The ecology of common heliotrope (*Heliotropium europaeum* L.)
in a Mediterranean dry-land cropping system

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‘Amid this dread exuberance of woe
Ran naked spirits wing’d with horrid fear,
Nor hope had they of crevice where to hide,
Or heliotrope to charm them out of view.’

- Dante Alighieri The Divine Comedy, Inferno Canto XXIV

‘I serve my perdition in this private hell
A thousand angers have kept me alive’

- Glen Danzig, ‘Evil Thing’, Danzig I
Abstract

Common heliotrope (*Heliotropium europaeum* L.) is an herbaceous Mediterranean summer annual that grows on areas devoid of vegetation in the dry-land cropping region located in the north-west of the state of Victoria, Australia. This region is known as the Mallee, and common heliotrope is considered a weed here because it transpires soil water that could otherwise be used by ensuing crops, and is toxic to livestock.

In this study, laboratory experiments have shown that germination of seeds of common heliotrope is not limited by light, cold treatment, or a leachable inhibitor. Temperature and water potential (and perhaps depth inhibition) are the principal environmental factors that limit germination. Although 100% of seeds will germinate under optimal conditions, these conditions are rarely met in the field, and the percentage of seeds that germinate at sub-optimal conditions changes seasonally and between Australian populations. This is the principal mechanism of dormancy in the species, ensuring that seeds do not germinate when conditions are unfavourable for continued growth and that in the field, germination of a seed population is fractional, spreading risk temporally. Germination of seeds of common heliotrope does not conform to the assumptions of the hydrothermal time model frequently used to predict field emergence of weed species.

Field observations and simulated rainfall experiments on a consistent soil type (Calcarosol with a clay loam surface texture and clay subsoil) indicated that approximately 20 mm of rainfall is the minimum amount required for germination and emergence of common heliotrope. Field experiments using lysimeters indicated that this is also the amount required for minimal reproduction on the same soil type. Although common heliotrope can successfully reproduce upon the rainfall event which causes its germination, its growth is indeterminate, and further access to moisture will result in massively increased reproductive output. Plants will continue to grow and produce seed over summer until they are killed by drought or senesce in autumn. Laboratory and field studies showed that root growth in common heliotrope is relatively slow, and is opportunistic in areas where moisture becomes available.

Simulation of soil water and temperature fluxes showed that soil type has a large impact on the amount and duration of water potential that seeds and plants are exposed to. In the case of common heliotrope, this is critical in determining regional prevalence and
distribution in the north-west of Victoria. It is recommended that studies of arid species reliant on isolated rainfall events for emergence should consider absolute water availability and not in terms of rainfall amount alone.

Analysis of long term summer rainfall data from the Victorian Mallee indicates that there is potential for reducing the cost of controlling common heliotrope by using residual pre-emergent sulfonylurea or triazine herbicides, instead of the traditional post-emergent herbicides or cultivation. More information is needed on the efficacy of such residual herbicides on common heliotrope and other summer weeds, and their impact on subsequent crops before the full potential of this management option is known. Reduced cost of control could also be achieved by economic analysis of the likely benefits of controlling each emerging cohort of common heliotrope, and a framework for decision making is suggested.
Declaration

This is to certify that;

(i) the thesis comprises only my original work towards the PhD except where indicated in the Preface,
(ii) due acknowledgement has been made in the text to all other material used,
(iii) the thesis is less than 100,000 words in length, exclusive of tables, maps, bibliographies and appendices.

James Robert Hunt, November 2005

Preface

The experiment recording the rate of root growth of common heliotrope at different temperatures as outlined in Section 4.4 was conducted in conjunction with DeAnne Price in partial fulfilment of the requirements of the degree of Bachelor of Agricultural Science (Honours) at La Trobe University.
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Chapter 1. General Introduction

1.1. Introduction

The semi-arid Mediterranean dry-land agricultural regions of southern Australia are of tremendous importance to the nation's food supply and economy (Linacre 2005; Martin 2005). These regions on average produce 16.4 million tonnes of cereals, oilseeds and pulses annually (ABARE 1999). Crop production is principally limited by water availability (Ridge 1986). Consequently, there is great potential benefit in preventing water that has fallen as rain being unproductively transpired by weeds. Competition for water from weeds can occur both directly within the crop, and indirectly over summer when fields are in fallow, awaiting sowing in the autumn. In-crop weeds have been extensively researched both within Australia and in comparable farming systems elsewhere in the world. Fallow or summer weeds have traditionally been paid little attention, perhaps due to the indirect nature of their competition with crops. The water relations and agricultural practices of the grain growing regions in Australia may also contribute to them being a uniquely Australian problem.

Some of the cropping regions in which summer weeds are of extreme agronomic importance are the Mallee regions of the states of Victoria, New South Wales, South Australia and Western Australia. These regions exist in the agriculturally marginal land between the higher rainfall regions associated with the Great Dividing Range, and the arid interior of the Australian continent.

*Heliotropium europaeum* L. (common heliotrope) is one of the most abundant and problematic summer weeds in the grain growing regions of southern Australia (S. R. Niknam, pers. comm.). Farmers have long considered control of this species necessary, but only in recent years has quantitative evidence of significant negative impact on crop yield been produced (see van Rees and Smallwood 2000). As a result, very little basic scientific work has been done on the species in a crop production context.

The aim of this thesis is to understand how the biological attributes of common heliotrope interact with the physical attributes of the ecological system it inhabits, and thereby determine its impact on a Mediterranean dry-land cropping system. This will undoubtedly assist in its management in the region.
1.2. Common heliotrope and its naturalisation in Australia

Common heliotrope is a summer growing herbaceous annual belonging to the family Boraginaceae and is native to the Middle East, East Asia and the region surrounding the Mediterranean sea (Bentham 1869; Cunningham, Mulham et al. 1981; Parsons and Cuthbertson 2001; Sheppard, Brun et al. 1996; Walsh and Entwistle 1999). Walsh (1999) describe it as having an erect habit up to 0.4 m in height with an indumentum of tubercle-based greyish hairs. The leaves are elliptic to ovate, 15 to 70 mm in length and 5 to 30 mm wide with an obtuse apex, cuneate base, flat margins and hair on both sides. They are connected to the stems by petioles that are up to 30 mm in length. Inflorescences are usually branched, sepals are lanceolate, 2.5 to 3.5 mm long, acute, shortly connate and do not elongate. The corolla is 4 to 5 mm long with a yellow, glabrous throat and white, hairy outside. The anthers are acute, the apices free and style very short. The stigma is about 0.75 mm long and papillate. The seeds are four dry, brownish mericarps per flower, which can be glabrous or pubescent, rugose and fall at maturity. Figures 1.1a-f show common heliotrope at various stages of its development.

Common heliotrope has been recorded in all states of Australia except Tasmania and the Northern Territory (Figure 1.2), being most abundant in southern New South Wales and Victoria inland of the Great Dividing Range, and in southern South Australia (Everest 1981; Harden 1992; Parsons and Cuthbertson 2001; Walsh and Entwistle 1999). Its distribution is limited to areas of dominant winter rainfall, principally between the 300 and 500 mm isohyets (Moore 1956). It is proclaimed noxious in Tasmania and certain regions of Western Australia (Parsons and Cuthbertson 2001). Common names within Australia include Barooga weed, caterpillar weed, Bishop's beard, European heliotrope, wild heliotrope, potato weed, tomato weed, blue weed and Wanderrie curse (Moore 1956; Parsons and Cuthbertson 2001). However, the accepted common name within Australia is common heliotrope (Anon. 1953; Hartley 1979).
Figure 1.1a. A seedling of common heliotrope several days old showing cotyledons and emerging first true leaves.

Figure 1.1b. A young common heliotrope plant 2-3 weeks old with 3 pairs of true leaves about to commence flowering and axillary growth.
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Figure 1.1d. A mature common heliotrope plant.
Figure 1.1e. Flowers of common heliotrope in an inflorescence (cyme) early in development.

Figure 1.1f. A well developed inflorescence (chyme) of common heliotrope illustrating indeterminate nature of flowering. Note un-opened flower buds at the top, and immature seeds at its bottom.
In the past, there has been some contention as to whether common heliotrope is native to southern Australia (Kloot 1983; Moore 1956; Sheppard, Brun et al. 1996). The controversy centres on a specimen collected at the head of Spencer's Gulf by Robert Brown in 1802, which he named *Heliotropium glandulosum* (Moore 1956). Bentham (1869) later cited this specimen as *H. europaeum*, and argued that the plant was native, as there was no known European contact with South Australia prior to the voyage of Mathew Flinders, in which Brown took part (Kloot 1983). However, Black (1909) considered Brown's specimen to be of another species, the native *H. eichwaldii*, and Kloot (1983) cites personal communication from D. E. Symon to the effect that the specimen in question is very poor in quality and its identity uncertain. In comparing Australian specimens to those from the Northern Hemisphere, Bentham (1869) himself states that he could find no character to distinguish Australian specimens from European material. Moore (1956) cites comparative studies undertaken by the Kew Botanic Gardens, which concluded that Australian specimens from a wide range of
localities were similar to European specimens, whilst those from Asiatic countries differed more widely from the European than did those from Australia. All things considered, it seems most likely that common heliotrope was introduced to southern Australia during the 19th century from France or Italy (Delfosse and Cullen 1980; Kloot 1983; Moore 1956; Walsh and Entwistle 1999)

Within Australia, common heliotrope is an economically important weed of both crops and pastures (Delfosse and Cullen 1980; Lazarides and Hince 1993). It is thought to infest 10 million hectares of agricultural land within Australia (Culvenor 1985) and is reputed to cost Australian agriculture over $46 million in bad years (Cullen and Delfosse 1990). According to Sheppard, Brun et al. (1996), who compared the demography of common heliotrope populations in Australia and southern France, frequency and intensity of infestations and magnitude of seed production are much greater in Australia than in its native habitat. Sheppard, Brun et al. (1996) concluded that this was largely due to differences in cultural practices between Australia and southern France. Common heliotrope establishes in late spring and early summer in areas devoid of other living plants after sufficient rainfall when temperatures are high enough to allow germination (Moore 1956; Sheppard, Brun et al. 1996). The farming systems in the pertinent regions of Australia principally utilise annual species for production, and leave much land devoid of vegetation over the summer months. In the plant’s native range, perennial species are dominant, leaving less bare earth during summer. The suitability of Australian farming systems to the growth of common heliotrope is discussed further in Section 1.1.2.

As a weed of crops, common heliotrope growing over the summer months can significantly decrease the yield of subsequent crops, particularly in dry years (Delfosse and Cullen 1980; Fromm and Grieger 2000; van Rees and Smallwood 2000). There is evidence that the remains of common heliotrope plants may have a deleterious allelopathic effect on the growth of crop plants (van Rees and Smallwood 2000). It may also be a host for crop pathogens during fallow periods (Boubourakas, Hatziloukas et al. 2004; Cordoba, Martinez-Priego et al. 2004; Katis, Kokinis et al. 1997; Mahiar and Khlaif 1999; Vanstone and Russ 2001). Under certain environmental conditions, common heliotrope seeds and foliage may be harvested with grain and become a contaminant (Anon. 1999; Gaul, Gallagher et al. 1994; Hill, Gaul et al. 1997). This is a
problem, as the above ground parts of common heliotrope contain high levels of pyrrolizidine alkaloids (O'Dowd and Edgar 1989), which are well established as hepatotoxins in animals and humans (Huxtable 1989). The frequently lethal toxamic effects of the pyrrolizidine alkaloids found in common heliotrope on sheep, cattle, pigs and poultry are well documented (Bull, Dick et al. 1956; Everest 1981; Gaul, Gallagher et al. 1994; Harper, Walker et al. 1985; Kinnaird, Chan et al. 1968; McLennan and Dodson 1972; Walker 1966). Common heliotrope pollen has also been identified as a source of pyrrolizidine alkaloids in samples of commercially available honey (Beales, Betteridge et al. 2004; Edgar, Roeder et al. 2002).

As a weed of pastures, common heliotrope becomes established in areas previously dominated by winter annuals such as barley grass (*Hordeum leporinum* L.), silver grass (*Vulpia bromoides* (L.) S. F. Gray), subterranean clover (*Trifolium subterraneum* L.), musky crowfoot (*Erodium moschatum* (L.) L'Hérit) and capeweed (*Arctotheca calendula* (L.) Levyns) (Everest 1981; Moore 1956). Animals grazing on pastures dominated by common heliotrope are susceptible to pyrrolizidine alkaloid poisoning. Culvenor (1985) estimated that the total annual loss from pyrrolizidine alkaloid poisoning by common heliotrope in south-eastern Australia as $(AUD) 7.5 million.

Within Australia, common heliotrope is largely controlled by cultivation, as control with herbicides is expensive and difficult to achieve under summer conditions (Fromm and Grieger 2000; Leys, Amor et al. 1990; van Rees and Smallwood 2000). With both these methods, if a cohort of common heliotrope establishes following rain and is successfully controlled, further rain will result in another cohort emerging which will also require control (Delfosse and Cullen 1980; Dellow and Seaman 1987; Moore 1956; Parsons and Cuthbertson 2001). This re-treatment can make the cost of controlling common heliotrope very expensive. Also, cultivation is only effective on younger plants, causes erosion and is damaging to the soil structure (Anon. 1999; Delfosse and Cullen 1980; Parsons and Cuthbertson 2001). Control by grazing is of limited value due to the plant's toxicity (Moore 1956). However, some farmers use flocks of ageing merino wethers for this purpose (A. Shepard, pers. comm.). The inadequacy of conventional control methods prompted interest in a biological control program, and the Commonwealth Scientific Research Organisation (CSIRO) began searching for possible organisms throughout the weed's native range in 1950. An account of this program,
which concluded in 1994, may be found in Delfosse (1980) and Sheppard (1994). Despite the release and establishment of the flea beetle *Longitarsus albineus* Foudras and rust fungus *Uromyces heliotropii* Sredinski as a result of this program, these biological control agents have not contributed to the control of common heliotrope (Cullen and Delfosse 1990; Sheppard 1994).

Common heliotrope is not the only member of its genus that is a weed of economic significance in Australia, although it is by far the most important. The other four species of *Heliotropium* accorded economic significance occasionally cause localised, but generally not severe problems (Delfosse and Cullen 1980). Blue heliotrope (*Heliotropium amplexicaule* Vahl), a native of South America, is a perennial weed of roadsides, fallows and degraded pastures in southern Queensland, South Australia and northern New South Wales, where in some shires it is classified as noxious (Harden 1992; Parsons and Cuthbertson 2001). The CSIRO undertook a survey of potential biological control agents for blue heliotrope which culminated in the release of the leaf-feeding beetle *Deuterocampta quadrijuga* in 2001 (Briese and Zapater 2001). Smooth heliotrope (*Heliotropium curassavicum* L.) is also native to South America and occurs on saline flats and wet areas in all mainland states (Harden 1992; Walsh and Entwistle 1999). Another European species, creeping heliotrope (*H. supinum* L.), is very similar in appearance to *H. europaeum* except for its prostrate habit. It is also a summer weed, but is restricted to heavy clay soils in the Mediterranean semi-arid regions of Australia (Harden 1992; Walsh and Entwistle 1999). Rough heliotrope (*Heliotropium asperrinum* R. Br.) is a native species restricted to damp, sandy situations (Harden 1992; Walsh and Entwistle 1999).

## 1.3. Farming Systems in the Victorian Mallee

The ‘Mallee’ is a peculiarly Australian land system named after the indigenous word for the growth habit (multiple stems protruding from a subterranean lignotuber) of the *Eucalyptus* species which dominated the native vegetation of the area (Clark and Heydon 2002). Examples of Mallee land systems may be found right across southern Australia, but for reasons of proximity, this study focuses on the area of Mallee found in the state of Victoria. The Victorian Mallee (Figure 1.3.) approximately encompasses the
triangle of land in the north west of the state formed by the 36th parallel to the south, the South Australian border to the west, and the flood-plains of the Loddon and Murray rivers to the north and east (Newell 1961). It is characterised by gently undulating plains of solonized brown soils, with associated dunes of siliceous sands and occasional playa lakes with fringing lunettes (Blackburn and Wright 1989). The climate of the region is typically Mediterranean, with hot, dry summers and mild, wet winters. The average annual rainfall of the region is around 300 mm, most of which falls in winter (Figure 1.4.).

Europeans first occupied the Victorian Mallee in the nineteenth century. In the late nineteenth and early twentieth centuries, much of the native vegetation in the Mallee was cleared to allow agricultural production. Initially the predominant land use was grazing of sheep and cattle, due to the presence of ‘mallee roots’ (the mallee eucalypt’s subterranean lignotubers), which made the land impossible to cultivate using the adapted European methods of the time. The invention of the stump-jump plough in 1876 overcame this problem, and along with the invention of the grain stripper (a simplistic form of combine harvester) allowed cropping to become a viable industry in the region (Callaghan and Millington 1956). The soils of the Victorian Mallee are very low in nitrogen (Blackburn and Wright 1989), and it wasn’t until the introduction of annual medic (Medicago spp.) in the 1930s (Cooke, MacLennan et al. 1989) as pasture legumes to be grown in rotation with cereal crops, that cropping came to rival sheep production as the dominant land use in the region. The farming system that subsequently evolved came to be known as ‘sheep and wheat’, and was a simple rotation of cereal crops, principally wheat (Triticum aestivum L.) but also barley (Hordeum vulgare L.) and oats (Avena sativa L.), winter pastures and fallow. Cereals under-sown with medic were planted following the ‘autumn break’, or first significant rainfall of the growing season. The cereals grew on winter and spring rainfall until they ripened and were harvested in early to mid summer. The under-sown medic would set seed that would germinate and form pasture the following autumn. Fallows were cultivated any time from late winter until autumn to conserve moisture. Today, this system has changed very little with regard to land use over summer, despite the advent of herbicides and a trend toward continuous cropping permitted by the introduction of oilseeds and grain legumes into the rotation. Even with the increasing implementation
of minimum tillage systems throughout the rest of the Australian cropping zones, much of the Mallee is still tilled over the summer months.

