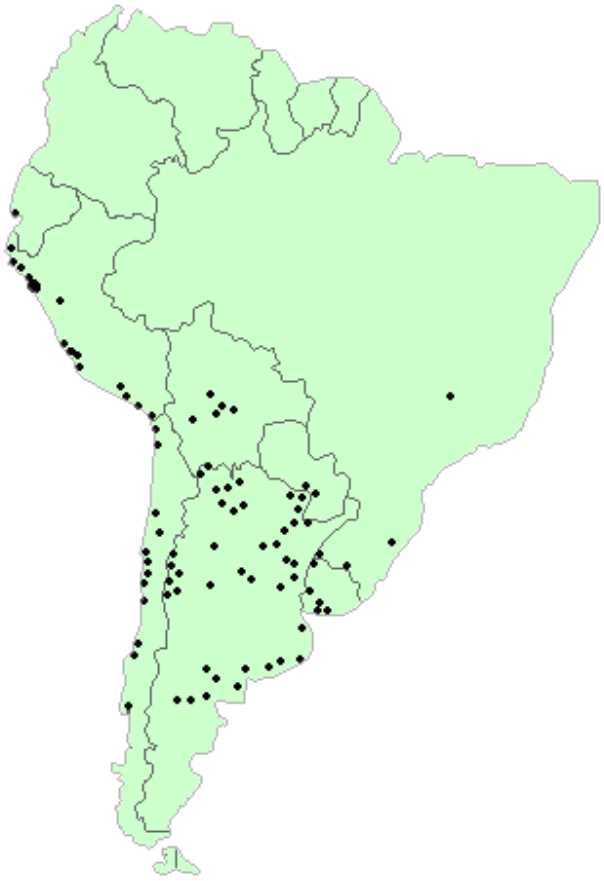
Phyla canescens is indigenous to sub-tropical and temperate South America (Figure 2.2), where it is apparently quite common and widespread in areas subject to seasonal flooding or adjacent to more permanent water-bodies. There are records from Argentina, Bolivia, Brazil, Chile, Ecuador, Paraguay, Peru and Uruguay (Kennedy 1992). Even within South America, there is evidence that the range of *P. canescens* is expanding (Conticello and Bustamante 2001).

2.2.2 World

Since at least the late 1800s, *P. canescens* has been promoted as a hardy garden plant, and still is in many places, including Australia. This has apparently led to its introduction to every continent (except Antarctica, Table 2.4). At many of these recipient sites *P. canescens* has become naturalised.

Phyla canescens was recorded as a component at four of six sites studied in the floodplain of the Guadiana River, Portugal (Aguiar et al. 2006). It was considered to be a dominant species of 'infrequently flooded' landforms, and was also a component of 'frequently flooded' and 'rarely flooded' landforms. All sites were impacted by livestock grazing.

Figure 2.2 Distribution of *Phyla canescens* in South America. The larger black dot on the west coast indicates the location of collection of the type specimen.



Redrawn from Kennedy (1992).

Table 2.4 The world distribution of *Phyla canescens* by continent, country and region. * Indicates type locality.

Continent	Country	Region	Reference
Africa	Algeria	Constantine	(Kennedy 1992)
	Botswana	Savuti River	
	Egypt	Abu Matamir	
	Guam	Nas Agana	
	Senegal	Dakar	
	South Africa	Cape Province	
Asia	Afghanistan	Jagdalek	(Kennedy 1992)
	Iraq	Mosul	(Townsend 1972)
Europe	France	Montblanc	(Kennedy 1992)
		Montpellier	(Tutin 1972)
		Corsica	
	Italy	Mainland	(Tutin 1972)
		Sardinia	
		Sicily	(Kennedy 1992)
	Portugal		(Tutin 1972)
			(Aguiar et al. 2006)
	Spain	Andalusia	(Kennedy 1992)
		Balearic Islands	(Tutin 1972)
		Toledo	(Hernandez 1985)
North and Central America	Mexico	Hildago	(Kennedy 1992)
		Jaltepec	
		Mexico	
		Valle De Mexico	
	USA	California	
		Hawaii	
		Nevada	
		North Carolina	
		Utah	
Oceania	Australia	South Australia	(Kennedy 1992)
	New Zealand	Prebbledon	
South America	Argentina	Buenos Aires	(Kennedy 1992)
		Catamarca	
		Chaco	
		Cordoba	
		Corrientes	
		Entre Rios	
		Formosa	
		Jujuy	
		La Rioja	
		Mendoza	
		Salta	
		Rio Negro	
		San Luis	
		Santa Fé	
		Santiago Del Estero	
		Tucuman	

Table 2.4 (continued)

Continent	Country	Region	Reference
South America* (continued)	Bolivia	Cochabamba	
		Santa Cruz	(Kennedy 1992)
		Tarija	
	Brazil	Rio Grande Do Sul	(Kennedy 1992)
	Chile	Arauco	(Kennedy 1992)
		Arica	
		Atacama	
		Concepcion	
		Coquimbo	
		Curico	
		Santiago	
		Tarapaca	
		Valdivia	
		Valparaiso	
	Ecuador	Galapagos	(Svenson 1935)
		Guayas	(Kennedy 1992)
	Paraguay	Rio Paraguay	(Kennedy 1992)
	Peru*	Ancash	(Kennedy 1992)
		Arequipa	
		Callao	
		Chosica	
		Huanoco	
		La Libertad*	(Kunth 1818) *
		Lambayeque	(Kennedy 1992)
		Lima	
		Piura	
		Tachna	
	Uruguay	Antigas	(Kennedy 1992)
		Florida	
		Montevideo	
		Rocha	
		Soriano	
		San Jose	

2.3 Biology of *Phyla canescens*

2.3.1 Ecology in Australia

There are several studies on the ecology of *P. canescens* in Australia, particularly within the Murray Darling Basin. The bulk of this literature is aimed at characterising flooding regimes associated with various components of riverine vegetation. Invasive species, including *P. canescens* are inevitably part of this vegetation.

Lower River Murray

In the Lower River Murray, between the confluence with the Darling River and the river mouth, Blanch *et al*. (1999) investigated the tolerance of a range of riverine plants to various flooding and exposure regimes. They found *P. canescens* to 'prefer' infrequently flooded sites. These sites were flooded from between 87 and 164 days out of the previous 730 days, with exposures of equal to, or greater than, 100 cm above water level for between 228 and 470 days out of 730. The longest time continuously without flood for sites with *P. canescens* was between 283 and 313 days. Therefore, these 'infrequently flooded' sites, which were between one and three metres above the weir pool level, were flooded at least annually in this study.

Another study from the same region, but across several weir pools, characterised the distribution of *P. canescens* as being typical of a floodplain species, with greater abundance scores at higher elevations (Blanch et al. 2000). The maximum elevation in this study was approximately six metres above pool level.

In comparing the distribution and habitat of *P. canescens* with a native perennial rhizomatous grass, *Sporobolus mitchellii* (Trin.) S.T.Blake, there was little overlap in the habitats occupied by the two species (Taylor and Ganf 2005). *Sporobolus mitchellii* tended to occupy sites with significantly higher soil electrical conductivity, finer textured surface soil and higher soil water content at 50–100 cm soil depth than sites with *P. canescens*. However, there was no significant difference between the minimum river discharge required for inundation of sites dominated by the two species. In potted plant-plant interactions, where water and nutrients were not limiting, final biomass of

Sporobolus mitchellii was unaffected by initial density (≥25%), or by the presence of *P. canescens*. However, final biomass of *P. canescens* was significantly lower with any initial density of *Sporobolus mitchellii* greater than or equal to 25%, than in pots without *Sporobolus mitchellii*. In small artificial wetlands, potted plants of both species were subject to two flooding regimes, one static (analogous to the currently regulated river) and the other ostensibly simulating a spring flood (analogous to a potential environmental flow). *Sporobolus mitchellii* had a higher growth rate than *P. canescens* under both regimes, but particularly under the static regime. It was suggested that this may be an artefact of the timing of the experiment, conducted in the warmer part of the year, and that this relationship may not hold under cooler temperatures. Regardless, relative growth rates are not necessarily good predictors of competitive outcomes (Harper 1977, p. 15).

Northern Darling River

In the north of the Murray Darling Basin, most work on *P. canescens* has centred on the Gwydir Wetlands. McCosker (1994a) conducted a soil seedbank study to determine if there were sufficient propagules of native wetland plants to re-establish a diverse vegetation community following delivery of environmental water allocations (artificial floods). The density of *P. canescens* seedlings varied across the four study sites from just 48 m^{-2} to 1128 m^{-1}. In a glasshouse comparison of the response of *P. canescens* and the native perennial rhizomatous wetland grass *Paspalum distichum* L., it was found that while *P. canescens* flowered while inundated to a depth of 1 cm, it grew poorly relative to *Paspalum distichum*. When flooded to 10 cm, *P. canescens* survived but barely grew, while *Paspalum distichum* grew prolifically. At the deepest water level in the study, 20 cm, both species survived but growth was minimal. In an extension of this work, Hobson (1999) investigated some broader competitive interactions between *P. canescens* and *Paspalum distichum*. In glasshouse trials, *P. canescens* had a higher relative growth rate at sites above water level, while *Paspalum distichum* had a higher relative growth rate when growing from shallowly submerged substrate (less than 20 cm). However, it should be noted that species distribution is better correlated with survival of flood events, rather than loss of biomass during flooding or rate of biomass recovery following flood subsidence, at least for perennial meadow species (van Eck et al. 2004).

In a later study of the Gwydir Wetlands, Mawhinney (2003) found *P. canescens* to be indicative of sites with a 'dry' long-term water regime. It was also suggested that by reintroducing a 'wetter' water regime, the native species *Paspalum distichum* and *Eleocharis plana* S.T.Blake would come to dominate some areas currently dominated by *P. canescens*, with the caution that this is likely to increase the abundance of another seriously invasive species, *Eichhornia crassipes* (Mart.) Solms.

Fensham (1998) studied the effects of grazing on the vegetation of the Darling Downs of south-eastern Queensland. It was concluded that *P. canescens* was associated strongly with flood-prone riverine grasslands with 81.8% frequency at sites with a mean elevation of 1.3 m above the nearest major waterway. *Phyla canescens* was also present in grassland (16.0%) and poplar box woodland (12.8%) of slightly higher elevation, 27.5 m and 27.9 m respectively, but was completely absent from all hill woodland sites with mean elevation of 103.4 m. *Phyla canescens* was recorded as one of very few introduced species capable of displacing native species without the aid of mechanical disturbance. No significant relationship was evident between the abundance of *P. canescens* and grazing intensity (Fensham 1998).

2.3.2 Ecology in South America

While there have been two recent Australian literature reviews of the biology of *P. canescens* (Earl 2003; Leigh and Walton 2004), neither have included work from its native range.

There is a substantial descriptive literature of the vegetation of South America. Some of these refer to *P. canescens*, which is apparently widespread and common in a variety of wetland/grassland/savannah assemblages, particularly in the Río de la Plata grassland region of northern Argentina, Uruguay and southern Brazil. The region is subdivided into the 'pampa' of the Argentine provinces of Buenos Aires, Entre Ríos, Santa Fé, Córdoba, La Pampa and San Luis and the 'campos' of Uruguay and southern Rio Grande do Sul, Brazil. *Phyla canescens* is listed as a characteristic component of vegetation of Rolling Pampa and Flooding Pampa in Argentina (Soriano et al. 1992).

Flooding Pampa

The majority of the relevant literature relates to the Flooding Pampa. The Flooding Pampa is a topographically flat region with endoreic or areic drainage, experiencing flooding most years and major flooding approximately each decade (Garbulsky and Deregibus 2004). This region has been relatively intensively studied because it is close to the major centre of Buenos Aires, and is less amenable to cropping because of the frequent and prolonged floods. Therefore, it still consists predominantly of native vegetation, albeit in a derived state. Other areas of the pampa and campos have been more heavily modified by intensive agriculture (Soriano et al. 1992).

Within the Flooding Pampa grasslands, Perelman *et al*. (2001) found *P. canescens* to be one of only six generalist species occurring in all eleven of the recognised community types. In a study of the structural role of *Paspalum quadrifarium* Lam., which is thought to have been the dominant species across much of the pampa (Perelman et al. 2003), *P. canescens* was found to be one of only three species with 100% frequency across three vegetation clusters. These clusters were related to vegetation units of the Flooding Pampa delineated in Perelman *et al.* (2001). The percent cover of *P. canescens* was highest in a group of sites aligned to Humid Prairies (extensive lowlands, subject to flooding), at an intermediate level of cover in Mesophytic Meadows (relatively elevated, convex terrains with well drained soils), and lowest cover in Halophytic Steppes (saline depressions, Perelman *et al.* 2001).

Lewis *et al*. (1985), studying the vegetation communities of south-eastern Santa Fé (Argentina), found *P. canescens* in 6 of the 21 identified communities. They considered *P. canescens* to be characteristic of three *Stipa* (now *Nassella*) dominated grasslands and related communities. Interestingly, *P. canescens* grew with *Paspalum distichum* L. in three communities, although the latter species was characteristic of more hydrophilous communities. This is a very similar relationship to that found in some Australian situations between these same two species (McCosker and Duggin 1993; Mawhinney 2003).

Saltmarshes

In studying the vegetation relationships in a saltmarsh landscape of central Argentina (west of Buenos Aires), Cantero *et al.* (1998) found *P. canescens* associated with higher relative topographic positions in areas where the (saline) water table was at greater depth. In contrast, Taboada *et al*. (1998), studying the deterioration of pastures of the introduced *Elytrigia elongata* (Host ex Beauv.) Nevski, included *P. canescens* only in the list of species characteristic of the lowest topographic zone studied. This zone was also considered to be subject to the longest inundation, as well as highest levels of salinity.

Ant-hills

Of the 23 vegetation communities of the Great Chaco (Argentina), *P. canescens* was common in seven (Lewis et al. 1990). From these same data, *P. canescens* was present in 14 of the 16 vegetation communities in which ant-hills (typically 0.6 m high and 1.0 m diameter) of *Camponotus punctulatus* (Mayr.), subfamily Formicinae, were located (Lewis et al. 1991). It is possible that *P. canescens*, and associated species, may have survived on these mounds when the surrounding floodplain was inundated. However, no information was provided regarding the degree of flooding in the different communities during the study period.

Vizcacha

When examining the influence of the burrow system (vizcachera) of the herbivorous rodent vizcacha, *Lagostomus maximus,* in wetland vegetation in the Paraná River delta of Entre Ríos Province, Argentina, Arias *et al.* (2005) found *P. canescens* to be one of four species dominating the areas of high rodent activity. The dominance of *P. canescens* and *Dichondra microcalyx* (Hallier) Fabris. on the vizcacheras was attributed to the planiform habit of these species, such that they incurred less defoliation under such high impact conditions. The authors also refer to the dietary preference of vizcacha, graminoids, thus allowing dicotyledonous species, such as *P. canescens*, to dominate. However, whether this dominance was a result of low growth habit or due to low palatability was not investigated. It was also noted that *P. canescens* was less abundant outside the areas of intensive grazing, where taller graminoids dominated (Arias et al. 2005).

Greater rhea

In a study of the habitat use of a population of greater rhea (*Rhea americana*) on a cattle ranch in Buenos Aires Province (Argentina), Herrera *et al*. (2004) suggested rheas preferred areas adjacent to streams, with a higher percentage cover of a suite of species forming a low 'lawn'. This 'lawn' included *P. canescens*, as well as *Bupleurum* sp., *Lolium multiflorum* Lam., *Plantago lanceolata* L., *Sida leprosa* (Ortega) K.Schum., *Stenotaphrum secundatum* (Walter) Kuntze, *Stipa* spp. and *Trifolium repens* L. The general preference by rheas for areas of low vegetation height was used to explain the observations. Habitat use was determined by faecal-pellet counts in 10 m x 10 m quadrats. This may have biased the results somewhat toward areas of low vegetation simply by the relative ease with which faeces may be detected in these areas, compared with tall, dense swards of vegetation. However, earlier work had found that in summer, the diet of rheas consisted primarily of low-growing dicots such as *P. canescens* and *Plantago lanceolata* (Yagueddú and Viviani Rossi 1985). Such species tend to be less prevalent in areas dominated by various tall sward-forming monocots.

Livestock grazing

There have also been several experiments in which livestock grazing was manipulated. In general, the abundance of *P. canescens* decreased when grazing was excluded from previously grazed sites, and increased again when grazing was resumed (Table 2.5).

Table 2.5 Response to disturbance in studies of *Phyla canescens* from Argentina

Disturbance type	Response of *Phyla canescens*	Reference	Community as per Sala *et al*. (1986)
Exclusion of constant grazing	Decrease ↓	Sala *et al.* (1986) Facelli *et al.* (1989) Chaneton *et al.* (2002)	Lowland
Reintroduction of constant grazing	Increase ↑	Facelli (1988)	Upland
Prolonged flooding in grazed area	Increase ↑	Chaneton *et al.* (1988)	Lowland
Prolonged flooding in ungrazed area	Decrease ↓	Chaneton *et al.* (1988)	Lowland
Fertiliser application	Increase ↑	Collantes *et al.* (1998)	?

Phyla canescens was one of a group of plants which decreased in basal area after 4 years grazing exclusion, compared with adjacent areas which continued to be grazed by cattle at approximately one head ha^{-1} (Sala et al. 1986). In comparing grazed areas with areas from which grazing had been excluded for periods of 6 to 28 years, *P. canescens* was one of only a few native species with greater cover in grazed than ungrazed areas (Chaneton et al. 2002).

Most grazing studies (such as those just mentioned) look at the exclusion of grazing from a previously grazed site, but in a reversal of this, Facelli (1988) reintroduced grazing to an area from which grazing had been excluded for the previous 9 years. *Phyla canescens* was one of a group of species which was abundant in the continuously grazed area, not detected in the permanently ungrazed area, and increased in abundance over time in the area with reintroduced grazing. Interestingly, 2 years after the reintroduction of grazing, *P. canescens*, along with *Mentha pulegium* L.*, Leontodon taraxacoides* and other species, was still not detected in the newly grazed site, which at that time had become dominated by short-lived ruderal species (e.g. *Conyza bonariensis* (L.) Cronquist, *Medicago* sp. and others). It was not until 5 years after the reintroduction of grazing that *P. canescens* (and associated species) were found, by which time the ruderals were mostly no-longer detected. This invasion time-lag of *P. canescens* (and other species) was attributed to their absence in the seedbank and low dispersal of propagules. The disappearance of most of the ruderal species was attributed to increasing soil compaction by the grazing animals. Unfortunately, no mention was made of flood events during the study period (Facelli 1988). *Phyla canescens* and *Mentha pulegium* were no longer detected after 13 years of grazing exclusion (Facelli et al. 1989).

Similarly, in another study, *P. canescens* was one of 17 species not detected in a one ha area of Flooding Pampa from which grazing had been excluded for the previous seven years, but it was in the surrounding grazed vegetation (Rusch and Oesterheld 1997). The ungrazed site was significantly lower in species number, particularly forbs. This included both native and introduced species.

Grazing and flooding

In an attempt to separate the effects of flooding and grazing, one study investigated the vegetation changes following a spring flood of unusually large extent and long duration (Chaneton et al. 1988). *Phyla canescens* increased in cover after the flood in an area that had been continuously grazed (at a stocking rate of approximately 0.5 cattle ha^{-1}), but decreased in cover in an adjacent ungrazed area, which became almost completely dominated by native graminoids (99.7% of vegetation cover compared with 86.7% in the grazed area).

Fertiliser

Phyla canescens also increased with the addition of artificial fertilisers under a simulated grazing regime (Collantes et al. 1998).

Fire

In a study of the impact of fire on the seedbank composition of a *Spartina argentinensis* Parodi dominated grassland, no change in the *P. canescens* seedbank was found over the four years after fire (Alzugaray et al. 2003). There were differences in the seedbank of *P. canescens* among years only in the unburnt area, where in the first and fourth years no *P. canescens* seeds were detected. As *P. canescens* seed was in approximately 5% of samples overall, this difference is presumably an artefact of the sampling design and patchiness of the seedbank rather than a real change in the seedbank. Fifty samples were taken randomly over 150 m x 150 m, so sometimes all samples may have simply 'missed' the *P. canescens* seed patches.

Range expansion

There is also evidence that *P. canescens* is undergoing range expansion within South America. In an assessment of potential agricultural weeds, *P. canescens* was cited as one of 6 species previously unrecorded, but now present in the upper Río Negro and Neuquén provinces of southern Argentina (Conticello and Bustamante 2001).

2.3.3 Phytochemistry and allelopathy

There has been much interest in the chemical constituents of plants for their potential use in a variety of commercial applications. Some of this interest has focused on the genus *Phyla*. Unfortunately, much of the literature on the phytochemistry continues to use the genus name *Lippia* for species otherwise established as *Phyla* (e.g. Elakovich and Stevens 1985). This problem persists with more recent studies, (e.g. Dongre et al. 2004) also publishing under the name *Lippia nodiflora*. Given the general state of taxonomic confusion within the genus, it is not clear if the species referred to as *Lippia nodiflora* is *P. nodiflora* or in fact *P. canescens*, or indeed another species. For many studies, the lack of nominated voucher specimens makes it difficult to ascertain which taxon was actually studied.

Medicinal uses: traditional and potential

Phyla nodiflora

Phyla nodiflora has been used to treat a wide variety of ailments. This may in part be due to the wide distribution of this pantropical species. Uses included are: analgesic/anti-inflamatory/antipyretic; diuretic; antimicrobial; antimalarial; antispasmodic; remedy for menstrual disorders; and for treatment of syphilis and gonorrhoea (Pascual et al. 2001). The leaves of *P. nodiflora* are also an ingredient of 'anna pavala sindhooram', a traditional Indian preparation used in the treatment of artheriosclerosis (Radha Shanmugasundaram et al. 1983).

Extracts of *P. nodiflora* have been shown to have moderate anti-bacterial activity. This has been found for ethanol extractions when tested on *Helicobacter pylori* (Wang and Huang 2005), the bacterium implicated in the formation of gastric ulcers. The essential oil, obtained from leaves, also displayed anti-microbial activity against strains of five bacteria: *Escherichia coli, Streptococcus lactis, S. thermoacidophilus, Bacillus subtilis* and *Lactobacillus bulgaricus* (Sarada and Prakasa Rao 2003).

Phyla canescens

In a revision of the traditional uses of 52 species attributed to the genus *Lippia* from South and Central America as well as tropical Africa, no traditional uses of *P. canescens*

were recorded (Pascual et al. 2001). However, a herbarium label from a Peruvian specimen suggests that it has traditionally been 'used as a tea against amoebas' (Kennedy 1992, p. 146).

Three flavones isolated from the extracts of aerial parts of *P. canescens* had antiproliferative activity against cultures of murine melanoma and human uterine carcinoma cells (Abe et al. 2002).

Allelopathy

Allelopathy is the phenomenon whereby plants inhibit the growth or reproduction of other plants by the excretion of chemical substances (Putnam 1985). A large range of chemicals, including terpenoids, are thought to have allelopathic effects (Rice 1984).

Phyla nodiflora

After preliminary experiments showed extracts of *P. nodiflora* produced a reduction in radical length of lettuce seedlings, a number of monoterpene and sesquiterpene hydrocarbons as well as oxygenated compounds, were identified in steam distillate from that species (Elakovich and Stevens 1985). Some of these chemicals have been implicated in allelopathy (Rice 1984).

Leachates from mature leaves of *P. nodiflora*, and seven other dominant weeds of Indian field crops inhibited the germination of blackgram, *Phaseolus mungo* L., Fabaceae (Dongre et al. 2004).

Phyla canescens

Both *P. canescens* and *P. nodiflora* contain similar and complex flavonoid sulphates, contrasting with the simplicity of the flavonoid pattern of the closely related *Lippia triphylla*, a species of drier habitats (Tomas-Barberan et al. 1987). Tomas-Barberan *et al.* (1987) compared their work with a previous study (Nair et al. 1973), which failed to find sulphates in *P. nodiflora* from India, but had found two glycosides unconfirmed by the later study. The explanation offered was infraspecific variation, but in the later study

samples from Spain, Israel, Egypt, Saudi Arabia and Malaysia had 'almost identical patterns'.

In a comparison of the germination response of several common agricultural species to various concentrations of extract from the stems and leaves of *P. canescens*, there was reduced probability and rate of germination in two leguminous species, *Trifolium subterraneum* L. and *Vicia villosa* Roth (Tan et al. 2007). The concentrations used were considered to be realistic field concentrations.

In a study of tumour-inducing *Agrobacterium tumefaciens* isolated from galls of *P. canescens* growing in Arizona, one strain had a host-range limited to *P. canescens*, *Nicotiana glauca* Graham and members of the Cucurbitaceae (Unger et al. 1985).

Phyla canescens did not produce either of two taxonomically significant bioactive caffeic acid esters characteristic of the Lamiaceae, subfamily Nepetoideae. These esters were not present in other subfamilies of Lamiaceae, nor in closely related families, including nine species from the Verbenaceae (Grayer et al. 2003).

2.4 Conclusion

Phyla canescens is apparently restricted to areas subject to flooding, both in its native range (Kennedy 1992; Soriano et al. 1992; Taboada et al. 1998) and in Australia (Munir 1993; Fensham 1998). Other species dominate where inundation becomes too frequent or prolonged in both South America (Lewis et al. 1985) and Australia (McCosker 1994a; Blanch et al. 1999; Blanch et al. 2000; Mawhinney 2003). On both continents, *P. canescens* has been noted to occupy sites adjacent to, but drier than those dominated by, *Paspalum distichum* (see Lewis *et al.* (1985) for Argentina; Mawhinney (2003) and McCosker & Duggin (1993) for Australia).

Nowhere is *P. canescens* considered to be a problem in annual cropping systems, either irrigated or dry-land. This is presumably a result of the high frequency of cultivation and/or herbicide application. The apparent inability of *P. canescens* to become dominant

in cropping systems has lead to the contentious practice of clearing native vegetation, ostensibly to control *P. canescens*.

Phyla canescens becomes more abundant in the presence of continuous grazing by livestock (Sala et al. 1986; Chaneton et al. 1988; Facelli 1988; Facelli et al. 1989; Chaneton et al. 2002), or in areas of continuous and intensive activity from wildlife, including rodents (Arias et al. 2005), large flightless birds (Herrera et al. 2004), or hill building ants (Lewis et al. 1991). However, it is unclear if the ability of *P. canescens* to become dominant in these sites is due to selective herbivory, general biopedturbation (animal induced soil disturbance), or simply a function of microtopography.

Chapter 3

Review of *Phyla* collections in Australian herbaria

3.1 Introduction

Accurate identification is fundamental to understanding ecological processes such as biological invasion. Furthermore, an understanding of the invasion history of species, such as *P. canescens*, can give potentially valuable insights into invasion patterns and habitat preferences. Herbaria provide a verifiable way of confirming the presence of plant species over historical periods of time, even through nomenclatural change.

Specimens of the genus *Phyla* are often incorrectly identified in Australia (Hosking et al. 1996). An initial focus of this project was to inspect herbarium specimens to consider the applicability of the currently accepted taxonomic treatment of the genus in Australia by Munir (1993). The intention was not a formal taxonomic revision. Patterns of invasion and ecological insights were gleaned from the specimen data, where possible.

3.2 Specimens

All *Phyla* specimens held at the State Herbarium of South Australia (AD), Queensland Herbarium (BRI), Australian National Herbarium (CANB), Herbarium of the Northern Territory (DNA), National Herbarium of Victoria (MEL), NCW Beadle Herbarium, University of New England (NE) and National Herbarium of New South Wales (NSW) were examined. A digital image of the one Tasmanian Herbarium (HO) specimen not duplicated in any of these other herbaria was obtained. After inspection of label data from the Western Australian Herbarium (PERTH) collection, digital images of five specimens (PERTH 04104498, PERTH 05392535, PERTH 05553202, PERTH 07215290 and PERTH 07254121) were obtained. These were the most southerly specimens labelled *P. nodiflora*, and also closest to Perth, the largest population centre, and were thought most likely to be *P. canescens*. Therefore, a total of 444 herbarium specimens were inspected in person, while high resolution digital images of a further six were obtained (Table 3.1, see Appendix 2 for a complete list of herbarium specimens examined).

Table 3.1 Numbers of specimens of *Phyla canescens* and *P. nodiflora* examined from Australian herbaria.

Herbarium		Date examined	No. specimens of *Phyla canescens* (post-1992)	No. specimens of *Phyla nodiflora*	No. of specimens redetermined from *P. nodiflora* to *P. canescens*
State Herbarium of South Australia	AD	26 September 2006	45 (8)	18	2
Queensland Herbarium	BRI	31 January 2005	54 (35)	83	2
Australian National Herbarium	CANB	4 November 2005	26 (7)	40	2
Northern Territory Herbarium	DNA	1 April 2005	0 (0)	38	0
* Tasmanian Herbarium	HO	July 2005	2 (1)	1	0
National Herbarium of Victoria	MEL	10 June 2004	41 (10)	33	4
NCW Beadle Herbarium, University of New England	NE	4 March 2008	4 (3)	3	1
National Herbarium of New South Wales	NSW	23 July 2004	28 (7)	39	7
† Western Australian Herbarium	PERTH	October 2006	5 (0)	37	0
	Total % redetermined		205 (72) 9% (25%)	252	18

*HO specimens: digital image of HO 23617 (*P. canescens*) inspected

† PERTH specimens: digital images of PERTH 4104498, PERTH 5392535, PERTH 5553202, PERTH 7215290 & PERTH 7254121 (all *P. nodiflora*) inspected. For all other HO and PERTH specimens, only label data was inspected.

In addition, a digital image of an isotype (duplicate of holotype) of *Lippia canescens* Kunth, basionym of *Phyla canescens* (Kunth) Greene was obtained from the Muséum National d'Histoire Naturelle, Paris, France (P 00108606, an undated collection by Bonpland from Truxillo, Peru). Also, a digital image of the lectotype (retrospectively designated type) of *Verbena nodiflora*, basionym of *Phyla nodiflora* (L.) Greene, (BM 000557561) from the George Clifford Herbarium held at the Natural History Museum, London, was obtained online (Linnaean Plant Names Database 2006).

Leaf, stem and inflorescence features were used to discriminate between the two species (Table 3.2). It was found that coarse features were sufficient to delineate the two species, so it was not necessary to examine finer details. The use of floral bract and calyx features, as outlined by Munir (1993), would have required the dissection of specimens. Flower colour was not used as this does not to preserve well, and is therefore often not apparent, particularly in older specimens.

Table 3.2 Features used to identify specimens of *Phyla* (based on Munir 1993).

Feature	*Phyla canescens*		*Phyla nodiflora*
Leaf size	Smaller, typically <20 mm long		Larger, typically >20 mm long
Leaf margin	Shorter, blunt teeth, leaf often entire		Longer, sharper teeth
Leaf venation	Obscure venation		Often distinct
Stolon	Slender,terete		Thicker, often ridged
Peduncle	Slender, shorter		Thicker, longer
Mature spike	More ovoid, often flowering in several adjacent whorls		More elongate, flowering confined to a single whorl

None of the features listed above represent definitive distinguishing features. Both species are remarkably variable, and display substantial morphological plasticity. While one or even several of the features on any given specimen were often inconclusive, the majority of features supported a particular diagnosis.

It is well established that there is substantial morphological variability within the current concepts of both *P. canescens* and *P. nodiflora* (see Munir 1993). During this study it was noticed that there appears to some geographical structure to the morphological variation of *P. canescens* in Australia. Munir (1993) noted that the corolla is 'usually lilac or somewhat pinkish'. It appears that this reflects material collected in South Australia, Victoria, southern New South Wales and that which is currently commercially available, but material from northern New South Wales and southern Queensland has a wholly white corolla, but no mauve/lilac/pink colouration. The younger flowers of both of these forms display the yellow corolla throats as described in *Phyla incisa* Small (Cruzen et al. 1988), which Kennedy (1992) considers a synonym of *Phyla nodiflora* (see Appendix 1). Other morphological differences between these two forms were also noted (Table 3.3).

Table 3.3 Variation within *Phyla canescens* in Australia.

Feature	Southern form	Northern form
Corolla colour	Mauve/lilac/pink 	White 
Indumentum	More canescent/hairy	Less hairy
Stolon	Thicker	Finer
Distribution	South from Lachlan River NSW	North from Macquarie River NSW
Native Range Distribution (see Kennedy 1992)	West of Andes	East of Andes

These differences also reflect those noted from South America, with the type material from west of the Andes being similar to the 'southern' form in Australia, and that from east of the Andes similar to that found in northern New South Wales and Queensland (see Kennedy 1992 for variation in South America). These differences have been noted in the field, but also among adjacent plants growing under glasshouse conditions; the observed differences, therefore, are unlikely to be due to different growing conditions. However, these differences are less apparent in herbarium specimens than live material and no quantitative analysis was undertaken. This variation, if it is found to have geographical coherence in South America, may warrant formal taxonomic recognition. Alternatively, it may just represent points on a more-or-less continuous phenotypic spectrum.

Exceptions to this pattern of variation in Australia include some urban populations in the north (e.g. Inverell, New South Wales), which are similar to material found in the southern part of the distribution, and may be of more recent origin, appearing to be material which continues to be sold in nurseries and garden centres. The first collected population in Australia, from Williamstown, a western suburb of Melbourne, is also an exception in that it is similar to the material found only in the northern part of the Australian distribution.

3.2.1 Redeterminations

Of the 444 herbarium specimens examined, 18 were redetermined from *P. nodiflora* to *P. canescens*. This represents approximately 9% of all *P. canescens* specimens and 25% of specimens lodged since the last systematic inspection of the material (Munir 1993). Of the 18 redetermined specimens, 10 were duplicates of specimens already redetermined at another institution. No specimens labelled *P. canescens* were determined to be *P. nodiflora*.

3.2.2 Australian distribution

In addition to the herbarium specimens, 70 specimens of *P. canescens* collected in a previous study were acquired (Earl 2003). A further 31 specimens were obtained from colleagues and friends as well as the author's own collections. All of these were

P. canescens and were included with the herbarium specimens in the distribution map (Figure 3.1). The distribution of *P. canescens* tends to be more temperate, with most collections inland or near large human population centres, whereas the distribution of *P. nodiflora* tends to be more tropical and coastal with only isolated collections inland.

3.2.3 Unique collections

The 205 *P. canescens* specimens represent 157 unique collections (where duplicates are excluded). Collections from all Australian states and the Australian Capital Territory are represented (Table 3.4). Collections from Queensland, South Australia, Victoria and New South Wales account for nearly 95% (149) of all Australian collections. Of these, 108 (69% of all Australian collections) were taken from within the Murray Darling Basin. The single most collected site is Williamstown, a western suburb of Melbourne (Victoria), with seven separate collections by seven different collectors, presumably due to its proximity to botanists.

The 300 *P. nodiflora* specimens represent 221 unique collections from New South Wales, Queensland, Western Australia and the Northern Territory (Table 3.5). Only two of these (MEL 583748 and NSW 231759) are from within the Murray Darling Basin, both from near Balranald (southern NSW), although these were collected over 70 years apart (1878 and 1955 respectively). The persistence of these populations and their genetic relatedness to other populations may warrant investigation.

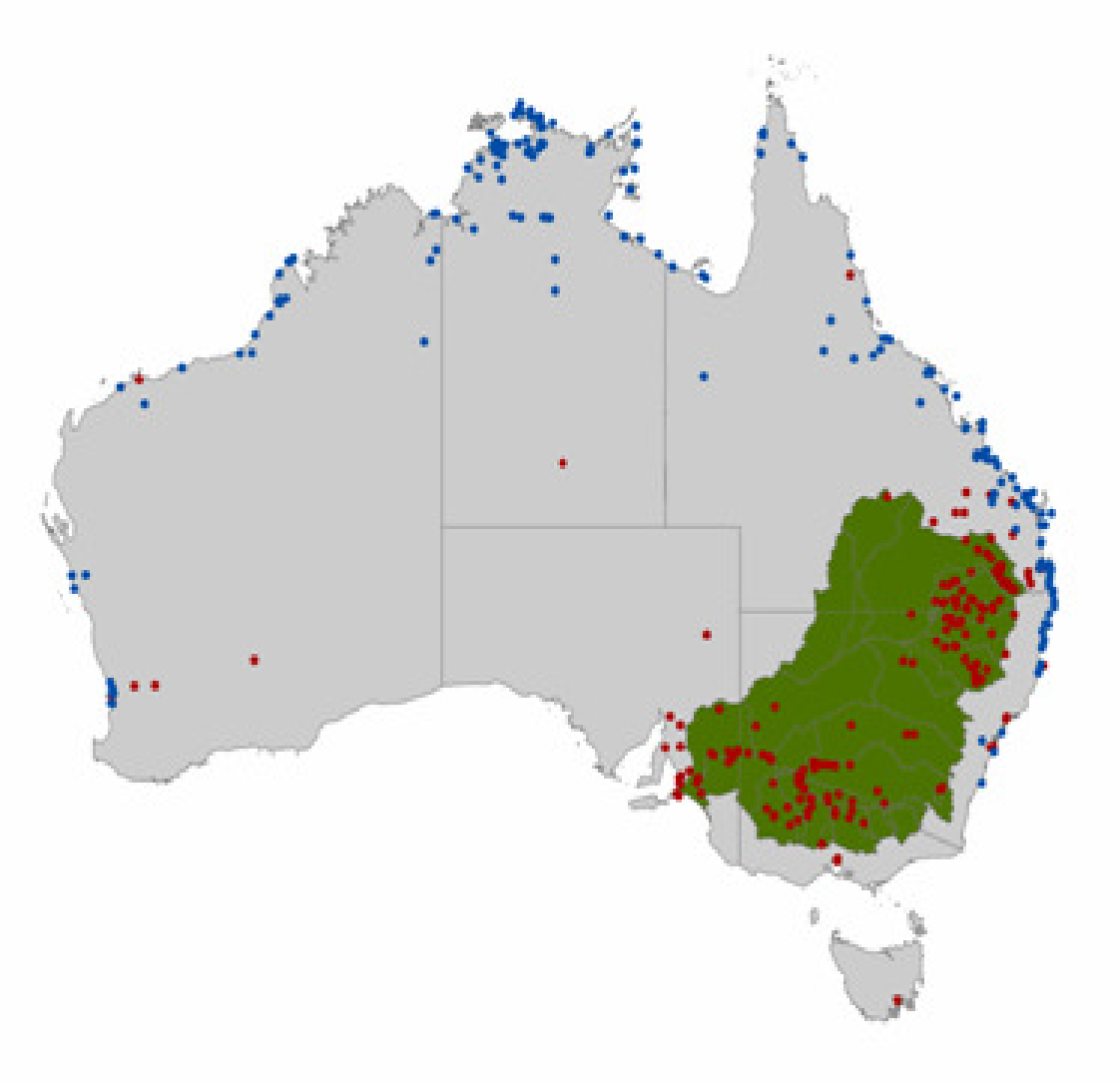


Figure 3.1 Distribution of *Phyla canescens* (●) and *P. nodiflora* (●) in Australia, also showing the Murray Darling Basin. Location data obtained from AD, BRI, CANB, DNA, HO, MEL, NE, NSW, PERTH collections, Earl (2003) and collections of the author, and author's colleagues and friends. Some outliers of *P. canescens* (including Karratha, Alice Springs, Mareeba and Hobart) were collected from gardens.

Table 3.4 Provenance by state or territory of unique collections of *Phyla canescens* held in Australian herbaria (AD, BRI, CANB, DNA, HO, MEL, NE, NSW, PERTH), and those collected from within the Murray Darling Basin (MDB).

State/Territory	Number of unique collections (% of total)	Collections from within MDB (% of State/Territory)
Queensland	50 (32)	38 (76)
South Australia	35 (22)	15 (43)
Victoria	33 (21)	26 (79)
New South Wales	31 (20)	27 (87)
Western Australia	4 (3)	0
Australian Capital Territory	2 (1)	2 (100)
Tasmania	2 (1)	0
Total	157	108 (69)

Table 3.5 Provenance by state or territory of unique collections of *Phyla nodiflora* held in Australian herbaria (AD, BRI, CANB, DNA, HO, MEL, NE, NSW, PERTH).

State/Territory	Number of unique collections (% of total)
Northern Territory	77 (35)
Queensland	76 (34)
Western Australia	38 (17)
New South Wales	30 (14)
Total	221

3.2.4 Habitat preferences and substrate

Herbarium labels often hold more information than just location and date of collection. Labels can also provide habitat information, such as co-occuring species, landform and soil type. However, many specimens, particularly from older collections, contain little of this information.

Collections were counted as from waterway/wetland or floodplain only where this is specifically mentioned on the label, not just a proximal locality; for example, 'Mildura' by itself is insufficient, but 'Mildura, Kings Billabong' is sufficient. Similarly for urban/garden collections, an urban locality alone is not sufficient for the specimen to be included in the count; some reference to urban structures (e.g. footpath, nature-strip) or cultivation is necessary.