Figure 1.3. A map of the Victorian Mallee, a region bordered by the 36th parallel to the south, the South Australian border to the west, and the flood-plains of the Loddon and Murray rivers to the north and east.

Figure 1.4. The climate of the Victorian Mallee. Monthly mean daily maximum temperature (hollow symbols) and monthly mean rainfall (solid symbols) for Mildura airport (squares), and the townships of Ouyen (diamonds) and Birchip (circles). These figures are from the Commonwealth Bureau of Meteorology and are averaged from records from 1946 to 2001 for Mildura, 1911 to 2001 for Ouyen, and 1898 to 1995 for Birchip.
Grain yield in the region is principally limited by water availability (Ridge 1986) and the principal purpose of fallow is water conservation. Cultivation of fallow paddocks kills living plants, which would transpire any existing or subsequently arriving soil moisture into the atmosphere. The tilth created also acts as a layer of hydraulic insulation between the moist sub-soil and the dry atmosphere (Fischer 1987). Sub-soil moisture harvested and conserved over summer and autumn can make a tremendous difference to crop yield, particularly in years of low growing season rainfall (Cooke, MacLennan et al. 1989; Fischer 1987; Ridge 1986). Consequently, the summer months see most of the arable land in the region covered in either sparse stubbles, hayed-off pastures, or more often than not, cultivated earth. These three states share a common theme in that they are devoid of living vegetation. Despite the bulk of the region’s annual rain falling in the winter (Figure 1.4.), a significant amount of rainfall arrives over the summer months (around 20%), principally in the form of sporadic and intense thunderstorms. Warm summer temperatures, bare earth and sufficient rain constitute the ideal conditions for the germination and emergence of common heliotrope (Moore 1956), and frequently Mallee landscapes are turned pale blue by its ensuing growth.

The growth of common heliotrope under these circumstances presents a serious agronomic problem. When present over summer in fields intended for crop production in the winter, common heliotrope competes for water with ensuing crops indirectly. It does so by establishing a hydraulic link between the atmosphere and the sub-soil moisture conserved by fallow and transpiring it into the atmosphere. It is principally because of this that common heliotrope is a weed of such economic importance in the Victorian Mallee. Ironically, control of common heliotrope, particularly by cultivation, creates disturbed habitat ideal for the growth of future cohorts of common heliotrope.

Common heliotrope is by no means the exclusive summer weed of the Victorian Mallee, but along with saltrop (Tribulus terrestris L.), it is by far the most important (Niknam, pers. comm.: van Rees and Jackman 2001). Other Mediterranean summer annual dicotyledons such as prickly paddy melon (Cucumis myriocarpus Naudin), camel melon (Citrullus lanatus (Thunb.) Matsum. & Nakai var. lanatus) and quenna (Solanum esuriale Lindl.) appear to be less widespread in the area and form patchy and inconsistent infestations. The same can be said for the annual grasses witchgrass
(Panicum capillare L.) and stinkgrass (Eragrostis ciliarisensis (All.) Vignolo ex Janchen).

1.4. The ecology of common heliotrope

1.4.1. Published information on the ecology of common heliotrope

There is a dearth of information within the literature pertaining to the ecology of common heliotrope. There are only three papers which deal directly with the topic: Moore (1956), Sheppard (1996) and Vasconcelos (1988). The most comprehensive of these works is that of Moore (1956), which still stands as the authority on the weed within Australia. Additional information may be gleaned from papers on related topics (e.g. biological control of common heliotrope, livestock poisoning), published floras pertaining to the species' range and general agricultural publications.

As mentioned in Section 1.2, common heliotrope germinates in late spring and early summer after sufficient rain. The exact moisture requirements for the successful germination and establishment of the weed have, up until this point, not been quantified (see Chapters 2-4). Sheppard (1996) suggested that 10 mm of rainfall may be sufficient to allow germination but that 25 mm is required to ensure population establishment. Fromm (2000) suggested that successful germination and emergence requires the amount of rainfall necessary to wet the top 250 mm of soil. The amount of rainfall required for successful germination and establishment of common heliotrope will vary with soil type, soil cover and weather conditions (Moore (1956), since it is both the amount and duration of soil water that seeds are exposed to that are the critical determinants of germination and emergence (see Chapter 4).

Relatively high temperatures are required for common heliotrope to germinate (Moore 1956). Moore observed that no seeds germinated in 3 weeks at 19ºC, but when the temperature was increased to 24ºC and 35ºC, percentage germination increased accordingly. Pre-treatment of seed kept moist at 0ºC for 24 hours and 10ºC for one week also gave a significant increase in percentage germination when compared to untreated controls. Moore also observed that germination did not occur in the field until mean air temperatures of around 18-24ºC were attained.
Moore (1956) states that after emergence, common heliotrope develops an extensive root system, and once established, it will withstand periods of drought provided there is sufficient sub-soil moisture. Development is rapid, and plants flower as little as three weeks after germination (Moore 1956) and can produce ripening seed by six to eight weeks after germination (Parsons and Cuthbertson 2001). Flowering and seed production are both indeterminate and concurrent with growth, which occurs continuously throughout summer until plants are killed by drought or autumn frosts (Moore 1956; Sheppard, Brun et al. 1996). In favourable seasons, reproductive effort can be enormous and seed rain as high as 1.4 million seeds m$^{-2}$ has been recorded in Australia (Sheppard, Brun et al. 1996).

Common heliotrope rarely establishes successfully in the presence of other living plants, but the mechanisms behind this observation have not been investigated. Moore (1956) observed that common heliotrope was in lower densities in areas where saffron thistle (Carthamus lanatus L.) was a prominent constituent of pastures and was not present in undisturbed areas dominated by native perennial grasses (e.g. Stipa spp. and Danthonia spp.). It has been shown that common heliotrope may be completely controlled with dense stands of lucerne (Medicago sativa L.) (Delfosse and Cullen 1980; Dellow and Seaman 1987). Moore (1956) suggested that common heliotrope could be controlled in wetter areas by maintaining pastures of phalaris (Phalaris tuberosa) and subterranean clover (Trifolium subterraneum L.) or perennial native grass species in drier areas. Control of common heliotrope by maintenance of competitive pasture species is not suitable in cropping systems such as those of the Victorian Mallee, as the pasture species will indirectly compete with ensuing crops in exactly the same manner as common heliotrope.

Seeds of common heliotrope appear to have considerable longevity. In a letter published in the Gardener's Chronicle and Agricultural Gazette, Charles Darwin cites an example from 19th century France, where seeds of common heliotrope were germinated after being buried in ancient Gaulish tombs for approximately 1500 years (Barrett 1977). Within Australia there are numerous, if less impressive, anecdotes of common heliotrope germinating en masse in favourable seasons when it has been absent for many years under less favourable conditions. Such anecdotes aside, Vasconcelos (1988) studied the longevity of seeds of common heliotrope buried at different depths and
found that more than 50% remained viable after 2 years, excluding those stored at the soil surface.

Common heliotrope grows on a wide range of soil types, principally loams but ranging from sands to clays (Cunningham, Mulham et al. 1981; Parsons and Cuthbertson 2001; Sheppard, Brun et al. 1996), and does not appear to show any marked preference (Moore 1956; Sheppard, Brun et al. 1996). Vasconcelos (1988) observed that light alkaline soils were best for propagation of the plant. Generally, soil-surface conditions (i.e. pasture composition and conditions, degree of litter accumulation, crop/stubble conditions) are more important than soil type in determining the occurrence of the plant (Delfosse and Cullen 1980; Moore 1956; Sheppard, Brun et al. 1996).

1.4.2. Field observations of the lifecycle of common heliotrope

The following section is based on observational data which was collected during the course of this thesis, and which provides further context to the statement of the research questions that follow. The data describe a typical life-cycle of common heliotrope, which commenced with a germinating rainfall event that occurred in the southern Victorian Mallee in the summer of 2002. The field chosen for the study is typical, both of fields used for crop production in the Victorian Mallee and of the agricultural habitat which common heliotrope infests. The site is at Jil Jil, approximately 22 km NNW of the township of Birchip in north western Victoria, Australia (Figure 1.3). The coordinates of the site are S 35°47' E 142°58' and the altitude is approximately 100 m above sea level. This site is a level plain within the Culgoa land system (Rowan and Downes 1963); the surface soil is described by Martin (2002) as a hard-setting and massive clay loam, and its Australian soil classification is an Epihypersodic, Pedal, Hypercalcic Calcarosol (Isbell 1996; Victorian Department of Primary Industries 2004). Observations were made in a rectangular paddock 650 m by 800 m, giving a total area of 52 ha. The paddock had supported a reasonably dense population of common heliotrope in the summer of 2000 - 2001, and was direct seeded to a pasture of vetch (Vicia sativa L.) and oats in the autumn of 2001. By late spring of 2001, the paddock had been heavily grazed by sheep, was devoid of living plants and sparsely covered by dead organic matter.
In the early spring of 2001, ten permanent 5 m x 1 m quadrats were positioned randomly in the paddock. The locations of the corners of the quadrats were marked with stainless steel pegs which were hammered in to the bottom of pits dug to 0.2 m (well below the tillage depth of implements used in the area) and had a 0.3 m length of stainless steel chain attached. These pits were then refilled such that only the end of the length of chain protruded from the soil. This allowed the quadrats to be marked permanently and subjected to the same cultural practises as the rest of the paddock without fouling or being disturbed by agricultural implements. Quadrat location was marked using a hand-held global positioning system (GPS) receiver (Garmin GPS 12 XL, Garmin Corporation, Olathe U.S.A.) and following cultivation, quadrats could be quickly relocated using the GPS receiver and a metal detector.

A Dataflow DS93 data logger (Dataflow Systems, Caboolture, Australia) recorded rainfall, air temperature and soil temperature at 20 mm and 50 mm depth hourly at the site. Rainfall was measured with a tipping bucket rain gauge, and air and soil temperatures with Dataflow 906 temperature sensors. The sensor recording air temperature was located at a height of 1.3 m above the ground and was shielded from direct solar radiation by two 0.2 m lengths of concentric white PVC pipe (50 mm and 90 mm diameter), with the open ends of the pipe facing north-south.

In late October of 2001, the soil seed bank of the site was sampled. This was achieved by taking intact soil cores of 17 mm diameter to a depth of 50 mm, and splitting these cores into 10 mm sections. Ten of these cores were taken from around each quadrat and bulked, giving a total of ten samples. The common heliotrope seeds in the cores were separated from the soil in nested 0.6 mm and 2 mm sieves. The seeds were then placed on two circles of Whatman No. 1 filter paper (Whatman, Maidstone, U.K.) in 90 mm Petri dishes with 5 ml of distilled water, sealed with paraffin film and then incubated at 35°C with a dark/light ratio of 10/14 hours for 21 days to test viability (these are optimal conditions at which near 100% of seeds will germinate, see Chapter 2 and 3). Table 1.1 shows the density and distribution of viable common heliotrope seed in the top 50 mm of the soil in late October 2001. It shows that densities are very low compared to those recorded by Sheppard, Brun et al. (1996), who recorded spring seed bank densities ranging from 30 000 to 250 000 seeds m⁻² by similar methods as outlined here. This is probably due to Sheppard, Brun et al.’s choice of severely infested sites for
the purposes of monitoring biological control agents. The values recorded here are similar to those recorded at other field sites in this study, and so can be regarded as typical of the seed densities found in broad acre cropping areas in the Mallee.

**Table 1.1.** The mean density of viable common heliotrope seeds at different soil depths at the Jil Jil field site on 25 October 2002. These values are the mean of bulked samples of ten soil cores taken at each quadrat (100 cores in total) of 17 mm diameter.

<table>
<thead>
<tr>
<th>Soil Depth (mm)</th>
<th>Seed Density (seeds m$^{-2}$)</th>
<th>Standard Error of Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-10</td>
<td>322</td>
<td>70</td>
</tr>
<tr>
<td>10-20</td>
<td>251</td>
<td>52</td>
</tr>
<tr>
<td>20-30</td>
<td>185</td>
<td>42</td>
</tr>
<tr>
<td>30-40</td>
<td>110</td>
<td>28</td>
</tr>
<tr>
<td>40-50</td>
<td>128</td>
<td>25</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>996</strong></td>
<td><strong>136</strong></td>
</tr>
</tbody>
</table>

On 21 and 22 January 2002, an intense and highly variable amount of rain fell on the area north of Birchip. At the field site, a total of 28 mm of rainfall was recorded. Air temperature and soil temperature at 20 mm depth following the rain are shown in Figure 1.5. These data show that according to Moore (1956), the thermal conditions were suitable for the germination of common heliotrope. It also shows that the environment in which common heliotrope seedlings must germinate and emerge is rather hostile with regard to temperature. Although both air and soil temperatures are depressed during and immediately following the rainfall, within two days maximum air temperatures are between 30 and 40°C, and soil temperatures are higher still, owing to high solar radiation (Figure 1.5). Soil surface temperatures well over 60°C have been recorded in the region. This, along with low humidity, rapid wind speed and little surface organic matter make the edaphic environment of emerging common heliotrope seeds very desiccating.

Following rainfall, the quadrats were checked for emergence daily. If plants had emerged, they were counted and removed. Seedlings were picked out of the soil intact using a pair of forceps and placed in a zip-lock bag containing water. The depth at which the seed of the emerging plant was located was calculated by measuring with digital callipers the distance between the root/shoot interface (assumed to be the position of the seed) and immediately below the cotyledons, assumed to be the position of the soil surface. Emergence began around three days after the germinating rainfall, and continued for about twelve days. Figure 1.6 shows the cumulative emergence at the
site, which resulted in a mean density of around 30 seedlings m$^{-2}$. The majority of seedlings originated from seeds located between 8 and 12 mm depth (Figure 1.7).

**Figure 1.5.** Soil temperature at 20 mm depth (-), air temperature (-) and radiation (●) following the germinating rainfall event in the summer of 2002. The temperature measurements were recorded at the field site; radiation was recorded by the Bureau of Meteorology at Mildura (approximately 200 km NNW).

**Figure 1.6.** The mean cumulative emergence of common heliotrope seedlings at the Jil Jil field site during summer 2002. The value for each date is the mean of ten 1 m x 5 m quadrats randomly distributed across the paddock; error bars are ± the standard error of this mean.
Figure 1.7. The mean germination depth of successfully emerging seedlings over time at the Jil Jil field site. The value for each date is the mean all plants emerging in ten 1 m x 5 m quadrats positioned randomly within the paddock; the error bars are ± the standard error of the mean.

As soon as was feasible after a rain, soil moisture at the site was recorded daily by taking soil cores as for the seed-bank sampling. The mass of the bulked cores was recorded to a precision of 1 mg, and they were then placed in an oven at 105°C for 48 hours before being re-weighed and gravimetric water content (GWC) calculated. Top-soil samples for each of the sites were taken and the soil water potential of samples with varying GWC were measured with a Decagon WP4 dewpoint potentiometer (Decagon Devices Inc., Pullman, U.S.A) before recording GWC. An empirical relationship between these two variables was established through simple linear regression of their natural logarithmic values (R² values are presented in Table 1.2.).

Table 1.2. Parameters and R² values for simple linear regression (y = ax + b) of the natural logarithm of GWC with respect to the natural logarithm of soil water potential.

<table>
<thead>
<tr>
<th>Quadrat</th>
<th>a</th>
<th>b</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>BQ01</td>
<td>-4.72</td>
<td>7.03</td>
<td>0.83</td>
</tr>
<tr>
<td>BQ02</td>
<td>-3.71</td>
<td>8.58</td>
<td>0.96</td>
</tr>
<tr>
<td>BQ03</td>
<td>-2.52</td>
<td>3.06</td>
<td>0.99</td>
</tr>
<tr>
<td>BQ04</td>
<td>-4.33</td>
<td>7.72</td>
<td>0.98</td>
</tr>
<tr>
<td>BQ05</td>
<td>-4.36</td>
<td>4.05</td>
<td>0.95</td>
</tr>
<tr>
<td>BQ06</td>
<td>-3.75</td>
<td>5.47</td>
<td>0.90</td>
</tr>
<tr>
<td>BQ07</td>
<td>-3.67</td>
<td>6.92</td>
<td>0.96</td>
</tr>
<tr>
<td>BQ08</td>
<td>-3.06</td>
<td>6.99</td>
<td>0.98</td>
</tr>
<tr>
<td>BQ09</td>
<td>-3.11</td>
<td>6.85</td>
<td>0.94</td>
</tr>
<tr>
<td>BQ10</td>
<td>-2.97</td>
<td>6.49</td>
<td>0.99</td>
</tr>
</tbody>
</table>
These relationships were used to calculate values of soil water potential in the top 50 mm of soil at the field site following rainfall (Figure 1.8). This figure shows that soil water potential in the zone of emergence (Figure 1.7) falls below wilting point within 3 to 5 days after rainfall, therefore germination following rainfall must be extremely fast. Figure 1.8 also shows that although the top layers of soil dry rapidly, those immediately below the surface (30-50 mm) take considerably longer to fall below wilting point. This is principally due to the absence of living plants and the hydraulic insulation created by the rapid drying of the upper layers. As a result, common heliotrope is able to emerge into an extraordinarily dry surface environment, relying on the moist soil below the surface for survival.

**Figure 1.8.** The soil water potential at 0-10 mm (○), 10-20 mm (●), 20-30 mm (▲), 30-40 mm (□) and 40-50 mm (■) at the Jil Jil site following the germinating rainfall. The values for each date are the mean of ten bulked samples of ten soil cores taken at each quadrat (100 cores in total) of 17 mm diameter.

No further significant rain fell at the site for the remainder of the season and plant growth was slow. Plants were approximately 100-150 mm high when they senesced in late April.
1.5. Formulation of research questions and thesis structure

Knowledge of certain attributes of common heliotrope’s biology could greatly improve efficiency of control, however published information on these attributes is lacking. Firstly, the ability to predict the occurrence of common heliotrope infestations in time and space will give great aid to planning and timing of control. Secondly, control of common heliotrope under all circumstances may not be economically justified, and knowledge of the resources that common heliotrope uses for growth will allow for intelligent decision making and thus more efficient control.