Of the 157 unique collections of *P. canescens*, 73 (47%) were collected from waterways, wetlands, or floodplains, while 38 (24%) were collected from urban or garden settings (Table 3.6). In contrast, no specimens of *P. nodiflora* were collected from explicitly urban settings. At least ten collections of *P. canescens* were noted to have come, or likely to have come from cultivated material (locations include: Hobart, HO 23617, MEL 2299549; Williamstown, MEL 698373, CANB 584178; Shepparton, MEL 621609; Swan Hill, MEL 2052804; Adelaide, AD 98587770, AD 98587737, CANB 352037; Canberra, CANB 637622; Deniliquin, NSW 231760; Burrumbuttock, NSW 231604 and Tamworth NSW 427373). No such reference, however, was found on any *P. nodiflora* collections. Therefore, there is no support for the idea that *P. nodiflora* has had a horticultural use in Australia. It is likely that all material sold under the name *P. nodiflora* in Australia is actually what we would now call *P. canescens*. Indeed, several retail outlets in NSW have been selling *P. canescens* during this project under the name '*Phyla nodiflora*'.

Unfortunately, the majority of specimens do not explicitly mention substrate characteristics (Table 3.7). Of those *P. canescens* specimens where the substrate is noted, most are from heavy clay soils, whereas most *P. nodiflora* were collected from areas of sandy soil.

Table 3.6 Habitat determined from *Phyla canescens* and *Phyla nodiflora* collections in Australia (from AD, BRI, CANB, DNA, HO, MEL, NSW and PERTH herbarium records).

Habitat	*Phyla canescens* No. specimens (% of total)	*Phyla nodiflora* No. specimens (% of total)
Waterway, wetland or floodplain	73 (46)	75 (34)
Coastal	0	47 (21)
Urban or garden	38 (24)	0
Other or insufficient labelling	50 (32)	108 (49)
Total unique collections	157	221

Note: Four *P. canescens* specimens were collected from waterways in urban areas and nine *P. nodiflora* specimens were collected from coastal waterways, so sum of percentages >100.

Table 3.7 Substrate determined from *Phyla canescens* and *Phyla nodiflora* collections in Australia (from AD, BRI, CANB, DNA, HO, MEL, NSW and PERTH herbarium records).

Substrate	*Phyla canescens* collections (% of those collections with soil noted)	*Phyla nodiflora* collections (% of those collections with soil noted)
Clay/mud	26 (59)	20 (29)
Clay-loam	3 (7)	0
Loam	6 (14)	2 (3)
Sandy-loam	6 (14)	3 (4)
Sand/gravel	3 (7)	44 (64)
Not recorded	113	152
Total	157	221

3.2.5 Early collections

The first known *Phyla canescens* specimen collected in Australia is from Williamstown, a western suburb of Melbourne, Victoria in 1914 (Table 3.8 and Munir 1993). In South Australia, *P. canescens* was collected from the shores of 'Torrens Lake' in Adelaide in 1927. The first collection from within the Murray Darling Basin (1938) is from Glenfalloch, near Clifton (45 km south of Toowoomba) on the Darling Downs of southern Queensland. Two collections from Hobart, Tasmania (both 1943) are from garden material, and *P. canescens* may not be truly naturalised in Tasmania because it has not been collected in that state since. The first collection from NSW was lodged in 1949 from Burrumbuttock, 30 km north of Albury and the Murray River. The collector noted that it was being cultivated as a lawn, and that the material had been obtained from South Australia. In the same year (1949) *P. canescens* was first collected in Western Australia from Mount Charlotte Reservoir, Kalgoorlie. However, apparently no specimen of *P. canescens* has been collected in Western Australia since 1969 (PERTH 1012509, no locality recorded).

Table 3.8 First collections of *Phyla canescens* by state (from AD, BRI, CANB, HO, MEL, NSW and PERTH herbarium records).

State/Territory	Year	Location	Collector	Specimen
Victoria	1914	Williamstown	JR Tooey	MEL 583749 MEL 663933
South Australia	1927	Adelaide	EH Ising	AD 96621097
Queensland	1938	Glenfalloch	J Webb	BRI 112178
Tasmania	1943	Hobart	RA Black	MEL 2299549
Western Australia	1949	Kalgoorlie	CA Gardener	PERTH 1012487
New South Wales	1949	Burrumbuttock	EJ McBarron	NSW 231604
ACT	1994	Deakin	BJ Lepschi	CANB 470001

Some of these earlier collections allude to the invasive nature of this species. For example, on the label of a collection from the Hunter Valley NSW in 1953, it is noted that it 'is getting a hold on to a farmer's paddock' (AJR Brown, NSW no accession #). Similarly, on a specimen collected in 1965 from Kings Billabong, near Mildura, Victoria,

the collector, J. Henshall, notes: 'Before the 1956 flood this plant was unknown on the river flats. Now it's everywhere' (MEL 583734). Others describe its hardiness, such as '[it] stayed green throughout the 1981–1982 drought (R. Vines, MEL 1529654)

The first *Phyla nodiflora* collection from Australia is from Shoalwater Bay, Queensland, collected 1802–1805 by Robert Brown (Munir 1993). This, and a number of other 19th century collections are held at Kew. The oldest collection held in an Australian herbarium is also from Queensland, collected in 1843 (Table 3.9). The most southerly collections on the east coast are from Jervis Bay, NSW at 35°05'55" south (CANB 15000 & CANB 2941) and on the west coast, from Perth (32°20' south), WA (CANB 303788, CANB 390797, PERTH 1010395, PERTH 1012444 & PERTH 5392535).

Table 3.9 First collections of *Phyla nodiflora* by state and territory (from AD, BRI, CANB, DNA, HO, MEL, NSW and PERTH herbarium records).

State/Territory	Year	Location	Collector	Specimen
Queensland	1843	?	Maconnell & Balfour	NSW 231782
Northern Territory	1855	Victoria River	F von Mueller	MEL 583741
New South Wales	1877	Ballina	HC Fawcett	MEL 583744
Western Australia	1895	Fortescue River	WH Cusack	MEL 560563

3.2.6 Cumulative collections

The cumulative number of collections of both *P. canescens* and *P. nodiflora* in Australia generally follow an exponential pattern (Figure 3.2). The number of collections of *P. canescens* rose steadily until 2000, when there was a rapid jump, attributable to the work of G.N. Batianoff (Queensland Herbarium), who lodged 16 *P. canescens* collections in 2001 alone.

Inferring invasion rates from herbarium collections is fraught with problems (Hosking et al. 1996), so interpretations from such data must be cautious. However, it appears likely that *P. nodiflora* was an earlier introduction into Australia than *P. canescens*. Whether

P. nodiflora was introduced after European settlement, (as suggested by Munir 1993), introduced by earlier traders (possibly as a contaminant of solid ballast) or is truly native remains unclear. There may be both native and introduced populations of *P. nodiflora* in Australia.

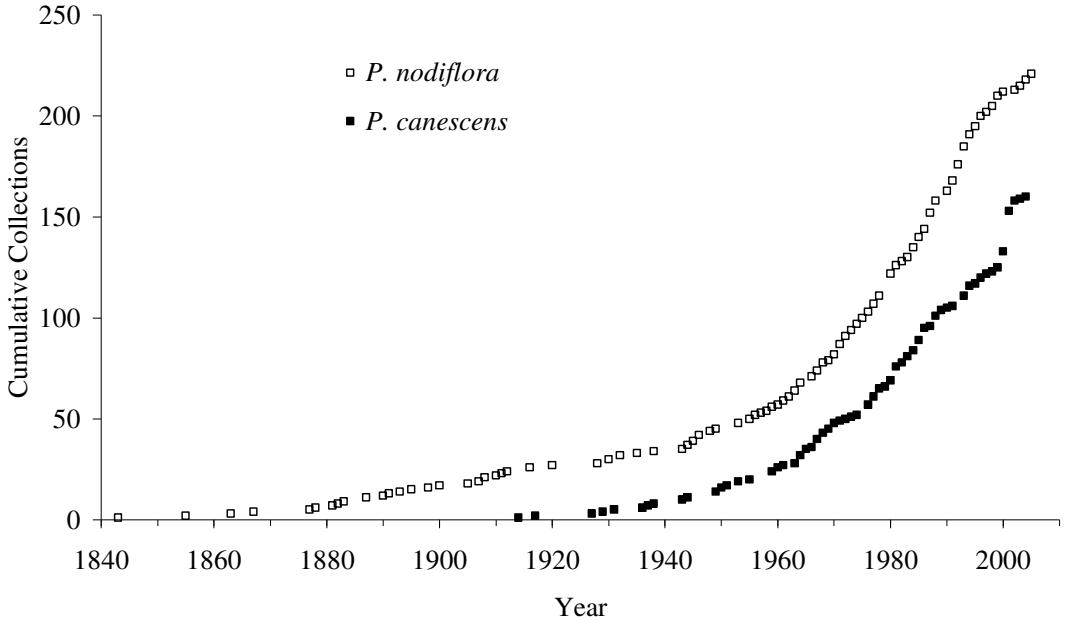


Figure 3.2 Cumulative unique collections of *Phyla canescens* and *Phyla nodiflora* in Australian herbaria (from AD, BRI, CANB, DNA, HO, MEL, NE, NSW and PERTH herbarium records).

3.3 Conclusion

From data on herbarium labels, it can be seen that both *P. canescens* and *P. nodiflora* are frequently found near waterways. *Phyla canescens* collections tend to be associated with heavy clays on floodplains or near waterways of the Murray Darling Basin, with a number of collections from urban sites (Table 3.10), which is not surprising for a species long promoted for its horticultural potential. In contrast, *P. nodiflora* tends to be associated with sandy soils of waterways in coastal areas.

Table 3.10 Summary of differences between *Phyla canescens* and *Phyla nodiflora* collections from Australia.

	Phyla canescens	*Phyla nodiflora*
Morphology	Finer	Coarser
Distribution	Temperate – subtropical Mostly inland	Subtropical – tropical Mostly coastal
Substrate	Mostly clay	Mostly sand
Introduction date	Later (late 1800s?)	Earlier (~1800?)
Used in horticulture	Yes	No evidence

Interestingly, no *P. nodiflora* collections suggested escape from horticulture, so it seems likely that this species has not been used in horticulture, and that all that has been sold under the name *P. nodiflora* is actually *P. canescens*. This is consistent with observations of gardens and nurseries during this study; all material in such situations was identified as *P. canescens*, despite being labelled *P. nodiflora* (as in Figure 2.1).

Chapter 4
Field sites

4.1 Regional context

Field studies were conducted on the extensive floodplains of the Namoi and Gwydir Rivers of the Murray Darling Basin, in the North Western Plains of NSW. These floodplains are both agriculturally productive and environmentally valuable.

The Namoi and Gwydir Rivers are fed from the western slopes of the Great Dividing Range to the east where rainfall is relatively high. The rivers flow in a generally westerly direction towards the flatter and drier interior. Floodwaters resulting form heavy rainfall are distributed through extensive networks of anastomosing channels which feed into the Darling River further west (Thoms et al. 2004). Sites of international environmental significance include the Ramsar listed Gwydir Wetlands (The List of Wetlands of International Importance 2007). The pre-European vegetation of these floodplains consisted largely of wetlands, grasslands and grassy woodlands, communities which are under-represented in the conservation reserve system (Benson et al. 2006).

This region is characterised by long hot summers (mean January temperature 33–36° C), and mild winters (mean July temperature 16–19° C with 8–18 frosts per year, mostly in June, July and August). The rainfall is summer dominated (November–March) and averages from 500 mm to 650 mm annually across the region, with a distinct gradient from west (lower) to east (higher). The summer storms, which typically bring this rain, can be extremely localised and therefore precipitation is highly variable. Historically, the area has been subject to extensive flooding (Bureau of Meteorology 2007; Webb et al. 2007).

The soils of these floodplains generally have a high clay content, exhibit extensive cracking when dry (vertosols), are usually of grey or black colour, and some are 'self-mulching' (CSIRO 2003). Major agricultural enterprises of these floodplains include irrigated and dryland cropping of cereals and cotton, and cattle grazing. The region's

grazing industry is generally reliant on pastures based on native perennial grasses. Substantial changes to the hydrological patterns of the catchments in the region have resulted from the construction of large water storages (Webb et al. 2007).

4.2 Nomenclature

Nomenclature follows Wheeler *et al*. (2002) for Poaceae and Harden (1992; 1993; 2000; 2002) for other taxa, except *Phyla canescens* (Munir 1993) and *Verbena gaudichaudii* (Michael 1997).

4.3 Field sites

Four field sites were selected, two in the Namoi River Catchment and two in the Gwydir River Catchment (see Figure 4.1 for map, Table 4.1 for a summary of site details). All sites were selected because they had patches of *Phyla canescens* sufficiently large to accommodate 12 m x 12 m stock exclosures. Field sites were selected to represent much of the variability among sites dominated by *P. canescens*, within logistical constraints. Three exclosures (A–C) were established at each of the four sites.

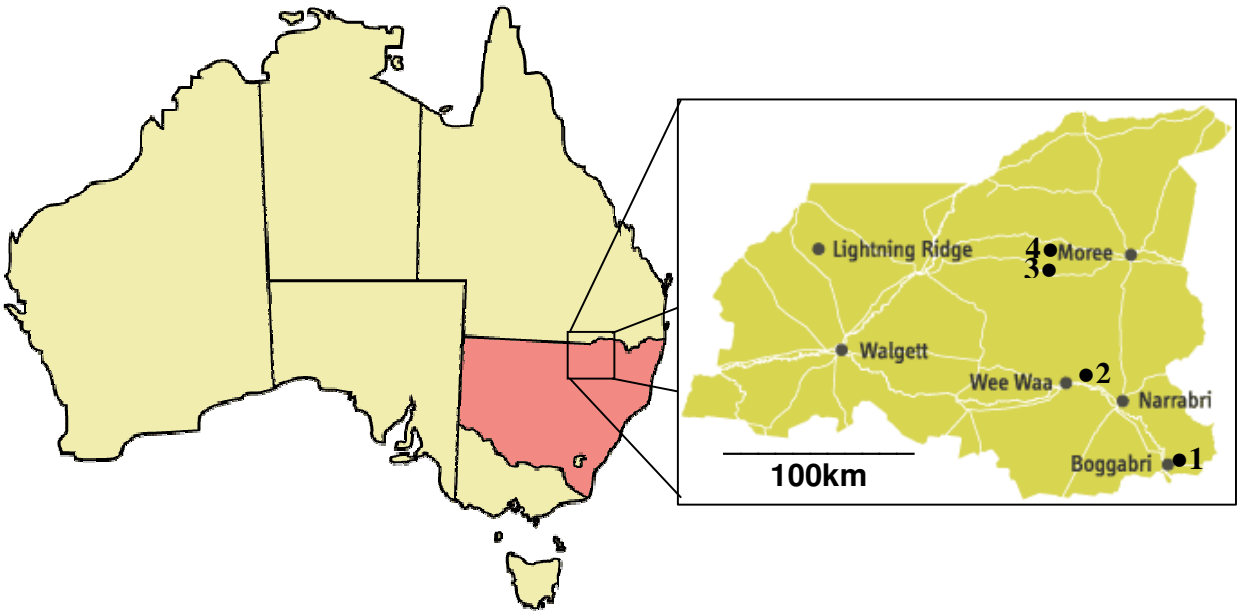


Figure 4.1 Location of field sites (1–4) in Northern NSW, Australia

Table 4.1 Location and description of experimental field sites.

Site	Property	Catchment	Location	Latitude Longitude	Description	Dominant Vegetation	Estimated initial cover of *Phyla canescens* within exclosures
1	'Kilmarnock'	Namoi	~1km east of Boggabri	30°42'S 150°03'E	Floodplain grassland east of Namoi River, undulating with billabongs	River Red Gum (*Eucalyptus camaldulensis*) with native and introduced grasses and forbs including species of *Medicago*, *Polygonum, Bromus*, *Paspalidium*	48 %
2	'Glen Arvon'	Namoi	~10km east of Wee Waa	30°11'S 149°31'E	Floodplain grassland north of Namoi River, undulating with billabongs	River Red Gum (*Eucalyptus camaldulensis*) with native and introduced grasses and forbs, including species of *Medicago*, *Dichanthium*, *Paspalidium*	66 %
3	'Old Dromana'	Gwydir	~50km west of Moree	29°19'S 149°17'E	Floodplain adjacent to Gwydir 'Big Leather' Wetland, Gwydir River	Coolibah (*Eucalyptus coolabah*) with native and introduced grasses and forbs, including species of *Sclerolaena*, *Medicago*, *Lachnagrostis*	40 %
4	'Moolabulla'	Gwydir	~50km west of Moree	29°15'S 149°23'E	Floodplain adjacent to 'Gingham Watercourse' Wetland	Coolibah (*Eucalyptus coolabah*) and Belah (*Casuarina cristata*) with native and introduced grasses and forbs, including species of *Marsilea*, *Eleocharis*, *Paspalum*	47 %

Numerous experiments were conducted within each exclosure (see Figure 4.2 for general layout within exclosures). Five disturbance treatments (Chapter 5) were randomly allocated to plots 1–5. Plot 6 was used for the fecundity and pollinator exclusion studies (Chapter 6), plots 7 and 8 were used in the seedbank studies (Chapter 7).

At each site, a data-logger was installed in one randomly chosen exclosure. Each data-logger (HOBO® Weather Station) was equipped with two soil moisture sensors (ECH_2O® Dielectric Aquameter, Decagon Devices) and two temperature sensors (Onset Computer Corporation 1996-2007). Soil moisture and temperature were measured approximately 2.5 cm below the soil surface in the most recently disturbed and control plots (see Chapter 5 for more detail on treatments). Ambient temperature was measured by placing a temperature sensor inside a 30 cm length of white PVC plumbing pipe (200 mm diameter) installed horizontally approximately 1.5 m above ground level. All measurements were logged at 15 minute intervals.

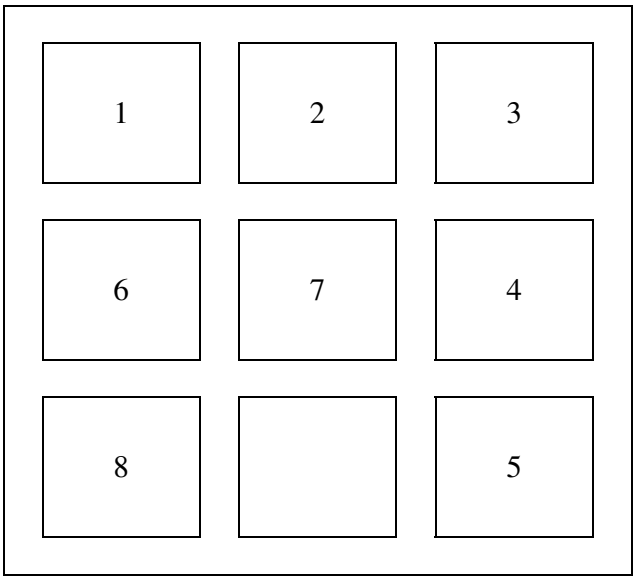


Figure 4.2 General exclosure layout (12 m x 12 m) with experimental plots (3 m x 3 m) numbered 1–8 and buffers (0.75 m). Plots 1–5 were randomly allocated to the disturbance treatments (Chapter 5), plot 6 the fecundity and pollinator exclusion studies (Chapter 6) and plots 7 and 8 the seedbank studies (Chapter 7).

4.3.1 Site 1: 'Kilmarnock' Boggabri, Namoi River catchment

This site was immediately adjacent to the eastern bank of the Namoi River, and was mostly treeless, with only some *Eucalyptus camaldulensis* remaining, particularly along the river itself (see Figure 4.3 for photograph, and Appendix 1 for list of vascular plants). This site had a lower overall cover of *Phyla canescens* than the other sites. The populations/occurrence of *P. canescens* was generally restricted to the 'flood-runners', shallow linear depressions which are the first areas to carry flood water when the river banks are exceeded. Compared to the other sites in this chapter, this site had probably the most recent invasion of *P. canescens* and had a diverse range of native (mostly perennial) and introduced (mostly annual, except for *P. canescens*) grasses and forbs. The experimental exclosures were within 200 m of the river bank. Rainfall records were obtained from the nearby Boggabri Post Office (*c.* 1 km west). Long term climate data (Figure 4.4) are for Gunnedah, approximately 35 km south-east. Mean daily maximum and minimum ambient temperatures and mean daily soil moisture contents were recorded from a data logger in Exclosure B (Figure 4.5). However, the logger was invaded by ants between 1 February and 13 March 2006, rendering it inoperable and was not replaced.

Figure 4.3 Photograph of Site 1 with *P. canescens* in left foreground and Namoi River to the right, 21 April 2004.

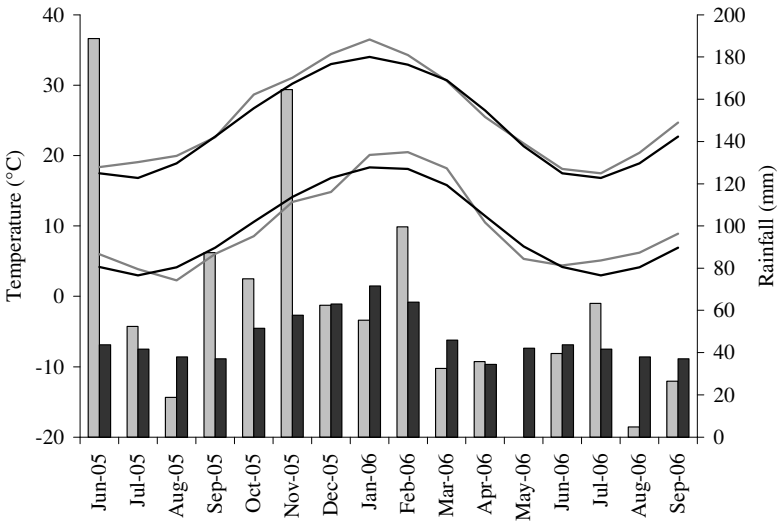


Figure 4.4 Site 1 monthly rainfall (▒) and monthly mean daily minimum and maximum temperature (— June 2005 to January 2006 from data logger on site, February to September 2006 for Gunnedah Pool), and long-term (1884–2007) monthly rainfall means (▒ for Boggabri Post Office) and temperature (—) for Gunnedah Pool, (Bureau of Meteorology 2007).

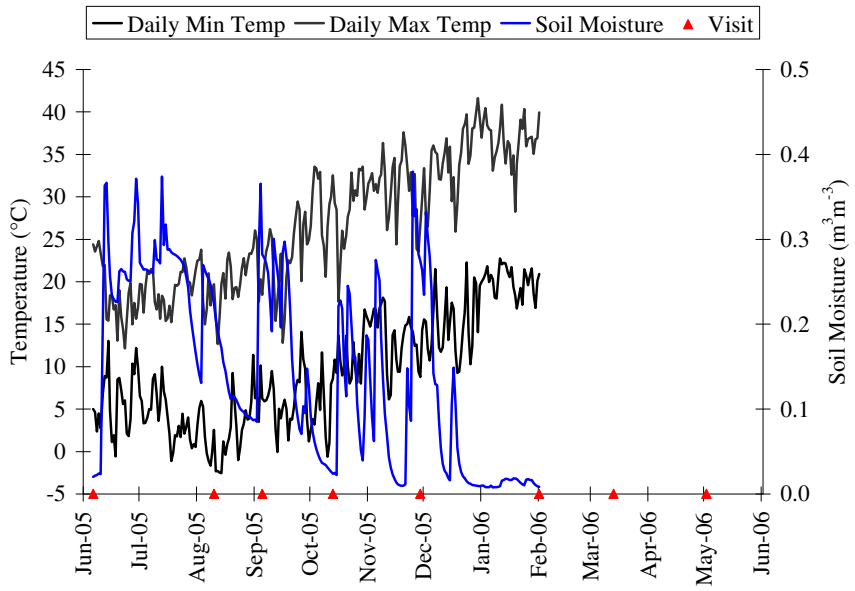


Figure 4.5 Site 1 daily minimum and maximum temperatures (—) and daily maximum soil moisture at depth of 2.5 cm (—) from data logger located in Exclosure B from June 2005 to February 2006. Red triangles (▲) show dates of site visits.

4.3.2 Site 2: 'Glen Arvon' Wee Waa, Namoi River catchment

This site was approximately 1 km north of the Namoi River and consisted of large old remnant trees (mostly *Eucalyptus camaldulensis*), a substantial and apparently increasing layer of *Acacia farnesiana* (1–3 m high), and an almost continuous cover of *P. canescens* (see Figure 4.6 for photograph, and Appendix 1 for list of vascular plants). There were many native grasses and forbs still present, however, mostly in patches not dominated by *P. canescens*. A billabong runs through the site and is usually dry, but can experience extended periods with water in it. It was dominated by an almost monospecific stand of *Eleocharis plana*. The experimental exclosures were within 100 m of this ephemeral billabong. Rainfall records were obtained from 'Glen Arvon' homestead (*c*. 1 km west). Long term climate data (Figure 4.7) are for Narrabri, approximately 30 km south-east. Mean daily maximum and minimum ambient temperatures and mean daily soil moisture contents were recorded from a data logger in Exclosure B (Figure 4.8). However, the logger was invaded by ants between 1 February and 13 March 2006, rendering it inoperable and was not replaced.

Figure 4.6 Photograph of Site 2, Exclosure B, with data logger, 11 August 2005.

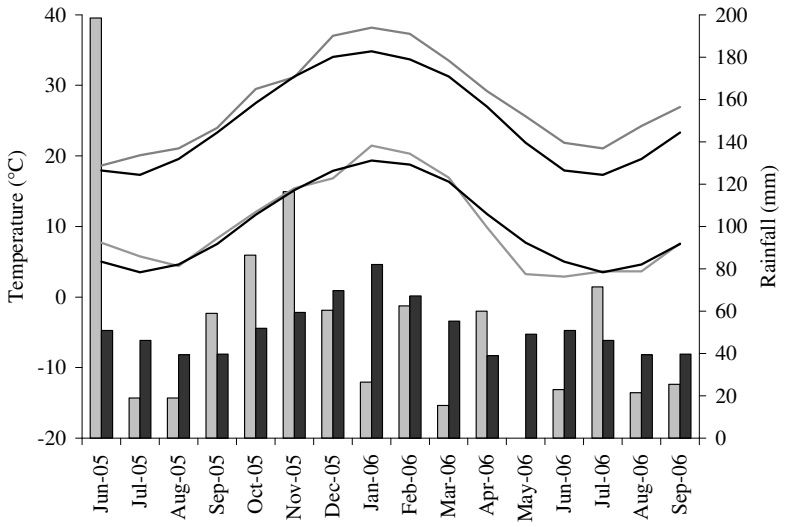


Figure 4.7 Site 2 monthly rainfall (for 'Glen Arvon' homestead) and monthly mean daily minimum and maximum temperature (— from data-logger on site), June 2005 to September 2006, and long-term (1870–2007) monthly rainfall means ( ) and temperature (—) for Narrabri (Bureau of Meteorology 2007).

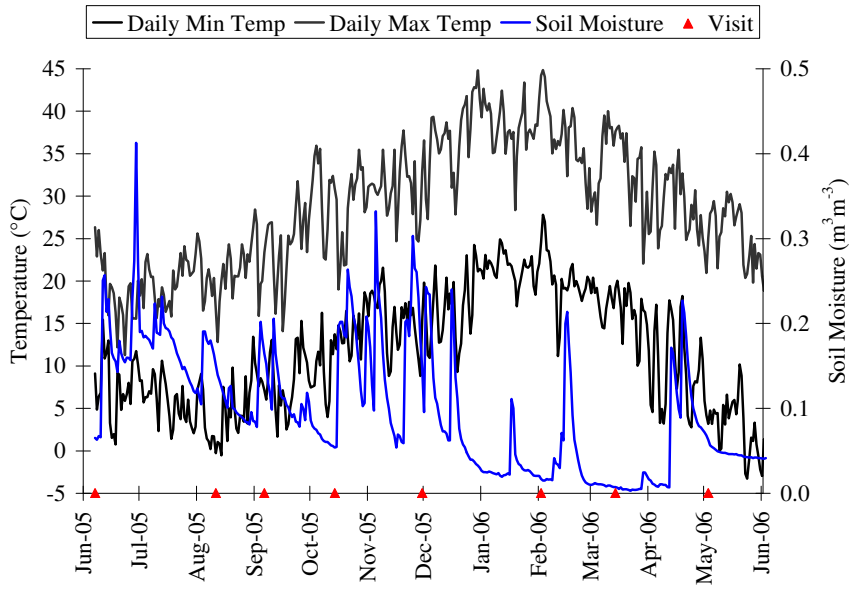


Figure 4.8 Site 2 daily minimum and maximum temperatures (—) and daily maximum soil moisture at a depth of 2.5 cm (—) from data logger located in Exclosure B from June 2005 to June 2006. Red triangles (▲) show dates of site visits.

4.3.3 Site 3: 'Old Dromana' Moree, Gwydir River catchment

This site was adjacent to the northern edge of the 'Big Leather' terminal wetland of the Gwydir River and the area had been effectively excised from the wetland proper by the installation of a stock and domestic water supply channel in the 1970s. This channel quickly drained any floodwaters that breached it or any surface flow from local rainfall events. Therefore, the site on the higher side (away from the wetland) received fewer floods of much shorter duration than the wetland proper. The vegetation at this site has apparently changed to a more terrestrial community rather than the semi-aquatic vegetation that was once present (McCosker 1994b). Experimental exclosures were within 100 m of this channel and the wetland itself, amongst scattered *Eucalyptus coolabah*. The site was essentially devoid of shrubs, and the ground-flora remained sparse for the duration of the experimental period (see Figure 4.9 for photograph). Apart from *P. canescens*, other abundant species were mostly annual or short-lived perennials (e.g. *Portulaca oleracea*, *Lachnagrostis filiformis*, *Sclerolaena* spp., see Appendix 1 for list of vascular plants). Rainfall records were obtained from 'Old Dromana' homestead (*c*. 7 km north-east). Long term climate data (Figure 4.10) are for Moree, approximately 55 km east. Mean daily maximum and minimum ambient temperatures and mean daily soil moisture content were recorded from a data logger in Exclosure C (Figure 4.11).

Figure 4.9 Photograph of Site 3, Exclosure B, with wetland to left, 21 May 2005.

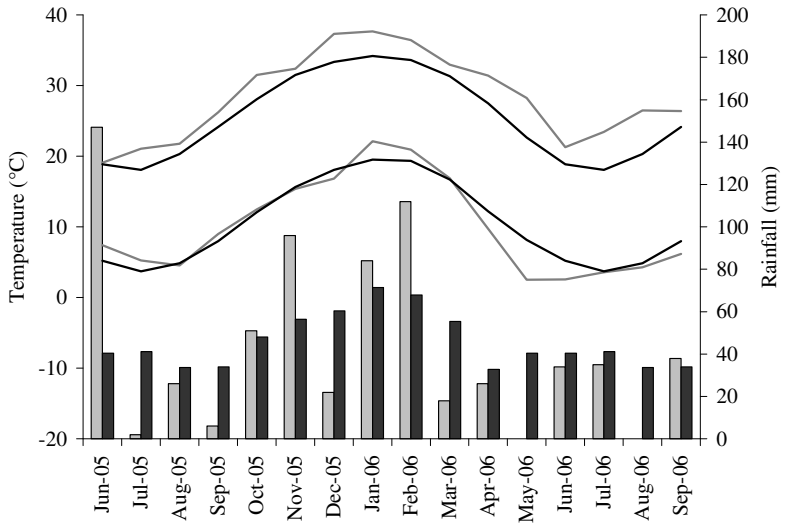


Figure 4.10 Site 3 monthly rainfall (▮ for 'Old Dromana' homestead) and monthly mean daily minimum and maximum temperature (— from data-logger on site), June 2005 to September 2006, and long-term monthly rainfall means (▮ 1879–2007) and temperature (— 1907–2007) for Moree (Bureau of Meteorology 2007).

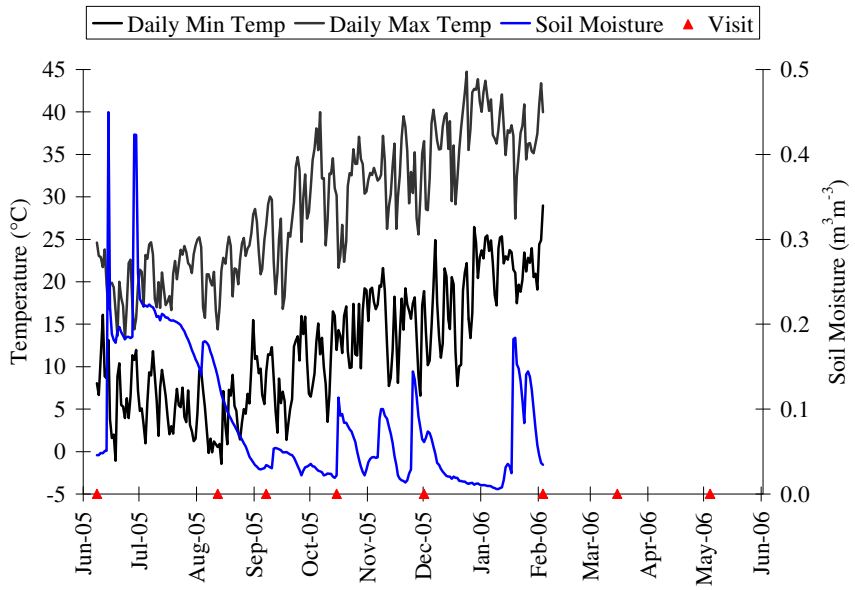


Figure 4.11 Site 3 daily minimum and maximum temperatures (—) and daily maximum soil moisture at a depth of 2.5 cm (—) from data logger located in Exclosure C from June 2005 to Februaury 2006. Red triangles (▲) show dates of site visits.

4.3.4 Site 4: 'Moolabulla' Moree, Gwydir River catchment

This site was immediately adjacent to the northern fringe of the Gingham Wetland, a terminal wetland of a Gwydir River anabranch (see photograph, Figure 4.12). The wetland itself was a complex mosaic of vegetation, with patches dominated by species such as *Typha orientalis*, *Eleocharis plana*, *Paspalum distichum* and *Juncus* sp. Unlike Site 3, the hydrology of this site has not been impacted by local engineering works. The experimental exclosures were placed in an area of relative uniformity of vegetation with occasional *Eucalyptus coolabah* and nearby patches of *Casuarina cristata*. However, this site contained gilgais, where elevational changes of 300 mm or more were expressed over a few metres. This topographic variation was reflected in the vegetation. Dominant species other than *P. canescens* included *Eleocharis plana* and *Marsilea drummondii* (see Appendix 2 for list of vascular plants). Rainfall records were also obtained from 'Old Dromana' homestead (*c*. 6 km south-east). Long term climate data (Figure 4.13) are for Moree, approximately 50 km east. Mean daily maximum and minimum ambient temperatures and mean daily soil moisture contents were recorded from a data logger in Exclosure A (Figure 4.14). The data logger was flooded on 4 July 2005, and replaced on 1 December 2006.

Figure 4.12 Photograph of Site 4, from within Exclosure B, with wetland in background, 15 October 2005.

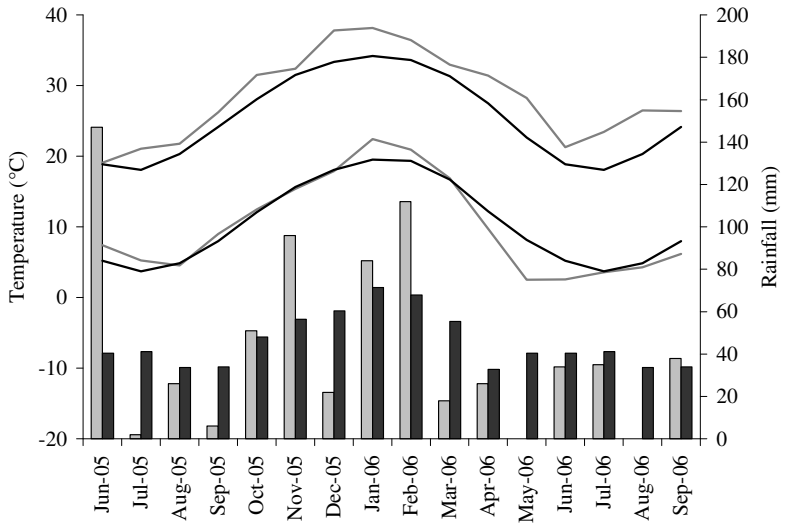


Figure 4.13 Site 4 monthly rainfall (▒ for 'Old Dromana' homestead) and monthly mean daily minimum and maximum temperature (— data from data-logger on site), June 2005 to September 2006, and long-term monthly rainfall means (▒ 1879–2007) and temperature (— 1907–2007) for Moree (Bureau of Meteorology 2007).

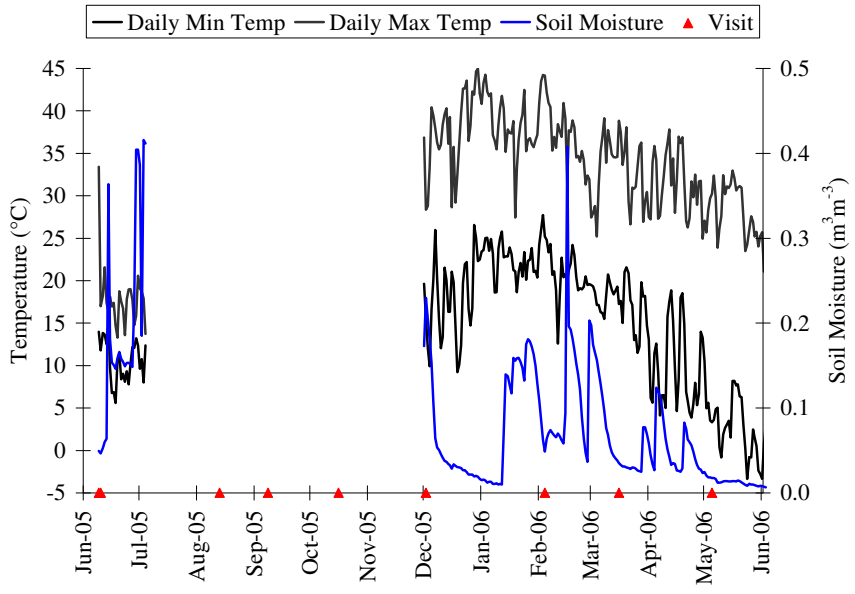


Figure 4.14 Site 4 daily minimum and maximum temperatures (—) and daily maximum soil moisture at a depth of 2.5 cm (—) from data logger located in Exclosure A from June 2005 to June 2006. Red triangles (▲) show dates of site visits. Data logger was flooded on 4 July and replaced on 1 December 2005.

Chapter 5
Germination

5.1 Introduction

Phyla canescens has the potential to spread by seeds and vegetative fragments. This species appears to be spread by floods (McCosker 1994a), and can develop substantial seedbank densities in Australia (2566 m^{-2} derived from McCosker 1994a) and in Argentina (3820 m^{-2} derived from Alzugaray *et al*. 2003). By better understanding the recruitment and seedbank processes, such as conditions required for germination, we anticipate being able to better target management interventions and reduce the impacts of this widespread and abundant species.

A series of experiments was undertaken to determine a suitable germination regime which could be used for future germination experiments (Chapters 6 and 7). An understanding of these germination requirements themselves also provides insights into some of the ecological constraints on *P. canescens*.

Previous studies have successfully germinated *P. canescens* on moistened filter paper placed over the convex side of a watch glass inside a Petri-dish partially filled with water at 30:20°C with a 12 h photoperiod (White 2004). However, because the seeds are susceptible to becoming dislodged from the filter paper, another method was required. A variety of substrata were tested under the same temperature and light conditions to determine which would be most reliable for future germination tests (Experiment 1). Once an optimal method of germinating *P. canescens* seeds was determined, further experiments investigated the effects of light (Experiment 2) and a range of constant and alternating temperatures (Experiment 3) on germination.

All experiments in this chapter used whole schizocarps, hereafter referred to as 'fruit'. I consider the fruit as the 'natural dispersal unit' and therefore the most appropriate unit for use in germination studies (Baskin and Baskin 1998). It is the fruit that is dispersed from the inflorescence, often still enclosed in the calyx, onto the soil surface. However, once

the fruit has become liberated from the enclosing calyx, it may split into its two component single-seeded mericarps (Munir 1993), hereafter called 'seeds'. Therefore, the seed population in the field will contain a proportion of single seeds as well as entire fruit, both of which are buoyant and may disperse further (Lucy et al. 1995). Fruit are also larger, more easily manipulated, and require less processing from field samples.

5.2 Methods

5.2.1 Experiment 1: Substrate

An incubator set at 30:20°C (light: dark) with a 12 h photoperiod (irradiance of approximately 20 μmol m^{-2} s^{-1}, measured with a 'LI-COR' model LI-250 light meter, John Morris Scientific), was loaded with five different substrate treatments. The treatments were:

1. fruit placed on a single moistened filter paper on an inverted watchglass sitting in water (as in White 2004)
2. fruit placed between two moistened filter papers on an inverted watchglass
3. fruit placed on commercially available germination card, atop a pad of Kimpak® cellulose wadding sitting in water
4. fruit imbedded into the surface of moistened sand
5. fruit inserted 1–2 mm into the surface of 1% agar gel.

Each treatment had five replicates of 25 fruit (50 seeds) in 90 mm diameter disposable Petri-dishes. The experiment was initiated on 15 May 2005 with seeds collected from Site 1 (see Chapter 4 for details) on 1 June 2004. Seeds were stored in airtight containers in the dark at room temperature. The number of germinants per treatment was counted after 14 days. A seed was considered germinated if the cotyledons had emerged from the seedcoat.

Data were square-root-transformed and analysed using Hsu's Multiple Comparisons with the Best ANOVA (Statistix 2003).

5.2.2 Experiment 2: Light

An incubator set at 30:20°C (light: dark) with a 12 h photoperiod, was loaded with two different light treatments. The treatments were:

1. fruit inserted 1–2 mm into the surface of 1% agar gel in a Petri-dish sealed with Parafilm®,
2. fruit inserted 1–2 mm into the surface of 1% agar gel in a Petri-dish sealed with Parafilm® and wrapped in aluminium foil.

Each treatment had five replicates. The seeds used and all other conditions were as described for Experiment 1 (above).

5.2.3 Experiment 3: Temperature

Multiple diel (daily) alternating temperature combinations can be simultaneously tested on a two-way thermogradient plate (Larsen 1971). A total of 9 day x 9 night temperature combinations were used (Figure 5.1).

For each trial, 25 fruit (50 seeds) were pushed 1–2 mm into the surface of 1% agar gel set inside aluminium foil shells approximately 50 mm square and 20 mm deep. These were arranged in each of the 81 cells of the thermogradient plate. Thermocouples were also imbedded in the agar gel at 17 locations and temperatures logged at 1 h intervals. Within an hour of each alternation, temperatures had approximated the nominated temperature. Light (irradiance approximately 25 μmol m^{-2} s^{-1}) was provided for 12 h each day in phase with the day temperatures on the thermogradient plate. Agar was moistened with deionised water as required to prevent dehydration. Each trial lasted 28 days. Treatments were then transferred to an incubation cabinet set at alternating temperatures of 30:20°C (light: dark) with 12 h thermo- and photoperiod for another 28 days (irradiance approximately 20 μmol m^{-2} s^{-1}). The initial trial was checked every 12 h and subsequent trials daily. Seeds were considered germinated when cotyledons emerged from the seedcoat.

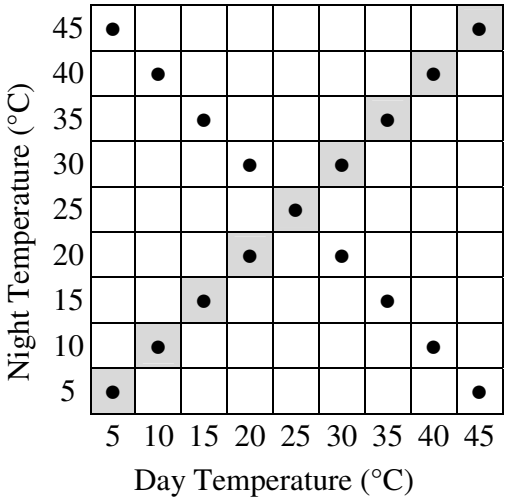


Figure 5.1 Two-way thermogradient plate layout, showing 81 diurnal temperature combinations with constant temperature cells shaded ( ), and location of the 17 thermocouples (●).

For the initial trial only, seeds which had not germinated after 56 days were bisected longitudinally and soaked in a 1% solution of tetrazolium chloride for approximately 4 h. Seeds which stained pink were considered viable, those which remained unstained were considered non-viable.

Two seed batches were used in this experiment. Seeds were collected from Site 1 (see Chapter 4 for site detail) on 1 June 2004 (the same batch as for Experiments 1 and 2) and germination trials commenced 4 months (132 days) and 16 months (498 days) after harvest. Seeds were also collected from Site 3 on 21 May 2005, and the germination trial commenced six months (178 days) after harvest. Seeds were stored in airtight containers in the dark at room temperature.

Germination percentages are the percentage of seeds placed in each treatment which subsequently germinated. Viability percentages are the sum of germination percentages and the percentage of the original seed sample which stained positive for each treatment.

Germination prediction surfaces were modeled using Geographical Information Systems (GIS)-based techniques (Tarasoff et al. 2005). Ordinary kriging was used with the ESRI® ArcGIS™ Geostatistical Analyst extension within ArcMap v9.0™ program (*ArcMap* 2004). The four nearest neighbours in the search radius were used in the spherical variogram model.

5.3 Results

5.3.1 Experiment 1: Substrate

Mean germination for seeds between two moist filter papers and imbedded into 1% agar gel (Treatments 2 and 5, respectively) were not significantly different. Mean germination on a single moist filter paper, germination card and sand (treatments 1, 3 and 4 respectively) were significantly lower than that of the best (agar) treatment (p = 0.05, Figure 5.2).

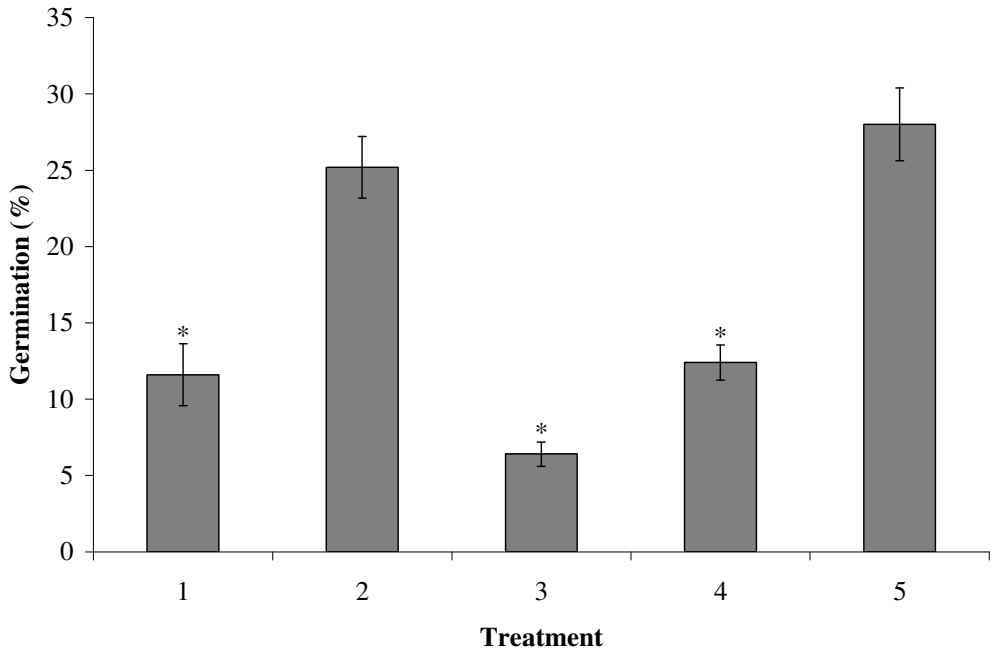


Figure 5.2 Germination of *Phyla canescens* seeds for five substrate treatments (1 = single filter paper, 2 = between two filter papers, 3 = germination card, 4 = sand, 5 = agar gel) ± SE. * = significantly different from the treatment with the highest germination (Hsu's Multiple Comparisons with the Best ANOVA, p = 0.05).

5.3.2 Experiment 2: Light

Phyla canescens seeds without light did not germinate after 14 days in any of the replicates. Under the same conditions, but with a 12 h photo-period, mean germination after 14 days was 28%.

5.3.3 Experiment 3: Temperature

Germination after 28 days was significantly lower for seeds subjected to constant (diel fluctuation ≤ 5°C) temperature treatments than for seeds from fluctuating (diel fluctuation ≥ 10°C) temperature treatments (Figure 5.3 and 5.4). There was also reduced germination in hot (maximum = 45°C) and cold treatments (15°C or below for seeds from Site 1 and 20°C or below for seeds from Site 3). After a further 28 days under 'optimal' temperatures (30:20°C), germination from seeds initially subject to constant and cold treatments was not significantly different from seeds initially subject to fluctuating temperatures. In contrast, germination of seeds from initially hot treatments, was still significantly lower than seeds from fluctuating temperature treatments, even after the 28 day fluctuating temperature period. After the remaining ungerminated seeds were tested for viability with tetrazolium staining, the total viability of seeds from hot initial treatments was still significantly lower than that of seeds from initially fluctuating treatments.

a)

b)

c)

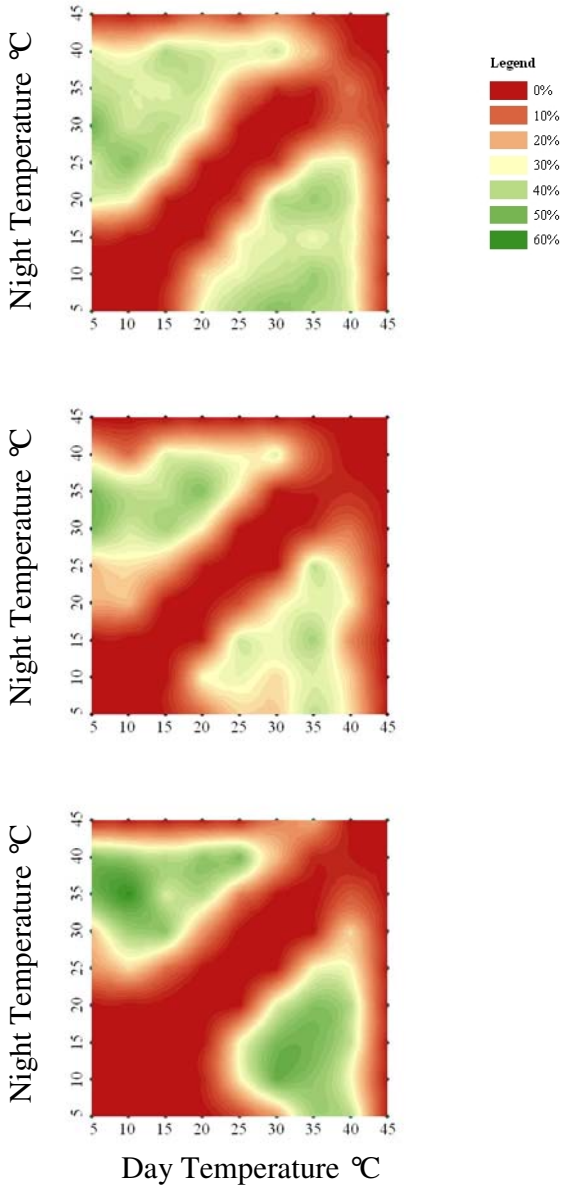


Figure 5.3 Prediction surfaces for percentage germination of *Phyla canescens* seeds collected from Site 1, a) four months, b) 16 months and c) seeds collected from Site 3 six months after harvest, showing low germination at constant temperatures.

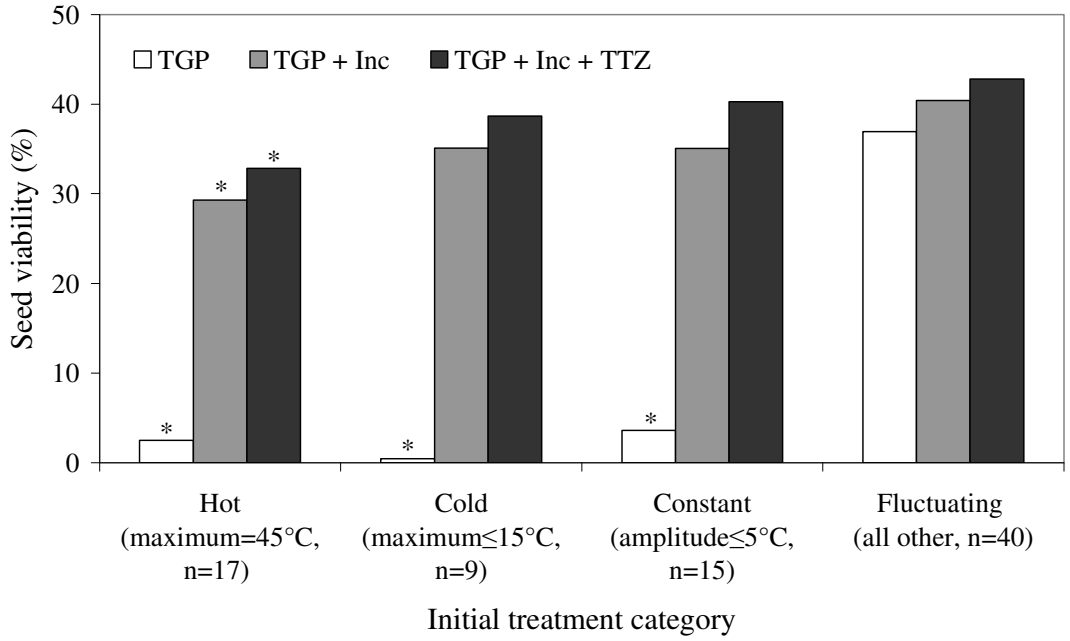


Figure 5.4 Percent viability of *Phyla canescens* seed, aged 4 months, as indicated by germination on thermogradient plate (TGP), germination in incubator (Inc) and positive tetrazolium viability stain (TTZ) for each of four categories of initial (thermogradient plate) temperature regime, n = number of cells per initial treatment category. Degree of significance (Chi-square test): * $p < 0.017$, with Bonferroni correction for multiple comparisons (equivalent to $p < 0.05$). Comparisons are between fluctuating and other initial treatment categories for each experimental stage (i.e. after TGP, after TGP + Inc and after TGP + Inc+ TTZ). Seeds were collected from Site 1.

5.4 Discussion

5.4.1 Experiment 1: Substrate

It appears that *P. canescens* seeds require free water for germination. Highest germination percentages were achieved when fruit was surrounded by water (i.e. either placed between two moist filter papers or imbedded into 1% agar gel, with additional water provided *ad libitum*). In contrast, some standard germination techniques (e.g. purpose made germination cards) resulted in little germination.

5.4.2 Experiment 2: Light

Light appears essential for the germination of *P. canescens* seed. While this was the case under the conditions of this study, it remains a possibility that there may be some germination under dark conditions at other temperature regimes, or with seeds from other populations or after a longer period of ageing. However, even if exceptions are found, the general conclusion still holds that only *P. canescnens* seeds from very near the soil surface are likely to germinate.

5.4.3 Experiment 3: Temperature

The germination response of *P. canescens* to temperature is characterised by reduced germination at constant temperatures. I have termed this response 'homothermophobia'. This does not appear to be a form of dormancy (*sensu* Baskin and Baskin 2004), rather simply quiescence, equivalent to a subset of Harper's (1977) 'enforced dormancy', i.e. enforced by the absence of conditions necessary for growth, not the state of the seed. Therefore, diurnally fluctuating temperatures are regarded simply as a 'normal physical environmental factor', without which this species will not germinate (Baskin and Baskin 2004). This is supported by the subsequent germination of seeds moved from constant temperature to fluctuating temperature conditions. These seeds showed the same pattern as those moved from positions apparently too cold for germination (Figure 5.4).

The term 'homothermophobia' is considered to more accurately describe the germination response to temperature than the obvious positive corollary, 'heterothermophilic'. This is because all constant temperature regimes suppressed germination, whereas not all combinations of alternating temperatures elicit a germination response, i.e. where temperatures are too high or too low (Figure 5.3).

The phenomenon of homothermophobia has been recorded to varying degrees in many species (though obviously not by this name). Mostly there is still substantial, though reduced, germination at constant temperatures, but there are also some species which seem to exhibit almost absolute homothermophobia. Examples include: *Cynodon dactylon* (L.) Pers., Poaceae; *Typha latifolia* L., Typhaceae (Morinaga 1926); *Lycopus*

europaeus L., Lamiaceae (Thompson 1969); *Fimbristylis littoralis* Gaudich., *Scirpus juncoides* Roxb., both Cyperaceae (Pons and Schröder 1986); and *Phalaris arundinacea* L., Poaceae (Leck 2004). Interestingly, these obligate homothermophobes, although from a range of families, all occupy aquatic, semi-aquatic or floodplain habitats: no obligate homothermophobic species were identified from non-flooding habitats. *Phyla canescens* appears to be a classic homothermophobe. This generalisation is consistent across two geographically disjunct populations, as well as with seed age.

The ecological and adaptive significance of homothermophobia is still a subject for speculation. Explanations include soil depth-sensing, ecological-gap-sensing and inundation-recession-sensing (Thompson and Grime 1983). Greater germination of *Sorghum halepense* (L.) Pers. has been recorded at shallower depths of burial and attributed to homothermophobia (Ghersa et al. 1992). Likewise, larger soil temperature fluctuations induced by a reduction in leaf canopy have been implicated in greater germination of *S. halepense* (Benech Arnold et al. 1988). Many wetland species require alternating temperatures to germinate (Thompson and Grime 1983). This was related to an increase in temperature fluctuations due to the diminution of the 'insulating effect' (thermal mass) of water as wetlands dry out. The seeds are, therefore, able to delay germination until there is bare, exposed ground.

All the species listed above which show a homothermophobic germination response are also listed as weeds somewhere in the world (Randall 2002). This may simply reflect the greater scientific attention weeds have received compared to 'well-behaved' species. However, it may represent an important biological trait for invasion success in aquatic/floodplain habitats.

How these competing detection hypotheses interact depends upon other aspects of the biology of the seeds and the habitat under study. Depth-sensing may be redundant in species which also require light for germination. This may be particularly true for small seeds because temperature fluctuations of sufficient amplitude for germination may penetrate deeper than the ability of the seeds to emerge (Thompson and Grime 1983). In

such cases, light would be a more sensitive 'depth-sensor', particularly in fine-textured soils. As *P. canescens* appears to also require light to germinate, we suggest that inundation-recession-detection is the main adaptive driver of homothermophobia in this species.

Approximately half of the seeds collected from both sampled populations were apparently not viable (Figure 5.3). This suggests the potential for increased fecundity. The factors limiting the viability of seed are not known, but reinforces the importance of understanding the breeding system, pollination and genetic variation in this species.

The majority of viable, freshly collected seeds appeared to be non-dormant. Under the conditions of this study, temperature does not appear to induce dormancy. The significance of the 4% of seed, which remained ungerminated across all initial treatment categories but stained positive for tetrazolium, is unknown. If this 4% is actually viable, it may make an important contribution to the seedbank. The reduced overall viability of seeds from hot initial regimes indicates some mortality under these conditions.

Homothermophobia may be pre-adaptive for general weediness (Thompson and Grime 1983). For *P. canescens*, it appears to be an important mechanism driving the ability to develop persistent seedbanks, and recruit successfully after flooding.

5.5 Conclusion

All these germination experiments indicate that *P. canescens* requires a fairly narrow range of conditions to achieve high levels of germination. This species appears to require a set of conditions (abundant moisture, light and alternating temperatures) most likely to be experienced on or very near the surface of bare soil as flood waters recede.

Chapter 6
Fecundity

6.1 Introduction

The number of seeds produced by a plant is fundamental to understanding the population dynamics of a given species (Shipley and Dion 1992). Indeed, propagule pressure, i.e. the number of introduction events and the number of individuals introduced, is thought to be a major factor in the success of invasive species (Williamson and Fitter 1996). Invasive species also tend to have higher fecundity than non-invasive species (Pysek and Richardson 2007).

Seed production can be influenced by many factors. The best predictors of seed output (across 57 herbaceous angiosperm species) are size (weight) of the parent plant and the average size (weight) of individual seeds (Shipley and Dion 1992). Clearly, a larger adult plant can invest more resources in reproduction than a smaller plant, all else being equal, and a plant producing larger seeds cannot produce as many seeds as a plant producing smaller seeds, with the same resources (Henery and Westoby 2001). There are many resources affecting plant size, and these would be expected to lead to corresponding changes in seed production. However, many factors can affect seed production beyond any size-dependent relationship. Seed production has been shown to vary with species, for example, species from disturbed habitats tend to have greater seed production than similar sized species from less disturbed habitats (Shipley and Dion 1992). Within a species, individual genotype (Aarssen and Clauss 1992), pollen and pollinator availability (Ashman et al. 2004), and root pathogenic fungi (Newsham et al. 1994) affect seed production beyond size-dependent associations. Increased nutrient supply can increase the number of seeds produced per flower (Campbell and Halama 1993), while damage by frost and seed predators can lead to increased fruit abortion (Stephenson 1981).

In addition, plant life-history can affect the size/fecundity relationship, such that monocarpic species show a closer relationship between plant size and seed output than polycarpic perennials, and for clonal perennials the relationship is weaker again, though

still significant (Aarssen and Taylor 1992). Clearly there is greater variation in fecundity among plants with a greater variety of ages, and hence greater chance of exposure to stochastic events such as herbivory, and potential future reproductive opportunities than cohorts of monocarps.

Indeed, one obstacle to the study of fecundity in polycarpic perennials is that very few studies extend over the entire life of a plant; most (such as Aarssen and Taylor 1992) are based on fecundity over a small proportion of the reproductive life (Herrera et al. 1998). This can bias estimates of lifetime reproduction, particularly in species with highly variable annual seed production, such as most polycarpic woody plants (Herrera et al. 1998). The analysis by Herrera *et al.* (1998) excluded polycarpic herbs because very few data sets of four years or more were available.

However, while lifetime fecundity is important in understanding potential evolutionary trade-offs, the annual rate of seed production (and its variability) is likely to drive short-term dispersal and seedbank dynamics, with potential consequences for populations of pollinators, vectors and seed-predators. Such annual fecundity data are available for many polycarpic perennials, including invasive species. Annual seed fall in the invasive perennial *Sporobolis indicus* (L.) R.Br. var *major* (Buse) Baaijens (Poaceae) was estimated at >146 000 seeds m^{-2} (± 17 600), but where seed production was prevented by regular defoliation for one seeding season, seedbanks declined by 62% compared to untreated control plots (Andrews et al. 1996). Similarly, the invasive perennial *Chromolaena odorata* (L.) R.M. King & H. Robinson (Asteraceae) produced an estimated maximum 260 000 seeds m^{-2} yr^{-1} in 10-year-old stands from sunny sites (Witkowski and Wilson 2001), which related to higher seedbank densities in sunny sites than shaded sites of similar age.

Recruitment of a species is dependent not only on the availability of seed, but also the availability of sites suitable for germination (Harper 1977). Seed-limited species are defined as those where an increase in abundance is observed with seed addition (Turnbull et al. 2000). In a comprehensive review of seed addition studies, approximately half of

the plant species from a sample of 90, including both invasive and non-invasive species, were found to be seed-limited (Turnbull et al. 2000). Seed-limitation was also found to be more common in early successional and short-lived species and in early successional habitats generally. However, in 19 of the 29 studies in which a disturbance treatment was also included, higher recruitment was found with both disturbance and seed addition than either disturbance or seed addition alone, implying that for many species, recruitment may be both seed and microsite-limited (Turnbull et al. 2000).

For a given species, the major determinant of fecundity is plant size (Aarssen and Taylor 1992). However, the difficulty of delimiting the extent of individual plants of stoloniferous species, such as *P. canescens*, where neighbouring individuals may overlap extensively, dictates that it is much more practical to quantify population parameters, such as fecundity, by unit area rather than by individual plants.

As propagule dispersal is generally a function of density (Nathan and Muller-Landau 2000), fecundity is an important contributor to the potential rate of spread (Higgins and Richardson 1999) and the development and persistence of a seedbank for a given species. Therefore, the fecundity of *P. canescens* was estimated across four sites to gain an understanding of the quantity and variability of seed production of *P. canescens*.

Annual seed production, the change in seed production with season, and the effect of other environmental conditions on seed production across a number of field sites was investigated. The effect of depriving plants of pollinators on seed production in a field population was also explored.

In this chapter, the term ‘fecundity’ is used exclusively to refer to the production of seed, not the production of vegetative fragments.

6.2 Methods

6.2.1 Flowering phenology

Flowering time was estimated using the month of collection of 152 reproducing (flowering or fruiting) herbarium specimens of *P. canescens* (from AD, BRI, CANB, HO, MEL and NSW herbaria, see Chapter 3 and Appendix 2 for specimen details).

Four 0.25 m x 0.25 m permanently marked quadrats were established within a 3 m x 3 m plot in each of the 12 experimental exclosures (described in Chapter 3). Within each of these quadrats, the number of immature inflorescences (buds), mature inflorescences (flowering) and infructescences (post-flowering) were recorded. Density for each exclosure is the mean of the four quadrats. Plots were monitored from June 2005 to September 2006 and visited approximately every 6 weeks.

6.2.2 Fecundity

The same quadrats were used to estimate fecundity. Once peduncles had become brown and dry, the infructescences were assumed to be mature and were picked and taken to the laboratory, where the fruit were manually extracted. These fruit were then counted and placed in 1% agar gel, with a thin film of deionised water maintained on the surface and incubated at 30:20℃ (light: dark) with a 12 h thermo- and photo-period (irradiance approximately 20 μmol m^{-2} s^{-1}). Germination was scored after 28 days. All measures are expressed per unit area, rather than per plant; this species is stoloniferous and it is extremely difficult to determine the extent of an individual plant in the usual sense,.

Inflorescence, fruit and germinable seed production data was log-transformed and tested for normality (Shapiro-Wilk) and homogeneity of variances (Cochrane's). Differences among sites were tested using Sheffe all-pairwise comparisons one-way ANOVA. Linear models were unweighted least squares linear regression and best subset regression (Statistix 2003).

Model variables included:

1. Site
2. Visit (time of year)
3. Time (days) since last visit
4. Percentage cover of *P. canescens* at time of seed collection
5. Percentage cover of all species other than *P. canescens*
6. Total rainfall since last visit
7. Total rainfall since last visit with 14-day lag
8. Mean daily minimum temperature since last visit
9. Mean daily maximum temperature since last visit
10. Mean daily soil moisture since last visit.

Variables 6 and 7 were calculated from rainfall data from nearby rain gauges, variables 8–10 were calculated from on-site data loggers (see Chapter 4 for details).

6.2.3 Pollinator exclusion

On 15 March 2006, ten virgin inflorescences (still in bud stage, with no flowers having opened) were selected within the 3 m x 3 m plot used in the fecundity experiment (above) for each of the three exclosures at Site 4. These inflorescences were each enclosed within a fine gauze mesh bag, the opening sealed around the peduncle with weather-proof tape. Another ten virgin inflorescences, adjacent to those bagged, were tagged with tape around the peduncle. The bagged and tagged infructescences were removed after 50 days (on 4 May 2006), by which time all peduncles were brown and shrivelled; the appearance of the peduncles was assumed to indicate that the fruit were physiologically independent of the parent. During this time some bags and tags disappeared.

Differences between treatments, bagged and open, for number of inflorescences, flowers, fruit and germinable seeds were tested using Kruskal-Wallis non-parametric one-way ANOVA.

6.3 Results

6.3.1 Flowering phenology

The main flowering period of *P. canescens* in Australia is from October to April, with over 90% (139 collections) of reproductive (flowering and fruiting) herbarium specimens being collected in this period (Figure 6.1). The small number of collections (13) from outside this period (September, May and July) includes specimens from Queensland (6), South Australia (3), NSW (2) and Victoria (2), i.e. there is no obvious geographic pattern.

The phenology of flowering observed at the four field sites followed a similar pattern to the herbarium collections (also Figure 6.1). Flowering was observed from October to May, with high inflorescence density from November to March.

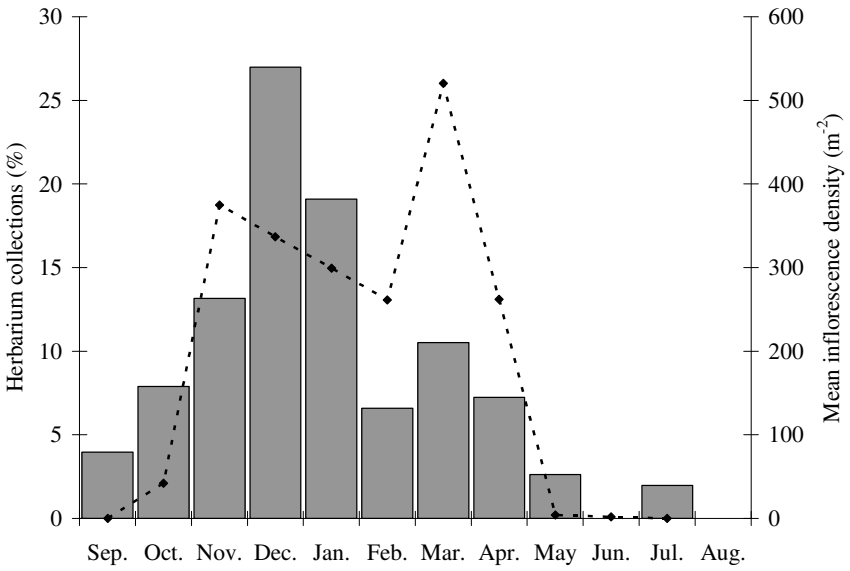


Figure 6.1 Percentage of herbarium collections (columns, left scale) per month for 152 reproductive (flowering and fruiting) *P. canescens* specimens (from AD, BRI, CANB, HO, MEL and NSW herbaria) and mean inflorescence density (m^{-2}) per visit (dotted line, right scale) for Sites 1–4.

The time taken for flowering and seed production, from the presence of a floral bud to a mature infructescence (with brown and dry peduncle and germinable seed) was less than 40 days (Figure 6.2). The shortest interval between visits during the flowering period of this study was forty days (1 February to 13 March 2006). Substantial quantities of infructescences matured completely within the inter-visit intervals at Sites 1 and 2 ($\Delta > 0$) during the first (64-day), second (40-day) and at Site 1 during the third (50-day) inter-visit interval. Some inflorescences did not persist up to the subsequent visit at Sites 3 and 4 ($\Delta < 0$) during the first interval and at Site 4 during the second interval. This attrition is attributed to predation or abortion of entire inflorescences.

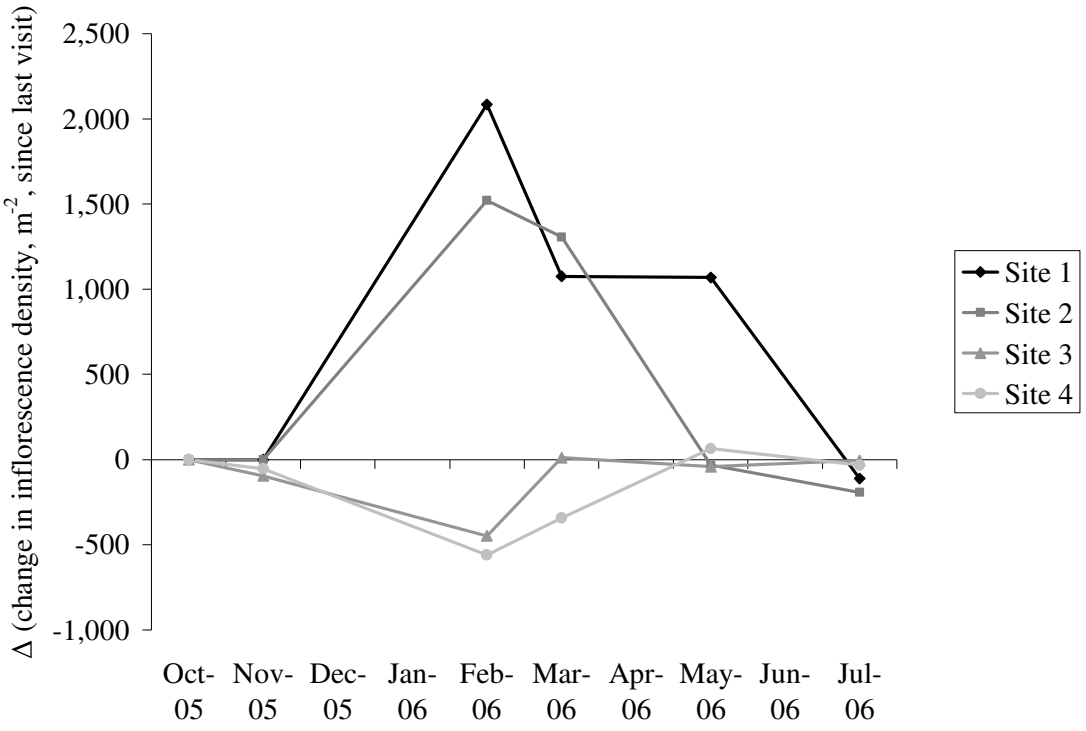


Figure 6.2 Change in inflorescence density (mature infructescences at time t – immature inflorescences at t-1) over time for each site. Where $\Delta > 0$, infructescences have completely matured in the inter-visit interval; where $\Delta < 0$, inflorescences have been predated or aborted.

6.3.2 Fecundity

The first germinable seeds were produced after the end of November (Figure 6.3). A high densities of seeds was produced early in the season at Site 2 (reaching 833 germinable seeds m^{-2} day^{-1} for 64 days from 30 November to the 2 February), whereas Site 4 produced more seeds later in the season (459 germinable seeds m^{-2} day^{-1} for 40 days from 16 March to 23 May). No germinable seeds were produced at any site after May.

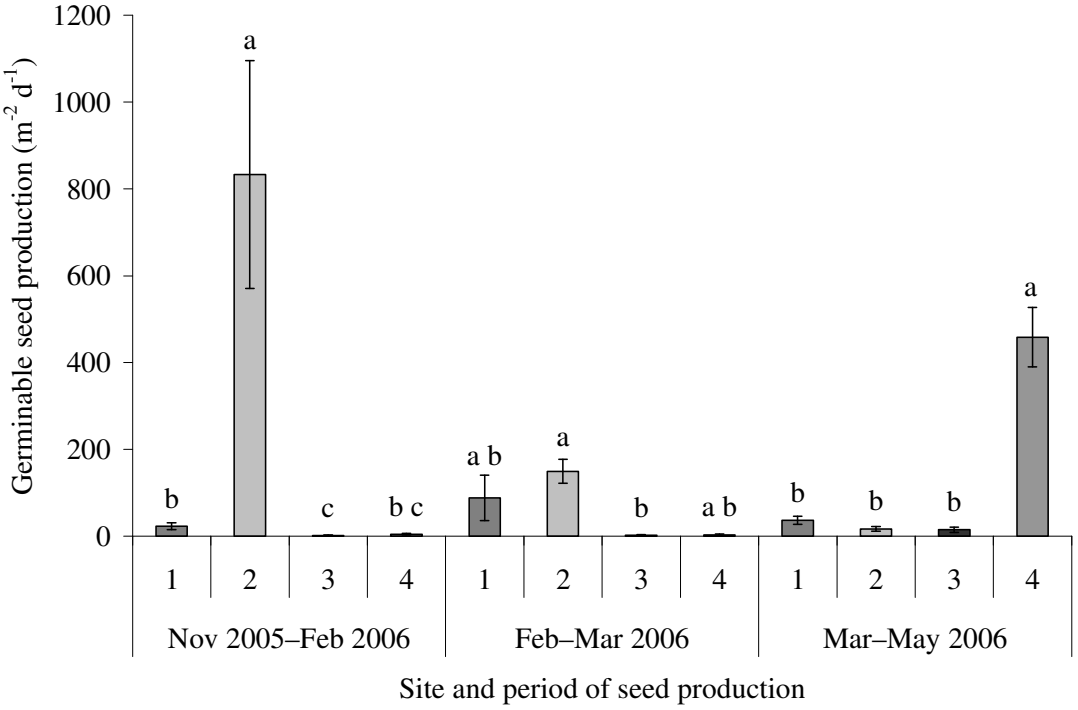


Figure 6.3 Germinable seed production (m^{-2} d^{-1}) by site for each visit over the 2005–2006 season. Means with the same letter are not significantly different from one another ($p < 0.05$). Sheffe all-pairwise comparisons one-way ANOVA among sites for each time of collection, not between collection times.

Site 1 produced a higher density of inflorescences over the 2005–2006 growing season than Sites 3 and 4 (Figure 6.4). However, Site 2 produced a higher density of fruit and germinable seeds than either Sites 1 or 3, and a higher density of fruit than Site 4. Sites 1 and 4 also had higher fruit and germinable seed production than Site 3. Germinable seed production reached 60 153 m^{-2} yr^{-1} at Site 2, but was only 936 m^{-2} yr^{-1} at Site 3.

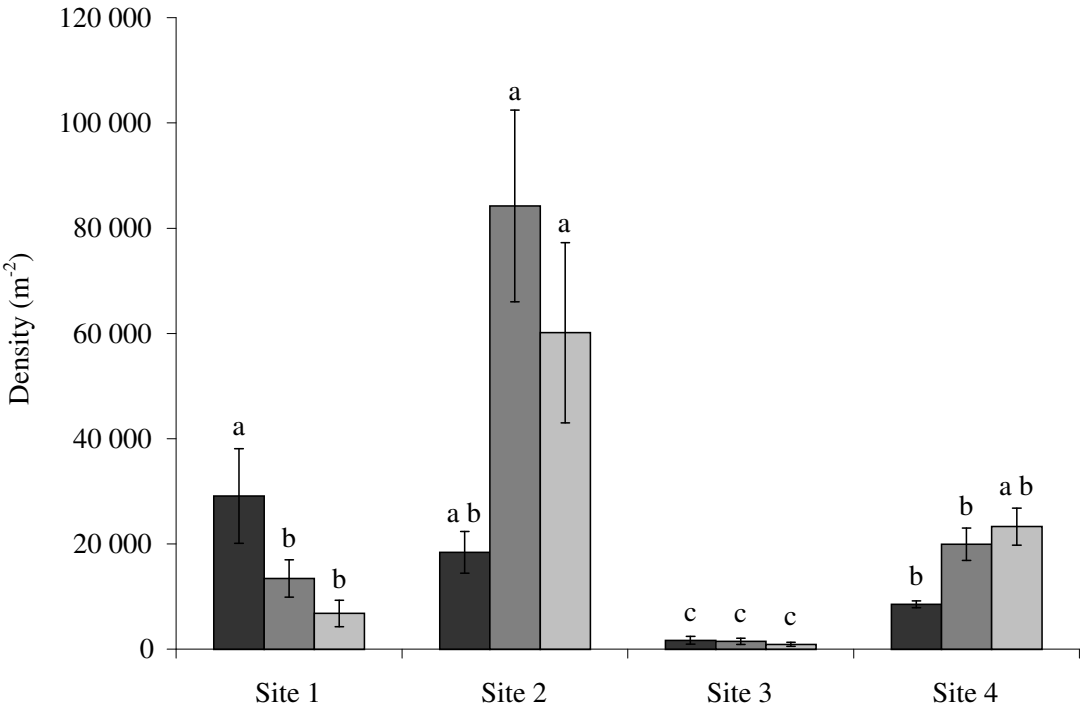


Figure 6.4 Inflorescence (■), fruit (■) and germinable seed (■) production (m^{-2}) ± SE for each site over the 2005–06 growing season (October–May). Columns with the same letter are not significantly different ($p < 0.05$). Sheffe all-pairwise comparisons one-way ANOVA among sites for each measure of fecundity, not between fecundity measures.

Germinable seed production was significantly associated with only two variables (Table 6.1): rainfall since last visit ($r^2 = 0.3032$, $p = 0.0003$) and cover of *P. canescens* ($r^2 = 0.1722$, $p = 0.0096$). The 'best' model to explain the variation in germinable seed production included four variables: total rainfall since last visit, cover of *P. canescens*, visit number, and total cover of all species other than *P. canescens* (Mallows' $C_p = -1.6$, adjusted $r^2 = 0.7221$).

Table 6.1 Unweighted least squares linear regression of germinable seed density.

Variable	r^2	p
Total rainfall since last visit	0.3032	0.0003
Cover of *P. canescens*	0.1722	0.0096
Visit (time of year)	0.1021	0.0505
Site	0.0851	0.0756
Mean daily maximum temperature since last visit	0.0638	0.1260
Total cover of all species other than *P. canescens*	0.0213	0.3822
Mean daily minimum temperature since last visit	0.0201	0.3962
Total rainfall since last visit with 14-day lag	0.0118	0.5167
Mean daily soil moisture since last visit	0.0035	0.7572
Time (days) since last visit	0.0001	0.9558

Fecundity, as measured by fruit and germinable seed production, had a positive but rather loose relationship to inflorescence density across the four sites (Figure 6.5). However, the production of germinable seeds is closely related to fruit production (Figure 6.6).

The mean number of germinable seeds produced per inflorescence was 5.22, but there was substantial variation among sites (Figure 6.7). Across all sites, the modal number of germinable seeds per inflorescence was zero. However, Sites 1 and 3 had a large percentage of inflorescences without any germinable seeds (61.3% and 48.2%, respectively).