So, the question that is first addressed in this thesis relates to the prediction of occurrence of common heliotrope: what endogenous attributes of common heliotrope, and exogenous attributes of the environment that it inhabits, limit its occurrence in space and time? This is the primary question that is addressed in this thesis, and it shall first be addressed at the seed and germination phase of common heliotrope’s life cycle.

Germination is universally a function of water and temperature, and frequently other factors such as light, which all vary greatly over time. Consequently, the specific research questions first addressed in this thesis (Chapter 2) are: what environmental conditions are required to allow seeds of common heliotrope to germinate?

Additionally, with prediction of occurrence through mathematical simulation in mind, how does variation in environmental conditions impact on germination?

It is known that populations of a species evolving in subtly different environments can evolve different germination responses to suit their environment (e.g. Dunbabin and Cocks 1999), and that the germination response of a single population of seeds can change over time (e.g. Karssen 1982). Hence the third question addressed (Chapter 3) is: how do the germination responses of populations of seeds of common heliotrope vary over space and time?

Given answers to these first three questions, the fourth question (Chapter 4) expands their implications to the growth and reproduction phase of common heliotrope’s life cycle: how does the germination response of common heliotrope relate to its life history, spatial and temporal distribution and function as a weed in a Mediterranean dry-land farming system? Furthering the distribution aspect of this question, the way in which a crucial change in the physical environment impacts on the variables that limit
common heliotrope forms the subject of the fifth (Chapter 5) research question: *how do differences in soil type change the amount and duration of water available to common heliotrope plants and seeds?* The final research question (Chapter 6) draws the answers gleaned from the previous questions together in a practical context: *what implications do the temporal and spatial distribution of common heliotrope, and the resources for which it competes with crops, have for the economics of different control methods in the Mediterranean dry-land farming system of the Victorian Mallee?*

Each of the above questions is addressed sequentially through experiments and simulations within this thesis. A summary of findings, with commentary on how they fit into the broader ecology of common heliotrope is given in Chapter 7, along with suggestions for further areas of study.

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Chapter 2 – The Germination Requirements of Common Heliotrope

2.1. Introduction

The presence and density of common heliotrope infestations in a given season are largely determined by the ability of seeds to germinate; yet the germination requirements of common heliotrope are poorly understood. Moore (1956), Dellow (1987) and Sheppard (1996) all noted similar general requirements for the appearance of common heliotrope. Principally, it germinates only in late spring or early summer after sufficient rainfall, and not in the presence of other living plants. However, beyond Moore's cursory study of thermal requirements for germination, no one has sought to reveal the mechanisms behind these observations. It is certainly not possible to predict field emergence accurately using the current literature.

The establishment of effective integrated weed management systems should incorporate a detailed understanding of weed biology and ecology (Bhowmik 1997). For example, the ability to predict seedling emergence in response to environmental conditions can improve the timing of control measures (Ghorbani, Seel et al. 1999). Successful prediction of weed emergence in the field requires quantification of the effect of relevant environmental processes on the distinctly separate processes contributing to emergence (Cousens and Peters 1993).

Quantification of the response of seeds of common heliotrope to the environmental factors limiting their germination is the first step in the creation of a model that will be capable of predicting the field germination and emergence of common heliotrope. Similar models have been created successfully for other annual weed species by Roman (2000), Harvey (1993) and Forcella (1993) for temperate environments. A similar model for common heliotrope would greatly enhance understanding of how this species functions as a weed in a cropping system, and hence could indicate opportunities for improved management. It could also potentially facilitate direct control of common heliotrope by predicting when infestations of the species will be at the seedling stage, which is when control by cultivation and post-emergent herbicide is most effective (Jackman 2001; Leys, Amor et al. 1990). Thus, the aim of this chapter is to identify and subsequently quantify the major environmental factors that limit the germination and thus the occurrence of common heliotrope.
The environmental variables studied in this section were selected on the basis of a simplistic model of understanding of the limits to germination of common heliotrope derived from logic and from the literature. In this model, light, cold treatment, leaching of an endogenous germination inhibitor, and satisfaction of hydric and thermal requirements are considered as 'switches' in series which require 'closing' before germination can occur (Figure 2.1). Subsequently, water and temperature are also considered variable resistors (rheostats), which will impact on the rate and extent of germination.

![Figure 2.1. A schematic representation of the model of understanding of the environmental controls of common heliotrope germination.](image)

This chapter consists of four sets of experiments aimed at determining which of these ‘switches’ are most important to the germination of common heliotrope. The first of these experiments (Section 2.2) are designed to determine if seeds of common heliotrope have an inherent or acquired light requirement for germination. The second set of experiments (Section 2.3) follows on from the observations of Moore (1956) and aims to determine if seeds of common heliotrope have a cold requirement for germination. The third set (Section 2.4) investigates whether germination of seeds of common heliotrope is prevented by a leachable inhibitor, as has been found to be the case with other arid species (Kigel 1995; Mayer 1986). The final set (Section 2.5.) quantifies the germination of populations of seeds of common heliotrope in response to varying temperatures and water potentials. The secondary aim of Section 2.5 is to determine how well germination of seeds of common heliotrope conform to the assumptions of Gummerson’s (1986) hydrothermal time model. This will determine the suitability of the model of hydrothermal time as a tool to aid the prediction of common
heliotrope occurrence. Much emphasis has been placed on the potential for prediction of weed emergence using a model of germination based on hydrothermal time (Bradford 2002).

2.1.2 Definitions

Dormancy

Before progressing further, it is necessary to define the terms 'germination' and 'dormancy' as they appear in this study. Vleeshouwers (1995) highlighted the disunity within the associated literature of the use and definition of the term 'dormancy', and proposed a definition aimed at increasing the understanding of seed dormancy and germination, and to help define ecological research questions. This definition is confined to the forms of dormancy named ‘physiological dormancy’ by Baskin (1998), and therefore does not consider dormancy caused by a hard seed coat or under-developed embryo. The definition of dormancy is:

“...a seed characteristic, the degree of which defines what conditions should be met to make the seed germinate. The wider the range of conditions at which a seed is able to germinate, the smaller its degree of dormancy."

This definition makes a distinction between both internal seed factors and external environmental conditions, and between germination and dormancy. Germination is a seed's response to an overlap in environmental conditions and its germination requirements, as defined by its degree of dormancy. Dormancy cannot be observed directly: the level of dormancy of a given population of seeds may only be approximated indirectly by observing their germination under a range of conditions.

A common opposite definition is that of Benech-Arnold (2000), who define dormancy as:

"...an internal condition of the seed that impedes its germination under otherwise adequate hydric, thermal and gaseous conditions."

Similarly, Foley (2001) defines dormancy as:
"...the temporary failure of a viable seed to germinate, after a specific length of time and in a particular set of environmental conditions that allow germination after the restrictive state has been terminated by either natural or artificial means."

These definitions are more general than that of Vleeshouwer's (1995) and, whilst they do extend to other forms of dormancy (e.g. physical dormancy), they are less useful for ecological study. It is explicit in the first definition that dormancy is not a fixed all-or-nothing 'block' to germination, whereas this is not the case in the second definition. Consequently, Vleeshouwer's (1995) definition is most suitable for an ecologically focussed study of germination, particularly as common heliotrope seeds appear to have only physiological dormancy. It will therefore be the definition of dormancy as used in this thesis.

Fractional germination

Brown (2002) refers to the incomplete germination of a seed bank under apparently adequate conditions as ‘fractional germination’, and this definition is adopted in this thesis. The evolutionary benefit of such a germination strategy, which spreads risk across time has been well documented (Baskin and Baskin 1998; Gutterman 1992).

Properties of cumulative germination

Two properties of cumulative germination are used for analysis in this thesis: the final percentage of viable seeds that germinated over the duration of the experiment (germination extent, Figure 2.2); and the time taken for 50% of final germination to be reached (median time to germination, Figure 2.3). Germination rate was taken as the reciprocal of median time to germination. Within the literature, it is frequently unclear as to how authors have calculated the time to germination of a given fraction of the seed population, as there are two distinct ways to determine population in this context. Many studies assume the population to be the total number of seeds sown in a treatment, or if viability is checked following an experiment, the total number of viable seeds sown. Subsequent calculation of germination ‘rate’ assuming either of these values as the population confounds germination rate and extent, as the time taken to reach a given percentile is influenced by the total number of seeds germinating. For example, if over 50% of seeds are dormant, germination of 50% of the total number of viable seeds sown
will not be achieved! Many of the germination indices used by seed scientists also confound rate and extent (Brown and Mayer 1988).

Median time to germination was calculated as the mean value of linear interpolation between the two data points in the cumulative germination curve either side of 50% germination for each replicate within a treatment. Median time to germination here is used as a measure of how rapidly seeds germinate under different treatments.

**Figure 2.2.** A representation of germination extent of idealised cumulative germination data of three hypothetical treatments A (●), B (□), and C (▲). The arrows indicate the values of germination extent for each of the treatments.

**Figure 2.3.** A representation of median time to germination of the same cumulative germination data used in Figure 2.3 standardised by dividing each data point by the germination extent. The arrows indicate the median time to germination of the treatments A (●), B (□), and C (▲).

### 2.1.3 Seed collection

Flowering of common heliotrope is indeterminate, and as a consequence the population of seeds found on a plant at any one time will exhibit a range of maturities. Moore (1956) harvested seeds for his germination experiments at a single point in time, and as a consequence a proportion of these seeds would have been immature. As seed maturity greatly influences germination behaviour (Baskin and Baskin 1998), this would have greatly confounded the results obtained by Moore. This is evident in the very low percentage germination that he observed. In order to avoid this problem, a method of harvesting mature seeds as they dehisce from maternal plants was devised for this study.
For each collection of seed made, transparent perforated plastic bags were placed over at least twenty plants at a site after the commencement of flowering and when the plants had attained a size of least 0.3 m diameter. The bags were secured at the base of the plants with plastic cable ties, such that all branches of the plant were inside the bag. The plants grew to fill the bags, and seeds were collected in the bag as they dehisced. Following senescence in autumn, the plants were uprooted and allowed to dry in the bags. The accumulated seeds were collected and separated from plant matter with a pair of nested sieves (perforations 1.8 and 1.1 mm in diameter) and a velvet board.

Although this method was successful in harvesting only seeds that were mature, owing to the lengthy flowering period of common heliotrope, any collection of seeds made using this method would contain fractions that developed under different environmental conditions. The maternal environment under which seeds develop can also influence their germination behaviour at maturity (Andersson and Milberg 1998). However, this variation in maturity within a seed population is representative of actual seed rain in any given year, and as such is ecologically valid. The transparent perforated plastic bags would have altered the maternal environment in which seeds developed. However, as this would have been consistent for all seeds, and would certainly not alter conditions beyond those experienced by common heliotrope in its natural range, it is assumed not to be a problem.

2.1.4. Experimental methods

This chapter consists of six separate manipulative germination experiments conducted in the laboratory, which share a certain amount of common methodology. The general methods used in all experiments in this chapter will be described here. Differences in treatments and deviations from this standard are dealt with in the pertinent sections.

For each experiment, common heliotrope seeds were counted into plastic Petri dishes (100 mm diameter) containing two discs of Whatman No. 1 filter paper (Whatman International Ltd., Maidstone, England). Five ml of distilled water (or other treatment solution) was added to each replicate and the dishes sealed with paraffin film. To prevent desiccation at the high temperatures used in these experiments, the Petri dishes were placed into zip-seal bags containing a small amount of water.
Petri dishes were placed at random into six identical temperature-controlled growth cabinets (Linder & May, Brisbane, Australia). These cabinets are fan-forced and their temperature is controlled by a two-phase thermostat accurate to 0.1 °C connected to separate heating and cooling units.

The light in each cabinet was provided by four 30 W ‘Grolux’ fluorescent neon tubes (NEC, Japan) and two 15 W incandescent tungsten globes (General Electric Lighting, Kingston-Upon-Thames, U. K.). The daily light regime was 14 hours light and ten hours darkness. This regime was chosen to represent day-lengths during summer in the Victorian Mallee.

Physiological processes leading to germination were assumed to have commenced as soon as water was added to the seeds; seeds were considered germinated when the radicle was visible to the naked eye. The length of time taken for this to occur was considered the time to germination. All treatments were checked at regular intervals and germinated seeds counted and discarded. Experiments were terminated after 21 days, and all un-germinated seeds were cut open and checked for viability. Seeds were considered viable if they contained fresh, white endosperm. This assumption was validated by viability tests using tetrazolium stain (Baskin and Baskin 1998) and by the work of A.W. Sheppard (pers. comm.).

Each Petri dish was assumed to be a replicate. However, it is acknowledged that because of the limited number of cabinets, for some of the treatments this is not strictly the case and that each dish is technically a pseudo-replicate of a given treatment (Morrison and Morris 2000). Replicate number to be used ($n$) was estimated using Equation 2.2, where $t$ is Student's $t$ value for a specified degree of certainty, $CV$ is the coefficient of variation (expressed as a %) of replicates observed in a pilot study and $E$ is the specified error limit.

$$n = \frac{t^2 CV^2}{E^2}$$  \hspace{1cm} (Equation 2.2)

For this study, a $t$ value of 2.8 was assumed, (giving a 95% certainty with 4 degrees of freedom) and $E$ was assumed to be 10% i.e. the sample mean calculated from $n$ replicates has a 95% chance of being within 10% of the population mean. In a pilot study, five replicates of one hundred seeds were germinated using similar methods as
outlined above. The coefficient of variation for the total germination was 6.4. Using this figure, \( n \) was calculated using Equation (2) as 3.2, therefore a minimum of 4 replicates within each treatment was used for the following experiments. Baskin and Baskin (1998) recommend a minimum of three replicates of sixty seeds for germination studies. In the following studies, a minimum of 60 seeds was used, and in some cases more.

2.2. Investigation of a light requirement for germination

2.2.1. Introduction

The possibility of a light response in seeds of common heliotrope is suggested by the generalisations of Grime (1981), who found that a large proportion of smaller seeded species (seed weight less than 1 mg) exhibited a light response compared to large-seeded species (seed weight greater than 1 mg). Common heliotrope seeds typically weigh around 0.7 to 1.2 mg, and are incapable of emerging from depths greater than 50 mm (data not presented here). Common heliotrope also has a persistent seed bank (Barrett 1977; Sheppard, Brun et al. 1996; Vasconcelos and Sa 1988), and Pons (1992) states, "The capacity for induction of dark dormancy appears to be of great importance for formation of the soil seed bank". Common heliotrope also shows a preference for open environments, an attribute that is common to many species whose seed show a light response (Górski 1975; Górski and Górska 1979; Górski, Górska et al. 1977; Górski, Górska et al. 1978). Also, Baskin (1985) found that germination of both fresh and buried seed of witchgrass (*Panicum capillare* L.), a species which shares many ecological attributes with common heliotrope and co-occurs in the Victorian Mallee, was greatly reduced in darkness across a range of germination temperatures and at different times of the year.

A positive germination response of seeds of common heliotrope to light would provide a possible explanation as to why common heliotrope is not seen to emerge in the presence of other living plants, and why only seeds in a narrow band located near the soil surface emerge (Chapter 1). A light response has been observed in many species (Pons 1992). In most cases it is a quantitative response, with a greater (sometimes less) percentage germination in light. The qualitative response may change with burial (Young 2001). In some cases light is the primary inducer of germination (Vleeshouwers
The ecological significance of light responses has been inferred from many studies, but proof of actual ecological significance is lacking in many respects (Pons 1992; Stoutjesdijk 1972).

The mechanism by which seeds are thought to sense light is through the photo-reversible phytochrome pigment (Pons 1992). This mechanism allows fresh seeds which have been buried to acquire a light response (Wesson and Wareing 1969), which is thought to be important in preventing seeds from germinating from too great a depth (Grime, Mason et al. 1981), and detecting soil disturbance and associated removal of existing vegetation (Sauer and Struijk 1964). Phytochrome hypothetically also allows seeds to detect quality of light, and hence the presence of living plants (Cumming 1963; Fenner 1980; Górski 1975; Górski and Górska 1979; Górski, Górska et al. 1977; Górski, Górska et al. 1978; Stoutjesdijk 1972; Taylorson 1970; Taylorson 1972; Taylorson and Borthwick 1969; Van Der Veen 1970). It has also been observed that prolonged exposure to white light inhibits germination in several species (Fenner 1985), but explanation of this phenomenon does not fit into the phytochrome model, and is thought to be to do with blue absorbing pigments (Pons 1992). It is seen as a mechanism for preventing germination in seeds located on the soil surface.

It is not the intention of this study to further understanding into the mechanism of light response, rather to pose a research question with the aim of explaining ecological observations of common heliotrope and assisting in the overall goal of prediction of its occurrence. Do seeds of common heliotrope show any germination response to light? If they do, then further quantitative experiments will be required, as seed response to light will plainly make an important contribution to the ecology of the plant. If the answer is no, then the effect of light may be crossed off the list of possible environmental limits to germination, and other more critical factors sought and investigated. The most basic of experiments in this case is a simple light exclusion experiment on both fresh and buried seed. If common heliotrope exhibits an ecologically significant response to light, it should be evident from such an experiment.
2.2.2. Methods

Seeds of common heliotrope were harvested at Dooen in north-west Victoria, Australia (36.67ºS, 142.30ºE, 91 m above sea level) in April 2000. They were placed into dry storage at 5°C until the time of the experiment (161 days). From this point until the termination of the experiment, all handling of seeds was conducted in a dark room under a green light. The germination experiment was conducted using the methods outlined in Section 2.1.4, with Petri dishes designated for dark treatment being wrapped in two layers of aluminium foil and the light treatments left exposed to the light conditions of the incubators. All treatments were incubated at a temperature of 35°C. Germination was checked twice daily for the first four days of the experiment.

To test for induced light sensitivity, seeds from the same batch were buried to a depth of 100 mm at Dooen in nylon mesh bags for 413 days. These seeds were exhumed on a moonless night with a green light and the laboratory experiment was repeated.

A two-tailed Student's t-test assuming unequal variance was conducted using the S-PLUS 2000 statistical package (MathSoft Inc., Seattle, U.S.A.) to test for significant differences between the means of treatments for germination extent and median time to germination.

2.2.3. Results

There was a significant positive effect of light on median time to germination in fresh seeds (p<0.05). Seeds in the light treatment reached 50% of total viable seed germinated 0.77 of a day faster than in the dark treatment (Table 2.1, Figure 2.4).

There was a slight significant positive effect of light on the median time to germination of seeds buried for 413 days (p<0.05). Seeds in the light treatment reached 50% germination 0.22 of a day faster than those in the dark treatment (Table 2.2, Figure 2.5). There was no significant effect of light on germination extent of seeds buried for 413 days (p>0.05).
Table 2.1. The effect of light on the median time to germination and germination extent of fresh seed. The standard error of the mean is given in parentheses.

<table>
<thead>
<tr>
<th>Light</th>
<th>Dark</th>
</tr>
</thead>
<tbody>
<tr>
<td>Median Time to Germination (days)</td>
<td>1.53 (0.02)</td>
</tr>
<tr>
<td>Germination Extent (%)</td>
<td>99.5 (0.5)</td>
</tr>
</tbody>
</table>

Figure 2.4. Effect of light on germination of fresh seeds, light (●) and dark (○). Error bars are ± the standard error of the mean.

Table 2.2. The effect of light on the median time to germination and germination extent of buried seeds. The standard error of the mean is given in parentheses.

<table>
<thead>
<tr>
<th>Light</th>
<th>Dark</th>
</tr>
</thead>
<tbody>
<tr>
<td>Median Time to Germination (days)</td>
<td>2.09 (0.04)</td>
</tr>
<tr>
<td>Germination Extent (%)</td>
<td>99.3 (0.3)</td>
</tr>
</tbody>
</table>

Figure 2.5. Effect of light on germination of buried seeds, light (●) and dark (○). Error bars are ± the standard error of the mean.
2.2.4. Discussion

The results from this experiment indicate that a light requirement for germination is not an ecologically important attribute in common heliotrope. There is a significant positive response of light on median time to germination in both fresh and buried seed, but it is unlikely that such a small decrease in time taken for 50% germination to occur would be of ecological significance in the field. A light requirement for germination was not induced in buried seeds of common heliotrope. The slight positive effect of light on both median time to germination and germination extent was reduced in buried seeds compared to fresh seeds (Table 2.1 and 2.2).

It is doubtful that the very small effect of light could account for common heliotrope failing to establish in the presence of other living plants, or to prevent germination of seeds buried at depth. Germination extent under both light and dark was very high (>90%). As shown in Chapter 1, seeds of common heliotrope germinate from a band located between 8 and 12 mm soil depth. Tester (1987) concluded that ecologically significant amounts of light rarely penetrate more than 4-5 mm in soil. At these depths, light would be strongly biased toward far red and inhibit rather than stimulate germination (Woolley and Stoller 1978). It is perhaps likely that the absence of common heliotrope growing in the presence of other living plants is better explained by the impact of living plants on hydrothermal conditions in the soil surrounding them and the sensitivity of common heliotrope seeds to water potential and temperature (see Section 2.5). The depth-specific germination of common heliotrope is probably best explained by 'depth inhibition'. It is known that germination is inhibited by soil depth (Holm 1972; Stoller and Wax 1973), but the biological reasons for this have not been clarified (Benvenuti, Macchia et al. 2001). Benvenuti (1995) suggests that this is not merely from lack of light, but that mechanisms such as temperature fluctuation (Roberts and Totterdell 1981) and gaseous environment (Benvenuti and Macchia 1995; Holm 1972; Karssen 1982) are also involved.
2.3. Investigation of a cold requirement for germination

2.2.1. Introduction

Seeds of species that are dispersed in autumn frequently require cold stratification to promote germination (Baskin and Baskin 1998). The effective temperatures for cold stratification range from 0 to 10°C, with about 5°C being optimal for many species (Stokes 1965). Moore (1956) observed a significant positive effect of cold treatment on germination of common heliotrope. However, as mentioned in the introduction of this chapter, the seeds used for that study were of varying maturities. It would make ecological sense for common heliotrope to have a cold requirement for germination of fresh seeds, as it would prevent new seeds germinating in late summer and early autumn when conditions are likely to become unfavourable for continued growth. As prediction of occurrence is reliant on an understanding of the constraints to germination, the aim of this experiment was to determine if germination of fresh seeds of common heliotrope harvested in an ecologically valid manner would be promoted by cold stratification.

2.3.2. Methods

Seeds of common heliotrope were harvested at Dooen in northwest Victoria, Australia (36.67ºS, 142.30ºE, 91 m above sea level) in April 2000. The seeds were placed into dry storage at 5°C until the time of the experiment (161 days). Cold stratification would not occur under these storage conditions, as seeds must be imbibed for cold stratification to be effective (Baskin and Baskin 1998; Stokes 1965). The germination experiment was conducted using the methods outlined in Section 2.1.4, with Petri dishes containing seeds destined for the cold treatment being incubated on moist filter paper at 5°C for 5 days while the comparison treatment were incubated at 15°C for 5 days. A comparison temperature of 15°C was used as it is outside the range of temperatures effective for cold stratification (Stokes 1965) whilst being below the temperature at which common heliotrope seeds will germinate. After the incubation period, both treatments were removed to an incubator set at a constant temperature of 35°C.
A two-tailed Student's t-test assuming unequal variance was conducted in the S-PLUS 4 statistical package (MathSoft Inc., Seattle, U.S.A.) to test for significant differences between the means of treatments for germination extent and median time to germination.

2.3.3. Results

There was a significant difference between median time to germination, but not in germination extent, of the two treatments (p<0.05) (Table 2.3, Figure 2.6). Seeds in the control treatment reached 50% germination 0.42 of a day faster than those in the cold treatment.

Table 2.3. The effect of cold treatment on the median time to germination and germination extent of common heliotrope seeds. The standard error of the mean is given in parentheses.

<table>
<thead>
<tr>
<th></th>
<th>5°C</th>
<th>15°C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Median Time to Germination (days)</td>
<td>1.95</td>
<td>1.53</td>
</tr>
<tr>
<td></td>
<td>(0.04)</td>
<td>(0.02)</td>
</tr>
<tr>
<td>Germination Extent (%)</td>
<td>98.5</td>
<td>99.5</td>
</tr>
<tr>
<td></td>
<td>(1.2)</td>
<td>(0.5)</td>
</tr>
</tbody>
</table>

Figure 2.6. The effect of cold treatment on the germination of common heliotrope seeds: 5°C (○) and 15°C (●). Error bars are ± the standard error of the mean.
2.3.4. Discussion

Despite Moore's (1956) observation to the contrary, there was no significant positive effect of cold treatment on germination extent of common heliotrope seed. There was a significant negative effect of cold treatment of time to median germination, but this different observation may perhaps be explained by pre-germination growth being more rapid at 15°C than at 5°C (Rowse, McKee et al. 1999).

The only major difference between this study and that of Moore’s is the maturity of seeds used, a result of the different harvesting methods (see Section 2.1.3.). This difference is then the most obvious explanation of the differences in outcomes of the two studies. As the seeds used in this study were collected at the level of maturity attained at seed dispersal, it can claim greater ecological validity over Moore’s under the protocols of Baskin (1998). Consequently, in the model of prediction described in Chapter 6, it is assumed that cold stratification is not a requirement for germination in seeds of common heliotrope.

2.4. Investigation of a leaching requirement for germination

2.4.1. Introduction

Leachable germination inhibitors occur frequently in species from arid regions (Kigel 1995), and they are thought to provide a mechanism whereby seeds can sense and respond to adequate rainfall for continued growth (Mayer 1986). The water in which common heliotrope seeds imbibe stains brown and has a strong, bitter odour. These observations led to the formulation of the hypothesis that germination of common heliotrope seeds may be prevented by chemical dormancy in the form of a leachable inhibitor.

Chemicals of varying constituents located in different parts of the seed and its surrounding structure, including the cotyledons (Ellery and Chapman 2000), seed coat (Bewley and Black 1994), structures exterior to the seed coat (Bradbeer 1988; Evenari 1949) and the embryo itself (Webb and Wareing 1972a; Webb and Wareing 1972b), have been found to inhibit germination of the seed embryo in some species (Bewley and Black 1982; Wareing 1965).
In some cases, germination is allowed by the leaching of inhibitors from seeds (Ellery and Chapman 2000; Hussain, May et al. 1968; Nikolaeva 1977; Thompson and Cox 1978; Thompson, Cox et al. 1979; Tissaoui and Côme 1973). Various compounds have been isolated and proven to have inhibitive properties at concentrations found in seeds, although in most cases the chemical in question is thought to be abscisic acid (Baskin and Baskin 1998; Bewley and Black 1982; Bewley and Black 1994; Bradbeer 1988). Of particular relevance to common heliotrope, alkaloids contained in both the seeds and vegetative structures of numerous species have been shown to inhibit germination (Evenari 1949). Seeds of common heliotrope contain high levels of pyrrolizidine alkaloids (Gaul, Gallagher et al. 1994), the major constituents being europine, heliotrine and lasiocarpine (O’Dowd and Edgar 1989). Although no specific studies have been done on the inhibitive properties of these compounds, it is possible that they may be inhibiting the germination of fresh seed of common heliotrope. It is known that the residue of common heliotrope plants can be strongly anti-bacterial (Nadir and Salih 1985) and reduce yield in wheat (Triticum aestivum, van Rees and Smallwood 2000), implying that the above-ground parts of the plant may contain a growth substance of some description. In order to determine whether such a growth substance inhibits germination, it is necessary to prove that the compound is present in the seed and that it prevents embryo growth and germination (Baskin and Baskin 1998). This is essentially an extension of the postulates of Koch, originally applied in the context of disease causing organisms (Evans 1976).

Hypothetically, common heliotrope would benefit ecologically from containing a leachable inhibitor in its seeds in two ways. Firstly, it would prevent fresh seeds from germinating at the end of the growing season when plants are likely to meet competition from winter annuals or be killed by frost. Winter rains falling when temperatures are not suitable for germination would leach the inhibitors, leaving a seed population more germinable when temperatures are suitable and moisture is sufficient for growth, i.e. in late spring and summer. Such a strategy has been found in the Mediterranean winter annual capeweed (Arctotheca calendula (L.) Levyns.) by Ellery (2000). Secondly, it could provide a mechanism for seeds to detect rainfall events of sufficient magnitude to allow reproduction. Seeds would only germinate after enough rain had fallen to leach the inhibitor. Kigel (1995) states that theoretically there should be a relationship between the amount of inhibitors in the dispersal unit and the minimal amount of
rainfall required for reproduction, but that no quantitative data on the subject have been published. The rate at which leaching occurs could also be dependent on temperature, such that effective leaching takes place only in the summer months.

Two experiments were formulated to test for the presence of a leachable inhibitor in the seeds of common heliotrope. The aim of the first experiment was to determine if leaching fresh seeds for different amounts of time at different temperatures would affect their germinability. The second experiment was designed to test whether leachate of varying concentrations made from fresh seeds of common heliotrope, which are known to be less germinable than seeds stored under field conditions, would inhibit the germination of highly germinable seed. As pointed out by Baskin (1998) and Bradbeer (1988), it is ecologically invalid to test the inhibitive effects of leachate on the seed of species other than that being studied (e.g. lettuce seeds or wheat embryos and coleoptiles), so highly germinable seeds of common heliotrope were used as the bioassay. The seeds in question had been buried after they had been harvested in autumn, and were known to be highly germinable.

2.4.2. Methods

Experiment 1. Seeds for this experiment were harvested at Normanville (S 35°49'54", E 143°43'26", 110m above sea level) in April 2002 and kept in dry storage at 5°C up until the time of the experiment (20 days). The germination experiment was conducted using methods outlined in Section 2.1.4, with the leaching treatments consisting of three different leaching times (0, 1 and 24 hours) after which the water and filter paper in the dishes was replaced, hypothetically removing any inhibitors which may have leached from the seeds at that time. Leaching took place in growth cabinets set at 5 different constant temperatures (10, 20, 25, 30 and 35°C), giving a total of 15 different treatments in a factorial design. All leaching treatments spent 24 hours at their respective leaching temperature before being transferred to a cabinet set at 35°C to germinate.

Experiment 2. Three leachate solutions of different concentration were made by adding varying amounts (0.2, 2.0 and 20.0 g) of fresh common heliotrope seeds harvested from Normanville in April 2002 to 40 ml of distilled water. The seeds were allowed to infuse in the water for 24 hours, after which they were removed. A further 10 ml of distilled
water was added to each solution to bring it up to the volume required for the experiment. The concentrations of these solutions are given as the mass of seeds per volume of water (mg ml$^{-1}$). Seeds of common heliotrope that had been harvested at Normanville in April 2002 and buried there to a depth of 100 mm were assumed to have any hypothetical inhibitor leached by autumn and winter rains by the time of the experiment (September 2002, the seed being buried for a total of 138 days). As shown in Section 2.6, common heliotrope seeds in the natural soil seed bank are particularly germinable at this time. This seed was used as a bioassay for the presence of a leachable inhibitor in fresh seed of common heliotrope. The germination experiment was conducted using methods outlined in Section 2.1.4, with 5 ml of the supernatant resulting from the infusion of the fresh common heliotrope seeds being added to each dish instead of distilled water in all treatments but the control. Germination took place in an incubator set at a constant temperature of 35°C.

A factorial analysis of variance using the S-PLUS 2000 statistical package (MathSoft Inc., Seattle, U.S.A.) was used to test for significant effects of treatments on median time to germination and germination extent. For germination extent, it was assumed that there would be unequal variance between treatments and the data were arcsine transformed accordingly prior to analysis. The Tukey method was used to test for significant differences between the means.

2.4.3. Results

Experiment 1. There was a very small significant effect of temperature (p<0.05) on germination extent; the pooled means of all temperatures are presented in Table 2.4. The only significant differences (p<0.05) were between the 10°C and 20°C treatments and the 10°C and 35°C treatments. There was no significant effect of time or an interaction of time and temperature on germination extent (see Appendix 2.1 for ANOVA table).
Table 2.4. The effect of leaching temperature on mean germination extent (%). Mean values are taken from pooled time treatments for each temperature (i.e. main effect of temperature). Arcsine-transformed values are given in parentheses; the standard error of the means is for arcsine transformed data.

<table>
<thead>
<tr>
<th>Leaching Temperature (°C)</th>
<th>10</th>
<th>20</th>
<th>25</th>
<th>30</th>
<th>35</th>
<th>S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean Extent (%)</td>
<td>82</td>
<td>89</td>
<td>88</td>
<td>85</td>
<td>90</td>
<td>(1.14)</td>
</tr>
<tr>
<td></td>
<td>(1.23)</td>
<td>(1.22)</td>
<td>(1.18)</td>
<td>(1.25)</td>
<td>(0.02)</td>
<td></td>
</tr>
</tbody>
</table>

Table 2.5. The combined effect of leaching time and temperature on median time to germination (days). The standard error of the means is given in parentheses.

<table>
<thead>
<tr>
<th>Leaching Time (hours)</th>
<th>Leaching Temperature (°C)</th>
<th>1</th>
<th>24</th>
<th>Control</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>9.4</td>
<td>7.6</td>
<td>8.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(1.0)</td>
<td>(0.6)</td>
<td>(0.9)</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>7.7</td>
<td>6.5</td>
<td>7.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.4)</td>
<td>(0.6)</td>
<td>(1.2)</td>
<td></td>
</tr>
<tr>
<td>25</td>
<td>7.5</td>
<td>8.5</td>
<td>5.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.4)</td>
<td>(0.6)</td>
<td>(1.0)</td>
<td></td>
</tr>
<tr>
<td>30</td>
<td>7.0</td>
<td>6.3</td>
<td>6.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.5)</td>
<td>(0.4)</td>
<td>(1.0)</td>
<td></td>
</tr>
<tr>
<td>35</td>
<td>7.2</td>
<td>6.1</td>
<td>8.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.5)</td>
<td>(0.6)</td>
<td>(0.6)</td>
<td></td>
</tr>
</tbody>
</table>

There was a significant difference (p<0.05) in median time to germination between the 10°C 1 hour treatment and the 25°C control treatment. There was also a significant interaction between time and temperature. There was no significant effect of time or temperature on median time to germination (Table 2.5, see Appendix 2.2 for ANOVA table).

Experiment 2. Germination was completely prevented in the 400 mg ml\(^{-1}\) treatment. There was no significant effect of the other leachate concentrations on germination extent (Table 2.6, see Appendix 2.3 for ANOVA table). There was, however, a significant effect of leachate concentration on median time to germination (Table 2.7, see Appendix 4 for ANOVA table). The 40 mg ml\(^{-1}\) treatment took significantly longer (0.90 of a day) to reach 50% germination in comparison to the 0 and 4 mg ml\(^{-1}\) treatments (p<0.05).

Table 2.6. The effect of leachate concentration on germination extent (%). Arcsine transformed values are given in parentheses.

<table>
<thead>
<tr>
<th>Leachate Concentration (mg seed ml(^{-1}))</th>
<th>0</th>
<th>4</th>
<th>40</th>
<th>400</th>
<th>S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean Extent (%)</td>
<td>98</td>
<td>98</td>
<td>95</td>
<td>0</td>
<td>(1.48)</td>
</tr>
<tr>
<td></td>
<td>(1.44)</td>
<td>(1.36)</td>
<td>(-)</td>
<td>(0.04)</td>
<td></td>
</tr>
</tbody>
</table>
Table 2.7. The effect of leachate concentration on median time to germination (days). Standard errors are given in parentheses.