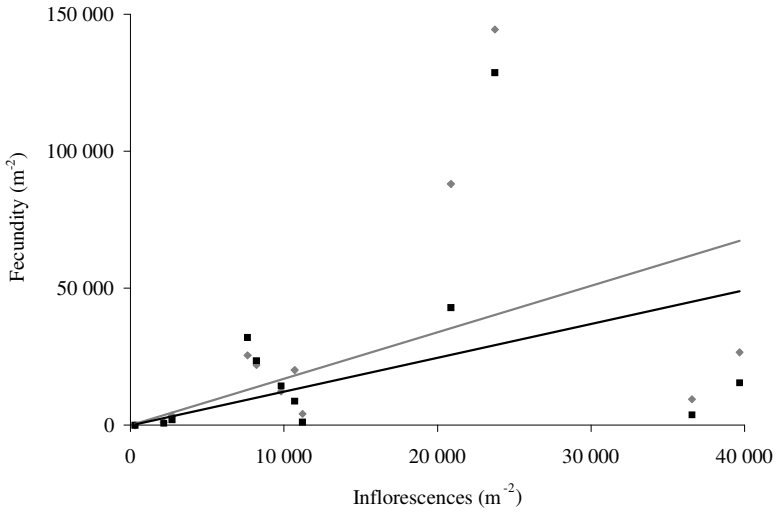


Figure 6.5 Fruit (◆) and germinable seed (■) production (m^{-2}) as functions of inflorescence density (m^{-2}) across all sites. Lines represents unweighted least squares regression, forced through the origin, for fruit (grey line —, y = 1.69819x, centred $r^2 = 0.0967$, p = 0.0192) and germinable seed (black line ─, y = 1.23229x, centred $r^2 = 0.0285$, p = 0.0424).

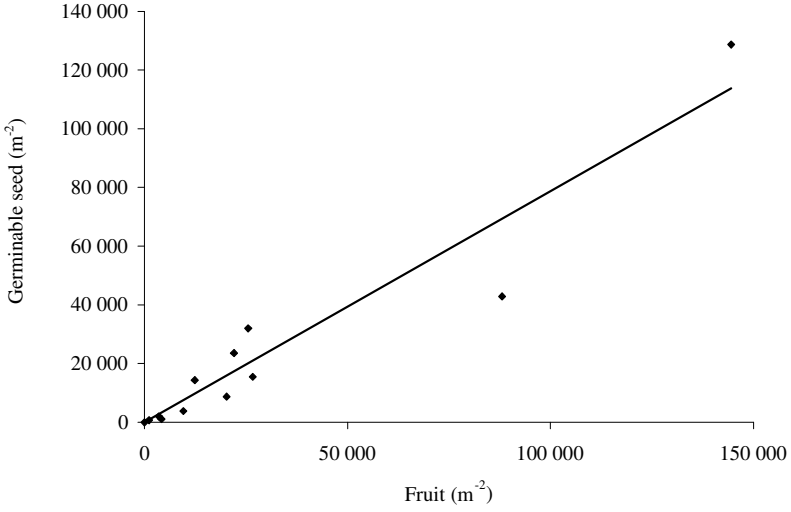


Figure 6.6 Germinable seed production (m^{-2}) as a function of fruit density (m^{-2}) across all sites. Line represents unweighted least squares regression, forced through the origin (y = 0.78751x, centred $r^2 = 0.9146$, $p < 0.0001$).

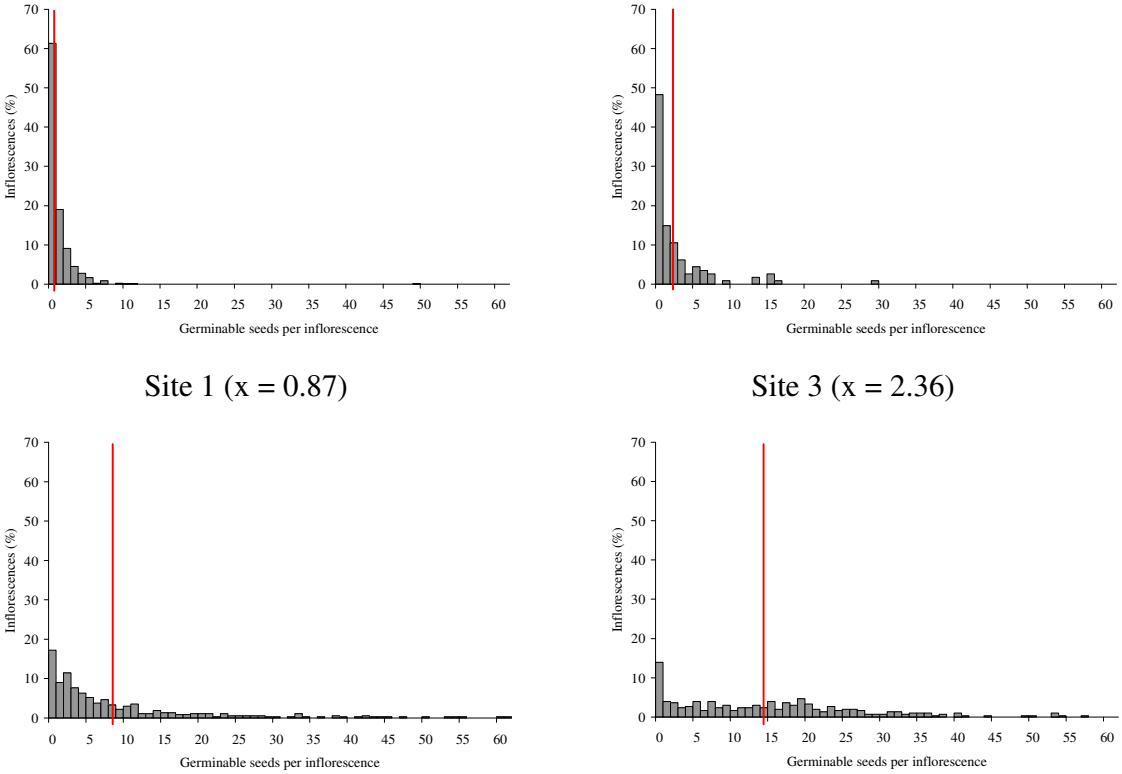


Figure 6.7 Number of germinable seeds per inflorescence for each of the 4 sites (x = mean germinable seeds per inflorescence for each site, shown as a red vertical line).

6.3.3 Pollinator exclusion

No fruit or germinable seed were produced by those inflorescences from which pollinators had been excluded (Table 6.2). Adjacent open-pollinated inflorescences produced 9.4 fruit (± SE of 1.4) and 8.5 (± 1.8) germinable seeds per inflorescence.

Table 6.2 Seed-set in *Phyla canescens* with and without pollinator exclusion from 15 March–4 May 2006 at Site 4 (N.S. = non-significant difference, * = significant difference, p = 0.05).

Treatment	Inflorescences	Flowers	% Fruit Set	% Seed Germinability
Open–Pollinated	16	296	51.0	45.0
Bagged	21	237	0.0	0.0
	N.S.	N.S.	*	*

While conducting this and other experiments, it was noticed that European honey bees (*Apis mellifera*) were frequent visitors to *P. canescens* inflorescences. Adult cotton boll-worm moths (*Helicoverpa armigera*) were also noticed visiting *P. canescens* flowers during the day at Sites 1 and 2 on 29 and 30 November 2005 respectively.

6.4 Discussion

6.4.1 Flowering phenology

Phyla canescens is a predominantly warm-season flowering species which can produce a large quantity of seeds (>60 000 m^{-2} yr^{-1}) under favourable conditions. Individual inflorescences can develop, grow and produce mature fruit within 40 days. Therefore, *P. canescens* appears to have the ability to respond quickly to the onset of favourable conditions by producing a pulse of seed, but can also extend seed production if conditions remain favourable over a longer period. Prolific flowering can occur from October to April. Long flowering period has been associated with invasive species in Australia (Lake and Leishman 2004) and Canada (Goodwin et al. 1999).

While some unaccounted for attrition of inflorescences was inferred (where the number of inflorescences left unharvested was greater than the number observed on a subsequent visit), no mechanism (e.g. herbivory) was noticed. It is possible that these inflorescences were aborted (as was the case for the 42% of all harvested inflorescences which produced no germinable seed), but were dislodged from the plant (e.g. by birds).

6.4.2 Fecundity

The large difference in production of germinable seeds among sites was best described with a four factor regression model. The model, which included: total rainfall in the preceding interval, cover of *P. canescens*, cover of other species and time of year, explained nearly three-quarters of the total variation. Total rainfall alone explained nearly one-third of the variation. The cover of *P. canescens* is the only other single factor which explains a substantial amount of the variation. Such a relationship is not surprising given the general relationship between plant size and fecundity (Aarssen and Taylor 1992; Shipley and Dion 1992).

However, the model is improved with the addition of the time of year (visit) and the cover of species other than *P. canescens*. The 'time of year' term encapsulates many seasonal factors, such as temperature and day-length. This and the other aggregated variable, site, individually made marginal contributions to explaining the overall variation. The cover of other species represents interspecific effects in addition to the direct effects on *P. canescens* cover. These interspecific effects were not significant as an individual factor because experimental plots were chosen for their uniform cover of *P. canescens*, and, therefore, inevitably with low cover of other species. If plots had been deliberately selected along a gradient of cover of other species, this effect may have been stronger.

Of the other variables included, mean daily maximum and minimum temperatures were incorporated into the 'time of year' variable. Total rainfall with a 14-day lag explained less variation than rainfall without a lag. Mean daily soil moisture was compromised as it

contained many missing values due to equipment failure. Time since last visit explained virtually none of the overall variation in germinable seed production.

Approximately one-quarter of the variation in germinable seed production remains unexplained by even the best model described here. This unaccounted for variation may have been reduced if visits had been conducted at shorter intervals. Other possible sources of this variation include: changes in pollinator activity over time, discrepancies between the rainfall recorded nearby and that at the actual sites, and variation among exclosures at each site.

The density of inflorescences is a poor predictor of fruit or germinable seed production. Attempts to estimate fecundity based on inflorescence counts, such as has been reported in other species (e. g. Andrews et al. 1996; Gardener et al. 2003), may be misleading for *P. canescens* populations.

6.4.3 Pollinator exclusion

From the pollinator exclusion experiment, it appears that *P. canescens* needs a pollinator to produce substantial quantities of viable seed. It is unclear if *P. canescens* is an obligate outcrosser proper, or if it simply requires the action of pollinator probing for intrafloral pollination, as has been observed in *Phyla incisa* (Estes and Brown 1973). From a management perspective, the difference is not important. Clearly, if the prevention of seed-set was considered a desirable management strategy, it does not matter if pollinators facilitate outcrossing *per se* or simply selfing (or both). If a reduction in pollinator density leads to a reduction in seed production, the precise mechanism may be largely irrelevant.

Honey bees (*Apis mellifera*) accounted for three-quarters of the pollinator visitations in a study of the related *P. incisa* Small in Costa Rica (Cruzen et al. 1988). *Phyla canescens* is considered a valuable source of pollen by apiarists in northern NSW and southern Queensland (Forno and Julien 2005) and it seems likely that honey bees are the main pollinator of *P. canescens* in Australia.

Although normally night-feeders, adult cotton boll-worm moths are known to sometimes feed during daylight hours, particularly when population density is high (Common 1990). It is not known if these moths are effective in pollinating *P. canescens*, but their frequency as floral visitors on *P. canescens* appeared less than honey bees by several orders of magnitude, although no observations were made at night. Due to small flower size, it has been suggested that for *P. nodiflora* 'only tiny flies or ants can act as pollinators' (Kumar and Dutt 1989, p. 351), although this was not actually tested.

6.5 Conclusion

Phyla canescens can produce over 80 000 fruit (160 000 seeds) m^{-2} yr^{-1}, of which over 60 000 seeds m^{-2} are germinable, under favourable conditions. This is of the same order of magnitude as the annual seed production of other invasive perennial herbs, such as *Sporobolus indicus* var. *major* (>146 000 seeds m-2, Andrews et al. 1996) and *Chromolaena odorata* (260 000 seeds m^{-2}, Witkowski and Wilson 2001). However, this seed production is overwhelmingly restricted to the warmer months (October to April in this study) and is influenced by recent rainfall, cover of *P. canescens*, cover of other species and the activity of pollinators.

Chapter 7
Seedbank dynamics

7.1 Introduction

Seedbanks can be seen as the temporal dispersal of plant propagules (Fenner 1995). The longevity of the seedbank is an important ecological and evolutionary trait, whereby persistent seedbanks are favoured in unpredictable environments (Cohen 1968). Persistent seedbanks have been found for species in 155 vascular plant families (Baskin and Baskin 1998). Many of the world's worst (agricultural) weeds develop persistent seedbanks (Holm et al. 1977), although seedbank studies have been heavily biased toward such agricultural (arable and grassland) habitats (Thompson et al. 1997).

Attempts have been made to classify seedbanks according to their longevity and seasonality (Thompson and Grime 1979; Bakker 1989; Poschlod and Jackel 1993). The overwhelming problem with the application of even simple systems, with only 3 or 4 categories, is that data for the vast majority of species are simply insufficient (Thompson et al. 1997). There is also the more fundamental problem of defining categories along what is essentially a persistence continuum, requiring arbitrary cut-offs, the location of which is driven more by convenience than any ecological meaning.

7.1.1 Seedbank longevity

Despite these drawbacks, there are some theoretically appealing and empirically supported generalisations regarding seedbank longevity. Monocarpic species, i.e. those with a single reproductive event, and also tending to be short-lived, are more likely to develop a persistent seedbank than polycarpic and generally longer-lived species, while species from stable habitats tend to have lower seed persistence than those from highly disturbed habitats (Thompson et al. 1998). The weight and sphericity of the seeds (diaspores) has been used to predict the ability of European species to develop a persistent seedbank, such that species with small, round seeds are very likely to develop seedbanks which persist for at least 5 years (Thompson et al. 1993). However, this

relationship does not hold for Australian (Leishman and Westoby 1998) or New Zealand flora (Moles et al. 2000). Another possible exception is the minute seeds of the Orchidaceae, for which no seedbank references were found in a comprehensive database of 2568 European taxa (Thompson et al. 1997). Seed mass is also associated with other traits, such as adult plant size (canopy area), adult density, reproductive lifespan and seed output, illustrating the importance of a whole-of-life-cycle perspective to perceived trade-offs (Moles and Westoby 2006).

Four prerequisites for the development of a persistent seedbank have been identified (Murdoch 2006), based on earlier models (Schafer and Chilcote 1969; Roberts 1972):

1) preservation of viability
2) prevention of germination
3) avoidance of predation
4) eventual germination.

The preservation of viability (i.e. not dying) is the most fundamental prerequisite for the persistence of any life-form. Much research has been concerned with the loss of viability of seeds under artificial storage conditions, which are clearly different from those experienced by seedbanks *in situ* (Cook 1980), but a correlation between *in situ* and *ex situ* longevity has been found across 28 species (Priestley et al. 1985), suggesting an intrinsic basis for seed longevity. However, imbibition may actually increase seed longevity due to the activity of cellular repair processes (Thompson 2000).

Germination may be the single largest cause of mortality in short-lived seeds (Cook 1980), implying that the prevention of germination is important in seedbank persistence. While seed dormancy is perhaps the most obvious preventative to germination, for many species, which develop persistent seedbanks, prevention of germination is attributable to exacting germination requirements, such as an absolute requirement for light (Grime et al. 1981), rather than dormancy *per se* (Thompson 2000).

Seed predation by animals has been most clearly demonstrated pre-dispersal, and post-dispersal, at, or near, the soil surface, where seed densities are highest and seeds most exposed (Crawley 1992). As seeds become incorporated into the soil and densities decrease, monitoring predation becomes increasingly difficult, although seed predation has been demonstrated by some animals (e.g. Hulme 1994; Edwards and Crawley 1999) and fungi (Kremer 1993).

Abiotic factors, such as fire and flood, can also influence the seedbank directly by increasing germination and seed mortality (Meney et al. 1994), or indirectly, such as by decreasing seedbank replenishment (Harrington and Driver 1995).

Ultimately, however, for the development of a seedbank to be a successful characteristic, some seeds must germinate and grow, and the resultant plants reproduce. For this, seeds must respond to environmental triggers associated with conditions suitable for survival (Murdoch 2006). Germination responses to specific light (Pons 2000) and temperature regimes (Probert 2000) have been interpreted as gap-detecting cues for many species.

Survivorship of seeds buried in soil is generally considered to follow a negative exponential curve, i.e. seeds have a constant probability of survival over time (see references in Baskin and Baskin 1998 for examples). However, some species appear to have high survivorship initially, but this declines over time (e.g. Lunt 1995). A study, in which *Sinapis arvensis* (Brassicaceae) seeds were buried in the same location in two consecutive years, found that the survivorship of seeds buried in the first year followed a negative exponential curve, whereas those buried in the second year followed a negative linear decline (Donald 1993). Therefore, the survivorship of seeds in soil is clearly a function of environmental conditions and is not an immutable species trait.

7.1.2 Seedbank density

The density of seedbanks is highly variable (Baskin and Baskin 1998). Densities of over 500 000 seeds m^{-2} have been recorded for highly modified environments (McIntyre 1985). While for the majority of species no data are available, most species studied from

north-west Europe have seedbank densities below 500 seeds m^{-2} and more than 90% have less than 5000 seeds m^{-2} (Thompson et al. 1997). Therefore, while seedbanks are an almost ubiquitous feature of vascular plant communities, species with large and persistent seedbanks are relatively few.

Seedbank density may be estimated in a number of ways. The most direct method is simply to quantify germination *in situ*, but this method is problematic for species, such as *P. canescens*, because the germination requirements may not be met (see Chapter 8) during the experimental period (Roberts 1981). Seedbank density estimates using this technique are also sensitive to the presence of live plants and dead plant litter (van der Valk 1986).

An alternative for estimating the magnitude of the seedbank is to take soil cores. Sampling errors are typically high, due to heterogeneity in the distribution of the seedbank (Roberts 1981), requiring large sample sizes for an acceptable degree of accuracy (Barralis et al. 1986; Dessaint et al. 1996; Ambrosio et al. 1997). Generally, the precision of seedbank estimates can be improved by taking many small samples rather than fewer large ones (Bigwood and Inouye 1988).

Once the soil samples are taken, the seedbank can be quantified either by:

1) physical extraction using various combinations of sieving and floatation (e.g. Malone 1967; Gross 1989; Buhler and Maxwell 1993; Tsuyuzaki 1994), followed by seed counting and preferably an assessment of viability, or
2) germination directly from the sample (emergence method, e.g. Roberts 1981; Poiana and Carter Johnson 1988).

These two methods can lead to disparate conclusions regarding both the density and species composition of the seedbank, as extraction includes dormant and non-viable seeds, while emergence includes only seeds that are germinable under the conditions provided. Extraction, therefore, will generally give higher estimates of seedbank density than emergence methods (Poiana and Carter Johnson 1988; Gross 1990; Brown 1992; Ter

Heerdt et al. 1996). An additional limitation of the emergence method is that where a large number of samples are taken, a substantial amount of glasshouse space, with conditions suitable for germination, will be required (Gross 1990; Brown 1992). To overcome this, concentration of samples by sieving to remove fine particles has been advocated (Ter Heerdt et al. 1996; Bossuyt et al. 2000). Perhaps not surprisingly, this can lead to underestimating the seedbank density of species with the smallest seeds (Traba et al. 1998). Estimates of the seedbank for an individual species, therefore, can vary substantially, depending on methodology (as discussed above and also the depth of soil sampled) and site characteristics (Thompson et al. 1997).

7.1.3 Artificial seedbanks

One method frequently used to assess the longevity of seeds in soil is to bury the seeds, then exhume them and test their viability. Perhaps the best known example of such experiments is one initiated by Beal in 1879 (Telewski and Zeevaart 2002), which showed that after 120 years of burial, nearly half (46%) of *Verbascum blattaria* (Scrophulariaceae) seeds remained germinable. However, the rate of depletion in seed viability does not just vary with species, but can also be influenced by aspects of the seed's environment (as discussed above) and even the environment of, and position on, the maternal plant (Gutterman 2000).

7.1.4 Seedbank pilot study

Since the sample size required to estimate the density of a seedbank with given accuracy varies with the abundance and patchiness of the seedbank, as well as the volume of the sample and the size of the soil core, a preliminary study is recommended (Thompson et al. 1997). A seedbank pilot study was undertaken, where soil cores were collected from Site 1 and incubated under conditions suitable for seeds of *P. canescens* to germinate directly from the soil. The aims of the pilot study were to determine:

1) the optimal number of samples to take
2) the depth distribution of the seedbank in the soil.

In addition, seedbank longevity of *P. canescens* in the field was determined by two methods: seedling emergence from sieved soil samples from plots where recruitment of new seeds to the seedbank had been prevented, and the burial and exhumation of an artificial seedbank.

7.2 Methods

7.2.1 Seedbank pilot study

All soil cores were taken from within dense (>80% cover) patches of *Phyla canescens* at Site 1 (see Chapter 4 for details) on 3 February 2005. Soil cores were cylindrical, 19 mm in diameter and 75 mm deep. The cores were transported in 20 mm diameter plastic canisters to minimise disintegration and mixing of depths during transit. The soil cores were subsequently cut into three soil depths: 0–25 mm, 25–50 mm and 50–75 mm. These sections were then manually crumbled into fine peds, and placed in Petri-dishes; the samples were covered with deionised water. Samples were incubated at 30:20° C (light: dark) with a 12 h photo- and thermo-period (irradiance of 20 μmol m^{-2} s^{-1}, measured with a 'LI-COR' model LI-250 light meter, John Morris Scientific). Deionised water was added as required to maintain saturation for 28 days, when seedlings were counted. The number of samples required to achieve a standard error of 20% of the mean was calculated (Thompson et al. 1997) from the sample mean, variance and an estimate of the binomial exponent, k (Elliot 1971). Depth data were analysed using Kruskal-Wallis non-parametric ANOVA all-pairwise comparisons.

7.2.2 Seedbank estimation and decline

One 3 m x 3 m plot within each of the three exclosures established at each of the four field sites (12 exclosures in total, see Chapter 4), was selected to estimate the change in *P. canescens* seedbank over time. From within this plot, 30 soil samples to a depth of 75 mm were taken with the 19 mm diameter soil corer (initial samples were taken on 6, 7, 8 and 9 June 2005, for Sites 1, 2, 3 and 4, respectively). Thereafter the plot was sprayed approximately every six weeks with Roundup™ herbicide (360 g L^{-1} glyphosate diluted 1:100 with water, equivalent to 9 L glyphosate ha^{-1}) in an attempt to kill existing plants

and prevent further seed production. Further samples were taken approximately every 12 weeks until September 2006.

The data from the first sampling trip are not reported as all 30 cores per exclosure were pooled and it is suspected that the concentrated sample was too deep (6–9 mm) to allow germination of the whole sample. Subsequently, three lots of 10 cores per exclosure were pooled and spread more thinly (2–3 mm) in separate Petri-dishes.

The soil cores were wet sieved and the fraction between 600 μm and 1180 μm was incubated in a Petri-dish at 30:20° C (light: dark) with a 12 h photo- and thermo-period (irradiance 20 μmol m^{-2} s^{-1}). Deionised water was added as required to maintain a cover of water for 28 days, when seedlings were counted. A seed was considered to have germinated when the cotyledons had emerged from the seedcoat. For the first collection only, the 500–600 μm fraction was also incubated, but as there was no germination from this fraction, this was not repeated for later collections. Individual seed sizes of a sample of 20 seeds were 0.7–1.0 mm wide, 1.0–1.7 mm long and 0.3–0.5 mm deep.

The number of germinable seeds was square-root transformed and differences among sites were tested with Tukey HSD all-pairwise comparison ANOVA. Changes in seedbank density over time were similarly transformed and subjected to unweighted least squares linear regression. Results are presented as germinable seed density for ease of interpretation.

7.2.3 Seed burial and exhumation

Fifty intact fruit (100 seeds) were encased inside 50 mm square nylon mesh envelopes, mesh size = 300 μm, with 10 cm^3 soil previously collected from the site. This soil had been sieved to remove fractions greater than 200 μm. All fruit used were collected from Site 3 (see Chapter 4) on 20 May 2005. Envelopes were buried at 1, 5 and 10 cm depths in each of the three exclosures on 10, 11, 12 and 13 August 2005 at Sites 1, 2, 3 and 4 respectively. Eight envelopes were buried at each depth per exclosure. At the conclusion

of this study, three sets of envelopes remained in the field at each of the 12 exclosures for future exhumation.

Upon exhumation, the fine soil within the envelopes was washed through the mesh with running water, leaving the seeds inside. The envelopes were then cut open and the seeds were subjected to a germination test. The seeds were placed 1–2 mm into the surface of 1% agar gel in Petri-dishes and incubated at 30:20 °C with a 12 h thermo- and photo-period (irradiance approximately 20 μmol m^{-2} s^{-1}). A thin film of deionised water was applied to the surface of the gel and maintained for 28 days, at which time the number of germinants was counted. Data were analysed using Kruskal-Wallis non-parametric ANOVA all-pairwise comparisons.

7.3 Results

7.3.1 Seedbank pilot study

Since the sample variance was greater then the sample mean, the distribution of germinable *P. canescens* seeds in the soil from this pilot study was assumed to follow a negative binomial (clumped, aggregated or contagious) distribution (Elliot 1971). Using the method outlined by Thompson *et al.* (1997), an estimated 90.9 soil cores would yield seedbank density estimates with a standard error of 20% of the mean. This is broadly consistent with the recommendation of Lopez *et al.* (1988) that taking 100–300 cores is sufficient to achieve 20% precision at 95% confidence level for seed densities of 500–2500 m^{-2}. Therefore, for the subsequent seedbank studies 90 cores per site (30 per exclosure) were taken.

More seeds germinated from near the soil surface than deeper in the soil profile (Figure 7.1). Approximately half (49.1%) of these seeds were from the top 2.5 cm of soil, a third (36.8%) from 2.5 to 5 cm deep and one sixth (14.0%) from 5 to 7.5 cm. In subsequent experiments, cores were, therefore, taken to the full depth of 7.5 cm.

The cores for this pilot study were taken from a discrete patch of *P. canescens*, smaller than the patches from which subsequent seedbank samples were taken (smaller patches

may be younger, assuming patch size is a function of age). The mean seedbank density in this pilot study, therefore, was not necessarily expected to be the same as within the exclosures, even for those from the same site.

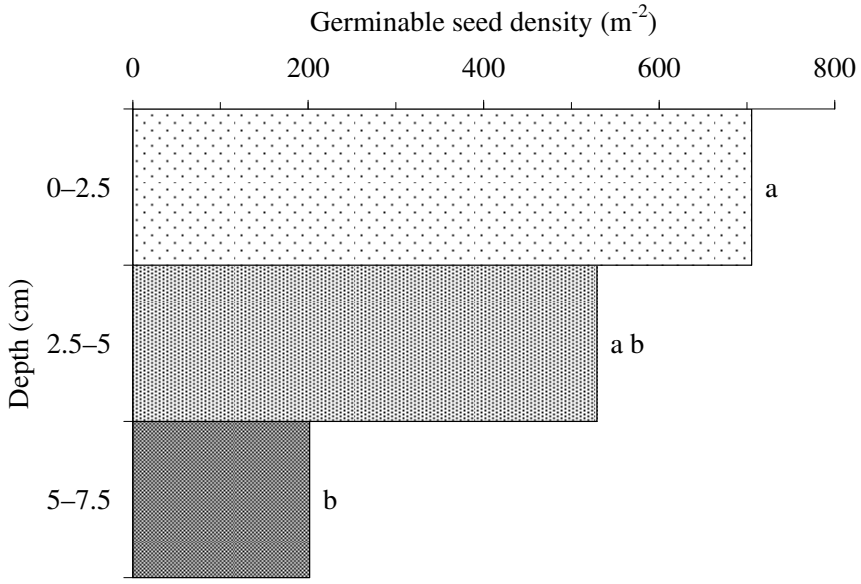


Figure 7.1 Distribution of *Phyla canescens* seeds at three depth classes from soil cores collected at Site 1. Depths with the same letter are not significantly different (p = 0.05).

7.3.2 Seedbank estimation and decline

Site 2 had the highest seedbank of germinable *P. canescens* seeds (Figure 7.2). The seedbank density at Sites 1, 3 and 4 were not significantly different.

There was very little decline in the soil seedbank during the 12 months of the experiment. However, the slope of the regression of germinable seedbank density over the duration of the experiment was significantly different from zero (p = 0.0041, Figure 7.3). This relationship was negative (-6.97), but was not a good fit (R^2 = 0.0453). In comparing regression lines among sites, there were no significant differences among variances (Bartlett's test of equal variances, p = 0.0526) or slopes (p = 0.2150). However, the comparison of elevations of the regression lines reveals significant differences in seedbank density among sites (p < 0.001).

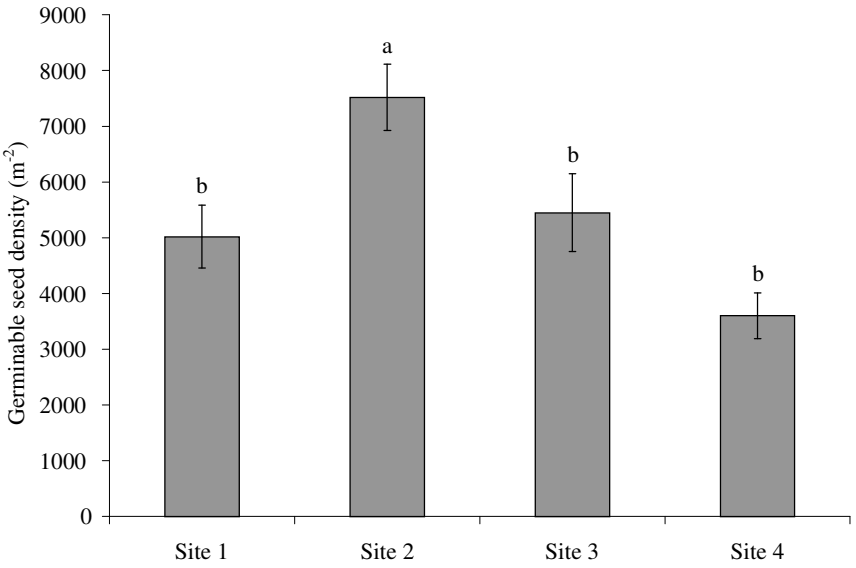


Figure 7.2 Soil seedbank density of *Phyla canescens* across four sites (± SE). Sites with the same letter are not significantly different (p = 0.05).

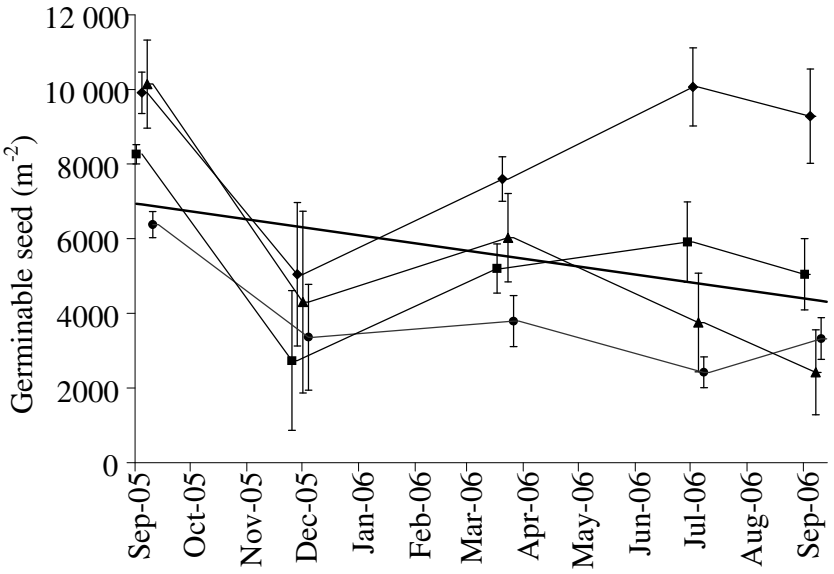


Figure 7.3 Mean seedbank density over time for Site 1 (■), Site 2 (◆), Site 3 (▲), Site 4(●) ± SE and overall linear regression (▬), y = 6 943 – 6.97x (R^2 = 0.0453, p = 0.0041).

7.3.3 Seed burial and exhumation

Significantly fewer seeds were retrieved after 391 days than after 64 days of burial (Figure 7.4). There were no significant differences in the number of seeds retrieved among sites or among burial treatment depths.

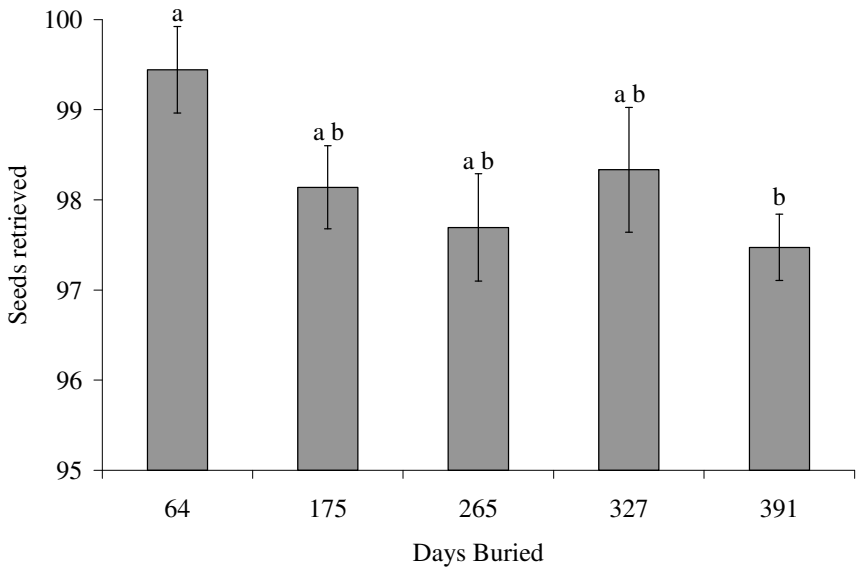


Figure 7.4 Mean number of *Phyla canescens* seeds retrieved per envelope by duration of burial (± SE). Treatments with the same letter are not significantly different (p = 0.05).

The proportion of germinated seeds exhumed from Site 2 was significantly lower than those exhumed from Sites 3 and 4 (Figure 7.5). There was no significant difference in the proportion of retrieved germinated seeds with depth or duration of burial treatments.

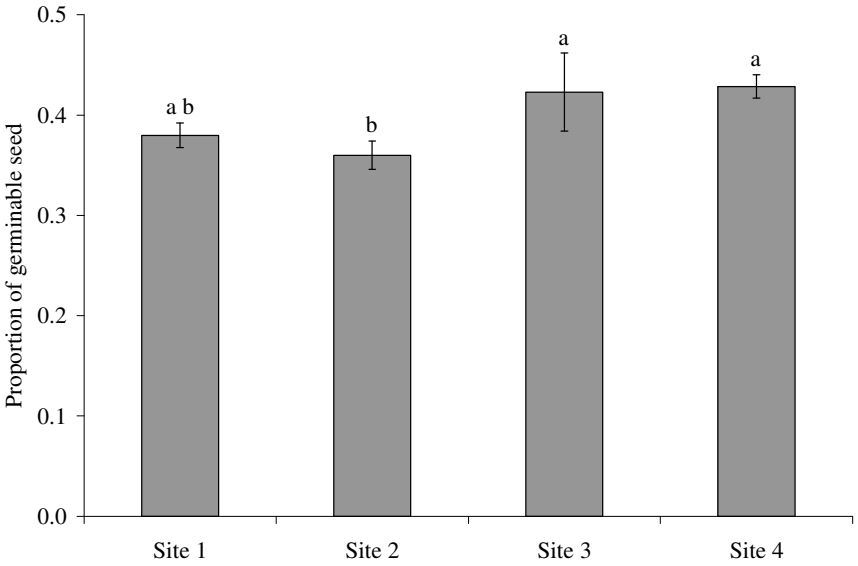


Figure 7.5 Proportion of exhumed *Phyla canescens* seeds which subsequently germinated from each of four sites (± SE). Sites with the same letter are not significantly different (p = 0.05).

7.4 Discussion

7.4.1 Seedbank pilot study

From the soil core pilot study, it was decided that taking 30 soil cores per exclosure (90 per site) was likely to yield sufficiently accurate soil seedbank density estimates. The obvious limitation was that without knowing the rate of seedbank decline in *P. canescens*, it was not possible to know how precise such seedbank estimates needed to be to detect a decline over a given period of time. The sample size of this study was consistent with other studies; 100–300 cores have been recommended where 500–2500 seeds m^{-2} are present (Lopez et al. 1988).

The depth distribution of seeds in the soil (i.e. higher density of seeds in surface layer than deeper layer) indicates that *Phyla canescens* may have a persistent seedbank which is short-lived (< 5 yr) (Thompson et al. 1997). This is based on the hypothesis that deeper seeds are older than shallower seeds, but the depth distribution of seeds, even from the same species is variable among sites (Bekker et al. 1998).

7.4.2 Seedbank estimation and decline

Site 2 had a significantly higher seedbank density than the other sites (Figure 7.2). Site 2 also had the highest seed production (Chapter 6). The observed differences amongst the sites appear to be a function of the initial seedbank density; there is no evidence of differential rates of seed mortality among the sites.

The germination of *P. canescens* seeds is associated with flooding (Chapter 5); there was a flood event at the beginning of July 2005 at Site 4, but this occurred while the seedbank sampling protocol was still being refined, and before the artificial seedbank was established. Because the particular germination requirements of *P. canescens* seeds were not met during the experimental period, the observed decline in seedbank density is unlikely to be due to germination. The detected decline is most likely attributable to loss of viability due to predation and/or ageing. If this rate of loss of viability remained constant (i.e. the survivorship followed a negative exponential curve), the seedbank would decline to 1% of the original density after 10 years. This is of course an extravagant extrapolation, and is intended more as an indication of the steepness of the observed decline rather than a prediction of longevity.

7.4.3 Seed burial and exhumation

The number of seeds retrieved per envelope generally decreased over time (Figure 7.4). However, there was not a similar decrease in either the number of germinable seeds, or the proportion of germinable seeds to retrieved seeds. This loss of seeds over the duration of the experiment seems likely to be attributable to the decomposition of non-viable seeds, rather than mortality of germinable seed. Because there is no significant decline in the number of germinable seeds retrieved over the duration of this experiment, it is not possible to describe a survivorship curve. However, if the survivorship of seeds in envelopes continued at the same rate (describing a negative exponential curve), the number of germinable seeds retrieved would reach 1% after 26 years. This extrapolation is even more speculative than that from the soil core data (above), and should be regarded primarily as a conceptual aid; as a prediction it must be treated with some scepticism.

Fewer seeds germinated from those envelopes which had been buried at Site 2 than at Sites 3 and 4 (Figures 7.5 and 7.6). This suggests that there may be increased mortality at Site 2. This may be related to the higher seedbank density at Site 2 leading to density-dependent mortality, but this explanation is speculative.

It has been shown that using an artificially high seed density in seed burial studies can lead to overestimation of soil seedbank depletion rates (Van Mourik et al. 2005). The densities used in this study (equivalent to approximately 40 000 seeds m^{-2} of soil surface) are consistent with seed production densities (up to 100 000 seeds m^{-2}, see Chapter 6). Also, there was no significant decline in germinable seedbank density in the seed burial experiment, therefore, it does not appear that overestimation of the rate of seedbank depletion is a problem in this study. The seedbank depletion rates in this study may be under-estimated due to the potential of mesh envelopes excluding soil-living seed predators (Westerman et al. 2003), but there is no direct evidence for this.

In light of the special conditions required for *P. canescens* seeds to germinate (Chapter 5), seedbank depletion is likely to be greatest following a flood event. Unfortunately, such an event did not occur at the sites during the experimental period for the soil core study or the burial and exhumation study. However, the three remaining (unexhumed) artificial seedbank samples offer some hope of quantifying such impacts were such a flood event to occur in the future.

7.5 Conclusion

The seedbank of *P. canescens* is clearly persistent, and is likely to remain sufficiently high to be of management significance for perhaps a decade, even without new seed input. Due to the relatively large seedbank of *P. canescens*, and scarcity of seedlings found in the field, it appears that recruitment from seeds in this species is likely to be microsite-limited rather than seed-limited. This has consequences for the search for biocontrol agents; introducing seed-predators for weeds whose recruitment is not seed-limited may not provide substantial control of existing populations (Hosking 1995).

The problems with inferring seedbank longevity from single plant traits can be illustrated, using *P. canescens* as an example. Taking just three traits, the seedbank longevity of this species is predicted to be anything from short-lived to long-term persistent (Table 7.1). Individual traits, therefore, even those supported theoretically and empirically, appear to be poor predictors of seedbank longevity for individual species. However, there is also ample evidence that the apparent seedbank longevity of a given species can be highly variable among sites (Bekker et al. 1998).

Table 7.1 Seedbank longevity predictions for *Phyla canescens* from various plant traits.

Plant trait	Predicted seedbank longevity	Reference
polycarpic	short-lived	Thompson *et al.* 1998
small and round seed	long-term persistent (> 5 yr)	Thompson *et al.* 1993
higher seedbank density at soil surface than deeper	short-term persistent	Thompson *et al.* 1997

It is clear that the seedbank of *P. canescens* has the potential to persist for many years in areas where this species has come to dominate the vegetation and a substantial seedbank has developed. Management of these areas must necessarily have a similar long-term focus, if the suppression of *P. canescens* is to be sustainable.

Chapter 8

Response to disturbance

8.1 Introduction

Recruitment of new individuals is essential to prevent extinction for all species. This recruitment must match the death rate in stable populations. Where recruitment exceeds mortality, as is the case for invading populations, an increase in density and/or range occurs. The ability to accurately predict recruitment is central to the development of efficient weed control strategies (Grundy 2003). Therefore, an understanding of the conditions required for the recruitment of a given species is essential for the development of such predictions. In theory, conditions can then be manipulated to minimise recruitment events, e.g. cover crops and mulches (Swanton and Booth 2004). Young plants are typically more vulnerable to mortality from adverse conditions, both biotic and abiotic, than established plants (Mack and Pyke 1984); where conditions favourable to recruitment cannot be manipulated directly, at least by understanding where and when recruitment is likely to occur land managers may make strategic management interventions, e.g. after fire (Thomas et al. 2006).

For recruitment to proceed, a propagule must experience conditions suitable for the development of that propagule (i.e. 'safe sites' of Harper 1977). In the case of *P. canescens*, a seed or vegetative fragment must experience conditions suitable for germination or root development. In this sense, recruitment does not necessarily imply survival to a reproductive stage, but is simply a collective term for all new individuals derived from all modes of reproduction. The conditions necessary for recruitment vary with species and, where a species produces more than one type of propagule, even with propagule type (Baskin and Baskin 1998). The conditions suitable for recruitment are generally interpreted as adaptations to optimise potential future reproductive success in a given environment. In environments with relatively predictable seasonal conditions, e.g. temperate regions of the northern hemisphere, where different resources may limit plant growth in a predictable seasonal pattern, recruitment is generally a response to

seasonal cues, with the seeds of many species requiring cold stratification before germinating in spring (Baskin and Baskin 1998). However, in less reliable environments, such as much of the Murray Darling Basin, where patterns of resource limitation are relatively unpredictable, recruitment is generally a direct response to those stochastically arising favourable periods, such as rainfall events (Baskin and Baskin 1998). The probability of survival to reproductive stage depends on conditions subsequent to recruitment. Again, in predictable environments, survivorship is highly season-dependent, whereas, in less predictable environments survivorship may depend on a 'fortuitous co-occurrence of a sequence of events where each event has a low probability of occurring' (Noble 1986, p. 4).

In general a 'competitor–free space' is suitable for the recruitment of many species (Bullock 2000). Such favourable sites can arise by the action of a number of natural or anthropogenic processes, ranging from the death or removal of a single individual to the large disturbances of fires, floods, storms and agriculture.

Many plant species show seasonal variation in recruitment (e.g. Van Assche et al. 2003). Even where the principle germination cue is not necessarily seasonal, the season of events, such as fire (Roche et al. 1998; Ooi et al. 2004) or flooding (Warwick and Brock 2003), can influence recruitment.

While there are no published data on the field recruitment of *Phyla canescens* in Australia, two studies have investigated *P. canescens* as a component of wetland seedbanks (McCosker 1994a; White 2004). Both of these studies involved collecting soil samples and observing germination under various watering regimes in a glasshouse. Based on the germination response to these treatments, McCosker (1994a, p. 8) concluded that 'the highest number of seedlings being likely to appear after drought-breaking rains and/or flooding after prolonged dry spells'. Little information is available concerning recovery of established plants of *P. canescens* following a single disturbance and the changes in its ground cover throughout the year at different sites and with different rainfall patterns.

The purpose of this study was to examine/monitor the effect/s of physical disturbances at different times of the year, i.e. seasonal disturbances, in providing field seedbanks of *P. canescens* the opportunity to recruit in different seasons. During the seasonal disturbances experiment, a recruitment event associated with a flood adjacent to the permanent exclosures at Site 2 (see Chapter 4 for site details) was observed and investigated opportunistically.

8.2 Methods

8.2.1 Seasonal disturbances

To facilitate recruitment of *P. canescens* in the field, dense patches of *P. canescens* with substantial soil seedbanks (see Chapter 7 for seedbank data) were subjected to physical soil disturbance. Treatment (disturbed) and control (undisturbed) plots (each 3 m x 3 m) were randomly allocated within each of the 12 exclosures (4 sites with 3 exclosures per site, see Chapter 4). To provide the greatest opportunity for recruitment, the existing vegetation was removed by intensive disturbance of the top 5–10 cm of the soil profile using a rotary-hoe. The treated area was raked to remove excess plant debris from the soil surface. Each plot was then hand-watered with 200 L of water, equivalent to 22 mm of rain.

These disturbances were repeated in another randomly selected plot within each exclosure at the beginning of each of the four seasons (see Table 8.1 for disturbance dates). The order of disturbance for sites was the same for each season for logistical reasons. This also reduced variation in the length of intervals between disturbance and subsequent monitoring visits.

Table 8.1 Dates of disturbance for each disturbance treatment for each site

	Winter	Spring	Summer	Autumn
Site 1	6 June 2005	5 Sept 2005	29 Nov 2005	21 March 2006
Site 2	7 June 2005	6 Sept 2005	30 Nov 2005	22 March 2006
Site 3	8 June 2005	7 Sept 2005	1 Dec 2005	22 March 2006
Site 4	9 June 2005	8 Sept 2005	2 Dec 2005	23 March 2006

Within each treatment and control plot, four 0.25 m^2 (0.5 m x 0.5 m) quadrats were arranged (as in Figure 8.1) and permanently marked with steel pegs at two opposite corners. The number of seedlings in these quadrats in each treatment and control plot was recorded approximately every 6 weeks. Percentage live (green) cover of each species was visually estimated for each quadrat. The visual estimation of cover was aided by using quadrats with diving wires which formed a grid of 25 (10 cm x 10 cm) units, each representing 4 % cover.

Data for species other than *P. canescens* with similar attributes were combined into the following functional groups (see Appendix 3 for a list of species and functional group):

1. Annual grass
2. Perennial grass
3. Other monocot
4. Annual legume
5. Perennial legume
6. Other dicots (plus the fern *Marsilea drumondii*).

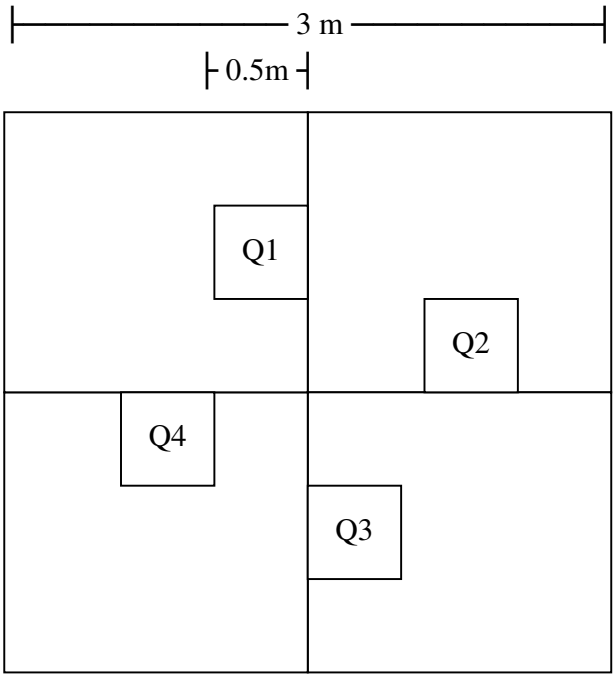


Figure 8.1 Position of four 0.25 m^2 quadrats (Q1–Q4) for 3 m x 3 m treatment and control plots.

Differences in germination among sites and treatments were tested using Kruskal-Wallis one-way non-parametric ANOVA all-pairwise comparisons. Means and standard errors are shown in figures for ease of interpretation. Cox's F Test was used in the survival analysis to compare the survivorship of seedlings of *P. canescens* in disturbed and control plots, as there was only one censored observation.

8.2.2 Opportunistic survey

A moderate flood event (as defined by Bureau of Meteorology 2007) occurred between 30 June and 3 July 2005, which inundated a billabong adjacent to the permanent exclosures at Site 2 on the Namoi River floodplain. On 6 September 2005, three 28 m transects were randomly placed across a 150 m length of this billabong. Each transect ran perpendicular to the edge of the billabong, and was divided into three zones (Table 8.2). The lower edge of Zone 1 (0 m elevation) was the water level at the time of sampling. The boundary between Zones 1 and 2 (0.16 m) was the upper extent of *Eleocharis plana*.

Zones 2 and 3 were separated by the strand-line, the height at which organic debris was stranded by the flood (0.42 m). Quadrats (0.25 m x 0.25 m) were placed at 1 m intervals along each transect, with the first quadrat being located at a random position in the first metre (closest to water) of each transect. The number of individuals of *P. canescens* per quadrat were recorded and categorised as one of the following plant types:

1. seedling – small erect plant with cotyledons
2. fragment – small (2.5 – 5 cm) horizontal piece of stem, rooting into the substrate
3. adult – well established individual, apparently present prior to the recent flood.

The site was grazed by sheep at the time. Frequency data for each plant type were subjected to chi square tests.

Table 8.2 Three zones adjacent to an ephemeral billabong (near Site 2), as defined by relative elevation and dominant vegetation at the time of sampling (6 September 2005).

Zone	Relative elevation (m)	Dominant vegetation
1	0–0.16	*Eleocharis plana*
2	0.16–0.42	Bare mud, *Phyla canescens*
3	0.42–1.07	*Phyla canescens, Medicago polymorpha*

8.2.3 Nomenclature

Nomenclature follows Wheeler *et al*. (2002) for Poaceae, and Harden (1992; 1993; 2000; 2002) for other taxa, except *Phyla canescens* (Munir 1993) and *Verbena gaudichaudii* (Michael 1997). Only vascular plants are included.

8.3 Results

8.3.1 Response to seasonal disturbances

Germination of *Phyla canescens*

No seedlings of *P. canescens* were recorded in any of the disturbance treatments inside the exclosures at Sites 1, 2 or 3, but other species did germinate at these sites. None of the exclosures at these three sites were flooded during the experimental period. However, *P. canescens* seedlings were found in both disturbed and control plots at Site 4 following a flood in early July 2005. No germination of *P. canescens* was recorded at any other time at this site, i.e. there was no germination of *P. canescens* when the exclosures were not flooded.

In total, 185 *P. canescens* seedlings were recorded after the flood event at Site 4. The density of seedlings was higher in winter disturbed plots (53.7 m^{-2}) than control (vegetated) plots (8.0 m^{-2}, $p < 0.05$, Figure 8.2). At the time of this flood, only the first (winter) disturbance had been completed, therefore no germination of *P. canescens* was recorded in other disturbance treatments. It was noticed that in the one control plot in which germination was recorded, the seedlings had germinated directly from mature infructescences, still attached to the parent plant (albeit in a partially decomposed state). This was not the case in the disturbed plot, as the mature infructescences still attached to the parent material had generally been dislodged by the disturbance process, but seedlings were frequently found in small (approximately 1 cm^2), dense patches (10 or more individuals).

Phyla canescens seedlings in the treatment (winter disturbed) plots survived longer than those in the control (vegetated) plots (Cox's F Test, $p < 0.0001$). Only one seedling survived the duration of the experiment in the disturbed plots, but none in the control plots (Figure 8.2).

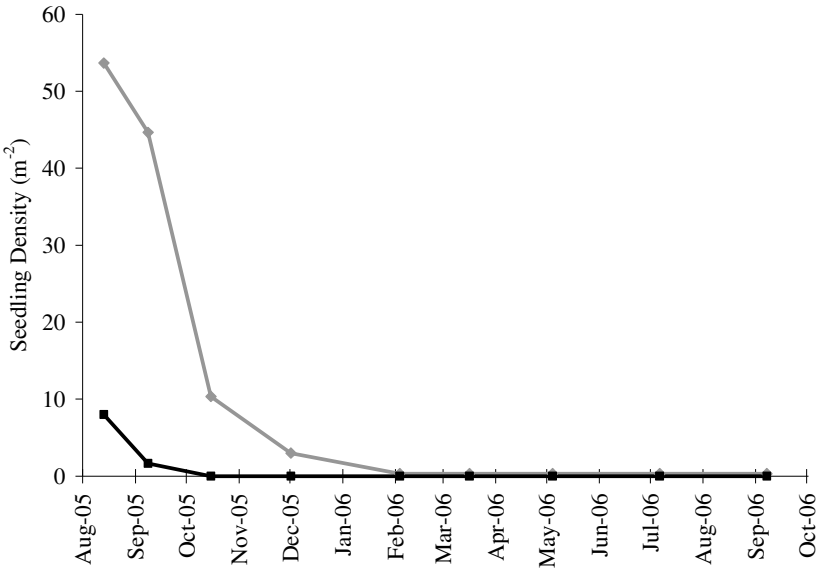


Figure 8.2 Survivorship of *Phyla canescens* seedlings in winter disturbed (◆) and control (■) treatments following a flood in July 2005 at Site 4. Note: One *Phyla canescens* seedling survived in the winter disturbed treatment until the end of the experiment (on 7 September 2006).

The exclosures at Site 4 were inundated following heavy rain in late June 2005. Soil moisture was elevated as a result of the rainfall event, and had begun to decline prior to the arrival of the flood (Figure 8.3). Unfortunately, on 4 July, the data-logger installed at the site to record temperature and soil moisture was damaged by the flood and ceased operating. Therefore, neither the longevity of the flood itself, nor the associated soil moisture is recorded.

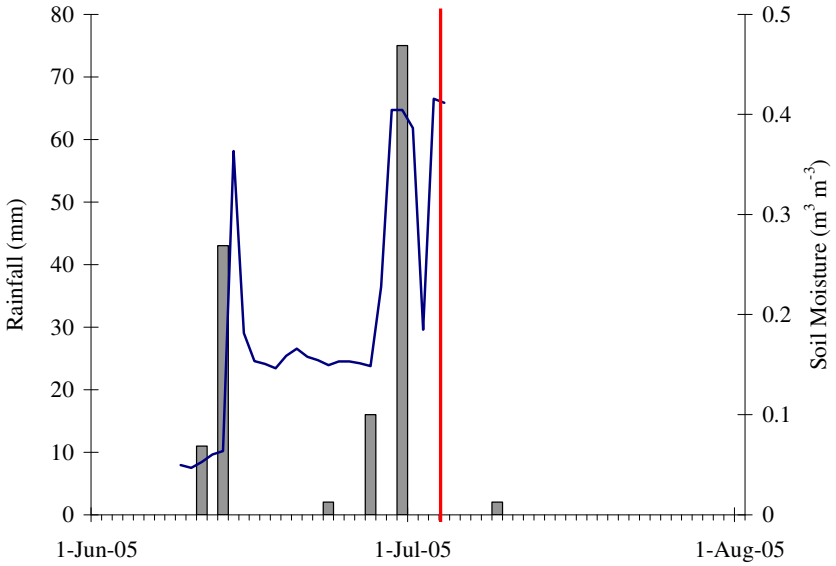


Figure 8.3 Rainfall records for 'Old Dromana' homestead, approximately 6 km south-east of Site 4 (column, left axis) and soil moisture (line, right axis) for June and July 2005 (flood event and logger failure, 4 July, indicated by a vertical line).

Cover of *Phyla canescens*

With each disturbance event, the live cover of all species was reduced to zero. However, the tap roots of some *P. canescens* and other perennial plants remained attached to the ground and were not severed by the disturbance. The cover of *P. canescens* in disturbed plots then recovered over time (Table 8.3) from the crowns of the surviving tap-roots, buried plant fragments and vegetative expansion from outside the disturbance. Cover of *P. canescens* in winter disturbed plots remained significantly lower than control plots until after 392 days past disturbance. Following spring disturbances, *P. canescens* reached over 50% cover (not significantly different from control plots) within 85 days of disturbance. However, with the onset of hot and dry conditions (during December and January), cover in the spring disturbed plots fell to levels significantly lower than the control plots. Summer disturbance plots recovered to control levels within 216 days, while in the relatively short period of monitoring after the autumn disturbance (168 days) *P. canescens* cover showed little sign of recovery, remaining well below control levels.

Table 8.3 Mean cover (%) of *Phyla canescens* (± SE) for treatment and control plots over the experimental period. Time (days) since disturbance is also included. Significantly different treatment and control cover scores are marked: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, Kruskal-Wallis one-way non-parametric ANOVA.

Visit	Control cover	Winter		Spring		Summer		Autumn	
		Days	Cover	Days	Cover	Days	Cover	Days	Cover
August 2005	50.4 ± 5.2	65	2.0 ± 0.6 ***						
September 2005	50.8 ± 5.8	91	4.5 ± 1.4 ***						
October 2005	56.8 ± 6.5	129	8.4 ± 3.1 ***	38	2.2 ± 0.8 ***				
December 2005	76.3 ± 6.0	176	26.3 ± 6.9 ***	85	51.1 ± 9.0				
February 2006	47.6 ± 10.6	240	15.4 ± 4.5 *	149	19.7 ± 5.4 *	64	22.0 ± 6.5 *		
March 2006	66.8 ± 6.2	280	35.9 ± 9.2 *	189	33.8 ± 7.0 **	104	39.3 ± 8.6 *		
May 2006	69.5 ± 6.7	330	32.8 ± 7.8 **	239	39.0 ± 7.2 **	154	45.7 ± 8.3 *	42	2.6 ± 1.0 ***
July 2006	38.2 ± 6.0	392	22.1 ± 5.1 *	301	23.4 ± 4.0	216	28.9 ± 5.3	104	4.2 ± 1.3 ***
September 2006	26.2 ± 3.9	456	15.4 ± 4.5	365	20.1 ± 3.6	280	21.5 ± 3.7	168	3.8 ± 1.1 ***

At the completion of the experimental period (7 September 2006), the percent cover of *P. canescens* was lower in autumn disturbed plots than any other treatment (Figure 8.4). The final cover in winter disturbed plots was also lower than the control (undisturbed) plots. Time since disturbance was 456, 365, 280 and 168 days for the winter, spring, summer and autumn disturbances respectively.

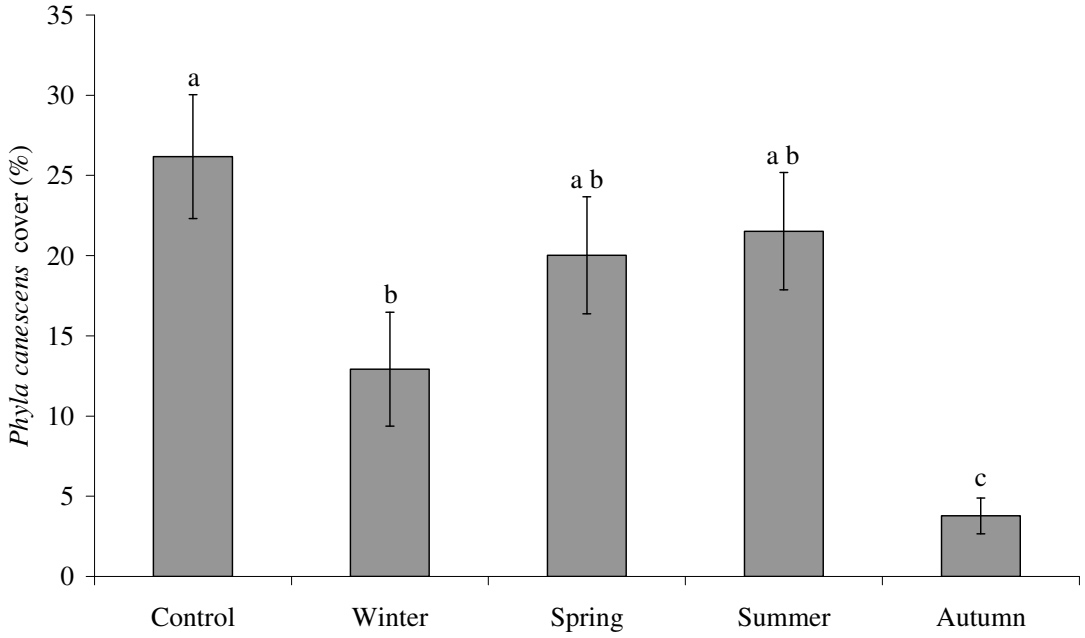


Figure 8.4 Mean cover (%) of *Phyla canescens* (± SE) at the completion of the experiment (September 2006) for each disturbance treatment across all sites. Means with the same letter are not significantly different ($p < 0.05$), Tukey's HSD all-pairwise comparisons ANOVA on root-transformed data.

Cover of *P. canescens* remained low from August to October, then rose significantly between mid-October and late November, coinciding with the demise of winter-growing annual species (Figure 8.5). However the cover of *P. canescens* declined from the end of November to early February, with the onset of hot and dry conditions. The recovery of *P. canescens* cover, between early February and mid-March, followed substantial rainfall across all sites in February (100 mm at Site 1, 63 mm at Site 2 and 106 mm at Sites 3 and

4, see Figures 4.4, 4.7, 4.10 and 4.13). Thereafter, *P. canescens* cover declined again through May and June with the onset of cooler temperatures. The total cover of all other species tended to trend with that of *P. canescens* during the summer months, reflecting rainfall as stated above. However, the rapid growth of winter annuals from July to early September, and their subsequent death as spring progresses runs counter to the seasonal fluctuations of *P. canescens*.

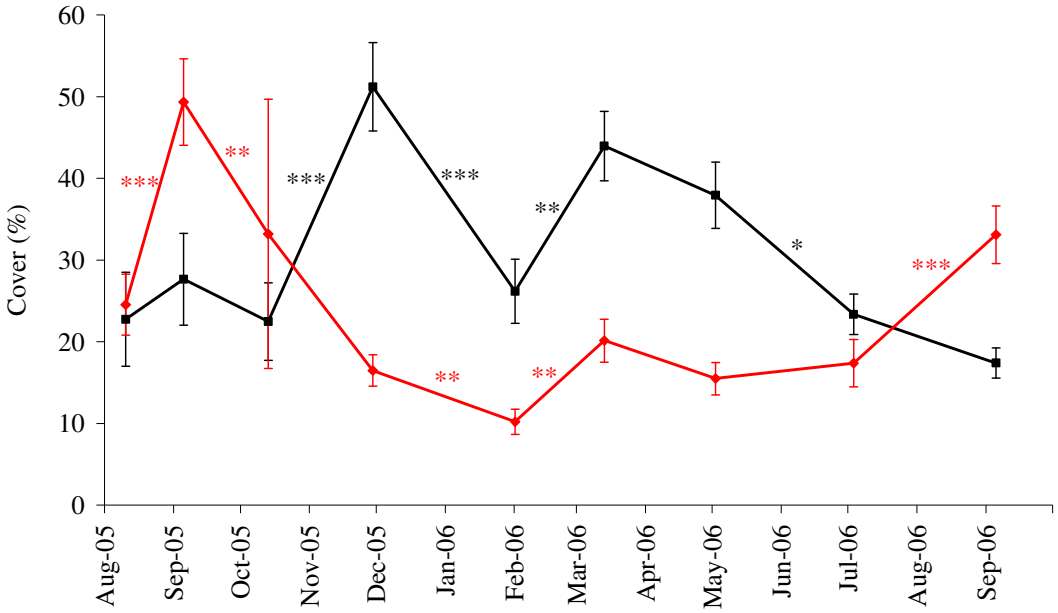


Figure 8.5 Mean cover (%) of *Phyla canescens* (■) and all other species (◆) across all sites and treatments for the duration of the experiment (± SE). Significant pairwise comparisons (Kruskal-Wallis one-way non-parametric ANOVA) between sequential cover scores have asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$); all other comparisons between sequential cover scores are not significant.

Germination of species other than *Phyla canescens*

Species other than *P. canescens* germinated at all four sites. Germination was generally dominated by annual species. Total germination was significantly higher at Site 2 than Sites 3 and 4 (Figure 8.6). Site 2 also had a higher density of annual legume germination (mostly *Medicago polymorpha*) than Sites 3 and 4, and higher germination of perennial legumes (mostly *Glycine tabacina*) than any other site. Site 1 had a higher density of annual grasses (largely due to *Lolium perenne* which behaves as an annual under the environmental conditions in this region) and perennial grasses (particularly *Paspalidium aversum*) than Sites 3 and 4. At Sites 1 and 2, germination was dominated by species such as *Medicago polymorpha*, *Lolium* spp., *Rapistrum rugosum* and *Cyclospermum leptophyllum*. Germination at Site 3 was dominated by *Medicago* spp., *Sclerolaena* spp., and *Lachnagrostis filiformis*, while Site 4 was dominated by *Brachyscome curvicarpa*, *Juncus usitatus* and *Rorippa eustylis* (see Appendix 3 for list of vascular plant species by site).

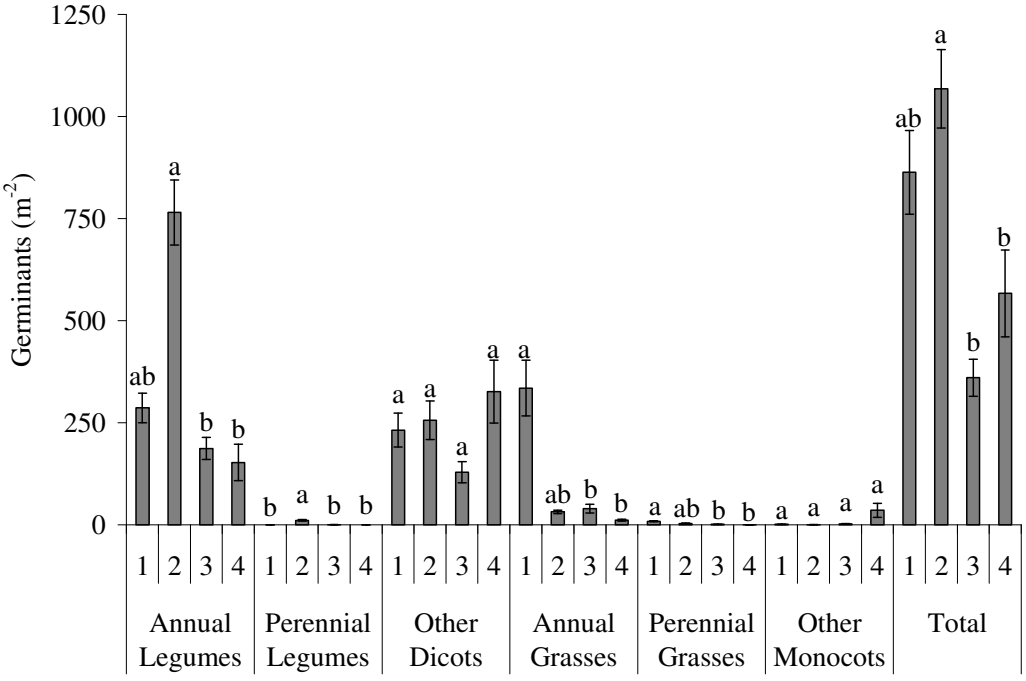


Figure 8.6 Density of seedlings (m^{-2}) of each functional group and total germination per site (± SE). Columns with the same letter are not significantly different ($p < 0.05$). Comparisons are among sites within functional groups only, not among functional groups, Kruskal-Wallis one-way non-parametric ANOVA.

Overall, germination was higher in disturbed than undisturbed plots ($p = 0.0001$). However, for individual seasonal disturbances, only summer and autumn disturbances resulted in significantly higher germination than the control plots for the same period (Figure 8.7). There was significantly higher germination after the winter and autumn disturbances than the spring disturbance, despite above average spring (September–November) rainfall at all sites.

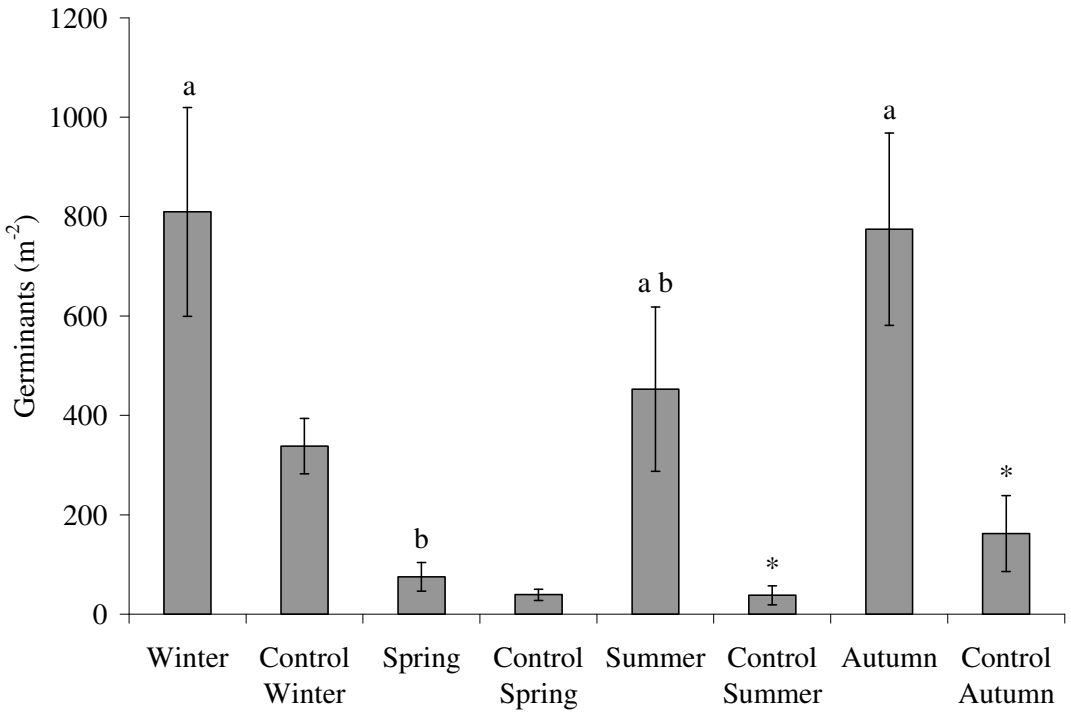


Figure 8.7 Density of seedlings (m^{-2}) of all species in seasonally disturbed plots and control (undisturbed) plots ± SE. New seedling counts were summed over the first three visits after each disturbance (i.e. 129, 149, 154 and 168 days for winter, spring, summer and autumn disturbance respectively). Columns with the same letter are not significantly different ($p < 0.05$). * = significant difference between treatment and control for that season ($p < 0.05$), Kruskal-Wallis one-way non-parametric ANOVA.

Cover of species other than *Phyla canescens*

Across all treatments and visits, Sites 1 and 2 had higher cover of species other than *P. canescens* than both Sites 3 and 4 (Figure 8.8).

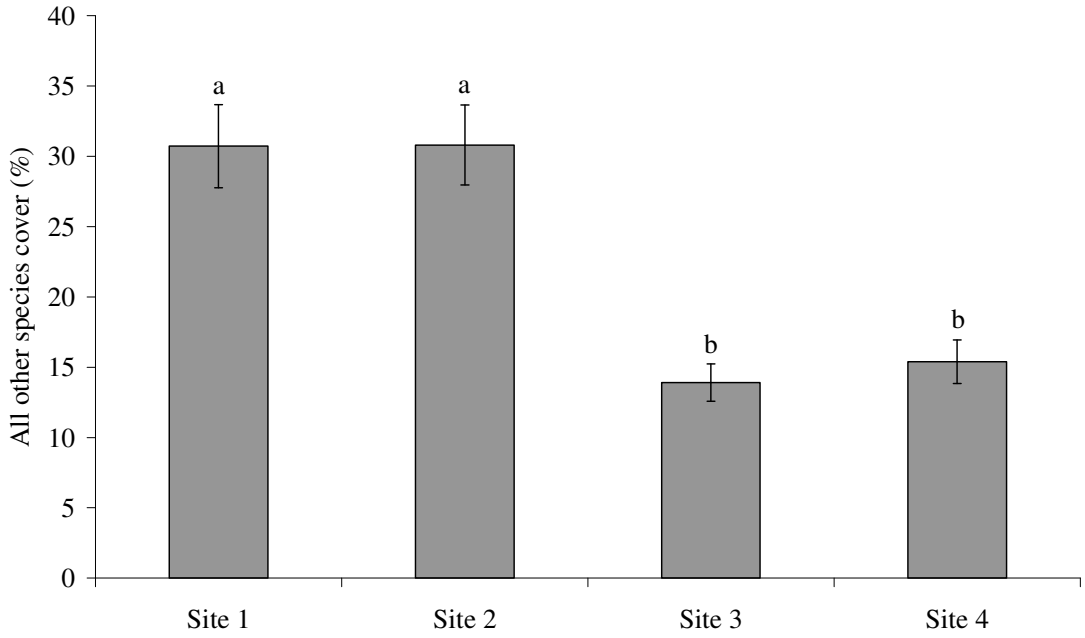


Figure 8.8 Total cover (%) of all species other than *Phyla canescens* at each site (± SE) across all treatments and visits. Columns with different letters are significantly different ($p < 0.05$), Kruskal-Wallis one-way non-parametric ANOVA.

Total cover of all species other than *P. canescens* was higher in winter disturbed plots than spring and summer disturbed plots, across all sites and visits (Figure 8.9). The spring disturbance also resulted in lower cover than the autumn disturbance or the (undisturbed) control.

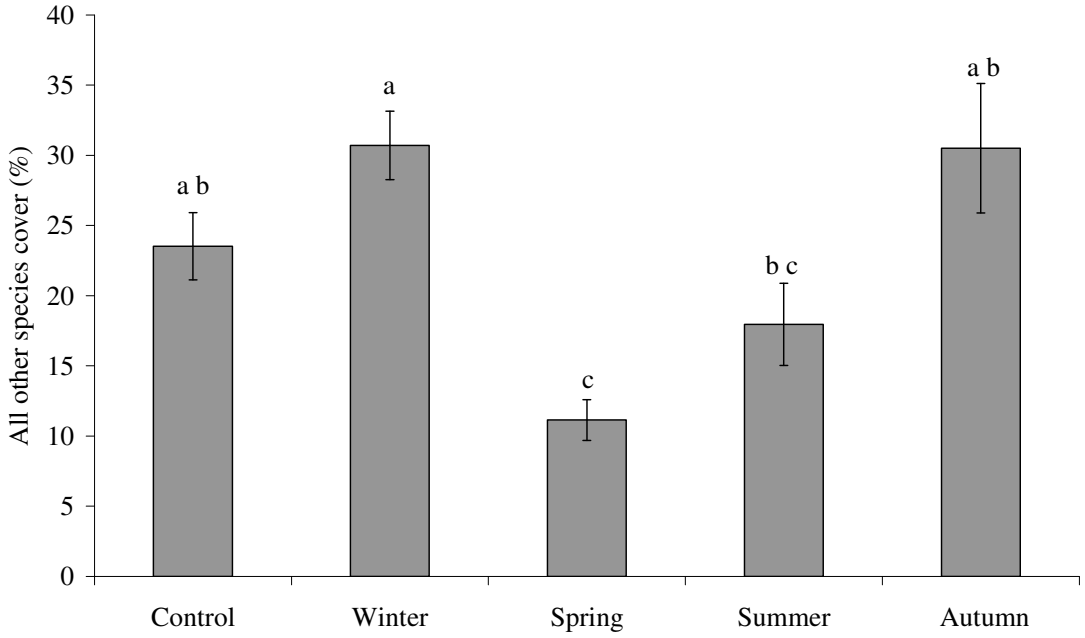


Figure 8.9 Total cover (%) of all species other than *Phyla canescens* for each treatment (± SE) across all sites and visits. Columns with different letters are significantly different ($p < 0.05$), Kruskal-Wallis one-way non-parametric ANOVA.

These patterns of germination and cover are generally consistent across all four sites, despite differences among the sites in the particular species involved. The patterns for each individual site are described in the following section.

8.3.2 Site-by-site patterns

Site 1

The winter disturbance (6 June 2005) was followed by nearly 200 mm of rain for the month (Figure 4.4). Soil moisture remained high until early September (Figure 4.5). Recruitment during this time was dominated by annual grasses (mostly *Lolium perenne*, which behaves as an annual in this environment) and legumes (mostly *Medicago polymorpha*, Figure 8.10). A subsequent germination of annual grasses (again, mostly *Lolium perenne*) and other dicots (mostly *Rapistrum rugosum*) occurred in this treatment in the following autumn (between March and May of 2006), presumably in response to 29 mm rainfall on 31 March and/or 36 mm rainfall over 18 and 19 April; no rainfall was recorded for May (Figure 4.4). The spring and summer disturbances were both followed by germination of *Lolium perenne*, *Rapistrum rugosum*, *Ammi majus*, and *Medicago polymorpha*. Germination following the autumn disturbance in 2006 was dominated by annual legumes (exclusively *Medicago polymorpha*), annual grasses (predominantly *Lolium perenne*) and other dicots (mostly *Ammi majus*). Germination in the control plots was dominated by the annual legume *Medicago polymorpha*. Peak seedling numbers were delayed by about two months in the control plots, compared to the winter disturbed plots (Figure 8.10).

Following disturbances, vegetation cover generally reflected those species which dominated recruitment (above). However, following winter disturbance, a substantial cover of *Bromus catharticus* contributed to the annual grass cover, while the dicots *Polygonum aviculare* and *Ammi majus* also attained high cover scores (Figure 8.11). *Eleocharis plana* (other monocots) *Paspalidium aversum* (perennial grasses) and *Polygonum aviculare* (other dicots) also contributed to cover following spring and summer disturbances, but *Amaranthus macrocarpus* var. *macrocarpus* dominated cover of other dicots. Cover following the autumn disturbance was dominated only by those species with prolific recruitment. In the control plots, species with substantial cover included *Ammi majus*, *Rapistrum rugosum* (other dicots), *Paspalidium aversum* and *Cynodon dactylon* (perennial grasses).

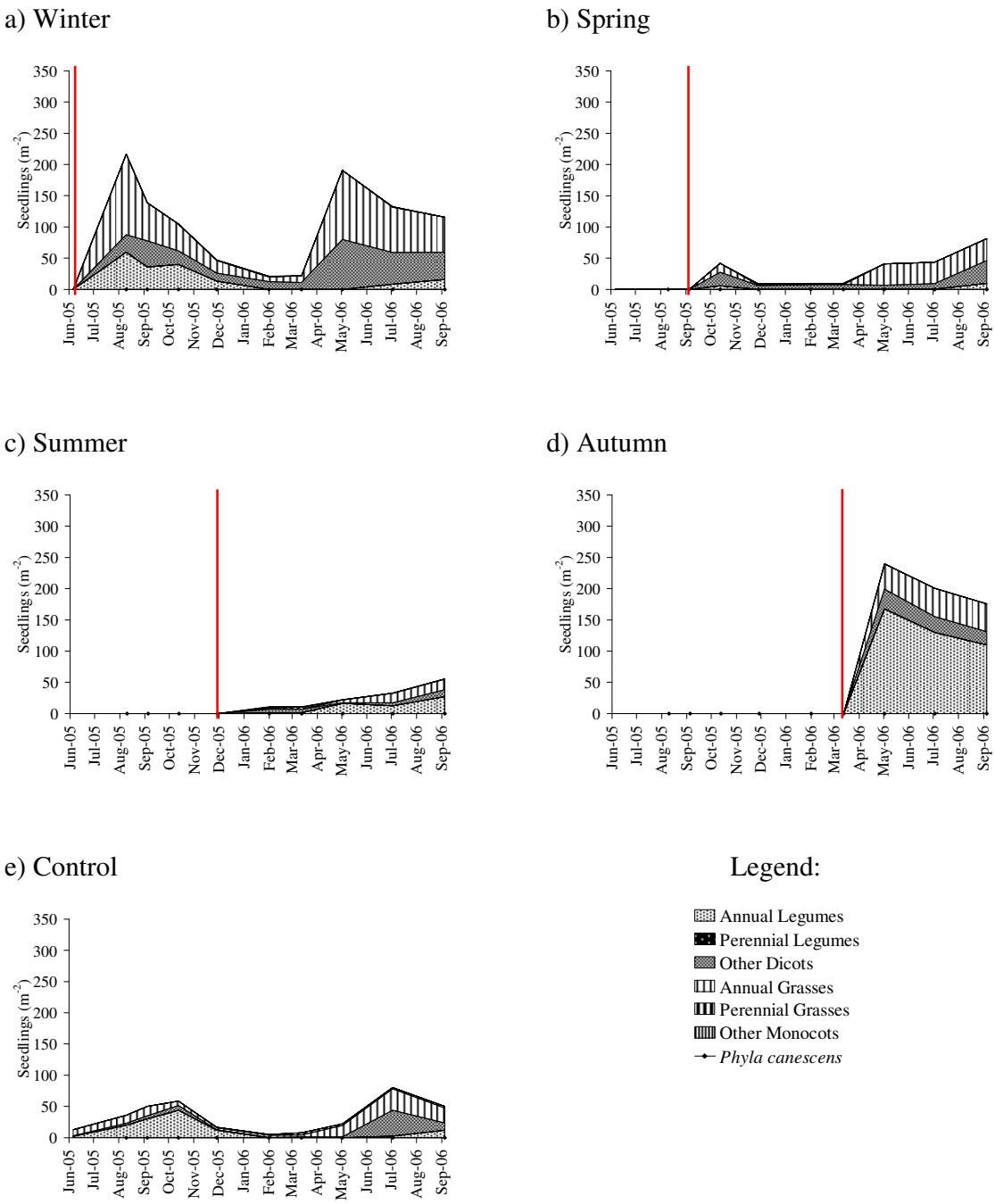


Figure 8.10 Site 1 seedling density (m^{-2}) of *Phyla canescens* and six functional groups for a) winter, b) spring, c) summer, d) autumn disturbances and e) control (no disturbance). The time of disturbance is indicated by a vertical line (|).