<table>
<thead>
<tr>
<th>Leachate Concentration (mg seed ml(^{-1}))</th>
<th>0</th>
<th>4</th>
<th>40</th>
<th>400</th>
</tr>
</thead>
<tbody>
<tr>
<td>Median Time to Germination (days)</td>
<td>2.3 (0.19)</td>
<td>2.1 (0.15)</td>
<td>3.0 (0.15)</td>
<td>- (-)</td>
</tr>
</tbody>
</table>

2.4.4. Discussion

These results show that although seeds of common heliotrope contain a leachable substance that interferes with germination, it is unlikely that such a substance plays an ecological role in preventing germination by acting as a chemical inhibitor. In the first experiment, there is no obvious relationship between leaching time and temperature and germination. In the second experiment, there was a significant effect of leachate concentration on germination extent only in the 400 mg ml\(^{-1}\) treatment, but its effect on the seeds was lethal rather than inhibitory, as no viable seeds were found in the treatment at the conclusion of the experiment. There was a statistically significant effect of leachate concentration on median time to germination between the three other treatments, but it was an amount insignificant in terms of preventing germination under conditions unsuitable for continued reproduction (<0.9 days).

Within the literature, there is little proof that biologically active chemicals frequently found in plants are responsible for preventing germination (Bewley and Black 1982). Fresh seeds of common heliotrope are most likely to be prevented from germinating at the end of summer by cyclic changes in hydrothermal germination requirements (see Sections 2.5 and 2.6 and Chapter 3).

2.5. Investigation of temperature and water requirements for germination

2.5.1. Introduction

Observations from the literature and simple physics strongly suggest that water availability and temperature are the principal environmental factors limiting the germination of common heliotrope. There has been very little research done on the germination of summer annuals in regions with Mediterranean climates, with the exception of a few weedy species. Generally, optimum and base germination
temperatures for such species are comparatively high (Baskin and Baskin 1998). It is logical to expect that temperature requirements for germination of Mediterranean summer annuals will be high, as this provides a mechanism for seeds to detect their temporal niche. In Mediterranean regions, reliable rain falls over winter and a great proportion of Mediterranean species are winter annuals (Buddenhagen 1990). Therefore a high temperature requirement is an indirect way of ensuring the absence of competition from living plants by only allowing germination at a time of year when there will be little competition from living plants.

Avoidance of competition by restricting germination to a period in time where conditions are frequently too dry to allow plant growth has an obvious risk associated with it. However, rain during summer in Mediterranean regions does fall, but it is unreliable in occurrence and amount (Buddenhagen 1990). Also, evaporation rates are such that any rain that does fall cannot be relied upon to sustain growth for the lengths of time necessary for plants to complete their lifecycle. Kigel (1995) argues that, in principal, summer annuals in semi-arid Mediterranean regions should have comparatively higher moisture requirements for germination to allow for faster evaporation. Mott (1974) put forward the theory that a high water requirement for germination in arid ephemerals is more like to result in reproductive success. In species such as common heliotrope that have adapted to arid environments, in addition to germinating when there is enough water for imbibition and germination, it is essential that the seeds respond to endogenous or environmental signals that indicate sufficient water for ensuing growth and reproduction (Kigel 1995).

The physiological basis of the interaction of temperature and water potential is largely unknown. The effect of the two is additive (Baskin and Baskin 1998), but it is unknown whether greater water potentials narrow the range of temperatures that are effective for germination (El-Sharkawi and Farghali 1985; Hegarty 1978), or vice versa (Bradford 2002). It has been shown that a greater percentage germination for many species is achieved under alternating, as opposed to constant, temperature regimes (Baskin and Baskin 1998). However, the collection of data intended for parameterisation of contemporary weed germination models (Roman, Murphy et al. 2000) requires quantification of germination response to constant temperatures. As the overall goal of
this study is to achieve prediction of common heliotrope occurrence, constant temperatures are used in these germination studies.

There were two principal aims to this experiment. The first was to quantify the combined effects of water potential and temperature on the germination of seeds of common heliotrope. From the previous discussion it can be hypothesised that both the temperature and water requirements for common heliotrope will be high in comparison with temperate species. The second aim was to test how well the germination behaviour of seeds of common heliotrope conform to the assumptions of Gummerson’s (1986) model of hydrothermal time. Much emphasis has been placed on the potential of this model for predicting weed field emergence (Bradford 2002; Forcella, Benech Arnold et al. 2000), modelling changes in dormancy (Bauer, Meyer et al. 1998; Bradford 2002), and comparative germination studies (Allen, Meyer et al. 2000). This model has been described at length in the literature (Bradford 1995; Gummerson 1986), but a brief summary follows.

The model of hydrothermal time is basically a threshold model, where $\theta_{HT}$ is the hydrothermal time (e.g. MPa-degree-days) required for germination of a given seed population, $\Psi$ and $T$ are the water potential and temperature of the germination medium, $T_b$ is the base temperature at or below which germination will not occur, $\Psi_b(g)$ is the base water potential at or below which germination of fraction $g$ of the population will not occur, and $t_g$ is the actual time required for germination of the fraction $g$.

$$\theta_{HT} = (\Psi - \Psi_b(g))(T - T_b)t_g$$  \hspace{1cm} (Equation 2.1)

The model assumes that $\theta_{HT}$ and $T_b$ are constant for a given seed population, while $\Psi_b(g)$ and $t_g$ vary with germination fraction (Figure 2.2). Distribution of $\Psi_b(g)$ is assumed to be approximately normal, with a mean $\Psi_b(50)$ and standard deviation $\sigma_{\Psi_b}$. The normal distribution of $\Psi_b(g)$ generates the characteristic cumulative inverse normal distribution of $t_g$ seen in germination time courses (Meyer, Debaene-Gill et al. 2000). The parameters $T_b$, $\theta_f(g)$ (thermal time to germination of the fraction $g$), $\Psi_b(g)$ and $\theta_H$ (hydro time to germination of the fraction $g$) can be estimated by
probit regression of germination time courses (Bradford 2002), although they also may be estimated by plotting the inverse of the time to germination of a given fraction of the seed population (germination rate, \( GR(g) \)) against temperature or water potential respectively. Figure 2.2 also illustrates the concept of cardinal germination temperatures (Roberts 1988): in addition to base temperature, seeds of a given population will also have an optimum temperature \( T_o \) for germination, and a ceiling temperature \( T_c(g) \) for germination of fraction \( g \). Under the assumptions of the hydrothermal time model, the relationship between \( GR(g) \) and sub-optimal temperature will be linear, with each population fraction having a common intercept \( T_b \), but different gradient \( (\theta_f(g)) \). The relationship between \( GR(g) \) and \( \Psi \) is also assumed linear, with each fraction having a common slope \( (\theta_H) \), but different x intercept on the water potential axis \( \Psi_b(g) \), assumed normally distributed as mentioned above.

Parameterisation of this model for a given species requires calculation of germination rate of different fractions of the seed population. The bulk of work pertaining to hydrothermal time assumes the population to be the total number of seeds (or viable seeds) sown in a treatment, which confounds germination rate and extent, as discussed in Section 2.1.2. The population may be taken as the total number of seeds that germinated in a given treatment (germination extent), as has been done in this thesis. Grundy (2000) calculated hydrothermal parameters for common chickweed (\textit{Stellaria media} L.) using both (a) the total number of seeds sown and (b) the total number of
germinated seeds as the population. For that particular species, there was little
difference in the resulting hydrothermal parameters estimated by the two different
methods. Grundy (2000) also points out that using the number of seeds germinated is far
more satisfactory for species that do not reach 100% germination in many treatments.
This is the case in many weed species, as one of the common characteristics of weeds is
their high levels of dormancy (Benech-Arnold, Sánchez et al. 2000). Contrary to this,
Bradford (2002) states that only the total number of seeds sown can be used for the
calculation of hydrothermal parameters, but gives no reason for this statement. It is
unclear as to why this should be the case. The bulk of species which Bradford has
worked on are crop species (Alvarado and Bradford 2002; Bradford 1990; Dahal,
Bradford et al. 1990), and would achieve close to 100% germination under all
treatments, making the results from the different methods of calculation very similar.

Parameterisation of the hydrothermal time model typically involves a factorial
experiment subjecting seeds to a range of constant temperatures and water potentials.
Although this model has been parameterised for numerous weed species (Grundy,
Phelps et al. 2000; Roman, Thomas et al. 1999a; Roman, Thomas et al. 1999b;
Shrestha, Roman et al. 1999), and much has been made of its potential for predicting
field emergence, the only application of the concept to a weed emergence model
validated with field data is that of Roman, Murphy et al. (2000). It is essential that the
assumptions of this model are fully tested before attempting to parameterise it for
common heliotrope.

2.5.2. Methods

Seeds of common heliotrope used for the water potential and temperature experiments
were harvested at Normanville (S 35°49'54", E 143°43'26", 110m above sea level) in
April 2001. The seeds were placed into dry storage at 5°C until the time of the
experiment (85 days).

Solutions of differing amounts of polyethylene glycol (PEG, average molecular weight
8000) were made according to equations from Michel (1983) to give six osmotic
potential treatments of 0, -0.1, -0.2, -0.3, -0.4, and -0.5 MPa at different incubator
temperatures. The germination experiment was conducted using the methods outlined in
Section 2.1.4, with 5 ml of each PEG solution being added to each Petri dish instead of distilled water in all but the 0 MPa treatment. This ratio of solution/paper volume was sufficient to satisfy the PEG objection of Hardegree (1990), which states that a sufficient paper/solution ratio must exist in order to prevent significant changes in water potential resulting from PEG exclusion by filter paper.

Each water potential treatment was then randomly placed into cabinets kept at constant temperatures of 20, 25, 30, 35 and 40°C. Twenty-four hours after imbibition had commenced, each of the treatments were moved to fresh filter paper and another 5 ml of the respective PEG solutions added before being re-sealed with paraffin film. This process ensured that the osmotic potentials of the solutions were not increased by PEG occlusion by seeds or evaporation (Bradford 1995). This process was repeated as necessary throughout the experiment to counter any increase in PEG concentration as a result of evaporation.

A factorial analysis of variance using the S-PLUS 2000 statistical package (MathSoft Inc., Seattle, U.S.A.) was used to test for significant effects of treatments on median time to germination and germination extent.

In order to estimate cardinal temperatures for common heliotrope for the purposes of comparison to other species, and to determine whether the germination behaviour of common heliotrope conformed to the assumptions of the model of hydrothermal time, the germination rates of different fractions of seeds of common heliotrope were plotted against temperature and water potential. For the calculation of cardinal temperatures and hydrothermal parameters, arbitrary germination percentiles such as 10, 50 and 90% are typically used (Bradford 1995). The 20°C treatment was excluded from analysis, as germination was not recorded in all replicates, and only one seed germinated in each of the remainder. Time to a given percentage germination was calculated by linear interpolation from the two data points either side of a given percentile for each replicate within a treatment, and then averaged to provide a mean germination rate for each treatment.

As in the idealised data presented in Figure 2.7, germination rate at the nominal near-optimal water potential of 0 MPa was plotted against temperature and a linear equation was fitted by least-squares regression to the series created by each germination
percentile. The linear equation was solved for germination rate = 0 to give an estimate of base temperature. The 40°C treatment was excluded from this regression as it was clearly supra-optimal for germination. Likewise, germination rate at the nominal near-optimal temperature of 35°C was plotted against water potential and a linear equation was fitted by least-squares regression to the series created by each germination percentile. The linear equation was solved for germination rate = 0 to give an estimation of base water potential.

2.5.3. Results

The optimum germination temperature for common heliotrope is 35°C, with both median time to germination and germination extent significantly increasing or declining respectively either side of this value. The optimum water potential for common heliotrope is 0 MPa; more negative potentials have a significant (p<0.05) negative effect on both median time to germination and germination extent (Figures 2.8 and 2.9, see Appendix 2.5 and 2.6 for ANOVA tables).

Germination of seeds of common heliotrope exposed to varying temperatures and water potentials do not conform to the assumptions of the model of hydrothermal time (Figures 2.10 and 2.11). Different fractions of seeds do not share a common base temperature, and values vary greatly for the different percentiles (Table 2.8). Also, the different fractions of the seed population do not share a common $\theta_H$ (Table 2.8). The estimates of these values will be imprecise, as the number of data points used in the regressions (Figures 2.10 and 2.11) is small, and the level of extrapolation high, principally owing to the small range and low resolution of temperatures.
Figure 2.8. The effect of temperature on germination extent (%) at 0 MPa (●), -0.1 MPa (○), -0.2 MPa (▲), -0.3 MPa (△), -0.4 MPa (■) and -0.5 MPa (□). Error bars are ± the standard error of the mean.

Figure 2.9. The effect of temperature on median time to germination (days) at 0 MPa (●), -0.1 MPa (○), -0.2 MPa (▲), -0.3 MPa (△), -0.4 MPa (■) and -0.5 MPa (□). Error bars are ± the standard error of the mean.
Table 2.8. Estimation of base water potentials and temperatures for different germination fractions from extrapolation of linear equation fitted by least-squares regression.

<table>
<thead>
<tr>
<th>Germination Percentile</th>
<th>Base Water Potential</th>
<th>R²</th>
<th>Base Temperature</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>-0.9</td>
<td>0.98</td>
<td>17.9</td>
<td>0.93</td>
</tr>
<tr>
<td>50</td>
<td>-1.0</td>
<td>0.86</td>
<td>11.7</td>
<td>0.74</td>
</tr>
<tr>
<td>90</td>
<td>-1.6</td>
<td>0.91</td>
<td>3.7</td>
<td>0.56</td>
</tr>
</tbody>
</table>

2.5.4. Discussion

Seeds of common heliotrope appear to have a very high temperature requirement in comparison with many species studied in the literature (germination extent approaches 0 at 20°C and is optimum at 35°C, which is supported by the work of Moore (1956), who found that seeds of common heliotrope would germinate when incubated at 24°C and 35°C, but not at 19°C). This is perhaps not surprising, as most seed germination studies are of temperate annual weeds or crop plants. For instance, Roman (2000) reports the base temperature of fat hen (*Chenopodium album* L.), a temperate summer annual, as 4.2°C, with an optimum germination temperature of 24.0°C. Weaver (1988) reports similar values for that species, and around 12°C for eastern black nightshade (*Solanum ptycanthum* Dun.) and 9°C for both powell amaranth (*Amaranthus powellii* S. Wats.) and green foxtail (*Setaria virdis* L.). Grundy (2000) found that common chickweed (*Stellaria media* L.), a temperate all-season annual, has a base temperature of 2°C and an optimum of 18°C. As mentioned in the introduction of this section, there has been
little research done on species with comparable life histories to common heliotrope. One notable exception is the study of Squires (1969), which found that seeds of caltrop (*Tribulus terrestris* L.), a species which shares many ecological attributes with common heliotrope and co-occurs during summer in the Victorian Mallee, only germinated between 20 and 40°C, with 32°C being optimal. The results from this study support the hypothesis that common heliotrope, being a Mediterranean summer annual, should have high temperature requirements for germination.

The germination of common heliotrope is also very sensitive to water availability, with final percentage germination being reduced by 28% at -0.5 MPa in comparison to 0 MPa under optimal temperature conditions (Figure 2.8). The response to water availability was even greater at non-optimal temperature conditions. This is again in contrast to the requirements of temperate annuals reported within the literature, which are comparatively less sensitive to water potential. As with temperature, the life strategy of common heliotrope suggests that its water requirements will be high. This hypothesis appears to be confirmed by these results. Whereas high percentages of temperate summer annuals, such as common chickweed, germinate at water potentials of up to -0.8 MPa at even non-optimal temperatures (Grundy, Phelps *et al.* 2000), germination extent of fresh seeds of common heliotrope is significantly reduced at only -0.5 MPa at optimum temperatures. This hypothesis is also supported by the study of Botha (1984) who found that Afghan melon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai), also a Mediterranean summer ephemeral and common in the Victorian Mallee, will not germinate at –0.43 MPa when incubated at 27°C.

It is thus concluded that the temperature and water requirements for germination of common heliotrope provide a mechanism for detection of its temporal and spatial niche. It will only germinate in warmer months, when there is unlikely to be competition, and only after sufficient rainfall, to allow sufficient growth to achieve reproduction (see Chapter 4 for a further investigation of this). Its sensitivity to temperature and water may also explain its absence in the presence of other living plants. The soil beneath living plant canopies would be cooler due to shading, important in spring when temperature is the environmental variable limiting germination (Moore 1956), and drier due to transpiration, important in summer months when moisture is limiting germination (Moore 1956). Complete quantification of water and temperature responses
of further species with Mediterranean summer annual life history (e.g. caltrop, *Tribulus terrestris* L.) would make for fruitful further study. Such a study could also be extended to species with similar constraints to life history, such as desert ephemerals.

Germination of seeds of common heliotrope exposed to varying temperatures and water potentials do not conform to the assumptions of the model of hydrothermal time, although the number of data points used to estimate hydrothermal parameters was small, and the level of extrapolation high. This was largely due to the small range and low resolution of temperatures used in this experiment - resource constraints prevented a greater range or resolution of temperatures being employed. Greater precision through shorter sampling intervals was also not possible for the same reasons. Such constraints aside, the behaviour of common heliotrope seeds would make it very difficult to reliably estimate hydrothermal parameters under any range of temperatures owing to the small percentage of seeds that germinate under sub-optimal conditions. As the model of hydrothermal time was principally created for crop species which typically achieve high percentage germination under sub-optimal conditions, it is not suited to the germination behaviour of common heliotrope without extensive modification.

As the ecology of common heliotrope differs markedly to the bulk of species for which emergence models have been created, it is perhaps not surprising that an approach to prediction of occurrence should also differ. The data obtained in this experiment are not sufficient to create a new model of germination for common heliotrope, and no attempt will be made to do so. Model development would require germination response to be recorded over a much greater range and resolution of temperatures and water potentials, and from seeds in the soil seed bank sampled at different times of the year (see Chapter 3). Obtaining such data and developing a more appropriate model could form the basis for an entire new study. However, the results of this experiment do provide useful insight into the germination ecology of common heliotrope, and provides a solid backdrop to the experiments and discussion outlined in subsequent chapters.
2.6. Conclusion – A mechanism for individual seed fastidiousness and population dormancy

The germination of common heliotrope appears to be principally limited by temperature and water requirements, which limit both rate and extent of germination of a seed population. My hypothesis of the mechanism which underlies the germination response of common heliotrope seed to temperature and water availability is as follows. In order for a seed to germinate, an endogenous physiological process must reach completion that requires exposure water for a certain amount of time. The results of this chapter indicate that such a process takes longer to reach completion at more negative water potentials. This may be due to different parts of the seed requiring longer to become hydrated (Mayer 1986). Presumably, there is a threshold potential below which the process stops and seeds will not germinate regardless of duration of exposure to sub-threshold potentials (Figure 2.12). The shape of the curve illustrated in Figure 2.12 is influenced by temperature, which has an impact on both the water potential below which the process will not progress, regardless of duration of exposure, and the rate at which the process progresses.

I propose that at the level of individual seeds within a population, the water potential at which this physiological process does not progress varies. This creates a population of seeds of varying fastidiousness in their germination requirements, which in turn defines the population’s level of dormancy, as defined in Section 2.1.2. Therefore, the proportion of seeds within a population that will germinate will decrease with increasingly negative water potential, as seen in the results of this chapter. This is further borne out by the observation that a proportion of the seeds that do not germinate at a certain negative water potential will germinate when they are exposed to a less negative water potential.
There is tremendous evolutionary logic to a mechanism such as this. If this hypothesis is correct, common heliotrope will germinate and emerge in higher densities when soil water amount and duration is higher, that is when there is likely to be a greater amount of water available for subsequent growth and reproduction. This has two distinct ecological advantages. Firstly, it provides a mechanism for common heliotrope to manage its plant density in response to the availability of the resource that primarily limits its growth (water), and thus maximise reproductive output to suit germination inducing rainfall events of any size. Secondly, it provides a mechanism for a population of common heliotrope seeds to spread their risk of emergence across time. It does this because at any given field emergence event, water and temperature requirements will undoubtedly be sub-optimal, which this chapter has quantified as less than 0 MPa (saturated soil) and 35°C. As a consequence, only the less fastidious fraction of the population will germinate, leaving the more fastidious portion of the population un-germinated in the soil for future rainfall events.

Such incomplete germination of the seed bank is an example of fractional germination as defined in Section 2.1.2. In the case common heliotrope, fractional germination is enhanced even further by the distribution of seeds in the soil profile, and the distribution of conditions of varying suitability in the soil profile after a germination event. For instance, hydrothermal conditions might be optimal at 10 to 20 mm depth in a given soil
type following rain, and as a consequence a vast majority of seeds at that depth will germinate. At the surface, or deeper down, hydrothermal conditions may become increasingly sub-optimal, and hence a lower proportion of the seed population located here will germinate (this may also explain the distinct depth of emergence noted in Chapter 1). This leaves a total population of seeds with varying fastidiousness in the soil seed bank. It is also possible that the fastidiousness of individual seeds (and hence the dormancy level of the population) may change over time. Because germination studies are through necessity based on the response of populations of seeds, the dynamics of this change are difficult to elucidate at the level of individual seeds. It could be that seeds that were once part of the highly fastidious portion of the population will become less so over time and vice versa. Chapter 3 addresses the changing dormancy level of seed populations of common heliotrope over time.

2.7. References


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Nikolaeva MG (1977) Factors controlling the seed dormancy pattern. In 'The Physiology and Biochemistry of Seed Dormancy and Germination'. (Ed. AA Khan) pp. 51-74. (Elsevier: Amsterdam)


2.8. Appendices

*Appendix 2.1. ANOVA table – effect of leaching time and temperature and interaction of leaching time and temperature on germination extent*

<table>
<thead>
<tr>
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Appendix 2.2. ANOVA table – effect of leaching time and temperature and interaction of leaching time and temperature on median time to germination

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Appendix 2.3. ANOVA table - effect of inhibitor concentration on germination extent

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Appendix 2.4. ANOVA table - effect of inhibitor concentration on median time to germination

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Appendix 2.5. ANOVA table - effect of temperature and water potential and interaction of temperature and water potential on arcsine transformed germination extent.

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Appendix 2.6. ANOVA table - effect of temperature and water potential and interaction of temperature and water potential on mean time to germination.

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Chapter 3. Temporal and Spatial Limits to Germination

The endogenous limits to germination of seeds frequently vary in space and time. It is the seeds’ sensing of their environment through endogenous mechanisms, and the prevailing conditions of that environment, that imposes limits on germination and hence occurrence. The germination response of a single population of seeds to varying environmental conditions (dormancy) can change seasonally. This is the case for many species (e.g. Baskin and Baskin 1985; Bouwmeester and Karssen 1993; Karssen, Derkx et al. 1988; Young 2001). It is then the level of dormancy that coincides with seasonally changing environmental conditions to allow a species to detect and germinate within its temporal niche.

Populations of a species from differing environments often have different germination responses (e.g. Dunbabin and Cocks 1999; Jain, 1982; Gill and Blacklow 1985; Naylor 1983; Smith, Cocks et al. 1996). This is seen as evolutionary fine tuning of a species’ germination ecology to suit the environment, and subtly different niches, that they inhabit.

One of the primary gaps in research that is addressed in this thesis is reliable prediction of the occurrence of common heliotrope infestations in time and space, which will be of immense benefit in planning and timing of control. Clearly, the way in which endogenous limits to germination behave in space and time is critical to predict occurrence. Hence, the aims of this chapter are to qualify and quantify any temporal and spatial variability that may exist in seeds of common heliotrope.

3.1. Investigation of cyclic dormancy in common heliotrope

3.1.1. Introduction

Seed populations can show degrees of relative dormancy, which can exhibit a distinct seasonal pattern. This can be viewed in light of the mechanism proposed in Chapter 2 as a change in the fastidiousness of germination requirements over time. As dormancy is released, the range of environmental conditions suitable for germination widens until it is maximal (Vleeshouwers, Bouwmeester et al. 1995). When dormancy is induced,
the range of conditions over which seeds can germinate narrows, until germination is no longer possible under any conditions and full dormancy is reached. Application of this concept within the literature has focussed on the range of temperatures over which seeds will germinate. It is thought that the observed field-emergence of temperate annuals such as fat hen (*Chenopodium album* L.) (Bouwmeester and Karssen 1993), wild radish (*Raphanus raphanistrum* L.) (Young 2001) and corn spurrey (*Spergula arvensis* L.) (Karssen, Derkx *et al.* 1988) is the combined result of seasonal periodicity in field temperature and seasonal periodicity in the widths of temperature ranges suited for germination. This seasonal pattern of behaviour was also found in the Mediterranean summer annual witchgrass (*Panicum capillare* L.) (Baskin and Baskin 1985). As water availability is the principal environmental factor limiting plant growth in Mediterranean climates (Buddenhagen 1990), it is plausible that dormancy could also be associated with a reduction in the range of water potentials over which seeds will germinate. An experimental investigation of this hypothesis has not been conducted (Bradford 1990), although both Bauer (1998) and Meyer (2000) modelled after-ripening as a function of changes in germination response to a range of water potentials.

The aim of the experiment to be described here was to quantify seasonal changes in the germination response of common heliotrope seeds in the soil. Seeds were extracted from the soil seed bank at different times of the year and subjected to a range of temperatures and water potentials.

### 3.1.2. Methods

The soil seed bank from which seeds were extracted was located in a paddock at Normanville (S 35°49'54'', E 143°43'26'', 110m above sea level) in the Victorian Mallee (see Figure 1.3). The paddock had supported a heavy infestation of common heliotrope in the summer of 2000/2001, but no plants had grown for a full year prior to the commencement of this experiment in February of 2002. Consequently, all seeds in the soil seed bank were at least twelve months old. Seeds were extracted from the soil by passing dry soil through nested sieves of 1.8 mm and 1.1 mm in diameter. Large organic material was trapped by the larger of the sieves, and a mixture of common heliotrope seeds and seed coats, sand and soil was trapped by the smaller of the sieves.
This mixture was further purified using an aspirator. As the amount of impurities and unviable seeds in this mixture was still high, seeds were not counted into Petri dishes, but a consistent weight (0.6 g) of seed + impurity mixture was added to each dish, aimed at giving around 100 viable seeds per dish (the percentage of viable seed in the mixture was calculated from pilot studies).

Solutions of differing amounts of polyethylene glycol (PEG, average molecular weight 8000) were made according to equations from Michel (1983) to give four osmotic potential treatments of 0, -0.2, -0.4, and -0.6 MPa at different incubator temperatures. The germination experiment was conducted using the methods outlined in Section 2.1.4, with 5 ml of each PEG solution being added to each Petri dish. This ratio of solution/paper volume was sufficient to satisfy the PEG objection of Hardegree (1990), which states that a sufficient paper/solution ratio must exist in order to prevent significant changes in water potential resulting from PEG exclusion by filter paper.

Each water potential treatment was then randomly placed into cabinets kept at six constant temperatures. Twenty-four hours after imbibition had commenced, each of the treatments was moved to fresh filter paper and another 5 ml of the respective PEG solutions added before being re-sealed with paraffin film. This process ensured that the osmotic potential of the solutions were not increased by PEG occlusion by seeds or by evaporation (Bradford 1995). This process was repeated as necessary throughout the experiment to counter any increase in PEG concentration as a result of evaporation.

The soil seed bank was sampled and the experiment repeated five times throughout 2002 at two-monthly intervals starting in February. This gave estimates of dormancy level for this population of seeds in February, April, July, September and November.

Temperatures in the cabinets were set to approximately 22, 25, 28, 31, 34 and 37°C (only the highest five treatments were used for the February sample, after which it was realised that lower temperatures would be needed). The temperature in each cabinet was monitored using four Dataflow 906 temperature sensors connected to a Dataflow DS93 data logger (Dataflow Systems, Caboolture, Australia). The recorded temperature in each cabinet was used for analyses, and cabinet temperatures were adjusted between experiments to achieve a more even spread of temperatures. Consequently, the temperature treatments are subtly different for each of the times the experiment was run.
A factorial analysis of variance using the S-PLUS 2000 statistical package (MathSoft Inc., Seattle, U.S.A.) was used to test for significant effects of treatments on median time to germination and germination extent. A separate two-way factorial analysis had to be conducted for each time of year, as the temperatures were slightly different each time the experiment was run. For germination extent, it was assumed that there would be unequal variance between treatments and the data were arcsine transformed accordingly prior to analysis. It was not possible to conduct an analysis of variance on median time to germination, owing to unequal variance between water potential treatments.

3.1.3 Results

Dormancy in seeds of common heliotrope clearly cycles seasonally. This is shown by the changes in germination extent and median time to germination across temperature and water potential treatments at different times of the year (Figures 3.1 and 3.2). The optimum temperature for germination appears constant at around 35°C for all times of the year, the optimum water potential is 0 MPa.

The effect of temperature and water potential on germination extent at all times of the year was significant (p<0.05, see Appendix 3.1 for ANOVA tables). There was a significant (p<0.05) interaction of temperature and water potential on germination extent for all months except September and November (see Appendix 3.1 for ANOVA tables). The interaction in these months was not significant because the lower levels of dormancy at that time resulted in close to 100% germination in all treatments. A wider range of treatments would be required to detect a significant interaction of temperature and water potential at this time of year.
Figure 3.1. The germination extent of common heliotrope seeds at different water potentials and temperatures at different times of the year. Each chart represents a time of the year. Each series represents a water potential treatment; 0 MPa (●), -0.2 MPa (○), -0.4 MPa (▲) and -0.6 MPa (□). Error bars are ± the standard error of the mean.
Figure 3.2. The median time to germination (MTG) of common heliotrope seeds at different water potentials and temperatures at different times of the year. Each chart represents a time of the year. Each series represents a water potential treatment; 0 MPa (●), -0.2 MPa (○), -0.4 MPa (▲) and -0.6 MPa ( □). Error bars are ± the standard error of the mean.
3.1.4 Discussion

Even though it is not possible to statistically test for a significant effect of time of year on germination extent, it is obvious from Figures 3.1 and 3.2 that by the definition of dormancy outlined in Chapter 2, dormancy in seeds of common heliotrope cycles seasonally. Dormancy is induced in seeds in late summer (February), reaches a maximum in autumn (April), and is then relieved from winter through until late spring (July, September, November). This observation is in agreement with those of other summer annuals in the literature (Baskin and Baskin 1985; Bouwmeester and Karssen 1993; Karssen, Derkx et al. 1988). The ecological advantage of such behaviour is clear; it provides a mechanism by which common heliotrope can detect its temporal niche, and thus minimise its risk of germination. By the pattern determined in this experiment, common heliotrope will germinate in greater numbers in response to lower temperature and water availability in late spring when evaporation rates, and hence risk of germinating without reproducing, is lower. By mid-summer, when the risk of germinating without reproducing is higher, a lower proportion of the seed population will germinate in response to the same conditions. By autumn, when the risk of germinating without reproducing becomes very high due to frost, the majority of the seed population will not germinate unless exposed to optimum conditions, which are almost certain not to occur.

Karssen (1988) investigated the environmental determinate of the similar cyclic pattern found in seeds of corn spurrey. This was achieved by incubating seeds under a temperature regime that condensed the annual temperature cycle of their study region into 73 days. They found that loss of dormancy was caused by rising ‘spring’ temperatures, and did not depend on exposure to low winter temperatures. Dormancy was then increased by falling temperatures in autumn. It is quite probable that this is also the case with common heliotrope, and an investigation of the environmental determinants of cyclic dormancy using the methods outlined by Karssen (1988) could be a fruitful endeavour for subsequent studies. Karssen (1988) stop short of proposing a physiological mechanism for their findings. Egley (1995) suggests that changes in dormancy in response to changing external conditions (temperature and water availability) are brought about through the cell membrane processes (fluidity as a result of changes in lipid composition) outlined by Mayer (1986).
The way that the seasonal pattern of dormancy found in seeds of common heliotrope relates to rest of its life cycle and the likelihood of reproductive success is discussed at length in Chapter 4.

The nature of the data recorded in this experiment prevents a quantified comparison of germination requirements at different times of the year. It is not possible to conduct a three way factorial analysis of variance on the germination extent or median time to germination data owing to the subtle difference in temperatures employed for each time of year. This was not foreseen as a problem during the design of the experiment, as the principal analysis was to be conducted on the hydrothermal parameters of seeds at different times of the year as outlined by Allen (2000) and (Bradford 2002). In species conforming to the assumptions of the model of hydrothermal time, seasonal cycling in dormancy can be expressed by change in the hydrothermal parameter $\Psi_s (g)$ (Alvarado and Bradford 2002; Bauer, Meyer et al. 1998). However, as observed in Chapter 2, the germination behaviour of common heliotrope is not amenable to the calculation of hydrothermal parameters.

An approach similar to that of Grundy (2000), who estimated upper and lower temperature and water potential 'thresholds' where germination extent approaches zero, would be more appropriate in the case of common heliotrope. Such an approach could not be used with this data set, as the range of temperatures and water potentials employed does not extend to values at which germination extent approaches zero for most of the times of the year studied. The cyclic behaviour of the germination response makes it very difficult to anticipate the range of temperatures and water potentials suitable for estimation of such thresholds. However, the approach of Grundy (2000) could be taken if a greater range and resolution of temperatures and water potentials were used for all times of the year (e.g. 12 to 50°C with 3°C intervals, 0 to -1 MPa with 0.1 MPa intervals). The results of such a range of treatments could be used to reliably generate some form of dormancy model in common heliotrope seeds at different times of the year. Unfortunately, time and resource constraints prevented this experiment being repeated with such a range of temperatures and water potentials.
3.2. Variation in seed dormancy of populations of common heliotrope

3.2.1. Introduction

Although restricted to areas with a Mediterranean climate, common heliotrope is geographically widespread within Australia, and consequently there is variation of the environments in which it exists. The hypothesis that seed dormancy characteristics of different populations will vary predictably with environmental characteristics and the major selection pressures acting on species has formed the basis of several studies (Dunbabin and Cocks 1999; Gill and Blacklow 1985; Jain 1982; Naylor 1983; Smith, Cocks et al. 1996).

Water and temperature are the principal environmental factors that limit common heliotrope germination (Chapter 2). It is the seed’s sensitivity to these parameters that allows it to detect its temporal and spatial niche and thus determines its reproductive success. Dormancy in common heliotrope is defined as a function of the range of temperatures and water potentials over which a given population of seeds will germinate. Theoretically, the ability of a seed to sense the suitability of its environment for continued growth and reproduction is an important fitness characteristic. It is thus reasonable to expect local adaptation of seed dormancy to climate and soil characteristics. Common heliotrope was naturalised in Australia approximately 200 years ago (see Chapter 1). Its spread, although not documented, undoubtedly followed the path of European farming systems throughout the country. As such systems have existed throughout much of Australia for at least 100 years, it is reasonable to assume that populations of common heliotrope growing under different climatic and edaphic conditions will have evolved different dormancy characteristics. Different levels of dormancy have been found in different populations of several weed species naturalised in southern Australia (Dunbabin and Cocks 1999; Gill and Blacklow 1985).

The aim of this experiment was to determine whether fresh seeds of common heliotrope from different populations within Australia display different dormancy characteristics with respect to the range of temperatures and water potentials over which they will germinate. It is hypothesised that dormancy level will be related to the climate characteristics of the regions from which the populations were taken, i.e. seeds of populations from regions with higher evaporation and lower soil water holding capacity.
will exhibit a more conservative response to water potential and seeds of populations from cooler regions will germinate more at lower temperatures than those from warmer regions.

3.2.2. Methods

Local agricultural extension officers collected seeds of common heliotrope at five locations across southern Australia (Figure 3.3). The locations were chosen as they represent a gradient in climate across the regions in which common heliotrope is considered a problem within Australia. The different populations are listed in Table 3.1, along with gross growing season climate data for each location.