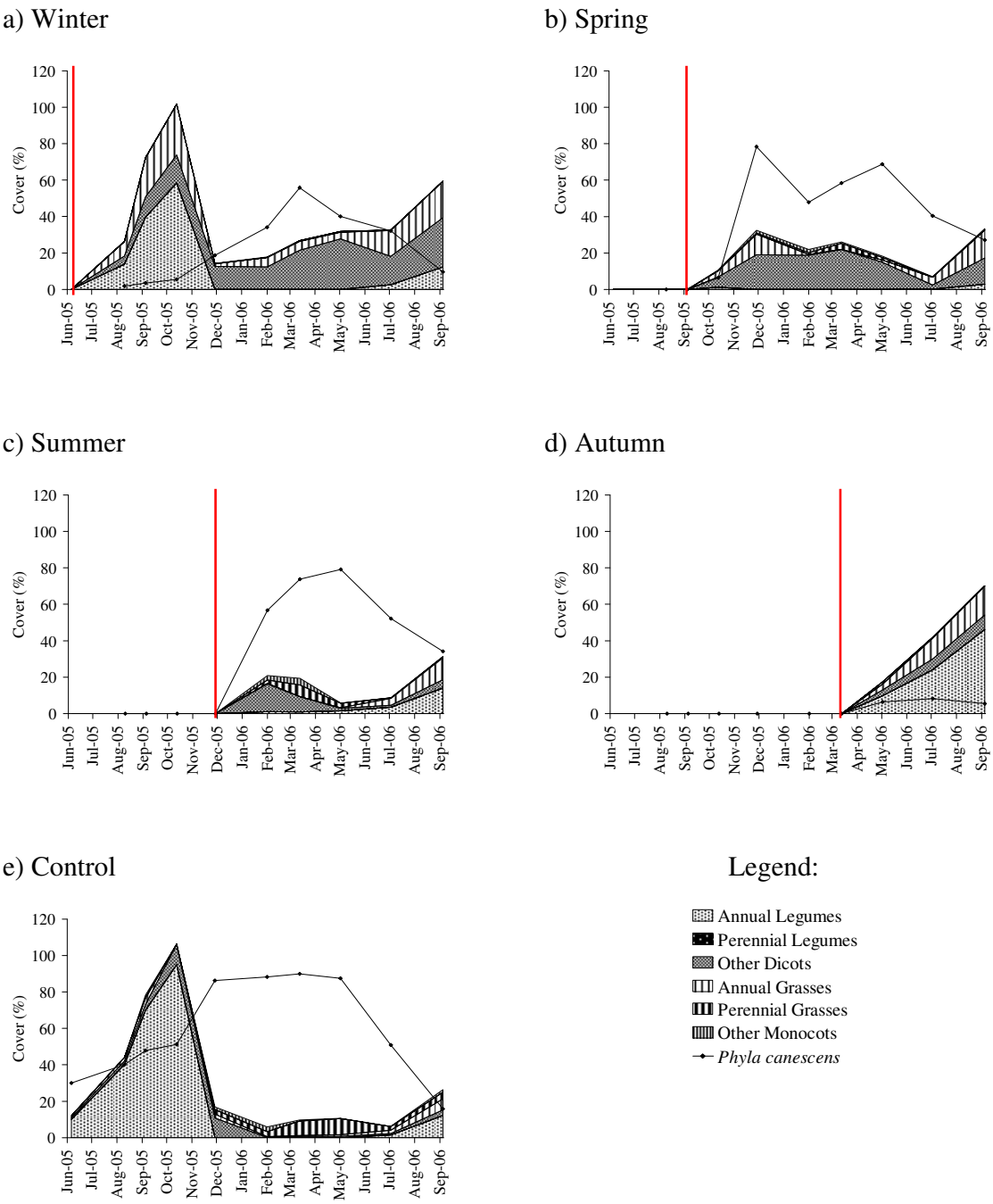


Figure 8.11 Site 1 vegetation composition (% cover) of *Phyla canescens* and six functional groups for a) winter, b) spring, c) summer, d) autumn disturbances and e) control (no disturbance). The time of disturbance is indicated by a vertical line (|).

Site 2

About 200 mm of rain fell at this site during June 2005 (Figure 4.7), followed by a flood at the end of June that did not reach the exclosures. Soil water remained high until January 2006 (Figure 4.8). Rainfall in February (at about average levels) resulted in a peak in soil water at the end of March (Figure 4.8).

A peak in seedling emergence occurred two months after the winter disturbance (Figure 8.12), mostly comprising annual legumes (particularly *Medicago polymorpha*) and other dicots (mostly *Cyclospermum leptophyllum* and *Rapistrum rugosum*). This was followed by another germination event of the same species in the late autumn and early winter of 2006. Similar germination events occurred at the summer and autumn disturbed sites with *Medicago polymorpha* and *Rapistrum rugosum* again dominant, but with the addition of *Amaranthus macrocarpus* var. *macrocarpus* in the summer disturbance treatment and annual grasses (mostly *Lolium rigidum*) following the autumn disturbance. Very little germination occurred following the spring disturbance (but still mostly *Medicago polymorpha* and *Rapistrum rugosum*). The germination pattern in the control plots was similar to that of the plots that were disturbed in the winter of 2005 (Figure 8.12).

In addition to the species dominating germination, *Paspalidium aviculare*, *Tribulus micrococcus* and *Einadia polygonoides* (other dicots) and *Glycine tabacina* (perennial legume) contributed substantially to the cover following winter disturbance (Figure 8.13). Following spring disturbances, the dicots *Einadia polygonoides*, *Tribulus micrococcus* and *Sonchus oleraceus* also had substantial cover, while *Physalis lanceifolia* contributed to cover after the summer disturbance. Vegetation cover following the autumn disturbance was dominated only by those species which dominated recruitment. The control plots were also dominated by the perennial grasses *Paspalidium aversum* and *Dichanthium sericeum* subsp. *sericeum* as well as *Glycine tabacina* (perennial legume) and *Einadia polygonoides* (other dicot).

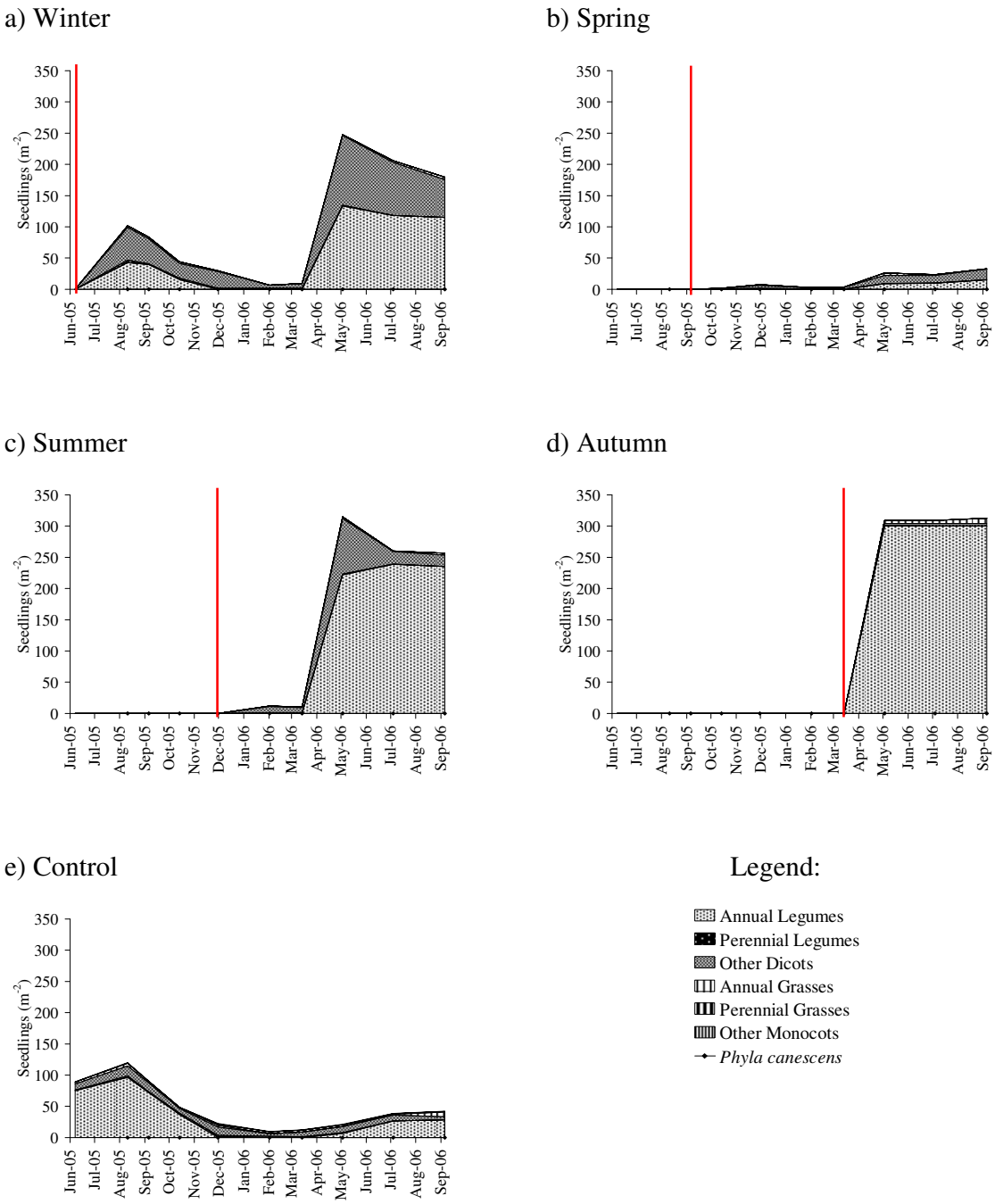


Figure 8.12 Site 2 seedling density (m^{-2}) of *Phyla canescens* and six functional groups for a) winter, b) spring, c) summer, d) autumn disturbances and e) control (no disturbance). The time of disturbance is indicated by a vertical line (|).

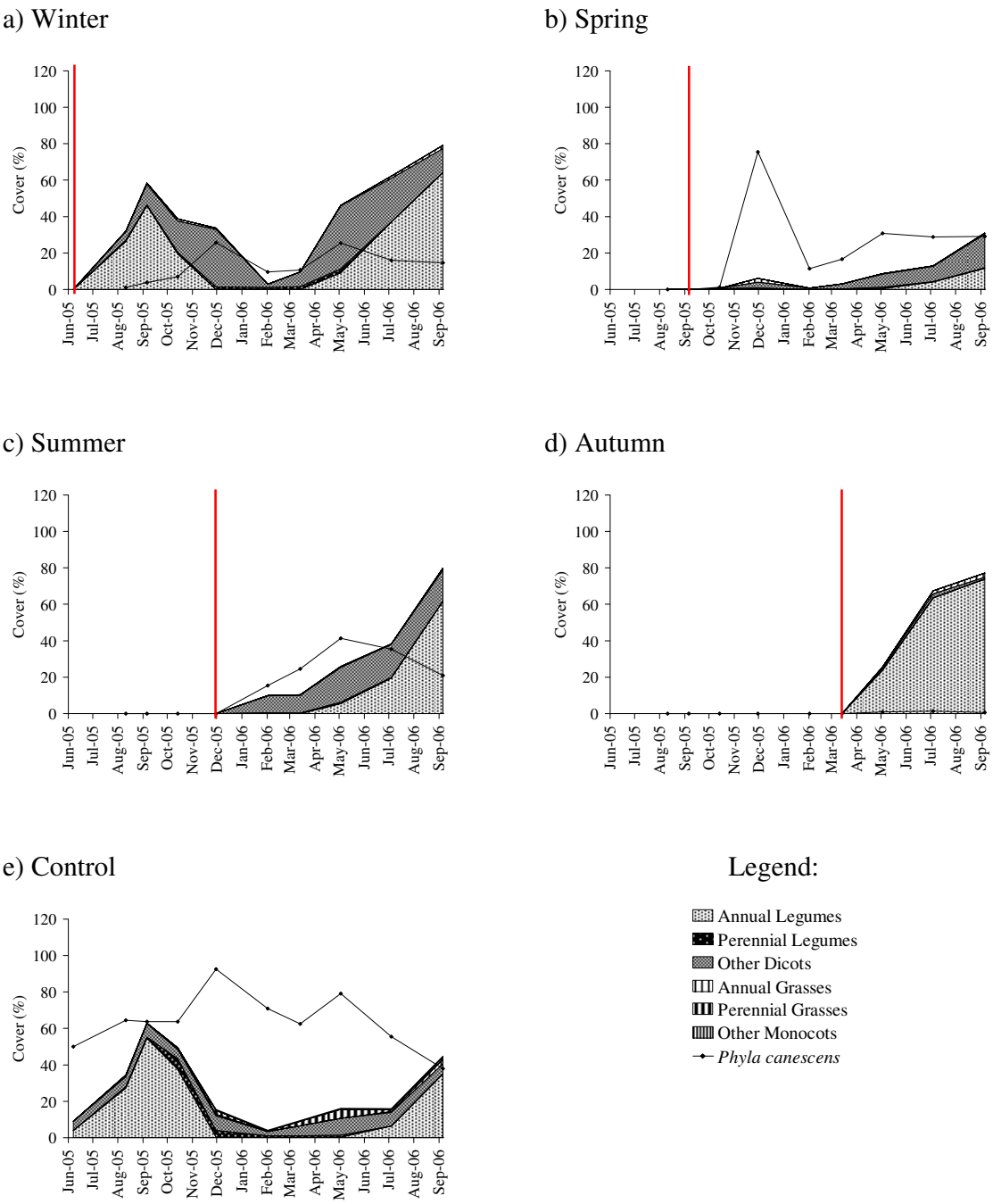


Figure 8.13 Site 2 vegetation composition (% cover) of *Phyla canescens* and six functional groups for a) winter, b) spring, c) summer, d) autumn disturbances and e) control (no disturbance). The time of disturbance is indicated by a vertical line (|).

Site 3

The June 2005 rainfall for Site 3 was only about 140 mm (Figure 4.10) and the soil water remained high until the end of winter (Figure 4.11). Immediately following the winter disturbance, germination was dominated by annual legumes (*Medicago minima* and *M. laciniata*) with small contributions from a wide variety of other dicots, while the autumn (March 2006) flush of germination was dominated by the same annual legumes (*Medicago* spp.) and the dicots, *Sclerolaena muricata* var. *muricata* and *Scleroblitum atriplicinum* (Figure 8.14). What little germination followed the spring disturbance was mostly *Sclerolaena muricata* var. *muricata* and *Scleroblitum atriplicinum*. Germination following the summer and autumn disturbances was almost entirely *Medicago* spp. In the control plots, the annual grass *Lachnagrostis filiformis* and the dicots *Rorripa eustylis*, *Ranunculus pumilio* var. *pumilio* and *Einadia polygonoides* were well represented, in addition to *Medicago* spp. (Figure 8.14).

The percentage ground cover at Site 3 was generally dominated by those species which germinated most prolifically. However, the consistent cover of other dicots after the winter disturbance and in the control plots (Figure 8.15) was also due to the presence of a few (relatively) large and persistent individuals of the perennial *Einadia polygonoides*, while *Echinochloa colona* was responsible for annual grass cover over summer in the control plots.

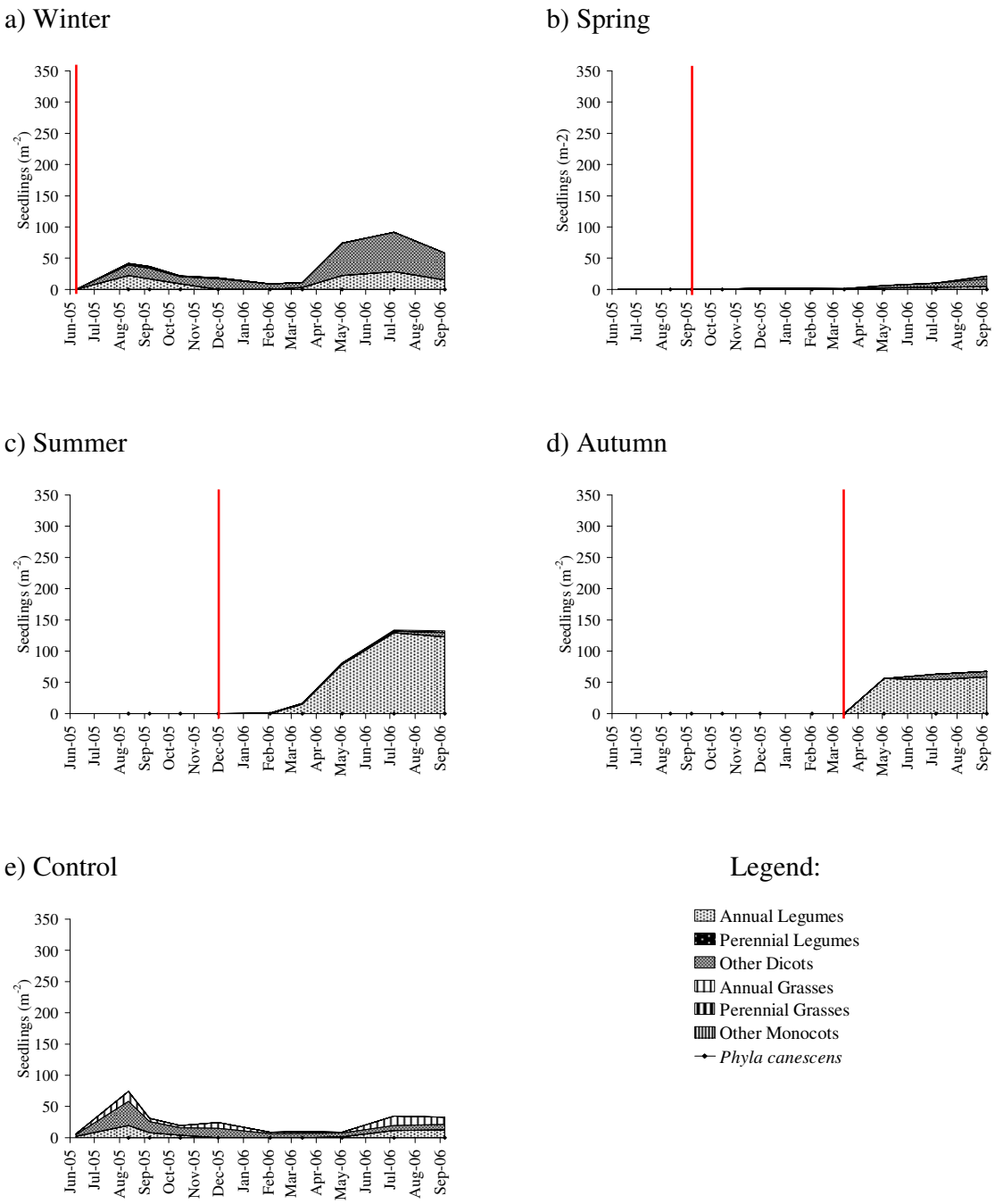


Figure 8.14 Site 3 seedling density (m^{-2}) of *Phyla canescens* and six functional groups for a) winter, b) spring, c) summer, d) autumn disturbances and e) control (no disturbance). The time of disturbance is indicated by a vertical line (|).

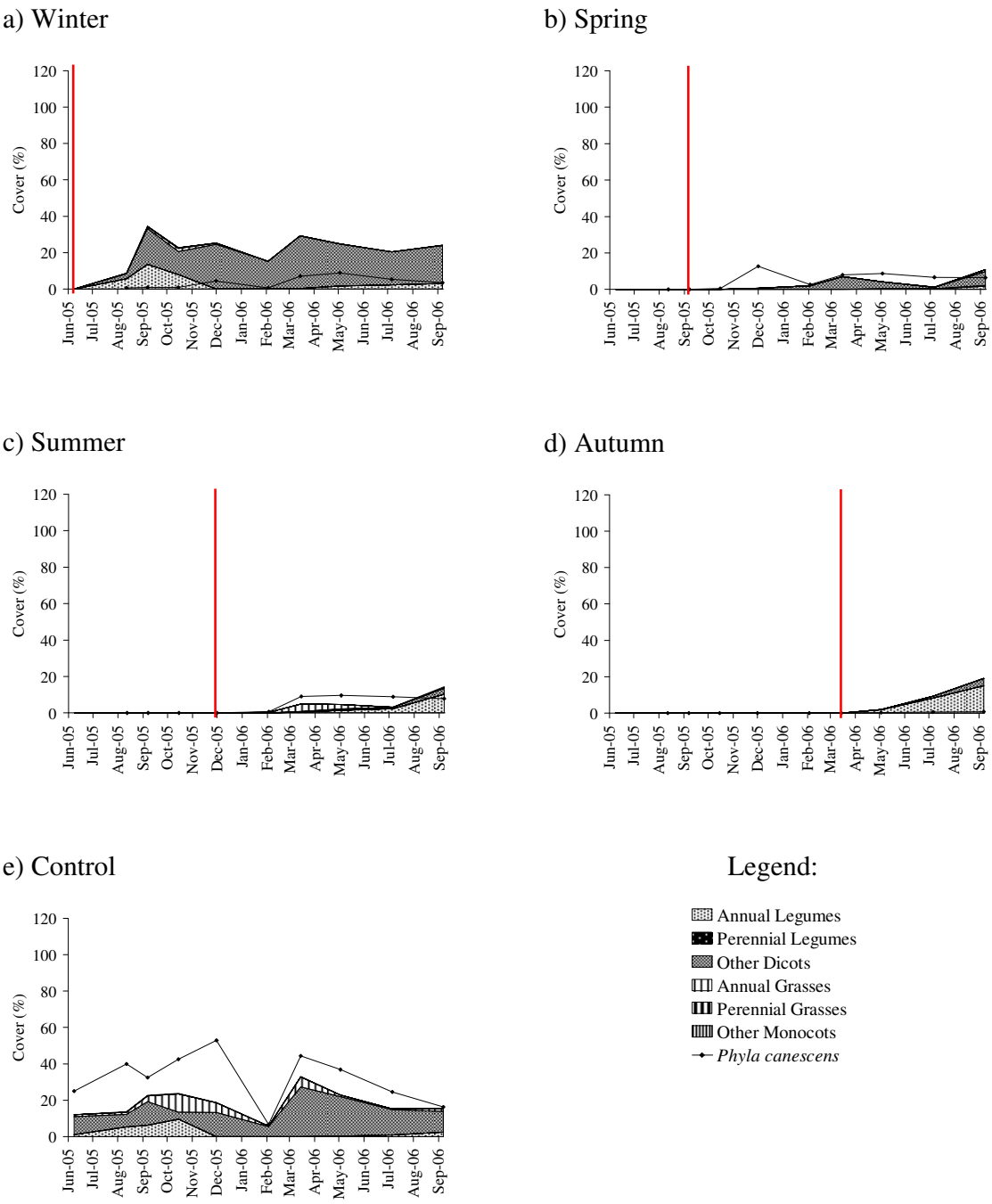


Figure 8.15 Site 3 vegetation composition (% cover) of *Phyla canescens* and six functional groups for a) winter, b) spring, c) summer, d) autumn disturbances and e) control (no disturbance). The time of disturbance is indicated by a vertical line (|).

Site 4

Site 4 was close to 'Old Dromana' homestead, (as was Site 3) and so the same rainfall records were used for both sites (Figure 4.13). Site 4 experienced a flood in early July 2005, but Site 3 did not.

This flood and associated rainfall resulted in germination of seedlings in the winter disturbed treatments, mostly a small unidentified annual member of the Cyperaceae and a small unidentified member of the Asteraceae, with contributions from *Brachyscome curvicarpa* and *Rorippa eustylis* as well as the seedlings of *P. canescens* previously described (Figure 8.16). Some germination of other dicots (mostly the same unidentified Asteraceae), plus *P. canescens* occurred in the control plots. Very little germination occurred following the other disturbance treatments. Following the spring disturbance the annual grass *Echinochloa colona* and the dicots *Rorippa eustylis* and *Chamaesyce drummondii* were the more common seedlings. The summer disturbance was followed by germination almost exclusively of *Echinochloa colona* and *Ranunculus pumilio* var. *pumilio*, whereas the autumn disturbance was dominated by germination of *Medicago* spp. and *Rorippa eustylis*.

The vegetation cover generally reflected those species which recruited most prolifically (Figure 8.17). Some notable exceptions were that, following the winter disturbance, *Eleocharis plana*, *Echinochloa colona*, *Marsillea drummondii*, and *Polygonum aviculare* all contributed substantially to total cover. The rhizomatous perennial grass *Paspalum distichum* was reasonably abundant following the spring, summer and autumn disturbances. *Eleocharis plana* and *Cyperus concinnus* and *Marsillea drummondii* were well represented in the control plots.

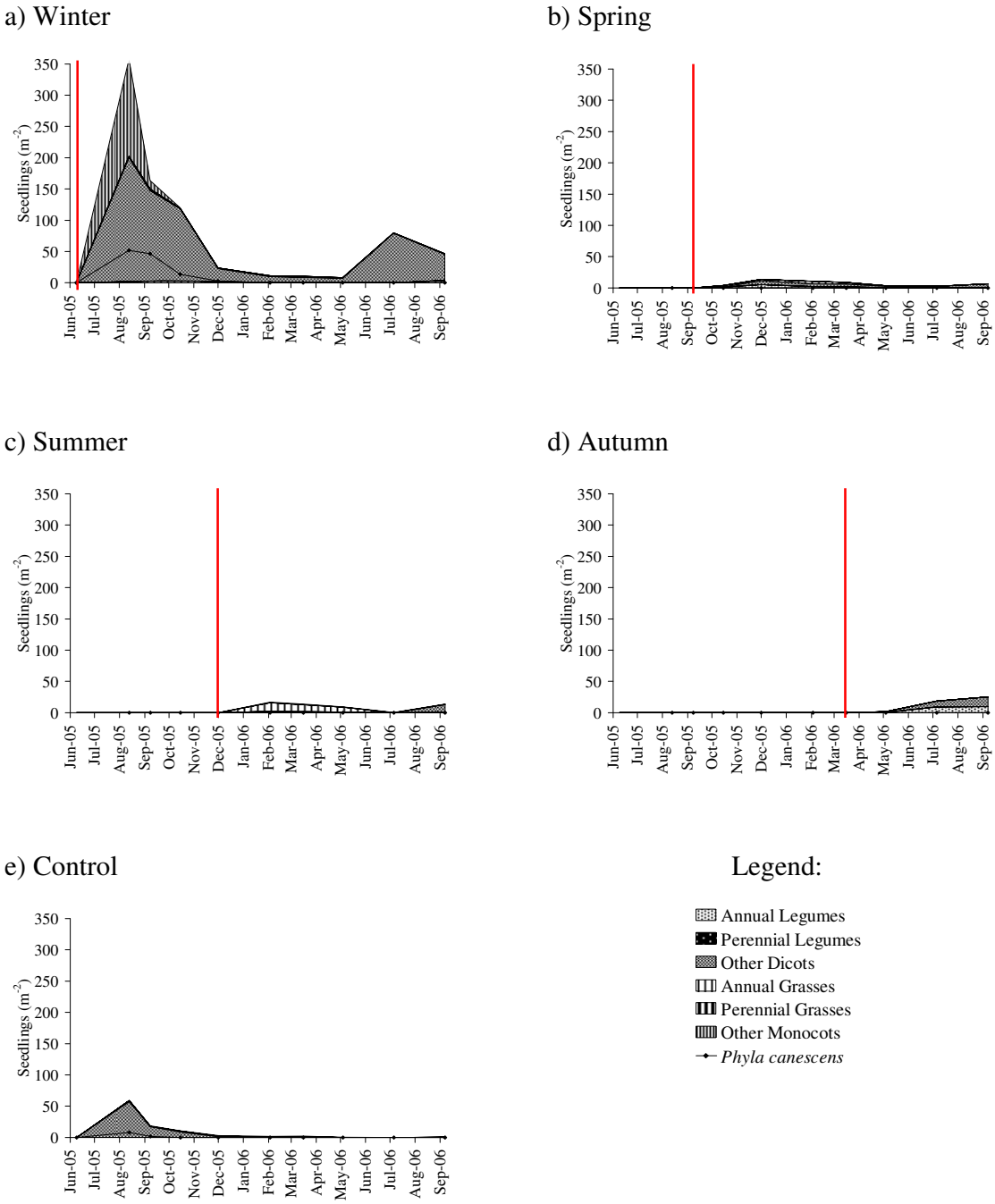


Figure 8.16 Site 4 seedling density (m^{-2}) of *Phyla canescens* and six functional groups for a) winter, b) spring, c) summer, d) autumn disturbances and e) control (no disturbance). The time of disturbance is indicated by a vertical line (|).

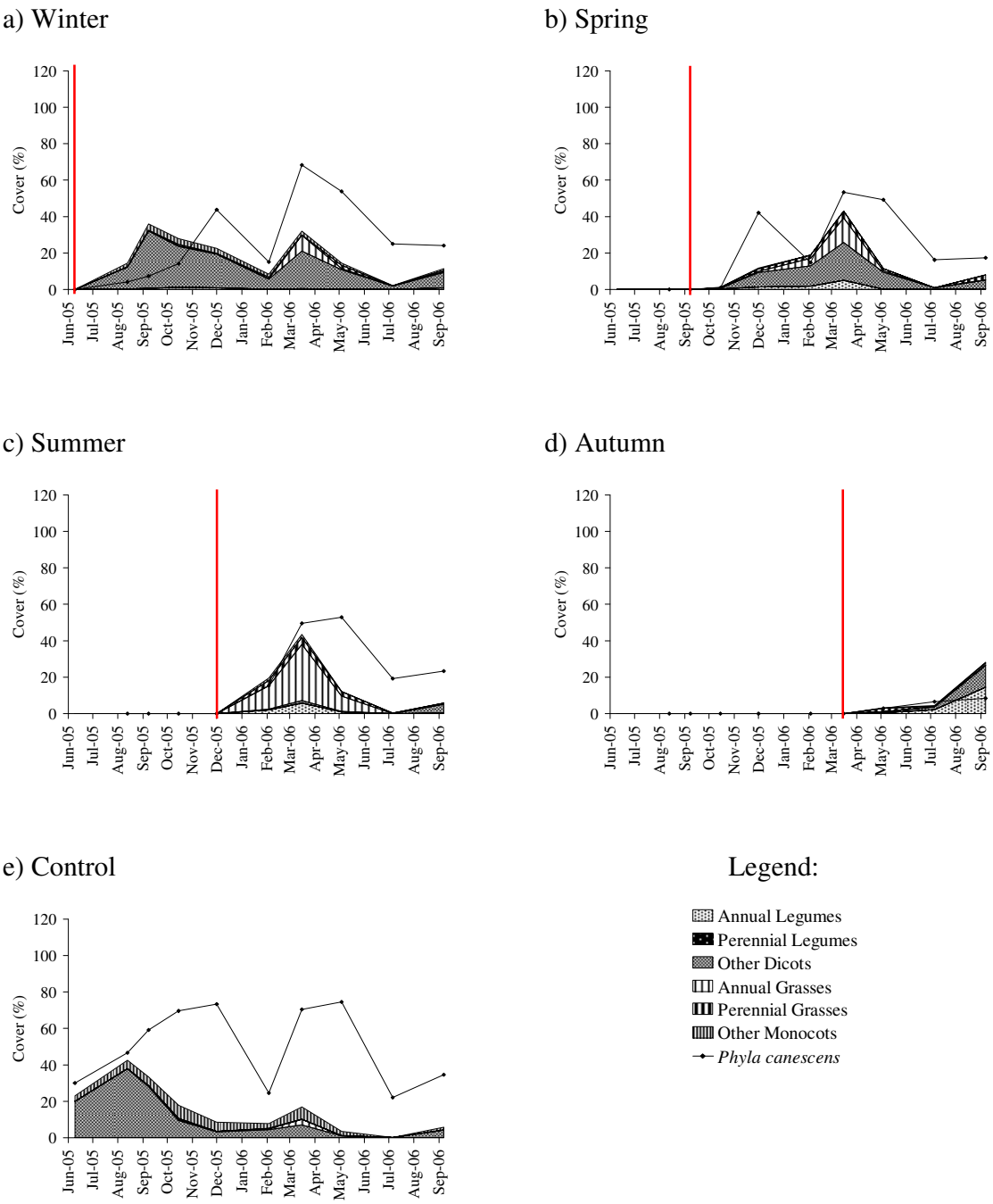


Figure 8.17 Site 4 vegetation composition (% cover) of *Phyla canescens* and six functional groups for a) winter, b) spring, c) summer, d) autumn disturbances and e) control (no disturbance). The time of disturbance is indicated by a vertical line (|).

8.3.3 Opportunistic survey

A total of 217 *P. canescens* recruits were recorded approximately two months after inundation, from 81 quadrats. Of these recruits, 147 were seedlings and 70 were vegetative fragments. Mean density was highest for seedlings in Zone 1 (45.6 m^{-2}, Table 8.4). With the exception of just three seedlings, all recruits were recorded below the flood strand-line (maximum extent of flooding). Of these three exceptions, two occurred in quadrats within 1 m horizontally and 50 mm vertically of the strand-line. Thirteen seeds were found to have germinated directly from sheep faeces.

Within plant types (i.e. seedlings, fragments, adults), no significant differences in frequency (number of quadrats in which plant type was present) were evident for comparisons between Zones 1 and 2 for seedlings ($p = 0.4142$) or fragments ($p = 0.0561$), and between Zones 2 and 3 for adults ($p = 0.3794$). All other comparisons represent significant differences (for all, $p < 0.0055$, accounting for Bonferroni adjustment for multiple comparisons). Between plant types, frequency of adults was significantly different from both seedlings ($p < 0.001$) and fragments ($p < 0.001$), but only in Zone 3. All other comparisons between plant types within zones were not significant.

Table 8.4 Mean density (m^{-2}) and percentage frequency in quadrats (% of quadrats occupied) of plant type for each zone.

Zone	Seedlings		Fragments		Adults		Number of Quadrats
	Density	Frequency	Density	Frequency	Density	Frequency	
1	45.6	44.4	7.7	40.7	3.0	11.1	27
2	39.7	55.5	33.8	66.7	32.6	74.1	27
3	1.8	11.1	0.0	0.0	18.4	63.0	27
Mean	29.0	37.0	13.8	35.8	18.0	49.4	81

8.4 Discussion

8.4.1 Response of *Phyla canescens* to disturbance

Germination

In the absence of flooding, no *P. canescens* recruitment occurred in any treatment despite soil disturbance and hand-watering with the equivalent of 22 mm of rainfall. Even up to 75 mm of rain in a single day and 200 mm over two weeks produced no recruitment, whereas recruitment of both seedlings and vegetative fragments was evident where flooding occurred.

Seedlings of *P. canescens* appeared following flooding at Site 4. There was a higher density of *P. canescens* seedlings in the disturbed than in the control plots. This implies that recruitment in this population is microsite limited. This limitation could arise from effects of the extant vegetation (e.g. competition) or other (e.g. soil) conditions changed by the act of disturbance.

Only one seedling of the perennial *P. canescens* was still alive at the end of the experiment in September 2006 (456 days after disturbance). All other *P. canescens* individuals within the quadrats in the (winter) disturbed plots had perished by 3 February 2006 (240 days after disturbance), while those in control plots had perished by 15 October 2005 (129 days after disturbance). This rapid mortality may have several causes. The flood event (late June to early July 2005), which induced the recruitment of *P. canescens* seedlings, was followed by below average rainfall for the remainder of July, as well as August and September. This dry period coincided with the highest mortality of *P. canescens* seedlings. However, these plots were also protected from grazing and therefore the seedlings of *P. canescens* were subject to competition from neighbouring plants. Had these sites been grazed, reducing the size and resource sequestration (particularly soil moisture) of competitors, the survival of the *P. canescens* seedlings may have been higher. Of course, these two explanations may be complementary, because competition can only act via limiting resources, i.e. if a resource is not limiting, then its use by another would have no effect. These data do not differentiate between the effects of competition and allelopathy.

Cover

The recovery of adult *P. canescens* plants was slowest following disturbance at the start of winter (taking 456 days). The cover of *P. canescens* after the autumn disturbance appeared to be recovering very slowly also, and full recovery was not achieved by the end of the experiment (168 days after disturbance). These data suggest that *P. canescens* growth is slowed during the cooler months. This represents an opportunity to establish other, more desirable vegetation. Without a sustained increase in the cover of perennial or warm-season species, it seems inevitable that the vegetation will revert to becoming dominated by *P. canescens* (some management options are discussed in Chapter 9).

The relatively fast recovery of *P. canescens* following the spring and summer disturbances indicates that *P. canescens* growth in the cooler months may be limited by temperature and limited by moisture availability under warmer conditions. This is consistent with the genus being distributed generally in tropical, sub-tropical and warm-temperate regions of the world (Atkins 2004).

8.4.2 Response of species other than *Phyla canescens*

Germination

Germination of species other than *P. canescens* was greater in disturbed than undisturbed plots, and is consistent with many previous studies (e.g. Fenner 1978). Most of the seedlings that appeared following disturbance and in the control plots were of annual species. This is to be expected, as the seedbank of annual species is generally higher than that of perennials (Thompson et al. 1998). These annuals generally produced seeds within the experimental period, except those following the autumn disturbance, which occurred only 168 days before the conclusion of the experiment.

The lower seedling density following spring disturbance, compared to that following winter and autumn disturbances (Fig. 8.3), was not a result of poor spring rains. Spring rainfall at all sites was above average, and more than that following either the winter or autumn disturbances. It appears that the lower germination following spring disturbance is almost entirely due to annual legumes, overwhelmingly *Medicago* spp., which

generally dominated the seedling population in other treatments, germinating poorly following the spring disturbance compared to other disturbances. This germination pattern is, therefore, largely due to the seasonal germination idiosyncrasies of just one genus.

Cover

The winter annuals, particularly *Medicago* spp. and *Lolium* spp., tended to be the dominant cover species of species other than *P. canescens* during late winter to spring (July to October). In contrast, the cover of other species (perennials and warm-season annuals) tended to follow a similar pattern to the cover of *P. canescens*.

8.4.3 Opportunistic survey

Seedlings and fragments both made substantial contributions to recruitment. Both appeared to be highly dependent on flooding, as indicated by their almost complete absence above the strand-line. The dispersal of vegetative fragments by flood was limited to at, and below, the height of the strand-line.

This is also the first record of *P. canescens* germinating from material that has undergone gut-passage (sheep faeces), which may be an important but manageable dispersal mechanism. Given that the proportion of seeds surviving gut passage is generally higher in cattle than sheep (Simeo Neto et al. 1987), at least some *P. canescens* seeds could also be spread through ingestion by cattle. However, the amount of *P. canescens* ingested by cattle may be lower, due to the prostrate habit of *P. canescens*, with cattle generally eating taller components of the pasture sward than sheep (Grant et al. 1985).

Adult plants were less frequent in Zone 1, suggesting a restricted ability of *P. canescens* to persist in this zone. Without 'before' data we cannot suggest if this pattern was due to mortality from prolonged inundation (McCosker, 1994a) during recent or earlier flood events, competition from species such as *Eleocharis plana* or other factors. The survivorship of these *P. canescens* recruits is not known.

8.5 Conclusion

It appears that the overwhelming majority of recruitment of *P. canescens* occurs following inundation. Also, recruitment was at higher density after disturbance than without disturbance. This suggests that by maintaining higher levels of vegetation cover, the recruitment of *P. canescens* seedlings can be reduced. The survival of seedlings was also reduced in the presence of other vegetation. The implication for management is that to minimise the recruitment and survivorship of those *P. canescens* recruits, the cover of other vegetation following floods should be maximised. Allowing the growth of such species by resting areas from grazing following floods may reduce the establishment of new *P. canescens* plants.

The flood (and recruitment) at both Site 2 and Site 4 resulted from the same widespread rainfall event during winter. Whether the same pattern of recruitment (i.e. germination being restricted to areas inundated by flood-waters) holds for warm-season storm events (when rainfall is generally highest in the areas studied) remains untested. Germination would presumably occur faster under the warmer conditions of a summer flood, but soil moisture would be lost more quickly due to higher rates of evaporation and transpiration.