![Figure 3.3. The location within Australia of the populations of common heliotrope used for this study.](image)

In order to account for the different harvesting methods and maternal environments experienced by the seeds, which result in differing levels of maturity (see Chapter 2),
fifteen plants from each population were grown from the seeds under field conditions at The University of Melbourne (-37.8075 S, 144.9700 E, 31 m height above sea level). The plants were grown in a randomised complete block design with three plants in each block. In order to prevent cross-pollination, perforated plastic bags of the type used by plant breeders were placed over the plants at the commencement of flowering. These bags also served to collect seeds as they ripened and dehisced. Seeds harvested in this manner were further purified using a system of nested sieves of 1.8 mm and 1.1 mm in diameter and velvet boards.

A germination experiment using a range of temperatures and water potentials was conducted as described in Section 2.5.2. Water potential was controlled using solutions of varying concentration of polyethylene glycol as described in Section 3.1.2 to give water potentials of 0, -0.2, -0.4 and -0.6 MPa. The temperature in each cabinet was monitored using four Dataflow 906 temperature sensors connected to a Dataflow DS93 data logger (Dataflow Systems, Caboolture, Australia). Actual mean cabinet temperatures were 23.0, 27.8, 29.0, 33.5 and 36.9°C.

A factorial analysis of variance was done using the S-PLUS 2000 statistical package (MathSoft Inc., Seattle, U.S.A.), to test for significant effects of population, recorded temperature and water potential on median time to germination and germination extent (see Appendices 3.2 and 3.3). For germination extent, it was assumed that there would be unequal variance between treatments and the data were arcsine transformed accordingly prior to analysis. A Tukey comparison was applied to germination extent and median time to germination data within each temperature and water potential treatment to determine whether the germination responses of the different populations were significantly different.
Table 3.1. Locations and climatic attributes of the different populations of common heliotrope used in the experiment. Data are taken from the Commonwealth Bureau of Meteorology web site (http://www.bom.gov.au). Where data were not available for specific locations, the data for the nearest station used is given in parentheses.

<table>
<thead>
<tr>
<th>Population</th>
<th>Location</th>
<th>Height above sea level (m)</th>
<th>Mean Nov-Jan rainfall (mm)</th>
<th>Proportion of total annual rainfall falling in Nov-Jan (%)</th>
<th>Mean Nov-Jan daily evaporation (mm)</th>
<th>Mean Nov-Jan daily maximum temperature (°C)</th>
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</thead>
<tbody>
<tr>
<td>Condobolin</td>
<td>-33.0664 S 147.2283 E</td>
<td>195</td>
<td>170</td>
<td>36</td>
<td>9.1</td>
<td>31.6</td>
</tr>
<tr>
<td>Longereno</td>
<td>-36.6719 S 142.2989 E</td>
<td>91</td>
<td>106</td>
<td>25</td>
<td>7.6</td>
<td>27.9</td>
</tr>
<tr>
<td>Normanville (Kerang)</td>
<td>-35.7250 S 143.9181 E</td>
<td>78</td>
<td>101</td>
<td>27</td>
<td>7.9</td>
<td>29.7</td>
</tr>
<tr>
<td>Walpeup</td>
<td>-35.1217 S 142.0022 E</td>
<td>105</td>
<td>95</td>
<td>29</td>
<td>8.2</td>
<td>29.7</td>
</tr>
<tr>
<td>Woodanilling (Kojonup)</td>
<td>-33.6886 S 117.5553 E</td>
<td>310</td>
<td>66</td>
<td>12</td>
<td>6.7</td>
<td>27.3</td>
</tr>
</tbody>
</table>
3.2.3. Results

The was a significant (p<0.05) effect of population on germination extent at lower temperatures, with seeds from the Walpeup population germinating to a lesser extent at 23°C than those from the other populations and seeds from Woodanilling germinating to a greater extent at lower temperatures than those from the other populations (Table 3.2, see Appendix 3.2 for ANOVA table). The other notable significant effect is the greater reduction in germination extent of seeds from the Condobolin population at increasingly negative water potentials in comparison to the other populations. For all treatments, there were significant effects (p<0.05) of temperature and water potential and the interaction of all main effects on germination extent and median time to germination (Table 3.2 and 3.3, see Appendix 3.3 for ANOVA table for median time to germination).

Table 3.2. Germination extent (%) for the different populations under different water and temperature treatments. Location means within temperature and water potential treatments with different letters are significantly different (p<0.05).

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>23</th>
<th>28</th>
<th>29</th>
<th>33</th>
<th>37</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>0 MPa</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Condobolin</td>
<td>46\textsuperscript{a}</td>
<td>85\textsuperscript{a}</td>
<td>88\textsuperscript{a}</td>
<td>87\textsuperscript{a}</td>
<td>90\textsuperscript{a}</td>
</tr>
<tr>
<td>Longerenong</td>
<td>58\textsuperscript{a}</td>
<td>94\textsuperscript{a}</td>
<td>97\textsuperscript{a}</td>
<td>98\textsuperscript{a}</td>
<td>93\textsuperscript{a}</td>
</tr>
<tr>
<td>Normanville</td>
<td>60\textsuperscript{a}</td>
<td>90\textsuperscript{a}</td>
<td>98\textsuperscript{a}</td>
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Table 3.3. Median times (days) to germination for the different populations under different water and temperature treatments. Location means within temperature and water potential treatments with different letters are significantly different (p<0.05).

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5.2.4. Discussion

As expected, the median time germination and germination extent of different populations varied at within treatments, i.e. inherent dormancy level varies. The most noticeable differences between the populations are that: seeds from Walpeup have a greater sensitivity to sub-optimal temperatures; seeds from Condobolin have a greater sensitivity to increasingly negative water potentials; and seeds from Woodanilling have a greater tolerance of sub-optimal temperatures. These differences can be explained to a certain extent by the gross growing season climatic differences of the different sites (Table 3.1). Condobolin has a higher mean growing season evaporation rate than the other locations, and this perhaps explains why seeds from that location have a greater...
sensitivity to water potential. Woodanilling has the lowest mean maximum growing season temperature, which may explain why seeds from that location were more tolerant of sub-optimal temperatures. An explanation for Walpeup's sensitivity to sub-optimal temperatures is not so obvious, as it is very similar climatically to Normanville and Longerenong. There are, however, many more subtle climatic, edaphic and cultural differences between locations, which may or may not constitute significant selection pressures. These include farming systems, length of cropping season and soil type, particularly with regard to soil water holding capacity (see Chapter 5).

The common hypothesis in previous studies of dormancy characteristics and environment is that dormancy will be more conservative in unreliable environments. Norman, Cocks et al. (2002) tested this hypothesis using the loss of hard-seededness in annual clovers from wet and dry environments. Norman, Cocks et al. (2002) found that although loss of hardseedendess varied between ecotypes, there was no correlation between hardseededness and mean annual rainfall. Philippi (1993), on the other hand, found a weak correlation between dormancy and mean winter rainfall in different populations of the desert annual Lepidium lasiocarpum. However, Jain, (1982) found that higher mean levels of dormancy in populations of annual rangeland species from sites with a higher probability of summer rainfall, which directly contradicts the hypothesis. The latter study, however, confounded the effects of maternal environment with those of genotype, as the seeds collected from different populations were not grown under a consistent maternal environment.

Generally, these studies support biological expectation: that populations growing for extended periods of time under differing climatic conditions have developed different dormancy characteristics. However, proving that dormancy characteristics vary predictably with particular quantifiable environmental characteristics (e.g. rainfall) is a lot more difficult. Research on this topic may be improved by obtaining a greater understanding of the mechanistic relationship between dormancy, climate, soil, competition and cultural practises on survivorship of a given species, rather than searching for correlations between dormancy and crude climate statistics such as mean annual rainfall. For instance, local rainfall pattern or the ability of soil to retain moisture may be a greater force in selection pressure than just growing season rainfall (Norman, Cocks et al. 2002). The genetics of dormancy are thought to be complex, but
the success of many weed species across a broad spectrum of climates and cultural practices may well be dependent on rapid adaptation to them (Naylor 1983).

It should be pointed out that this experiment, as with many others, is a dormancy ‘snap-shot’ of fresh seeds from the different populations. As shown in Section 3.1, dormancy of seeds of common heliotrope (as with many other species) is cyclic in nature, and it is likely that the precise seasonal behaviour of each of the populations will also differ. Gill (1985) considered such temporal issues and found that the duration of dormancy of seeds of *Bromus diandrus* (a Mediterranean winter annual) from different populations in southern Australia corresponded with the duration of dry summers at the different sites from which they were collected. Dunbabin (1999) likewise found that the seasonal dormancy pattern of different populations of *Arctotheca calendula* varied with environment.

The results of this experiment support the argument that different populations of weed species are likely to have different dormancy characteristics, whether or not they vary predictably with measurable climatic attributes. This should be taken into consideration when attempting to quantify the limits to germination of weed species.

### 3.3. References


### 3.4. Appendices

**Appendix 3.1. ANOVA tables – effects of temperature and water potential and interaction of temperature and water potential on arcsine transformed germination extent at different times of the year.**

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Appendix 3.2. ANOVA table – effects of population, temperature and water potential and factorial interaction of all three on arcsine transformed germination extent.

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Appendix 3.3. ANOVA tables – effects of population, temperature and water potential and factorial interaction of all three on median time to germination.

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Chapter 4 – Water Relations & Physiology

4.1. Introduction

Plants growing in arid regions are frequently found to possess unique biological attributes which provide them with strategies to increase their chances of survival and reproduction in these environments, where water availability is uncertain and is the primary limit to growth. Many plants, including common heliotrope, endure unfavourable conditions as durable seeds, germinating only once conditions are perceived as favourable for growth and reproduction. The success of ephemeral annual species such as common heliotrope depends on its seeds germinating during periods when the environment is suitable for completion of the life cycle, and not germinating when it is unsuitable (Freas and Kemp 1983).

In arid species, the environmental cue for germination is usually associated with the availability of water arriving in discrete, infrequent rainfall events (Guttermann 1993). This is in contrast to most published work existing on germination ecology, which has focussed on species from environments where growth is not limited by water availability (Baskin and Baskin 1998). The timing and quantity of water delivered by individual rains, not total seasonal rainfall, are the parameters critical to the germination ecology of arid species (Beatley 1974). This is certainly the case for common heliotrope, where field emergence is triggered by discreet summer rainfall events, which in the plant's range are highly variable in both timing and magnitude. Given this uncertainty, germination in response to rainfall events that are too small to support plant growth to the point of successful reproduction is an enormous risk, as no further rain may fall for the remainder of the season. This would result in plants suffering, quite literally, a fruitless death. This constitutes an enormous selection pressure on common heliotrope to germinate only in response to rainfall events of sufficient magnitude to give a high probability of sustaining growth up to the production of viable seed. The central hypothesis of this chapter is that selection in common heliotrope has occurred through the underlying relationship between fecundity (or the probability of reproduction, rather than simply seed production under good conditions) and the magnitude of the rainfall event which triggers germination (Figure 4.1).
It is known that seeds of arid annual species germinate only after a threshold amount of rain has fallen (Tevis 1958). Kigel (1995) states that the amount of rain required for germination in species growing in regions where water is the primary limit to growth is not merely a function of moisture requirements for germination, but also for continued reproductive success. Therefore, it is my hypothesis that the minimum threshold amount of rain required for emergence of common heliotrope corresponds to the minimum amount of rain required to sustain growth until plants have successfully reproduced. That is, that germination in the species is directly sensitive to environmental factors favourable for reproduction.

![Figure 4.1](image-url)  
**Figure 4.1.** The underlying relationship between the magnitude of the initial rainfall event which triggers germination in common heliotrope and fecundity.

Such a strategy is also likely to exist in other species with similar niches. Within the literature, similar hypothesised germination strategies observed in arid species have been termed 'predictive germination'. Smith, Riley *et al.* (2000) defined predictive germination as germination that is directly sensitive to environmental factors associated with conditions favourable for immediate seedling growth. However, it is a term also used to describe the positive relationship between emergence densities and suitability of conditions for growth (Freas and Kemp 1983; Pake and Venable 1996). The positive relationship between emergence densities and suitability of conditions for growth is viewed as a species both 'managing' its density to achieve maximum reproductive output for the prevailing conditions, and spreading the risk of failure by maintaining ungerminated seeds in the soil. As stated in this thesis, other workers have concluded that the amount and temporal distribution of available soil moisture are the primary
environmental variables upon which predictive germination behaviour in arid species is likely to be based (Gutterman 1993; Smith, Riley et al. 2000). As mentioned previously, the amount of rain required for germination in species growing in regions where water is the primary limit to growth is not merely a function of moisture requirements for germination, but also for continued reproductive success (Kigel 1995). I therefore suggest that the definition of predictive germination be strengthened by specifying that it is germination that is directly sensitive to environmental factors associated with conditions under which there is high probability of growth being sustained until plants have successfully reproduced.

The bulk of the literature regarding the germination ecology of arid species tends to focus on seed dormancy (Smith, Riley et al. 2000), and little attempt has been made to quantify and link conditions which result in emergence with conditions required for reproduction. If such a link can be made, it would provide clear evidence of a strategy of obvious importance to the success of species growing in arid and uncertain environments. This chapter is divided into three sections, the first two of which investigate such a link in common heliotrope. The first section describes an experiment using simulated rainfall to estimate the minimum threshold amount of rainfall that will result in emergence of common heliotrope under typical field conditions. The second section describes an experiment using plants of common heliotrope grown in lysimeters under typical field conditions to estimate the minimum amount of rainfall required for common heliotrope to achieve a minimal reproductive output. The third section focuses on the root growth of common heliotrope, another biological feature that is critical to the success of the species in an arid environment. It consists of a controlled laboratory experiment that measured rate of root elongation at different temperatures, observations that described root development following emergence in the field, and a description of the growth of lateral roots in mature plants in response to rainfall.

4.2. Emergence in response to simulated rainfall

4.2.1. Introduction

Simulation of rainfall is a useful method for measuring the emergence response of arid and semi-arid species reliant on discrete rainfall events for germination. Recent studies
that have made use of the technique include that of Brown (2002), who studied the
effect of differing amounts of simulated rainfall on the density, biomass and floristic
composition of arid winter annual communities in Kuwait. Smith et al. (2000) used line-
source irrigation (Johnson, Rumbaugh et al. 1982) in a greenhouse to determine the
minimum amounts of simulated rainfall required for significant emergence of different
populations of the perennial desert grass Digitaria californica.

No attempt has previously been made to experimentally quantify the minimum amount
of rainfall required for emergence of common heliotrope, nor the effect (if any) of
increased rainfall amount on emergence density. Such information would not only be
useful for forecasting occurrence, but potentially of tremendous biological interest with
regard to the concept of predictive germination discussed in the introduction to this
chapter.

It is known that seeds of arid annual species germinate only after a threshold amount of
rain has fallen (Tevis 1958), but this is something of a simplification. Seeds themselves
cannot perceive an actual amount of rainfall, but germination rate and extent are greatly
influenced by the water potential that seeds are exposed to (Chapter 2). It is my
hypothesis that that the mechanism which underlies emergence only in response to a
threshold amount of rainfall is the individual seed’s germination response to water
potential and time, as outlined in Chapter 2. In order for a seed to germinate, a
physiological process must reach completion that requires exposure to water potential
for a certain duration. The results of Chapter 2 indicate that such a process takes longer
to reach completion at more negative water potentials. Presumably, there is a threshold
potential below which the process stops and seeds will not germinate regardless of
duration of exposure to sub-threshold potentials (Figure 2.11).

Soil water potential at the top of the soil profile approaches zero during and
immediately after rainfall, and then starts to decrease as the soil drains and the water
evaporates. Following rainfall, the water potential that seeds in the soil are initially
exposed to is a function of the rainfall amount and the structure and composition of the
soil. The duration for which seeds in the soil are exposed to a given water potential is a
function of soil structure, composition and surface conditions (e.g. mulch, living plants)
and meteorological conditions. The response of seeds of common heliotrope to the
magnitude and duration of water potentials that they are exposed to is a function of
temperature (Chapter 2) and endogenous control mechanisms (dormancy) which cycle seasonally and vary between populations (Chapter 3). If a seed in the soil is not exposed to water potentials above the process threshold for the required length of time, the process will not reach completion and the seed will not germinate. Rainfalls of greater magnitude result in soil water potentials being less negative for longer than comparatively smaller rainfalls. This is due to the effect of the volume of water on soil water potential, duration of actual rainfall, and reduction in evaporation due to higher humidity. Consequently, I propose that the critical parameters associated with this hypothetical physiological process have been naturally selected for, such that given the climatic generalities of common heliotrope’s environment, satisfaction of the requirements of the process is provided by a threshold amount of rainfall. However, the threshold amount of rain required for emergence of common heliotrope will be subtly specific to soil type and surface condition, prevailing meteorological conditions, population and dormancy level. The effect of different soil types on water availability and duration is considered in Chapter 5.

The aim of this experiment was to determine the effect of simulated rainfall amount on the density of common heliotrope emergence, and to determine a minimum rainfall amount that leads to the emergence of common heliotrope in the field. If, as Kigel (1995) suggests, the minimum threshold amount of rain required for the emergence of common heliotrope is associated with the amount of water required for successful reproduction, the former parameter is likely to be relatively high. This is suggested by the high evaporation rates inherent within the plant’s spatial and temporal range. A high minimum threshold amount of rain for emergence is also suggested by the results of Chapter 2, which found that the germination of seeds of common heliotrope were comparatively sensitive to increasingly negative water potentials.