Chapter 9

Conclusions and management recommendations

9.1 Ecology

9.1.1 Taxonomy

The most recent taxonomic study of *Phyla* in Australia suggests there are two species, and although they are both variable, they are distinguishable on morphological grounds, with little overlap in distribution and habitat preferences (Munir 1993). Observations of field populations and inspection of herbarium material support Munir's treatment.

The observed variation in *P. canescens* in Australia appears to have geographic coherence, which reflects the pattern found in South America (Kennedy 1992). Material from the north of the Australian distribution (north from the Macquarie River catchment) appears akin to that from east of the Andes in South America, whereas the material from the southern part of the Australian distribution (south from the Lachlan River catchment) appears more like the type material, west of the Andes (Chapter 3).

These morphological differences imply multiple introductions. Given multiple introductions, and the subsequent widespread (virtually ubiquitous) dissemination of plants throughout Australia for horticultural purposes, *P. canescens* has clearly been the beneficiary of high propagule pressure.

The potential for hybridisation between these separately introduced forms may lead to novel genotypes not encountered by natural enemies, and potential biocontrol agents, in the home range. This situation appears to be similar to that of the closely related *Lantana camara*, where biocontrol agents are performing poorly on hybrid forms (Zalucki et al. 2007). The continued sale of new forms of *P. canescens* into areas with existing naturalised populations of previously introduced forms has the potential to fuel such post-introduction adaptation, potentially reducing the effectiveness of the biocontrol program currently underway. Questions of the genetic structuring of introduced and native

populations of *P. canescens* (and whether the current treatment of *P. canescens* includes more than one taxon) are the subject of current research (M. Fatemi personal commumication), which will inform the selection of candidate biocontrol agents.

The extreme paucity of Verbenaceae in Australia's indigenous flora (of the 1100–1200 species, a maximum of 5 are native, Chapter 2), may proffer a degree of novelty to *P. canescens*, such that only the most general of indigenous herbivores will consume it. During this study, a larva of *Junonia vallida* (meadow argus butterfly, Nymphalidae) was found on a specimen collected near Narrandera (NSW), and raised to maturity on a diet consisting exclusively of *P. canescens* leaves. Similarly, larvae of *Orgyia* sp. (tussock moth, Lymantriidae) were observed grazing on *P. canescens* glasshouse plants. Neither of these species hold any real hope of significantly impacting field populations of *P. canescens* as they are both known to feed on a wide range of native and introduced species (Common 1990; Common and Waterhouse 1995).

In situations such as this, where indigenous competitors are burdened by attack from generalist herbivores and their own suite of specific enemies, species subject only to generalist attack (such as *P. canescens*) may be at a relative advantage. However, determining the precise role of herbivores in invasion processes can be difficult (e.g. Maron and Montserrat 2001).

The role of phytochemicals in the resistance of *P. canescens* to flooding, grazing and competition remains largely unexplored. However, given the suggested correlation between phytochemicals and habitat, with species from moist habitats producing phytochemicals, but those from dryer habitats not (Tomas-Barberan et al. 1987), the adaptive role of these chemicals may be for microbial defence under inundation (Sarada and Prakasa Rao 2003; Wang and Huang 2005), rather than competitive allelopathy (Dongre et al. 2004; Tan et al. 2007). However, this habitat correlation is confounded with morphology and taxonomy.

9.1.2 Flooding and grazing

It is clear that *P. canescens* grows in areas subject to flooding in its native range (Chapter 2), and therefore it is those areas in Australia that are most vulnerable to invasion (Munir 1993; McCosker 1994a; Earl 2003; Mawhinney 2003). While there are reported examples of *P. canescens* spreading into areas higher in the landscape (e.g. Earl 2003), suitable habitat is likely to be limited to near water-bodies and in drainage lines. Therefore, the potential for *P. canescens* to form large, continuous areas of high cover (and thus causing substantial economic harm, as it does on floodplains) in upland sites is probably low.

Flooding appears necessary for *P. canescens* to become established (Chapter 8), but continuous grazing by introduced or native herbivores is necessary for widespread dominance. Planiform species, such as *P. canescens*, are well adapted to constant grazing by generalist herbivores. Taller herbaceous species form the bulk of the diet of domestic herbivores, particularly cattle (Grant et al. 1985), and under constant grazing are prevented from effectively competing with the planiform *P. canescens*. Unless the grazing regime is altered, as dominance of *P. canescens* develops, grazing pressure on the taller species intensifies, providing positive feedback to exacerbate the dominance of *P. canescens*.

Changes to patterns of flooding, the introduction of livestock grazing and the cessation of burning have changed the disturbance regime of the recipient habitat. Such changes may have rendered the habitat less favourable to the resident native species, which were presumably adapted to the previous regime, allowing species better adapted to the new regime to become dominant. This could be interpreted as a reduction in the biotic resistance of the recipient community.

9.1.3 Fecundity

Phyla canescens is a prolific seeder, with seed production reaching over 60 000 germinable seeds m^{-2} yr^{-1} (Chapter 6), which is of a similar magnitude to that of other seriously invasive species (e.g. Andrews et al. 1996; Gardener et al. 2003). However, seed production is highly variable, largely dependent on rainfall, but is reduced where

pollinators are excluded, and, not surprisingly, where the cover of *P. canescens* is reduced.

Phyla canescens differs from many invasive plants with large seed production in that *P. canescens* is also capable of vegetative reproduction. The focus on reproduction from seeds in this study, and the relative exclusion of vegetative reproduction (but see Chapter 8) does not imply that vegetative reproduction is not an important aspect of the life-history of *P. canescens*. It simply reflects the limitations of this study.

Flowering was observed from October to May in the field, though evidence from herbarium specimens suggests there is potential for year-round flowering. However, with over 95% of inflorescences observed from November to March, the small amount of 'off-season' flowering is unlikely to have a major influence on population dynamics. With inflorescences undergoing complete development from bud to production of fruit within 40 days, *P. canescens* has the ability to produce seeds quickly in response to summer rainfall events.

Perhaps the lower summer rainfall (and therefore possibly reduced seed production) in the southern parts of the Australian range goes some way to explain why it is considered less of a problem there than further north. However, latitude is confounded with apparent morphological differences. It is possible that as the northern (and currently more invasive) form migrates south (as it presumably will with flood events flowing generally south along the Darling River) it may become more invasive than the resident southern form.

9.1.4 Seedbank

Seeds incorporated into the soil seedbank, which reached over 7500 germinable seeds m^{-2}, (Chapter 7), are likely to be sufficiently long-lived to be of management significance for at least a decade after the commencement of any management intervention, even where all new seed production is prevented. However, one or more flood events, which are likely to promote germination of at least some of this seedbank, particularly that

portion buried sufficiently shallowly that it is within reach of light, are likely to accelerate this draw-down in seedbank, provided these new recruits do not reach reproductive maturity. There are no data available on how rapidly flood events deplete the soil seedbank.

9.1.5 Recruitment

The particular combination of conditions required for the germination of *P. canescens* seeds (Chapter 5) appears to predispose this species to germinate prolifically following flood events and not germinate in the absence of inundation. This idea is not new, and is supported by earlier work from Australia (Munir 1993; McCosker 1994a) and South America (Kennedy 1992; Soriano et al. 1992). It is also supported by field surveys (Chapter 8), where recruitment from fragments and seeds occurred below the maximum water-level of a flooded billabong, but not in adjacent areas which were not flooded, despite 200 mm of rainfall. The minimum duration of a flood needed for *P. canescens* seeds to germinate remains unclear.

Recruitment from seeds also appears to be influenced by vegetation cover. Where there is vegetation cover, not only is recruitment reduced, the subsequent survival of those seedlings is also reduced. This pattern is common to many species, including weeds (e.g. Gardener et al. 2003) and is the foundation of weed management systems which minimise the extent of bare ground (e.g. Teasdale and Daughtry 1993).

Interestingly, the flood event adjacent to the exclosures at Site 2 induced recruitment from both vegetative fragments and seeds, but at Site 4, the only recruits recorded were seedlings (i.e. no fragments). Several explanations for this can be suggested. The first is that perhaps the flood event at Site 4 was not of sufficient duration to induce the physical disintegration of the local *P. canescens* plants (as described by Hobson 1999; Taylor and Ganf 2005). Secondly, there may have been no (or very little) immigration of fragments from upstream, which may have been effectively filtered out of the floodwater by standing vegetation (as suggested by Earl 2003). Another possible explanation is simply that prevailing winds may have blown floating *P. canescens* fragments (and other

flotsam) away from Site 4 to the other side of the wetland. However, given that no information was available about the duration of flood and hence prevailing winds at either site, no conclusions can be drawn concerning the lack of recruitment from fragments following the flood at Site 4.

9.2 Management

Some management recommendations can be made on the basis of the information presented in this thesis for areas currently without, but likely to be invaded by, *P. canescens* and areas with existing populations. Not surprisingly, there is considerable commonality in the recommendations for both of these. However, they are presented separately to emphasise that:

1. there are alternatives to allowing *P. canescens* to become dominant before taking action
2. continuation of the management regime that has lead to *P. canescens* becoming dominant is very likely to result in its continued dominance.

9.2.1 Prevention

In areas where *P. canescens* is likely to invade, i.e. floodplains of the Murray Darling Basin, particularly downstream of existing dense populations, a number of actions appear likely to reduce the density of *P. canescens* recruitment and its subsequent survival. These are based on generally accepted principles of sustainable grazing management, modified where necessary for *P. canescens* and the environments it tends to invade.

1. Livestock sourced from areas already invaded by *P. canescens* should be quarantined for at least 1 week to allow passage of potentially ingested seeds (Simeo Neto et al. 1987). These quarantine paddocks would, where possible, be located on sites less favourable to *P. canescens*, i.e. on higher ground with lighter soils, and near frequently used infrastructure, such that regular inspections (particularly after floods) will allow new patches of *P. canescens* (and other weeds) to be treated before they reproduce. Ideally, livestock could be held at the source property for this period before transport, i.e. a withholding period, in an area free of *P. canescens*.

2. Fodder should not be sourced from areas with high cover of *P. canescens*. Where this is not possible, feeding areas should be located in quarantine areas as outlined above.

3. Pasture cover needs to be maintained where possible, particularly before and after floods, to reduce recruitment from propagules dispersed by the flood. This cover can also reduce the survivorship of any recruitment which does occur.

4. Familiarity with *P. canescens* and the sites where it is most likely to establish, e.g. waterways and depressions, particularly following floods, will allow new patches to be located and treated before they become large and reproductive.

9.2.2 Remediation

The typical pattern of invasion by *P. canescens* appears to be that patches appear in grazing land following flooding (McCosker 1994a). The maintenance of the same stocking rate once invasion has started will place the reduced area occupied by palatable species under increased grazing pressure. This will increase the competitive advantage of less palatable species, such as *P. canescens*, and result in a higher cover of the invading species.

The most desirable way to prevent this progression towards higher cover of *P. canescens* is to encourage the cover of taller and more desirable species by instigating strategic rests from grazing. Maintaining higher cover of desirable species will not only lead to lower seed production of *P. canescens*, by reducing *P. canescens* cover itself, (Chapter 6), but will also reduce the amount of bare ground which will reduce recruitment of *P. canescens* and also reduce the survivorship of recruitment that does occur (Chapter 8).

Seed production in *P. canescens* is prevented in the absence of pollinators (Chapter 6). This could be due to prevention of outcrossing, geitonogamy and/or pollinator mediated autogamy. It is not yet clear which vector is responsible for pollinating *P. canescens* in Australia. If feral honey bees are found to be significant pollinators, this may represent a

case of mutualistic facilitation among invasive species of disparate origin. A trial to determine the reduction in seed production as a result of preventing pollination by feral bees could be established, as has been recommended for reducing seed set in *Lantana camara* (Goulson and Derwent 2004).

Some success has been achieved in replacing *P. canescens* with introduced pasture species (see Dellow et al. 2001). Such treatment may be appropriate in areas of highly degraded biodiversity values, but the replacement of one introduced species with another in areas of conservation significance is generally undesirable (Mack et al. 2000). However, even with introduced pasture species, grazing management needs to maintain high pasture cover for sustained suppression of *P. canescens* (Dellow et al. 2001).

Some promising work is being undertaken in the grazing management of native grassland and wetland communities to restore productivity and biodiversity in areas with high cover of *P. canescens*. Such work is based on managing grazing, whereby the vegetation is periodically rested from grazing, allowing the more palatable, and desirable, species to recover (J. Price personal communication). Where such regimes lead to an increased cover of desirable perennial species, they have been shown to increase productivity (Kemp et al. 2000; Michalk et al. 2003) and decrease weed dominance (Huwer et al. 2005) in a range of grazed communities. However, the success of such systems appears to depend on tailoring the management regime to the biological system. Flexible grazing management based on ongoing vegetation assessment is critical for sustainability of these systems (Huwer et al. 2005), and probably even more so in the unpredictable environments which have been invaded by *P. canescens*.

In such unpredictable systems, characterised by long droughts interrupted by occasional flooding, the opportunity for fastest recovery of desirable vegetation may be following flood events (Mawhinney 2003). At such times, many of the native floodplain species respond with a period of vigorous growth and reproduction. Allowing these species to grow and reproduce by withholding grazing will not only increase the cover of these species (to the detriment of *P. canescens*), but also contribute to replenishing the seedbank of these desirable species, such that, following future floods, the density of

recruitment of these species may be greater. To expect complete recovery following just a single flood is unrealistic, but over a sequence of floods, where the desirable vegetation is allowed to complete its life-cycle and increase in cover, a staged recovery may be possible. Therefore, the sustainability of floodplain vegetation communities is dependent on sustaining a favourable flooding regime more than the characteristics of any single flood event (Mawhinney 2003).

The apparently slower recovery of *P. canescens* following autumn and winter disturbance represents an opportunity, the exploitation of which could take many forms. In areas unable to be cropped, e.g. due to the presence of gilgais or trees, damage to *P. canescens* may be achieved using the impact of very high livestock densities for short periods of time. In less sensitive areas, options include sowing a winter annual crop and a summer growing perennial pasture simultaneously, the perennial pasture seeds remaining dormant until after the crop is harvested, then the pasture seeds germinate and become established (R.D.B. Whalley personal communication). Such a system has the advantage of minimising tillage in flood and erosion prone areas. The options are limited primarily by the imagination. However, whichever approach is pursued, it seems inevitable that, without change to the subsequent grazing management, the vegetation will quickly revert to becoming dominated by *P. canescens*.

In addition to reinstating more frequent flooding of wetland sites, which will allow the native vegetation, particularly *Paspalum distichum* and *Eleocharis plana*, to maintain dominance over *P. canescens*, as advocated by previous authors (McCosker 1994b; Mawhinney 2003; but see Taylor and Ganf 2005), a number of management interventions, which can be implemented immediately, seem feasible.

9.2.3 Biological control

We need not wait for the introduction of biological control agents to more effectively manage existing populations of *P. canescens*. Indeed, that biological control can deliver effective control of *P. canescens* is not certain, particularly given the emerging parallels with the closely related *Lantana camara*, for which a total of 41 biological control agents

have been released world-wide. Despite 26 of these agents becoming established and causing some level of damage to *Lantana camara*, they are not achieving adequate control (Zalucki et al. 2007). While there are some outstanding successes where widespread control of an invasive species has been achieved by biological agents alone, such as with *Opuntia* spp. (though it should be noted that some 50 agents were introduced into Australia for that purpose, Dodd 1959), biological control programs are likely to be most effective when incorporated into an integrated management program. The effects of invertebrate herbivory and competition are expected to be multiplicative, where herbivory reduces biomass and competition reduces growth rate (Rees and Brown 1992). Therefore, greater reductions in weed performance would be expected where biological control agents and pasture competition impact together, rather than either in isolation (e.g. Sheppard et al. 2001). Even if the search for effective biological agents for control of *P. canescens* is successful, their widespread deployment will be years to decades away – a considerable wait.

Given the fresh insights into the ecology of *P. canescens* presented in this thesis, and a large number of potential biocontrol candidates being found in the native range (M. Julien personal communication), what attributes might be most beneficial in a biocontrol agent? Clearly seeds are important for dispersal of *P. canescens* in Australia, but given the poor performance of seed predators in controlling established populations of other invasive plants with large seed crops (Crawley 1992), seed predators may give poor reward for investment. This is particularly the case for *P. canescens*, where seed production may be reduced by other means, such as increasing competition and reducing pollination services. However, seed predators may slow the rate of spread where the full potential distribution of the invasive species is yet to be realised (e.g. Syrett et al. 1999). From casual observations, it appears that an important element in the ability of *P. canescens* to respond quickly following periods of stress is the woody tap-root. Therefore, a root-borer, equivalent to the root-mining weevil, *Hylobius transversovittatus* Goeze, for control of purple loosestrife, *Lythrum salicaria* L. (Malecki et al. 1993), may be of value.

If such biocontrol agents are found, and shown to be effective, then we may say that enemy release was a factor in the success of this species, as has been demonstrated for other species (Torchin and Mitchell 2004). However, if such a success was not accompanied by a recovery of palatable and desirable plant species, we may equally say that invasion by *P. canescens* has been symptomatic of changes in disturbance regime. There is the potential that in solving the *P. canescens* problem, if the underlying causes of its proliferation are not addressed, other invasive species may replace it, with no net benefit to the sustainability of either primary production or biodiversity conservation.

9.3 Conclusion

The invasion by *P. canescens* in Australia can be seen as a typical plant invasion. Plant invasions tend to follow repeated, deliberate and widespread introductions of species with extensive native ranges. The most invaded habitats have highly modified disturbance regimes. Once widespread and abundant, short of wholesale land-use change, multiple, coordinated management strategies are likely to be required. Specific details of successful management in one area are unlikely to apply over the entire distribution, but approaches based on recognising and utilising local resources are likely to offer the best sustainable management, not just of *P. canescens* but of those resources themselves.

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Appendix 1

Species of *Phyla*, with synonyms, from † International Plant Names Index (2006) and * Kennedy (1992).

Species	Basionym	Other Synonyms	Excluded Names
Phyla betulaefolia (Kunth) Greene 1899*†	*Lippia betulaefolia* Kunth 1818*†	*Cryptocalyx nepetaefolia* Benth. 1839*	
Phyla canescens (Kunth) Greene 1899*†	*Lippia canescens* Kunth 1818*†	*Lippia nodiflora* var. *minor* Gill. & Hook. 1830* *Zapania nodiflora* var. *rosea* D. Don 1834* *Lippia filiformis* Schrader 1834*† *Lippia uncinuligera* Nees ex Walp. 1843* *Zapania canescens* (Kunth) Gibert 1873* *Lippia litoralis* Phillippi 1895* *Lippia caespitosa* Rusby 1896* *Lippia nodiflora* var. *canescens* (Kunth) Kuntze 1898† *Lippia nodiflora* var. *pussila* Briq. 1904* *Lippia subterranea* Rusby 1920* *Phyla subterranea* Moldenke 1937† *Phyla nodiflora* (L.) Greene var. *canescens* (Kunth) Moldenke 1934† *Phyla nodiflora* var. *reptans* f. *copiapina* Acevedo 1951* *Phyla filiformis* Meikle 1985†	*Lippia nodiflora* var. *rosea* (D. Don) Macbr. 1960 *nom. Illegit.* (combination previously made by Munz)*
Phyla cuneifolia (Torrey) Greene 1899*	*Zapania cuneifolia* Torrey 1826*	*Lippia cuneifolia* (Torrey) Steudel 1841*	
Phyla dulcis (Trevir.) Moldenke 1934†*	*Lippia dulcis* Trevir. 1826†*	*Dipterocalyx scaberrima* Schldl. 1853*	*Lippia asperifolia* Reichb. 1827* *Phyla scaberrima* (Juss.) Moldenke 1936 belongs to genus *Lippia**
Phyla fruticosa (Miller) K. Kenn. ex Wunderlin & B.F.Hansen 2003†	*Verbena fruticosa* Mill. 1768*	*Lippia queretarensis* Kunth 1818* *Lippia strigulosa* Martens & Galeotti 1844* *Lippia nodiflora* var. *normalis* f. *sericea* Kuntze 1891* *Phyla yucatana* Moldenke 1946* *Phyla strigulosa* (M. Martins & Galeotti) Moldenke 1947*† *Phyla nodiflora* var. *antillana* Moldenke 1978* *Phyla nodiflora* var. *galapagensis* Moldenke 1979* *Lippia fruticosa* (Miller) K. Kenn. ex Wunderlin & B.F.Hansen 2001†	

Species	Basionym	Other Synonyms	Excluded Names
Phyla lanceolata (Michx.) Greene 1899*†	*Lippia lanceolata* Michx. 1803*†	*Lippia nodiflora* var. *lanceolata* (Michx.) Wood 1847† *Lippia nodiflora* var. *acutifolia* Kuntze 1891* *Lippia nodiflora* var. *lanceolata* Kuntze 1891† *Lippia lanceolata* var. *recognita* Fern. & Grisc. 1935* *Phyla lanceolata* f. *ahlesii* Moldenke 1952*	*Verbena scabra* Muhlenb. ex Sprengel. 1825 *nomen nudem* (no published description)* *Lippia nodiflora* var. *lanceolata* (Michx.) Kuntze 1891 *nom. illegit.* Combination previously made by Wood*
Phyla linearis (Kunth) Troncoso & Lopez-Palacios 1974*	*Lippia linearis* Kunth 1818*		
Phyla nodiflora (L.) Greene 1899*†	*Verbena nodiflora* L. 1753*†	*Phyla chinensis* Lour. 1790*† *Verbena capitata* Forssk. 1775* *Lippia nodiflora* (L.) Michx. 1803*† *Verbena repens* Bertol. 1806* *Lippia sarmentosa* Sprengel 1825* *Lippia nodiflora* var. *arenaria* Walper 1844* *Lippia nodiflora* var. *debilis* Walper 1844* *Lippia nodiflora* var. *vulgaris* Walper 1844* *Lippia nodiflora* var. *normalis* f. *brevipes* Planchon ex Kuntze 1891* *Phyla incisa* Small 1903* *Phyla nodiflora* var. *longifolia* Moldenke 1941* *Phyla nodiflora* f. *spathulata* Moldenke 1953* *Lippia nodiflora* var. *subsessilis* Wornb. ex Moldenke 1959* *Phyla nodiflora* var. *texensis* Moldenke 1973*	*Lippia reptans* Kunth 1818 apparently a hybrid between *Phyla nodiflora* & *P. fruticosa**
Phyla stoechadifolia (L.) Small 1909*†	*Verbena stoechadifolia* L. 1753*†	*Zapania reclinata* Lam. 1791* *Lippia stoechadifolia* (L.) Kunth 1818*† *Lippia longifolia* Sesse & Moc. 1894*	

Appendix 2.1

Herbarium specimens of *Phyla canescens*, in chronological order of collection (see Chapter 3). Includes unique collection number (collections from the same location, on the same date, by the same collector are not considered unique), specimens redetermined by the author from *P. nodiflora* to *P. canescens* are indicated by the inclusion of the date of retermination in the 'redet.'column, herbarium where held (AD, State Herbarium of South Australia; BRI, Queensland Herbarium; CANB, Australian National Herbarium; HO, Tasmanian Herbarium; MEL, National Herbarium of Victoria; NE, Beadle Herbarium, University of New England; NSW, National Herbarium of New South Wales; PERTH, Western Australian Herbarium), accession number, date, state, latitude, longitude and nearest locality of collection. Some latitude and longitude coordinates were retrospectively assigned by the author (using the website: Geosciences Australia 2007), indicated by an * after the longitude.

Unique collection	Redet.	Herbarium	Accession number	Date	State	Latitude	Longitude		Nearest locality
1		MEL	583749	Jan-1914	VIC	-37.9	144.9		Williamstown
		MEL	663933	Jan-1914	VIC	-37.9	144.9		Williamstown
2		MEL	1561970	Mar-1917	VIC	-37.9	144.9		Williamstown
3		AD	96621097	24-Jan-1927	SA	-34.9	138.6		Adelaide
4		AD	97621091	5-Jan-1929	SA	-34.9	138.6		Adelaide
5		AD	96612037	Jan-1931	SA	-34.9	138.6		Adelaide
6		AD	98587770	17-Dec-1936	SA	-34.9	138.6		Waite Institute
7		MEL	583483	4-Apr-1937	VIC	-37.9	144.9		Williamstown
		MEL	583484	4-Apr-1937	VIC	-37.9	144.9		Williamstown
8		BRI	112178	Nov-1938	QLD	-27.9	151.6		Glenfalloch
9		MEL	2299549	27-Feb-1943	TAS	-42.9	147.3	*	Hobart
10		HO	23617	16-Dec-1943	TAS	-42.9	147.3		Hobart

Unique collection	Redet.	Herbarium	Accession number	Date	State	Latitude	Longitude		Nearest locality
11		BRI	112177	19-Jan-1944	QLD	-27.9	151.6		Tummaville
12		PERTH	1012487	Nov-1949	WA	-30.7	121.5		Kalgoorlie
13		AD	98587742	17-Nov-1949	SA	-34.9	138.6		Waite Institute
14		NSW	231604	12-Dec-1949	NSW	-35.8	146.8	*	Burrumbattock
15		MEL	583732	10-Apr-1950	VIC	-37.9	144.9		Williamstown
16		BRI	112173	4-Dec-1950	QLD	-27.5	151.5		Toowoomba
17		BRI	112172	14-Nov-1951	QLD	-26.9	150.9		Warra
18		NSW		9-Feb-1953	NSW				Hunter Valley
19		PERTH	1012452	2-May-1953	WA	-31.6	117.5		Tammin
		PERTH	1012460	2-May-1953	WA	-31.6	117.5		Tammin
20		NSW	231764	13-Feb-1955	NSW	-34.1	141.9	*	Wentworth
21		BRI	112176	15-Jan-1959	QLD	-27.9	149.6		Westmar
		CANB	79411	15-Jan-1959	QLD	-27.9	149.6		Westmar
22		BRI	112171	29-Jan-1959	QLD	-27.6	151.3		Cecil Plains
23		NSW	48590	18-Mar-1959	NSW	-34.1	141.9	*	Wentworth
24		BRI	112168	Nov-1959	QLD	-24.9	146.9		Mt. Playfair
25		AD	97336028	1-Jan-1960	SA	-34.9	138.6		Adelaide
		CANB	398283	1-Jan-1960	SA	-34.9	138.6		Adelaide
26		CANB	84565	15-Mar-1960	VIC	-34.2	142.2		Mildura
27		BRI	112174	26-May-1961	QLD	-28.3	149.9		Toobeah
28		AD	96445402	28-Jan-1963	SA	-33.1	138.6		Adelaide
29		PERTH	1012479	Apr-1964	WA	-31.7	116.7		Northam
30		BRI	112179	24-Jul-1964	QLD	-27.6	152.6		Lowood
31		AD	98587768	Dec-1964	SA	-35.0	138.6		Adelaide
32	4-Nov-04	CANB	655685	18-Dec-1964	NSW	-35.6	144.5		Deniliquin
		NSW	231765	18-Dec-1964	NSW	-35.8	144.5	*	Deniliquin
33		BRI	112169	6-Mar-1965	QLD	-24.8	150.1		Kianga
34		MEL	583734	Nov-1965	VIC	-34.2	142.2		Mildura

Unique collection	Redet.	Herbarium	Accession number	Date	State	Latitude	Longitude		Nearest locality
35		AD	98587779	16-Dec-1965	SA	-33.8	138.6		Claire
		CANB	168134	16-Dec-1965	SA	-33.8	138.6		Claire
36		AD	96710029	4-Dec-1966	SA	-33.9	138.0		Bute
		MEL	583730	4-Dec-1966	SA	-33.9	138.0		Bute
37		BRI	112180	Jan-1967	QLD	-27.5	153.1		Brisbane
		MEL	583735	Jan-1967	QLD	-27.5	153.1		Brisbane
38		MEL	1517689	10-Mar-1967	VIC	-36.0	142.9		Birchip
		AD	98103314	10-Mar-1967	VIC	-36.0	142.9		Birchip
	23-Jul-04	NSW		10-Mar-1967	VIC	-36.0	142.9	*	Birchip
39		AD	96807908	28-Jul-1967	VIC	-34.1	141.9		Wentworth
40		BRI	112181	23-Nov-1967	QLD	-25.1	151.9		Ferry Hills
41		BRI	112175	Dec-1968	QLD	-27.6	150.3		Cecil Plains
42		AD	96903094	1-Dec-1968	SA	-34.9	138.6		Adelaide
43		AD	96916062	10-Dec-1968	SA	-34.9	138.6		Adelaide
44		PERTH	1012509	Oct-1969	WA				?
45	4-Nov-04	CANB	332085	23-Oct-1969	NSW	-33.9	151.1		Sydney
		NSW	231620	23-Oct-1969	NSW	-33.9	151.1	*	Sydney
46		MEL	1517822	27-Mar-1970	VIC	-34.3	142.2		Redcliffs
47		NSW	231766	9-Apr-1970	NSW	-29.1	147.9	*	Angledool
48		BRI	112182	18-Dec-1970	QLD	-26.3	152.0		Murgon
49		NSW	231763	17-May-1971	NSW	-33.1	141.7	*	Brokenhill
50		AD	97312088	31-Dec-1972	SA	-35.1	139.3		Murray Bridge
51		AD	97339002	22-Mar-1973	SA	-35.5	139.4		Blanchtown
52		NSW	231767	27-Dec-1974	NSW	-29.3	149.5		Moree
53		NSW	231758	27-Apr-1976	NSW	-34.1	141.3	*	Wentworth
54	23-Jul-04	NSW		17-Sep-1976	NSW	-33.1	145.5	*	Roto
55		NSW	231622	11-Nov-1976	NSW	-33.8	151.2	*	St Leonards
56		AD	97704791	23-Dec-1976	SA	-35.2	138.6		McLaren Flat

Unique collection	Redet.	Herbarium	Accession number	Date	State	Latitude	Longitude		Nearest locality
57		AD	98340227	24-Dec-1976	SA	-35.2	138.6		McLaren Flat
58		MEL	575355	1-Jan-1977	VIC	-35.2	143.4		Nyah
59		NSW	231760	12-Mar-1977	NSW	-35.5	145.0	*	Deniliquin
60		CANB	398286	26-Apr-1977	VIC	-35.7	143.8		Kerang
		MEL	1517823	26-Apr-1977	VIC	-35.7	143.9		Kerang
61		MEL	1502258	8-Dec-1977	VIC	-37.8	144.9		Melbourne
62		AD	97914303	8-Mar-1978	SA	-34.2	140.7		Renmark
		AD	98587729	8-Mar-1978	SA	-34.2	140.7		Renmark
63		BRI	264560	27-Mar-1978	NSW	-29.2	149.3		Weemelah
	23-Jul-04	NSW		27-Mar-1978	NSW	-29.2	149.3		Weemelah
64	23-Jul-04	NSW		5-Dec-1978	NSW	-34.3	142.3	*	Monak
65		AD	97950088	11-Sep-1979	SA	-34.0	140.9		'Bunyip Reach'
66		CANB	291893	13-Mar-1980	NSW	-30.8	148.0		Macquarie Marshes
67		CANB	8008100	27-Nov-1980	SA	-34.0	140.9		Queens Bend
68		CANB	293959	16-Dec-1980	NSW	-30.8	147.6		Macquarie Marshes
69		NSW	231762	13-Jan-1981	NSW	-34.6	143.6	*	Balranald
70		NSW	231761	28-Jan-1981	NSW	-29.5	149.8	*	Moree
71		BRI	362100	5-Feb-1981	QLD	-27.8	151.4		Brookstead
		CANB	365655	5-Feb-1981	QLD	-27.8	151.4		Brookstead
72		MEL	621609	11-Mar-1981	VIC	-36.4	145.4		Shepparton
73		MEL	1584242	29-Apr-1981	VIC	-36.5	143.3		Lake Cope Cope
74	23-Jul-04	NSW		16-Nov-1981	NSW	-33.4	148.0	*	Forbes
75		CANB	310173	17-Dec-1981	SA	-35.5	138.5		Victor Harbour
		AD	98587789	17-Dec-1981	SA	-35.5	138.5		Victor Harbour
76		AD	98821214	Apr-1982	SA	-34.4	140.5		Loxton
		AD	98821230	Apr-1982	SA	-34.4	140.5		Loxton
77		MEL	667329	31-Dec-1982	VIC	-34.8	143.4		Priambie State Forest

Unique collection	Redet.	Herbarium	Accession number	Date	State	Latitude	Longitude	Nearest locality
78		AD	98629215	20-Jan-1983	SA	-34.3	140.6	Martin Bend
		AD	98587699	20-Jan-1983	SA	-34.3	140.6	Martin Bend
		CANB	342123	20-Jan-1983	SA	-34.3	140.6	Martin Bend
79		MEL	629045	26-Jan-1983	VIC	-35.1	142.3	Wulpeup
80		NSW	231626	29-Nov-1983	NSW	-33.4	147.7	Jemalong
81		AD	98414298	25-Jan-1984	SA	-35.2	138.6	Chapel Vale
		AD	98587736	25-Jan-1984	SA	-35.2	138.6	Chapel Vale
		CANB	352054	25-Jan-1984	SA	-35.2	138.6	Chapel Vale
82		AD	98587737	13-Feb-1984	SA	-35.0	138.6	Glandore
		CANB	352037	13-Feb-1984	SA	-34.9	138.6	Glandore
83		MEL	1584240	13-Mar-1984	VIC	-36.9	141.0	Mullinger Swamp
84		MEL	1529654	Jan-1985	VIC	-36.6	146.0	Benalla
85		MEL	680462	2-Sep-1985	VIC	-36.1	143.7	Boort
86		MEL	680461	6-Sep-1985	VIC			Cemetery Forest
87		MEL	680460	7-Sep-1985	VIC			Cemetery Forest
88		MEL	680463	25-Nov-1985	VIC	-36.1	143.7	Boort
89		AD	98950082	1-Jan-1986	SA	-34.9	139.3	Mannum
		BRI	595236	1-Jan-1986	SA	-34.9	139.3	Mannum
		NSW	270608	1-Jan-1986	SA	-34.9	139.3	Mannum
90		AD	98631078	15-Mar-1986	SA	-34.7	139.0	Mt Crawford
91		MEL	696225	6-Oct-1986	VIC	-36.3	142.4	Ailsa
92		MEL	696223	7-Oct-1986	VIC	-36.3	142.4	Warracknabeel
93	10-Jun-04	MEL	2181599	29-Dec-1986	NSW	-34.1	141.9	Wentworth
94		CANB	626686	5-Oct-1987	SA	-35.0	139.3	Mannum
95		AD	98847322	25-Sep-1988	SA	-34.0	140.9	Chowilla Floodplain
96		AD	98844094	6-Oct-1988	SA	-34.0	140.9	Chowilla Floodplain
97		AD	98847323	6-Oct-1988	SA	-34.0	140.6	Chowilla Floodplain
98		CANB	398291	23-Nov-1988	VIC	-36.1	144.8	Goulburn/Murray R.
		MEL	1581687	23-Nov-1988	VIC	-36.3	144.8	Goulburn/Murray R.

Unique collection	Redet.	Herbarium	Accession number	Date	State	Latitude	Longitude	Nearest locality
99		BRI	466211	16-Dec-1988	VIC	-35.2	143.4	Vinifera
		MEL	115564	16-Dec-1988	VIC	-35.7	143.4	Vinifera
100		AD	98949055	18-Feb-1989	SA	-34.1	139.9	River Murray
101		AD	98949054	19-Feb-1989	SA	-34.1	139.9	River Murray
102		AD	98947133	1-Jul-1989	SA	-32.5	140.2	Manunda Station
103	Date?	NE	86133	3-Jan-1990	QLD	-28.6	150.0	Toobeah
104		BRI	502131	12-Dec-1990	QLD	-28.2	152.0	Warwick
105		CANB	584178	21-Jan-1991	VIC	-37.9	144.9	Williamstown
		MEL	698373	21-Jan-1991	VIC	-37.9	144.9	Williamstown
106		AD	99304248	12-Jan-1993	SA	-32.8	138.2	Melrose
107		MEL	2013980	16-Jan-1993	VIC	-36.1	145.5	Numurkah
108		AD	108929	24-Oct-1993	QLD	-26.8	150.6	Chinchilla
		BRI	683050	24-Oct-1993	QLD	-26.8	150.6	Chinchilla
		CANB	466689	24-Oct-1993	QLD	-26.8	150.6	Chinchilla
109		AD	99432304	6-Nov-1993	SA	-29.8	139.7	Moolwatana
110	26-Sep-06	AD	103480	16-Jan-1994	VIC	-34.2	142.2	Mildura
	31-Jan-05	BRI	681218	16-Jan-1994	VIC	-34.2	142.2	Mildura
		CANB	526233	16-Jan-1994	VIC	-34.2	142.2	Mildura
	10-Jun-04	MEL	2097924	16-Jan-1994	VIC	-34.2	142.2	Mildura
		NSW	285031	16-Jan-1994	VIC	-34.2	142.2	Mildura
111		CANB	470001	21-Jan-1994	ACT	-35.3	149.1	Canberra
		NSW	502453	21-Jan-1994	ACT	-35.3	149.1	Canberra
112		BRI	626655	20-Mar-1994	QLD	-27.1	151.1	Dalby
113		BRI	654645	13-Apr-1994	QLD	-28.2	152.0	Warwick
114		CANB	547357	28-Nov-1994	NSW	-30.9	150.5	Lake Keepit
		MEL	264518	28-Nov-1994	NSW	-30.9	150.5	Lake Keepit
		NSW	414080	28-Nov-1994	NSW	-30.9	150.5	Lake Keepit
		NE	64651	28-Nov-1994	NSW	-30.9	150.5	Lake Keepit
115		BRI	601328	12-Feb-1995	QLD	-27.4	151.4	Dalby

Unique collection	Redet.	Herbarium	Accession number	Date	State	Latitude	Longitude	Nearest locality
116		BRI	585378	9-Feb-1996	QLD	-24.8	151.1	Monto
117		BRI	489367	3-Apr-1996	QLD	-27.5	151.3	Cecil Plains
118		BRI	653074	15-Oct-1996	QLD	-25.5	150.0	Taroom
119		NSW	427373	1-Feb-1997	NSW	-31.1	150.9	Tamworth
120		MEL	2038951	4-Mar-1997	VIC	-36.6	143.0	Gre Gre
121		MEL	2064613	17-Apr-1998	NSW	-35.3	143.6	Swan Hill
122	23-Jul-04	NSW	434953	10-Jan-1999	NSW	-30.1	148.9	'Inglewood' Station
123	26-Sep-06	AD	109326	7-Oct-1999	QLD	-26.4	151.1	Dingaroo
		BRI	606717	7-Oct-1999	QLD	-26.4	151.1	Dingaroo
	10-Jun-04	MEL	302014	7-Oct-1999	QLD	-26.4	151.1	Dingaroo
	23-Jul-04	NSW	506846	7-Oct-1999	QLD	-26.4	151.1	Dingaroo
124		CANB	637622	15-Feb-2000	ACT	-35.4	149.0	Canberra.
125		BRI	497004	3-Oct-2000	QLD	-28.2	152.0	Warwick
126	10-Jun-04	MEL	2071063	11-Oct-2000	VIC	-36.1	142.1	Patchewollock
127		AD	131061	6-Nov-2000	VIC	-34.2	142.2	Mildura
128		BRI	494330	7-Nov-2000	QLD	-25.8	148.8	'Springrock' Station
129		BRI	718492	22-Nov-2000	QLD	-27.4	151.5	Dalby
130		BRI	718489	24-Nov-2000	QLD	-26.5	150.1	Condamine
131		MEL	2092250	27-Nov-2000	VIC	-35.0	143.3	Boundary Bend
132		BRI	492457	22-Jan-2001	QLD	-27.4	153.0	Enoggera
133		BRI	718668	9-Apr-2001	QLD	-28.2	152.0	Warwick
134		BRI	718677	26-Apr-2001	QLD	-28.2	151.9	Leslie
135		BRI	669996	29-Sep-2001	QLD	-25.5	149.7	Taroom
136		BRI	554812	5-Dec-2001	QLD	-28.0	151.6	Leyburn
137		BRI	554820	5-Dec-2001	QLD	-28.0	151.8	Leyburn
138		BRI	555426	5-Dec-2001	QLD	-28.1	151.8	Pratten
139		BRI	556229	5-Dec-2001	QLD	-28.2	151.8	Pratten
140		BRI	556250	5-Dec-2001	QLD	-28.1	151.8	Pratten

Unique collection	Redet.	Herbarium	Accession number	Date	State	Latitude	Longitude		Nearest locality
141		CANB	553817	4-Nov-2001	NSW	-31.3	150.5		Breeza
		MEL	2202608	4-Nov-2001	NSW	-31.6	150.5		Breeza
		NE	79749	4-Nov-2001	NSW	-31.6	150.5		Breeza
142		AD	143544	5-Dec-2001	QLD	-28.0	151.6		Leyburn
143		BRI	557169	6-Dec-2001	QLD	-28.8	151.2		Texas
		HO	523196	6-Dec-2001	TAS	-28.8	151.2	*	Texas
144		BRI	775737	10-Dec-2001	QLD	-28.6	148.9		Thallon
145		BRI	776208	11-Dec-2001	QLD	-28.6	149.6		Talwood
146		BRI	775239	11-Dec-2001	NSW	-28.7	149.2		Mungindi
147		BRI	775939	12-Dec-2001	QLD	-28.6	150.3		Goondiwindi
148		BRI	775950	12-Dec-2001	NSW	-28.6	150.3		Goondiwindi
149		BRI	776060	12-Dec-2001	QLD	-28.5	150.3		Goondiwindi
150		BRI	776069	12-Dec-2001	QLD	-28.6	150.4		Goondiwindi
151	31-Jan-05	BRI	555400	4-Jan-2002	QLD	-28.0	152.7		Boonah
152		BRI	553336	21-Jan-2002	QLD	-27.9	151.7		Clifton
153		NSW	498271	17-Mar-2002	NSW	-34.5	145.4	*	Hay
154		BRI	772647	9-May-2002	QLD	-28.6	151.4		Inglewood
155		BRI	733370	9-May-2002	QLD	-28.8	151.1		Texas
156		BRI	763133	10-Dec-2003	QLD	-27.8	152.6		Mutdapilly
157		MEL	2238693	13-Feb-2004	NSW	-32.8	151.7		Raymond Terrace
		AD	164506	13-Feb-2004	NSW	-32.8	151.7		Raymond Terrace
		CANB	583948	13-Feb-2004	NSW	-32.8	151.7		Raymond Terrace
		NE	84416	13-Feb-2004	NSW	-32.8	151.7		Raymond Terrace

Appendix 2.2

Herbarium specimens of *Phyla nodiflora*, in chronological order of collection (see Chapter 3). Includes unique collection number (collections from the same location, on the same date, by the same collector are not considered unique), herbarium where held (AD, State Herbarium of South Australia; BRI, Queensland Herbarium; CANB, Australian National Herbarium; DNA, Herbarium of the Northern Territory HO, Tasmanian Herbarium; MEL, National Herbarium of Victoria; NE, Beadle Herbarium, University of New England; NSW, National Herbarium of New South Wales; PERTH, Western Australian Herbarium), accession number, date, state, latitude, longitude and nearest locality of collection. Some latitude and longitude coordinates were retrospectively assigned by the author (those from a duplicate specimen held at another institution, or from the website: Geosciences Australia 2007), indicated by an * after the longitude.

Unique collection	Herbarium	Accession number	Date	State/ Territory	Latitude	Longitude		Nearest locality
1	NSW	231782	17-Nov-1843	QLD				?
2	MEL	583741	Oct-1855	NT	-15.2	133.0	*	Victoria River
	BRI	112197	1863	QLD	-27.5	153.5		Brisbane River
3	CANB	352652	1863	QLD	-27.5	153.5		Brisbane River
	NSW	231778	1863	QLD	-27.5	153.5		Brisbane River
4	MEL	583723	10-Oct-1867	QLD	-23.4	150.5		Rockhampton
5	MEL	583744	1877	NSW	-28.9	153.6		Ballina
6	MEL	583748	1878	NSW	-34.6	143.6		Balranald
7	MEL	583722	1881	NSW	-29.4	152.6		Clarence River
8	MEL	583728	1882	QLD	-27.5	151.8		Gowrie Creek
9	MEL	583721	1883	NT	-15.2	133.0		Elsey River
10	BRI	112199	Feb-1887	QLD	-27.4	153.1		Sandgate

Unique collection	Herbarium	Accession number	Date	State/ Territory	Latitude	Longitude		Nearest locality
11	BRI	112203	Dec-1887	QLD	-27.5	153.5		Stradbroke Island
12	MEL	583729	1890	QLD	-18.1	144.0		Einasleigh River
13	NSW	231610	Nov-1891	NSW	-28.8	153.6		Lennox Head
	MEL	583745	Nov-1891	NSW	-28.8	153.6		Lennox Head
14	MEL	583743	1893	QLD	-12.0	141.9		Cullen Pont
15	MEL	560563	1895	WA	-21.0	116.1	*	Fortescue River
16	NSW	231618	Nov-1898	NSW	-28.7	153.6		Byron Bay
	MEL	583747	Nov-1898	NSW	-28.7	153.6		Byron Bay
17	NSW	231621	1-Mar-1900	NSW	-33.3	151.5		Tuggerah Lakes
18	AD	98532017	2-May-1905	QLD	-27.4	153.2		Brisbane River
19	NSW	231772	1907	NT	-11.4	132.9	*	Malay Bay?
20	BRI	112206	29-Jan-1908	NSW	-28.3	153.6		Tweed Heads
21	BRI	112200	Nov-1908	QLD	-27.3	153.1		Redcliffe
22	NSW	231624	17-Nov-1910	NSW	-33.6	150.7		Richmond
23	NSW	231615	8-Jun-1911	NSW	-30.3	153.1		Coffs Harbour
24	NSW	231613	1-Mar-1912	NSW	-30.3	153.1		Coffs Harbour
	AD	97940082	1-Mar-1912	NSW	-30.3	153.1		Coffs Harbour
25	BRI	112195	Apr-1916	QLD	-27.5	153.5		Stradbroke Island
	NSW	231623	Apr-1916	QLD	-27.5	153.5		Stradbroke Island
26	NSW		1-Sep-1916	NSW	-28.4	153.6	*	Byron Bay-Tweed Heads
27	BRI	112205	Mar-1920	QLD	-23.5	150.5		Yeppoon
28	BRI	112194	Apr-1928	QLD	-28.1	153.4		Currumbin
29	BRI	112192	20-Apr-1930	QLD	-27.4	153.4		Stradbroke Island
	BRI	112193	20-Apr-1930	QLD	-27.4	153.4		Stradbroke Island
30	BRI	112188	15-Oct-1930	QLD	-25.5	153.5		Fraser Island
31	BRI	112202	2-May-1932	QLD	-27.4	153.1		Sandgate
32	PERTH	1012932	22-Aug-1932	WA	-21.6	117.1		Deep Reach
	PERTH	1012940	22-Aug-1932	WA	-21.6	117.1		Deep Reach
33	BRI	112201	26-Dec-1935	QLD	-25.9	153.3		Double Island Point

Unique collection	Herbarium	Accession number	Date	State/ Territory	Latitude	Longitude		Nearest locality
34	BRI	112187	1-Jan-1938	QLD	-24.9	152.4		Bundaberg
35	CANB	9511	1943	NT	-12.4	131.5		Koolpinyah
36	BRI	467895	29-Oct-1944	QLD	-27.2	153.1		Redcliffe
37	CANB	12596	14-Dec-44	QLD	-22.5	150.1		Toorilla
38	BRI	327131	18-Apr-1945	QLD	-22.3	150.8		Toorilla
39	BRI	112191	Apr-1945	QLD	-26.6	153.1		Coolum
40	BRI	327132	15-Sep-1946	NT	-12.3	131.5		Lake Finniss
	DNA	A0070622	15-Sep-1946	NT	-12.3	131.5	*	Lake Finniss
41	CANB	13152	Oct-1946	WA	-20.3	118.6		Port Hedland
42	NSW	231944	1-Jan-1948	NSW	-29.5	153.4		Clarence Heads
43	BRI	112209	13-Oct-1948	NT	-12.3	133.1		Oenpelli
	CANB	27904	13-Oct-1948	NT	-12.3	133.1		Oenpelli
	AD	96145034	13-Oct-1948	NT	-12.3	133.1		Oenpelli
	PERTH	3207609	13-Oct-1948	NT	-12.3	133.1		Oenpelli
	NSW	231776	13-Oct-1948	NT	-12.3	133.1		Oenpelli
	MEL	583750	13-Oct-1948	NT	-12.3	133.1		Oenpelli
44	BRI	416942	26-Dec-1949	QLD	-17.9	146.1		Mission Beach
45	NSW	22080	18-Jan-1953	NSW	-30.9	153.1		Arakoon Bay
46	PERTH	1012495	20-Feb-1953	WA	-31.9	115.8		City Beach
47	NSW		20-Feb-1953	NT	-12.6	131.1	*	Humpty Doo
48	NSW	231759	25-Feb-1955	NSW	-34.1	143.5	*	Balranald
49	CANB	2941	22-Jul-1955	NSW	-35.1	150.7		Jervis Bay
50	NSW	37337	30-Apr-1956	NSW	-30.0	153.2		Corindi Beach
51	BRI	112184	19-Nov-1956	QLD	-20.4	148.6		Georgana
	CANB	38764	19-Nov-1956	QLD	-20.4	148.6		Georgana
52	BRI	112211	1-Oct-1957	NT	-12.6	131.3		Humpty Doo
53	DNA	A0009283	22-Jan-1958	NT	-12.7	131.5	*	Connellans Camp
54	CANB	81280	14-Jan-1959	NT	-13.6	131.4		Humpty Doo
55	BRI	368522	20-May-1959	QLD	-25.9	153.1		Eight Mile Rocks

Unique collection	Herbarium	Accession number	Date	State/ Territory	Latitude	Longitude		Nearest locality
56	BRI	112190	21-Jun-1960	QLD	-22.4	150.1		Couti-outi
57	BRI	112208	23-Mar-1961	NT	-12.6	131.3		Beatrice Hill
	CANB	32961	23-Mar-1961	NT	-12.7	131.3		Beatrice Hill
	CANB	100289	23-Mar-1961	NT	-12.7	131.3		Beatrice Hill
	DNA	A0007989	23-Mar-1961	NT	-12.7	131.3	*	Beatrice Hill
	NSW	231774	23-Mar-1961	NT	-12.7	131.3		Beatrice Hill
58	BRI	112196	10-May-1961	QLD	-26.1	152.1		Boonara
59	BRI	112183	1-Feb-1962	QLD	-19.3	146.8		Townsville
60	BRI	112204	21-Apr-1962	QLD	-23.6	151.3		Curtis Island
61	CANB	123714	13-Mar-1963	NT	-12.6	131.3		Humpty Doo
	DNA	A0018031	13-Mar-1963	NT	-12.6	131.3	*	Humpty Doo
	DNA	D0000632	13-Mar-1963	NT	-12.6	131.3	*	Humpty Doo
62	DNA	D0000634	19-Apr-1963	NT	-12.6	131.3	*	Humpty Doo
63	AD	97306357	May/Jun-1963	QLD	-17.0	139.5		Bentinck Island
	AD	97306317	May/Jun-1963	QLD	-17.0	139.5		Bentinck Island
64	AD	96410161	16-Jan-1964	QLD	-19.3	146.8	*	Townsville
65	DNA	D0000633	22-Jan-1964	NT	-12.6	131.3	*	Humpty Doo
66	DNA	A0028253	24-Mar-1964	NT	-12.6	131.3	*	Humpty Doo
67	DNA	A0011411	1-Aug-1964	NT	-11.3	131.9	*	Cobourg Peninsula
68	CANB	15000	23-Feb-1966	NSW	-35.1	150.7		Jervis Bay
69	BRI	326769	28-Mar-1966	QLD	-23.6	151.3		Cutis Island
	CANB	339853	28-Mar-1966	QLD	-23.6	151.0		Curtis Island
70	NSW	231609	25-June-1966	NSW	-29.1	153.4		Evans Head
71	BRI	112189	29-Jan-1967	QLD	-27.8	153.5		Stradbroke Island
72	CANB	22083	12-May-1967	NSW	-30.2	153.2		Emerald Beach
73	NSW	231608	29-Oct-1967	NSW	-30.3	153.1		Coffs Harbou
74	BRI	112185	13-Jan-1968	QLD	-19.3	146.9		Townsville
75	CANB	188257	26-May-1968	NSW	-31.2	153.0		Crescent Head
76	DNA	A0052115	27-May-1968	WA	-18.0	122.4	*	Broome

Unique collection	Herbarium	Accession number	Date	State/ Territory	Latitude	Longitude		Nearest locality
76	PERTH	1611720	27-May-1968	WA	-17.9	122.5		Broome
77	DNA	A0024084	3-Oct-1968	NT	-11.1	132.1		Smith Point
	AD	96946045	3-Oct-1968	NT	-11.1	132.1		Smith Point
78	PERTH	1010417	2-Nov-1969	WA	-14.8	128.8		Thespesia Lagoon
79	BRI	144263	28-Mar-1970	QLD	-24.2	151.9		Bustard Bay
80	DNA	A0071362	1-Jul-1970	NT	-13.1	131.2	*	Tortilla Flats
81	BRI	112207	28-Nov-1970	NT	-11.1	132.1		Cobourg Peninsula
82	NSW	231607	1-Jan-1971	NSW	-31.0	153.1	*	Hat Head
83	NSW		21-Feb-1971	NSW	-29.4	153.3		Yamba
83	BRI	144264	21-Feb-1971	NSW	-29.4	153.3		Yamba
84	NE	78042	27-Mar-1971	NSW	-30.1	153.2		Arrawarra
85	CANB	220503	7-Jun-1971	NT	-15.6	136.4		Bing Bong Station
	DNA	A0031038	7-Jun-1971	NT	-15.6	136.4	*	Bing Bong Station
	MEL	583733	7-Jun-1971	NT	-15.6	136.4		Bing Bong Station
86	NE	28211	Nov-1971	NSW	-30.1	153.2	*	Arrawarra
87	DNA	D0003937	3-Nov-1971	NT	-12.4	131.4	*	Woolner Road
	DNA	D0003937	3-Nov-1971	NT	-12.4	131.4	*	Woolner Road
	CANB	220682	3-Nov-1971	NT	-12.4	131.4		Woolner Road
88	CANB	8008408	Dec-1971	QLD	-28.0	153.4		Southport
89	CANB	231753	25-Jan-1972	NT	-12.6	131.3		Humpty Doo
	DNA	D0131933	25-Jan-1972	NT	-12.6	131.3	*	Humpty Doo
	DNA	A0032527	25-Jan-1972	NT	-12.6	131.3	*	Humpty Doo
90	DNA	A0036255	11-Jul-1972	NT	-14.9	135.7	*	Maria Island
91	DNA	A0036705	24-Sep-1972	NT	-11.1	132.6	*	Croker Island
	CANB	239888	24-Sep-1972	NT	-11.4	132.6		Croker Island
92	BRI	8347	25-Nov-1972	QLD	-26.5	153.1		Maroochydore
93	CANB	239478	7-Feb-1973	NT	-12.4	133.0		Cannon Hill Airstrip
	DNA	D0006195	7-Feb-1973	NT	-12.4	133.0	*	Cannon Hill Airstrip
94	NSW	231731	7-Feb-1973	NSW	-29.5	153.4		Angourie

Unique collection	Herbarium	Accession number	Date	State/ Territory	Latitude	Longitude		Nearest locality
95	BRI	13866	9-Oct-1973	QLD	-27.3	153.5		Moreton Island
96	PERTH	1012517	3-Mar-1974	WA	-31.9	115.8		Herdsman Lake
97	PERTH	6174620	31-Jun-1974	WA	-18.5	122.1		Dampier District
98	DNA	D0009051	25-Oct-1974	NT	-13.2	130.1	*	Peron Island
	CANB	398284	29-Oct-1974	NT	-13.2	130.0		Peron Island
	CANB	398285	29-Oct-1974	NT	-13.2	130.0		Peron Island
99	BRI	97681	9-Dec-1974	QLD	-12.7	141.8		Weipa
100	DNA	A0072378	27-May-1975	NT	-17.6	133.5	*	Elliott Swamp
	AD	98421159	27-May-1975	NT	-17.6	133.5		Elliott Swamp
101	DNA	A0047752	21-Jul-1975	NT	-12.0	135.7	*	Elcho Island
102	CANB	283235	2-Jun-1976	QLD	-25.2	152.1		Maryborough
	CANB	283236	2-Jun-1976	QLD	-25.2	152.1		Maryborough
103	BRI	176233	8-Nov-1976	QLD	-26.6	153.1		Coolum Beach
	CANB	273087	8-Nov-1976	QLD	-26.6	153.1		Coolum Beach
104	DNA	D0012939	16-Dec-1976	NT	-12.6	132.4	*	Kapaga
105	DNA	D0012268	23-Jan-1977	NT	-13.9	136.6	*	Groote Eylandt
106	BRI	265713	13-Jul-1977	QLD	-23.3	150.8		Emu Park
107	BRI	292516	15-Jul-1977	QLD	-23.4	150.8		Cattle Point
108	CANB	274994	24-Jun-1977	NT	-13.5	130.5		Daly River
109	DNA	D0035651	12-Feb-1978	NT	-12.6	132.4	*	Kapalga
110	BRI	344747	7-Jun-1978	QLD	-12.3	143.1		Temple Bay
111	MEL	2119799	7-Aug-1978	NT	-15.1	133.2		Elsey Creek
112	PERTH	1010387	20-Dec-1978	WA	-31.7	115.8		Lake Joondalup
113	BRI	411455	19-Feb-1980	QLD	-23.3	150.9		Emu Park
114	BRI	411828	17-Mar-1980	QLD	-24.8	152.5		Bargara
115	DNA	D0017149	17-Apr-1980	NT	-12.2	131.2	*	Adelaide River
	NE	39080	17-Apr-1980	NT	-12.2	131.2	*	Adelaide River
116	DNA	D0017147	28-Apr-1980	NT	-14.9	131.8	*	Scott Creek
117	DNA	D0017148	7-May-1980	NT	-12.5	131.3	*	S Tommy Policeman Lagoon

Unique collection	Herbarium	Accession number	Date	State/ Territory	Latitude	Longitude		Nearest locality
118	DNA	D0017560	14-May-1980	NT	-12.4	131.5	*	Lake Finniss
119	CANB	295602	14-May-1980	NT	-12.7	132.5		Nourlangie
	DNA	D0140722	14-May-1980	NT	-12.8	132.7	*	Nourlangie
120	DNA	D0017406	25-Jun-1980	NT	-12.4	131.5	*	Woolner Station
121	CANB	8005439	15-Aug-1980	NT	-12.4	133.0		Kakadu National Park
122	BRI	343997	17-Aug-1980	QLD	-12.7	141.8		Weipa
	MEL	579456	17-Aug-1980	QLD	-12.7	141.8		Weipa
123	CANB	303788	12-Sep-1980	WA	-32.3	115.8		Lake Cooloongup
124	PERTH	1012525	26-Apr-1981	WA	-31.9	115.8		Herdsman Lake
125	NSW	231780	10-May-1981	QLD	-23.4	150.5	*	Rockhampton
126	NSW	231733	4-Sep-1981	NT	-15.6	136.4		Bing Bong Station
127	DNA	D0033118	30-Sep-1981	NT	-12.2	132.4	*	Alligator River
128	NSW	254689	25-Mar-1982	NSW	-28.8	153.6		Lennox Head, north side
129	NSW		21-May-1982	WA	-17.9	122.5		Broome
130	BRI	397081	8-Aug-1983	QLD	-12.0	141.9		Mapoon Peninsula
131	DNA	D0021591	21-Aug-1983	NT	-12.6	135.0	*	Arafura Floodplains
132	PERTH	1012444	14-Jan-1984	WA	-32.3	115.8		Rockingham
133	DNA	A0075211	21-May-1984	NT	-15.6	136.4	*	Bing Bong Station
134	PERTH	1611712	20-Jun-1984	WA	-17.0	122.5		Dampier Peninsula
135	PERTH	1012401	8-Oct-1984	WA	-18.0	122.5		Roebuck Plains
136	AD	98542117	1-Dec-1984	QLD	-16.7	138.3		Wentworth Station
	DNA	A0076816	1-Dec-1984	QLD	-16.7	138.3	*	Wentworth Station
137	DNA	D0025855	22-Jan-1985	NT	-12.6	131.3	*	Fogg Dam
138	DNA	D0025854	2-Feb-1985	NT	-12.6	131.3	*	Fogg Dam
139	CANB	364556	21-Apr-1985	WA	-31.7	115.8		Lake Joondalup
	PERTH	1012436	21-Apr-1985	WA	-31.7	115.8		Lake Joondalup
140	PERTH	2032961	26-Apr-1985	WA	-16.1	128.8		Lake Argyle
141	DNA	D0026379	11-Jul-1985	NT	-11.5	132.9	*	Murgenella
142	DNA	D0029292	14-Oct-1986	NT	-11.6	133.5	*	Goulbourn Island

Unique collection	Herbarium	Accession number	Date	State/ Territory	Latitude	Longitude		Nearest locality
143	BRI	431928	26-Nov-1986	QLD	-20.0	145.6		Charters Towers
144	BRI	560205	10-Dec-1986	NT	-12.5	132.9		Magela Point
	DNA	D0161160	10-Dec-1986	NT	-12.5	132.9	*	Magela Point
	NSW	274509	10-Dec-1986	NT	-12.5	132.9		Magela Point
145	NSW		17-Dec-1986	NSW	-30.0	153.2		Red Rock
	CANB	398290	17-Dec-1986	NSW	-30.0	153.2		Red Rock
	MEL	696227	17-Dec-1986	NSW	-30.0	153.2		Red Rock
146	DNA	D0051088	5-Feb-1987	NT	-11.3	132.9	*	Murgenella
147	PERTH	1010395	19-Mar-1987	WA	-32.3	115.8		Lake Cooloongup
	CANB	390797	19-Mar-1987	WA	-32.3	115.8		Lake Cooloongup
148	DNA	A0081756	6-Jun-1987	NT	-16.3	137.7	*	Calvert River
149	PERTH	1010409	22-Jun-1987	WA	-17.9	122.5		Roebuck Plains
150	NSW	206590	28-Aug-1987	NT	-11.4	133.0		Murganella
151	BRI	437014	22-Sep-1987	QLD	-20.6	139.6		Lake Moondarra
152	NSW	197256	23-Nov-1987	NSW	-29.5	153.4		Angourie Head
	MEL	696226	23-Nov-1987	NSW	-29.5	153.4		Angourie Head
153	BRI	436599	19-Dec-1987	QLD	-23.8	151.3		Facing Island
154	PERTH	1012428	20-Feb-1988	WA	-31.9	115.7		Metters Pool
155	BRI	480192	11-Apr-1988	WA	-16.5	122.9		Chile Head
	PERTH	1619861	11-Apr-1988	WA	-16.5	122.9		Chile Head
	NSW	231768	11-Apr-1988	WA	-16.5	122.9		Chile Head
	DNA	D0034706	11-Apr-1988	WA	-16.5	122.9	*	Chile Head
156	BRI	484001	31-May-1988	NT	-11.4	133.0		De Courcy Head
	CANB	9104742	31-May-1988	NT	-11.4	133.0		De Courcy Head
	DNA	D0051634	31-May-1988	NT	-11.4	133.0	*	De Courcy Head
	AD	98906219	31-May-1988	NT	-11.4	133.0		De Courcy Head
157	DNA	D0051643	2-Jun-1988	NT	-11.4	132.9	*	Annesley Point
	AD	98904222	2-Jun-1988	NT	-11.4	132.9		Annesley Point
	MEL	1598688	2-Jun-1988	NT	-11.4	132.9		Annesley Point

Unique collection	Herbarium	Accession number	Date	State/ Territory	Latitude	Longitude		Nearest locality
158	DNA	A0084313	23-Jul-1988	NT	-15.7	137.0	*	Vanderlin Island
159	PERTH	4104498	4-Sep-1988	WA	-31.5	115.7		Yanchep National Park
160	BRI	470552	3-Mar-1990	QLD	-12.7	141.8		Weipa
161	CANB	440608	5-Apr-1990	NT	-15.0	132.2		Elsey Park
	DNA	D0049090	5-Apr-1990	NT	-15.0	132.2	*	Elsey Park
	MEL	1582951	5-Apr-1990	NT	-15.0	132.2		Elsey Park
162	DNA	D0050698	20-May-1990	NT	-12.6	135.0	*	Arafura Swamp
	MEL	1586921	20-May-1990	NT	-12.6	135.0		Arafura Swamp
163	PERTH	1411373	2-Jul-1990	WA	-21.6	117.1		Millstream Pools
164	DNA	D0051962	27-Dec-1990	NT	-12.6	131.3	*	Fogg Dam
165	BRI	507274	30-Jul-1991	QLD	-19.3	147.0		Townsville
166	DNA	D0063056	16-Oct-1991	QLD	-11.9	142.0	*	Port Musgrave
	BRI	514381	16-Oct-1991	QLD	-11.9	142.0		Port Musgrave
167	AD	99241220	13-Nov-1991	NT	-12.3	133.1		Port Musgrave
	DNA	D0061537	13-Nov-1991	NT	-12.3	133.1	*	Port Musgrave
	MEL	1611832	13-Nov-1991	NT	-12.3	133.1		Port Musgrave
168	BRI	508726	18-Nov-1991	QLD	-25.3	152.8		Dundowran
	AD	99216113	18-Nov-1991	QLD	-25.3	152.8		Dundowran
169	PERTH	3151522	29-Jan-1992	WA	-17.8	122.7		Lake Campion
170	DNA	D0061991	3-Feb-1992	NT	-11.9	131.0	*	Melville Isle
171	BRI	545208	16-Feb-1992	QLD	-21.1	149.2		Slade Point
172	AD	99250313	29-Mar-1992	WA	-16.4	123.0		Nellie Point
	PERTH	3151638	29-Mar-1992	WA	-16.4	123.0		Nellie Point
	PERTH	2160137	29-Mar-1992	WA	-16.4	123.0		Nellie Point
173	BRI	518273	22-Jul-1992	NT	-11.7	136.8		Truant Island
	DNA	D0064640	22-Jul-1992	NT	-11.7	136.8	*	Truant Island
174	DNA	D0066340	20-Aug-1992	NT	-12.6	132.5	*	Kakadu National Park
175	DNA	D0065859	12-Oct-1992	NT	-11.4	132.9	*	Murganella
	MEL	713745	12-Oct-1992	NT	-11.4	132.9		Murganella

Unique collection	Herbarium	Accession number	Date	State/ Territory	Latitude	Longitude		Nearest locality
176	BRI	633165	17-Nov-1992	QLD	-21.3	149.7		Mackay
177	BRI	565769	22-Jan-1993	QLD	-18.6	144.7		Conjuboy
178	PERTH	4181913	10-Feb-1993	WA	-14.8	128.7		Kununurra
179	BRI	564613	10-Feb-1993	QLD	-21.5	148.3		Lake Elphinstone
180	BRI	533847	11-Apr-1993	WA	-31.8	115.8		Carine Swamp
181	DNA	D0077975	4-May-1993	NT	-13.3	136.4	*	Cape Shield
182	BRI	621070	10-Aug-1993	QLD	-22.5	150.7		Port Clinton
183	BRI	626554	15-Oct-1993	NT	-12.3	136.9		Yirrkala
	DNA	D0076737	15-Oct-1993	NT	-12.3	136.9	*	Yirrkala
184	DNA	D0076710	16-Oct-1993	NT	-13.2	136.8	*	Nhulunbuy Lagoon
185	BRI	622260	19-Nov-1993	QLD	-25.1	152.6		Woodgate
	NSW	414856	19-Nov-1993	QLD	-25.1	152.6		Woodgate
186	AD	99250312	29-Jan-1994	WA	-17.8	122.7		?
187	CANB	478207	4-Feb-1994	NT	-11.2	132.2		Cobourg Peninsula
	MEL	1617640	4-Feb-1994	NT	-11.2	132.2		Cobourg Peninsula
	BRI	626555	4-Feb-1994	NT	-11.2	132.2		Cobourg Peninsula
	NSW	414850	4-Feb-1994	NT	-11.2	132.2		Cobourg Peninsula
	DNA	D0076375	4-Feb-1994	NT	-11.2	132.2	*	Cobourg Peninsula
188	DNA	D0072676	16-Feb-1994	NT	-12.3	136.8	*	Gove
189	CANB	547356	17-Feb-1994	NT	-14.9	133.1		Mataranka
	DNA	D0076240	17-Feb-1994	NT	-14.9	133.1	*	Mataranka
190	BRI	633730	12-Nov-1994	NSW	-29.5	153.4		Yamba
191	BRI	634602	25-Nov-1994	QLD	-25.5	153.1		Fraser Island
192	DNA	D0123102	18-Apr-1995	NT	-11.1	132.6	*	Croker Island
193	BRI	571577	19-May-1995	QLD	-24.4	151.5		Bororen
194	NSW	406169	Sep-1995	NT	-12.6	131.3		Beatrice Lagoon
	NSW	406170	Sep-1995	NT	-12.6	131.3		Beatrice Lagoon
	NSW	406168	Sep-1995	NT	-12.6	131.3		Beatrice Lagoon
195	DNA	D0125002	17-Oct-1995	NT	-12.3	132.1	*	Wildman River

Unique collection	Herbarium	Accession number	Date	State/ Territory	Latitude	Longitude		Nearest locality
196	BRI	585377	11-Feb-1996	QLD	-24.8	151.2		Bancroft
	MEL	287620	11-Feb-1996	QLD	-24.8	151.2		Bancroft
197	BRI	652231	26-Jun-1996	QLD	-27.9	153.4		Southport
198	BRI	599126	12-Aug-1996	QLD	-12.8	143.5		Weipa
199	BRI	572564	21-Oct-1996	QLD	-24.6	152.1		Yandaran
200	BRI	603545	23-Oct-1996	QLD	-25.1	152.6		Woodgate
	MEL	285703	23-Oct-1996	QLD	-25.1	152.6		Woodgate
	AD	99746360	23-Oct-1996	QLD	-25.1	152.6		Woodgate
201	DNA	D0132982	12-Aug-1997	NT	-12.9	130.5	*	Finniss River
202	PERTH	5507634	14-Aug-1997	WA	-19.8	120.9		Mooglie Well
203	DNA	D0135985	10-Nov-1998	NT	-12.2	131.2	*	Adelaide River Crossing
204	BRI	677167	8-Dec-1998	QLD	-27.3	153.4		Moreton Island
205	BRI	676053	10-Dec-1998	QLD	-25.0	151.1		Mulgildie
206	BRI	490033	19-Jan-1999	QLD	-25.1	151.1		Abercorn
207	PERTH	5392535	9-Feb-1999	WA	-32.3	115.7		Lake Richmond
208	DNA	D0145306	2-Jun-1999	NT	-15.3	130.3	*	Bradshaw Station
209	BRI	492328	10-Aug-1999	QLD	-20.5	148.7		Goorganda Plain
210	PERTH	5770068	11-Oct-1999	WA	-19.8	121.4		Mandora Marsh
211	PERTH	5553202	22-Mar-2000	WA	-31.9	115.8		Lake Monger
212	BRI	494309	30-Oct-2000	QLD	-19.7	144.4		Gregory Spring
213	BRI	772166	17-Nov-2002	QLD	-17.1	139.6		Sweers Island
214	PERTH	6840582	23-Sep-2003	WA	-16.5	128.5		Lissadell Station
215	PERTH	7215290	15-Nov-2003	WA	-31.9	115.8		Scarborough
216	PERTH	6592996	13-Feb-2004	WA	-27.7	114.2		Kalbarri
217	PERTH	7158777	17-Sep-2004	WA	-19.1	121.5		Calenjadie Well
218	DNA	D0167346	27-Nov-2004	NT	-12.4	131.0	*	Howard River
219	PERTH	7296711	10-Aug-2005	WA	-19.4	128.3		Lake Willson
220	AD	186854	4-Sep-2005	NT	-12.4	135.0		River Glyde
221	PERTH	7254121	30-Nov-2005	WA	-31.9	115.8		Scarborough

Appendix 3

All taxa recorded from quadrats within exclosures at each of the four sites. Also included are life-form and functional group (see Chapter 8). Introduced species are indicated with an *. Nomenclature follows Wheeler *et al*. (2002) for Poaceae and Harden (1992; 1993; 2000; 2002) for other taxa, except *Phyla canescens* (Munir 1993) and *Verbena gaudichaudii* (Michael 1997).

	Species	Family	Life-form	Functional group	Site 1	2	3	4
*	*Abutilon theophrasti*	Malvaceae	Annual	Other dicot		+		
	Aeschynemone indica	Fabaceae	Annual	Annual legume				+
	Alternanthera denticulata	Amaranthaceae	Annual	Other dicot	+	+		+
*	*Amaranthus powellii*	Amaranthaceae	Annual	Other dicot	+			
*	*Amaranthus macrocarpus* var. *macrocarpus*	Amaranthaceae	Annual	Other dicot	+	+		
*	*Ammi majus*	Apiaceae	Annual	Other dicot	+	+		
	Amphibromus nervosus	Poaceae	Perennial	Perennial grass		+	+	+
*	*Argemone ochroleuca* subsp. *ochroleuca*	Papaveraceae	Annual	Other dicot		+		
*	*Argemone subfusiformis* subsp. *subfusiformis*	Papaveraceae	Annual	Other dicot	+			
*	*Aster subulatus*	Asteraceae	Annual	Other dicot	+		+	
	Atriplex semibaccata	Chenopodiaceae	Perennial	Other dicot			+	
	Austrodanthonia bipartita	Poaceae	Perennial	Perennial grass	+	+		
	Austrostipa aristiglumis	Poaceae	Perennial	Perennial grass	+	+		
	Brachycome curvicarpa	Asteraceae	Annual	Other dicot			+	+
	Boerhavia dominii	Nyctaginaceae	Perennial	Other dicot	+	+		
*	*Bromus catharticus*	Poaceae	Annual	Annual grass	+	+		
	Bulbine semibarbata	Asphodeliaceae	Annual	Other monocot			+	
	Carex inversa	Cyperaceae	Perennial	Other monocot		+		
	Chamaesyce drummondii	Euphorbiaceae	Perennial	Other dicot	+		+	+
	Chenopodium pumilio	Chenopodiaceae	Annual	Other dicot		+	+	+
*	*Cichorium intybus*	Asteraceae	Perennial	Other dicot	+			

	Species	Family	Life-form	Functional group	Site 1	2	3	4
	Chloris truncata	Poaceae	Perennial	Perennial grass	+	+		
*	*Cirsium vulgare*	Asteraceae	Annual	Other dicot			+	+
	Convolvulus erubescens	Convolvulaceae	Perennial	Other dicot		+		
*	*Conyza bonariensis*	Asteraceae	Annual	Other dicot	+	+	+	+
	Cotula australis	Asteraceae	Annual	Other dicot	+			
*	*Cucumis myriocarpus*	Cucurbitaceae	Annual	Other dicot	+	+		
	Cullen tenax	Fabaceae	Perennial	Perennial legume			+	
*	*Cyclospermum leptophyllum*	Apiaceae	Annual	Other dicot	+	+	+	+
	Cynodon dactylon	Poaceae	Perennial	Perennial grass	+		+	+
	Cyperus bifax	Cyperaceae	Perennial	Other monocot	+		+	
	Cyperus concinnus	Cyperaceae	Perennial	Other monocot				+
	Dichanthium sericeum subsp. *sericeum*	Poaceae	Perennial	Perennial grass	+	+		
	Echinochloa colona	Poaceae	Annual	Annual grass	+	+	+	+
	Einadia polygonoides	Chenopodiaceae	Perennial	Other dicot	+	+	+	+
	Enteropogon ramosus	Poaceae	Perennial	Perennial grass		+	+	
	Eleocharis plana	Cyperaceae	Perennial	Other monocot	+		+	+
	Eragrostis parviflora	Poaceae	Annual	Annual grass			+	
	Eriochloa procera	Poaceae	Perennial	Perennial grass		+		
	Erodium crinitum	Geraniaceae	Annual	Other dicot				+
	Euchiton sphaericus	Asteraceae	Annual	Other dicot	+	+	+	+
*	*Fumaria* sp.	Fumariaceae	Annual	Other dicot	+			
	Glycine tabacina	Fabaceae	Perennial	Perennial legume		+		
	Juncus usitatus	Juncaceae	Perennial	Other monocot				+
	Lachnagrostis filiformis	Poaceae	Annual	Annual grass		+	+	+
*	*Lactuca serriola*	Asteraceae	Annual	Other dicot	+	+	+	
*	*Lamium amplexicaule*	Lamiaceae	Annual	Other dicot	+			
*	*Lepidium africanum*	Brassicaceae	Annual	Other dicot	+	+		
*	*Lepidium bonariense*	Brassicaceae	Annual	Other dicot			+	
	Lepidium fasciculatum	Brassicaceae	Annual	Other dicot			+	

	Species	Family	Life-form	Functional group	Site 1	2	3	4
*	*Lolium perenne*	Poaceae	Annual	Annual grass	+			
*	*Lolium rigidum*	Poaceae	Annual	Annual grass		+		
	Lythrum hyssopifolia	Lamiaceae	Annual	Other dicot				+
*	*Malva parviflora*	Malvaceae	Annual	Other dicot	+		+	+
	Marsilea drummondii	Marsileaceae	Perennial	Other dicot	+		+	+
*	*Medicago laciniata*	Fabaceae	Annual	Annual legume			+	
*	*Medicago minima*	Fabaceae	Annual	Annual legume			+	
*	*Medicago polymorpha*	Fabaceae	Annual	Annual legume	+	+	+	+
*	*Medicago truncatula*	Fabaceae	Annual	Annual legume			+	+
*	*Melilotus indicus*	Fabaceae	Annual	Annual legume	+			
	Oxalis perennans	Oxalidaceae	Perennial	Other dicot	+	+	+	+
	Panicum decompositum var. *tenuior*	Poaceae	Perennial	Perennial grass	+	+	+	
	Panicum laevinode	Poaceae	Perennial	Perennial grass			+	
	Paspalidium aversum	Poaceae	Perennial	Perennial grass	+	+		
	Paspalum distichum	Poaceae	Perennial	Perennial grass	+		+	+
	Persicaria lapathifolia	Polygonaceae	Perennial	Other dicot				+
	Persicaria prostrata	Polygonaceae	Perennial	Other dicot	+			
*	*Phalaris paradoxa*	Poaceae	Annual	Annual grass	+	+		
*	*Phyla canescens*	Verbenaceae	Perennial		+	+	+	+
*	*Physalis lanceifolia*	Solanaceae	Annual	Other dicot		+		
	Plantago turrifera	Plantaginaceae	Annual	Other dicot			+	
*	*Polygonum aviculare*	Polygonaceae	Annual	Other dicot	+	+	+	+
	Portulaca oleracea	Portulacaceae	Annual	Other dicot	+		+	
	Ranunculus undosus	Ranunculaceae	Perennial	Other dicot			+	+
	Ranunculus pumilio var. *pumilio*	Ranunculaceae	Annual	Other dicot			+	+
*	*Rapistrum rugosum*	Brassicaceae	Annual	Other dicot	+	+	+	
	Rorippa eustylis	Brassicaceae	Annual	Other dicot			+	+
	Rumex brownii	Polygonaceae	Perennial	Other dicot	+	+		
	Rumex tenax	Polygonaceae	Perennial	Other dicot				+

	Species	Family	Life-form	Functional group	Site 1	2	3	4
	Salsola kali var. *kali*	Chenopodiaceae	Annual	Other dicot			+	
	Scleroblitum atriplicinum	Chenopodiaceae	Annual	Other dicot			+	+
	Sclerolaena limbata	Chenopodiaceae	Perennial	Other dicot			+	
	Sclerolaena muricata var. *muricata*	Chenopodiaceae	Perennial	Other dicot	+	+	+	+
	Sclerolaena muricata var. *villosa*	Chenopodiaceae	Perennial	Other dicot	+		+	
	Senecio runcinifolius	Asteraceae	Perennial	Other dicot			+	
	Senna clavigera	Fabaceae	Perennial	Perennial legume		+		
	Sida spinosa	Malvaceae	Perennial	Other dicot	+	+		
	Solanum esuriale	Solanaceae	Perennial	Other dicot	+			
*	*Sonchus oleraceus*	Asteraceae	Annual	Other dicot	+	+	+	+
	Sporobolus creber	Poaceae	Perennial	Perennial grass	+			
	Stellaria augustifolia	Caryophyllaceae	Perennial	Other dicot			+	+
	Tribulus micrococcus	Zygophyllaceae	Annual	Other dicot		+		
*	*Tribulus terrestris*	Zygophyllaceae	Annual	Other dicot	+			
*	*Urochloa panicoides*	Poaceae	Annual	Annual grass	+			
	Verbena gaudichaudii	Verbenaceae	Perennial	Other dicot		+		+
*	*Verbena supina*	Verbenaceae	Annual	Other dicot		+		
*	*Veronica peregrina*	Scrophulariaceae	Annual	Other dicot			+	+
*	*Vicia sativa* subsp. *nigra*	Fabaceae	Annual	Annual legume	+			
*	*Vicia villosa* subsp. *eriocarpa*	Fabaceae	Annual	Annual legume	+			
	Vittadinia pterochaeta	Asteraceae	Perennial	Other dicot		+	+	
	Wahlenbergia gracilenta	Campanulaceae	Annual	Other dicot			+	+
*	*Xanthium orientale*	Asteraceae	Annual	Other dicot	+	+		
*	*Xanthium spinosum*	Asteraceae	Annual	Other dicot			+	+
	Unidentified Asteraceae	Asteraceae	Annual	Other dicot			+	+