4.2.2. Methods

Black plastic rings 0.45 m in diameter and 0.4 m in depth were buried in the field at Normanville (see Section 2.4.2 for location information) in autumn 2001. The soil type at the site is an Epihypersodic, Pedal, Hypercalcic Calcarosol (Isbell 1996) with a clay loam surface texture and clay subsoil. Soil horizon integrity was preserved by returning
them in the reverse order to which they were removed. Approximate bulk density was preserved by ensuring that all soil was replaced into the same volume from which it was initially removed. The rings were located in a randomised complete block design with five replicates of each treatment. Winter annuals were allowed to germinate in the rings (principally capeweed, *Arctotheca calendula*, and barrel medic, *Medicago truncatula*). In spring 2001, rain shelters were placed over the rings to prevent natural rainfall causing germination. In January 2002, the rings were watered with four different simulated rainfall treatments: 15, 25, 50 and 100 mm. The water used in the experiment was rainwater collected from the roofs of agricultural out-buildings and stored in concrete tanks. The water was applied at a rate of approximately 50 mm hour\(^{-1}\) using drip-irrigation in order to prevent ponding, and associated dispersion of soil aggregates and draining of water through preferred pathways. The rings were then covered with hessian for 48 hours after watering to simulate post-rainfall climatic conditions. *This experiment was initially attempted without the use of hessian in February 2001, and again in December 2001, and no germination of heliotrope was recorded. This was attributed to simulated rainfall being unable to successfully mimic equivalent amounts of genuine rainfall due to the absence of other climatic conditions associated with rainfall, such as increased humidity and depressed temperature and radiation. This resulted in the small areas of moist soil that had received simulated rainfall drying out much quicker than if genuine rain had fallen on the entire region. This phenomenon has been observed by Keya (1997) and Tevis (1958), and is considered further in Section 4.2.4. The hessian was used to increase the relative humidity of the air immediately above the soil in the rings, and to decrease radiation reaching the soil, and thus mimic the climatic effects associated with rainfall.*] Emergence was counted daily, and emerged cotyledons removed.

### 4.2.3. Results

Figure 4.2 shows that emergence density increased with increasing rainfall, and that while no emergence was observed in the 15 mm treatment, a small number of plants emerged in the 25 mm treatment. The minimum threshold amount of rainfall that results in emergence must therefore lie between 15 and 25 mm. To estimate the minimum threshold, the 15 mm treatment was discarded and a rectangular hyperbola
was fitted using the MLP software package (Ross 1987) to the remaining three points (Figure 4.2.1.).

For values of \( y \) greater than zero, this curve is plausible as it assumes a flat topped response, reflecting the maximum emergence density that will be reached (\( a \)), beyond which greater rainfall will have no effect. The fit was weighted, using \( \frac{1}{\sigma^2} \) for each of the rainfall treatments as the weight so as to correct for unequal variances. The estimated value of the upper asymptote was 475 plants m\(^{-2}\) while the minimum threshold amount of rainfall required for the germination of common heliotrope (the value of \( x \) when \( y = 0 \)) was estimated as 24.2 mm (standard error = 2.5).

\[
y = a + \frac{b}{1 + dx}
\]

Equation 4.1

**Figure 4.2.** Mean density of the number of emerged common heliotrope plants in the different simulated rainfall treatments (●), and the rectangular hyperbola (solid line) fitted to the three non-zero data points. Error bars are ± the standard error of the mean.

### 4.2.4 Discussion

The results of this experiment indicate that 24 mm of rain is the threshold amount required for germination of common heliotrope in this particular soil and under these temperatures (Figure 4.2). A slight overestimation of the minimum threshold amount of rain required for germination is suggested by the smallest rainfall resulting in emergence recorded in three years of field observation being 17 mm (Table 4.1). A
minimum threshold amount of rain required for emergence of common heliotrope of about 24 mm is supported by the observations of other workers. Sheppard (1996) suggests that 10 mm may be sufficient to allow germination but that 25 mm is required to ensure population establishment. Fromm (2000) suggests that the minimum threshold rainfall resulting in germination may be the amount required to wet the top 0.25 m of soil to field capacity, which is equivalent to 26 mm on the soils in which that study was conducted (sandy loam with field capacity in top 0.25 m of soil of 21.9 % volumetric water content, air dry water volumetric water content 11.4 %, N. Dalgliesh, A. Jackman and R. Liston unpublished data). Studies carried out on other summer annuals in arid environments indicate similar threshold amounts of rainfall across many species. Mott (1974) reported that in order for the soil surface to remain at field capacity for the 48 hours required for the germination of the summer flora in the arid Murchison region of Western Australia, at least 25 mm of rain must fall. This is the same amount of rainfall required for emergence of summer ephemerals in the Mojave desert (Tevis 1958). Wester (1986) found that 11 mm of rain was not sufficient to allow emergence of the grasses *Eragrostis curvula* and *Panicum coloratum*, but that 19 mm was.

The value of 24 mm found here is likely to be in the upper range of reasonable estimates for a number of reasons. Firstly, the experiment was conducted during the month of January, which is when evaporation rates in the area are at a yearly maximum. This means that the water potentials that the seeds are exposed to become more negative at a greater rate than if evaporation rates were lower. It is also approximately at this time of year that dormancy starts to increase (Chapter 3). If the experiment had of been conducted in November, the threshold amount of rainfall is likely to have found to be lower. That is, the impact of rainfall on emergence is different at different times of the year due to cyclic dormancy and prevailing environmental conditions, and that this experiment was conducted at a time of year when minimum threshold rainfall is likely to be very high. Thirdly, the curve was fitted to only three data points, which makes estimation of curve parameters prone to error. Finally, as discussed subsequently, there are inherent differences between real and simulated rainfall which frequently result in underestimation of emergence density in simulation studies (Keya 1997; Tevis 1958).

However, significantly less rainfall has been found to result in the emergence of *Tribulus terrestris*, a species which shares many ecological attributes with common
heliotrope and co-occurs in the Victorian Mallee. Squires (1969) reported that a rainfall of 11 mm was sufficient to allow emergence of *T. terrestris* in south eastern Australia, while Ernst (1988) found that rainfall in excess of 10 mm resulted in germination of that species, and the invasive semi-arid annual grass *Tragus berteronianus*, in semi-arid regions of Botswana. This was in contrast to the 20 mm required for the germination of indigenous species in the same region (Veenendaal and Ernst 1991). This observation highlights a point made by Brown (2002), that species-specific minimum rainfall thresholds result in floristic differences dependent on the amount of rain falling in given germination events. For example, in an agricultural field in south-eastern Australia with seed banks of both common heliotrope and *T. terrestris*, an initial germinating rainfall of less than 15 mm will hypothetically result in an infestation of caltrop, but not common heliotrope. A rainfall in excess of 24 mm will result in a mixed infestation, which has implications for control.

Whilst lower threshold rainfall could indicate that *T. terrestris* has a temporal niche different to that of common heliotrope (e.g. emerges earlier in spring when evaporation rates are lower), observations made during the course of this study indicate that it emerges at the same time as common heliotrope. However, its reproduction has been observed to be very rapid, perhaps more so than that of common heliotrope.

Table 4.1. Rainfall events that did and did not result in the emergence of a cohort of common heliotrope. Only rainfall events between 5 and 30 mm are shown. Rainfall was recorded at all field sites using methods described in Chapter 1.

<table>
<thead>
<tr>
<th>Emergence</th>
<th>Rainfall (mm)</th>
<th>No Emergence</th>
<th>Rainfall (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jil Jil 22 January 2002</td>
<td>28</td>
<td>Normanville 21 March 2001</td>
<td>9</td>
</tr>
<tr>
<td>Normanville 22 December 2000</td>
<td>17</td>
<td>Normanville 22 January 2002</td>
<td>9</td>
</tr>
</tbody>
</table>

Figure 4.2 shows that there was a significant positive relationship between rainfall amount and density. An increase in emergence density with increased rainfall in arid annual species is a common trait (Freas and Kemp 1983; Pake and Venable 1996; Smith, Riley *et al*. 2000; Tevis 1958). In the case of common heliotrope, the germination requirements are now thoroughly understood (see Chapter 2 & 3), and it is possible to hypothesise that this observed increase in density with rainfall is a result of the reduction in percentage germination at the sub-optimal water potentials and temperatures found in the field. Given that the optimum water potential for germination
is 0 MPa (free water); seeds in the soil will almost always be exposed to sub-optimal water potentials, and as a result only a fraction of the seed bank population will germinate and emerge.

To some degree, all species will exhibit increased emergence density with increased rainfall due to the well established relationship between germination rate and extent and water potential. However, how emergence in arid annual species responds to increasing water availability in comparison to temperate species would be a research question of great interest. It can be hypothesised that arid annual species will show a more conservative and gradual increase in density with water availability, whereas temperate species will be less conservative as water availability is not such a crucial limit to their reproductive success (Figure 4.3). Such a comparative study could further elucidate whether the increased germination seen in common heliotrope with increased rainfall is a trait crucial to the reproductive success of arid annual species, or is purely due to germination requirements and is ecologically irrelevant.

![Figure 4.3. The hypothetical response in emergence density to increasing water availability of an arid and a temperate annual species.](image)

Theoretically, increased emergence density with increasing rainfall is ecologically sensible given the habitat and biological attributes of common heliotrope. The soil water available from a germinating rainfall event is a finite resource, and if the establishing population density is too great, it may all be transpired before plants can reproduce. If, however, a lower population density establishes, minimum reproduction is more likely, and if further rain falls or sub-soil moisture reserves exist, the indeterminate growth and flowering of common heliotrope can compensate for low density. The mechanism
behind increasing germination with rainfall would be a varying fastidiousness in germination requirements among a population of seeds as described in Chapter 2. In this context, varying fastidiousness would be selected for in individual seeds as chances of reproductive success would be increased if germination were temporally disparate for different fractions of the population, reducing intra-specific competition and thus increasing the chance of reproductive success for individuals that do germinate. Such a trait would also be selected for in a population as it spreads temporal risk of germination, and will also benefit non-germinating individuals by reducing the intra-specific competitive pressure on them when they germinate.

Differing variation in fastidiousness would result in the different hypothetical emergence responses of an arid and temperate annual to increasing rainfall described in Figure 4.3. The arid annual would not only have more fastidious germination requirements with respect to water availability, but also have greater variation in this fastidiousness.

There are several shortcomings associated with field simulation of rainfall that deserve discussion. As mentioned in Section 4.2.2, the environmental effects of rain extend beyond a given amount of water falling onto the soil surface, which is essentially all that simulated rainfall replicates. A myriad of environmental effects associated with rainfall, principally decreased radiation and temperature and increased humidity and resultant decreased evaporation, are near impossible to simulate realistically. Consequently, a given amount of artificial rain will be significantly less, biologically speaking, than an equal amount of genuine rain, as the soil water potential will become more negative at a greater rate. This is particularly the case in the top few centimetres of soil, which has greater exposure to atmospheric conditions in comparison to deeper layers, and is where the emerging seeds are located. This has been previously alluded to by Tevis (1958): "...real rain demonstrated an extraordinary superiority over the artificial variety to bring about a high rate of germination.", but is frequently ignored in studies featuring artificial rainfall (Brown 2002; Freas and Kemp 1983; Lafond and Fowler 1989), and in some cases completely misinterpreted. Keya (1997), for instance, found that emergence did not occur in the field following application of amounts of simulated rainfall equivalent to genuine rainfall events after which germination occurred. After noting that potential evapotranspiration in the study area decreased from
13 mm day$^{-1}$ to 4 mm day$^{-1}$ immediately prior to rain and 1 mm day$^{-1}$ during rain, he concluded that seeds contain some form of 'biological clock' which requires triggering by a combination of environmental factors, such as increased humidity and decreased radiation, before germination can occur. A lengthening of the duration of soil moisture sufficient to allow germination caused by a reduction in evaporation due to the climatic effects associated with rainfall is a far more parsimonious explanation. This explanation is also given support by the initial failure of this experiment before the problem of replicating genuine rainfall conditions was countered by using a hessian bag covering the treatments to approximate crudely the radiation and humidity conditions associated with rainfall. The realism that the hessian was able to achieve is unknown, but the 24 mm outcome is well within the limits of reasonable results. Smith (2000) appears to have attempted to overcome the same problem by waiting until a three day period of 60% relative humidity was forecast before commencing watering experiments. Such a technique is of tremendous validity, but places serious constraints on the timing of an experiment.

Despite these limitations, simulated rainfall is a useful method for studying the germination ecology of species whose emergence is limited by rainfall. This is particularly the case if results are combined with field observation or determination of minimum rainfall by mechanistic simulation. As mentioned in Chapters 2 & 3, it was the initial aim of this project to mechanistically estimate minimum rainfall requirements for common heliotrope emergence. This was to be achieved by coupling a model of hydrothermal time parameterised for common heliotrope with a model of soil temperature and water flux (Daamen and Simmonds 1996). However, as mentioned in previous chapters, this was not possible to achieve owing to non-conformity of common heliotrope to the assumptions of the model of hydrothermal time and inadequacy of data to create an alternative model.

4.3. Lysimeter growth of common heliotrope

4.3.1. Introduction

Given the strengthened definition of ‘predictive germination’ made in Section 4.1, common heliotrope provides an excellent model with which to enhance understanding
of the germination behaviour of arid summer annuals. The minimum amount of rainfall required for germination has been measured experimentally (Section 4.1), as have environmental and temporal limits to germination (Chapters 2 & 3). If the amount of water required by common heliotrope to reach a minimal reproductive output were to be quantified, the relationship between these biological attributes would offer a previously hidden glimpse into the mechanisms of arid germination ecology. Thus the aim of this experiment was to quantify the amount of water common heliotrope must transpire under field conditions to produce a minimal reproductive output.

The existence of predictive germination will be strongly supported if the minimum threshold emergence rainfall approximates the cumulative amount of water transpired by common heliotrope and evaporation up to the point of minimal reproductive output. Even though the environment which common heliotrope inhabits is extraordinarily desiccating (Chapter 1), the actual amount of water lost from the soil to transpiration and evaporation will not be as high as crude pan evaporation rates, which average around 8 mm day\(^{-1}\) in the region from November through to January (2004). As mentioned in Chapter 1, evaporation from deeper layers of soil devoid of vegetation is limited owing to the hydraulic insulation provided by the dry upper layers (Dalgliesh and Foale 1998). Also mentioned in Chapter 1, the phenology of common heliotrope is extraordinarily rapid, with flowering commencing three weeks after germination when plants have developed only their third pair of true leaves. As a result, leaf area up to minimal reproductive output, and consequently transpiration, is relatively low.

4.3.2. Methods

Plastic stormwater pipe, 90 mm in diameter, was cut into 0.4 m lengths. The resulting tubes were hammered into soil at Normanville (see Section 2.4.2 for location), which was an Endohypersodic (and Vertic) Pedal Hypercalcic Calcarosol (Isbell 1996), of sandy loam in texture and with a bulk density 1.27 Mg m\(^{-3}\). These tubes were then dug out so that an intact core of the soil profile remained in each tube. The bottom of the tube was covered with a fine plastic mesh to prevent soil from falling out, and the tops of the pots were moistened by spraying them with water. Seeds of common heliotrope harvested at Normanville in April 2002 and kept in cold storage were then sown in each
pot and approximately 10 mm of wet soil was added to the top of each pot in order to cover the seeds. The pots were then watered daily until at least one seedling had emerged in each pot. Whilst the seedlings were still in the cotyledon stage, the soil in the tubes was saturated by allowing them to soak almost entirely submerged in water for 2 hours. After this period, the pots were drained for 1 hour and then sealed at the top and bottom with 90 mm Petri dish lids and plastic cement such that they were air- and water- tight, except for a small hole (5 mm diameter) through which the growing heliotrope seedling protruded. The tubes were weighed and then buried at the Normanville field site on 22 January 2003 such that only the above-ground parts of the plants were protruding from the soil. Control tubes were also buried which had been likewise soaked, drained, sealed and weighed but had no plants in them. These tubes were used to estimate the evaporative loss out of the 5 mm aperture in the lids of the pots.

The plants were allowed to grow for two weeks before the first harvest. At each harvest, five pots with plants in them and five controls were removed at random and were weighed. The leaf area, rooting depth and dry weight of above- and below- ground parts were recorded. Harvests were repeated three times at two-week intervals. The amount of water used by each plant was calculated by subtracting the harvest weight of the pots and dry matter weights from the initial weight of the pots, and then further subtracting the amount of evaporation from the control pots. It was initially intended that more harvests would be made. However, the plants died of drought after the third harvest.

4.3.3. Results

Table 4.2 shows the volume of water used by the plants at the different harvest times, their status and reproductive output. In the 43 days from when they were placed in the field, the common heliotrope plants were able to achieve a minimal reproductive output whilst each transpiring a mean total of 494 ml of water.
Table 4.2. Mean volume of water used by the plants over the growth period, status of plants and reproductive output. Evaporation as calculated from the control tubes has been subtracted. Standard errors are given in parentheses.

<table>
<thead>
<tr>
<th>Time (Days)</th>
<th>Water Transpired (ml)</th>
<th>Status</th>
<th>Seed Production (seeds per plant)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>Alive</td>
<td>0</td>
</tr>
<tr>
<td>15</td>
<td>98 (14)</td>
<td>Alive</td>
<td>0</td>
</tr>
<tr>
<td>30</td>
<td>304 (41)</td>
<td>Stressed</td>
<td>10 (6)</td>
</tr>
<tr>
<td>43</td>
<td>494 (10)</td>
<td>Dead</td>
<td>43 (12)</td>
</tr>
</tbody>
</table>

In order to estimate an amount of rainfall from the volume of water transpired by successfully reproducing individual plants of common heliotrope, several assumptions about the biotic and physical environment of common heliotrope were made. The amount of water available to a single common heliotrope plant is a function of rainfall amount, plant density and evaporation.

\[
\text{water} = \left( \frac{\text{rain}}{\text{density}} \right) - \text{evaporation}
\]

Equation 4.2

Calculations were based on a density of 30 plants m\(^{-2}\), which is a typical field infestation density observed in the Victorian Mallee after germinating rainfalls of 20-30 mm (see Chapter 1). Plants were assumed to be evenly distributed and intra-specific competition assumed equal for all plants, and thus not considered. This effectively simplifies the system into single plants occupying individual soil 'cells' of an area dependent on plant density. The amount of water available to an individual plant is assumed to be the amount of rain falling in its cell, minus evaporation. With a density of 30 plants m\(^{-2}\), the area of the surface of each plant's cell is 33.3 x 10\(^{-3}\) m\(^2\).

The volume of water required for transpiration leading to a minimal reproductive output in the experiment is 494 ml, or 4.94 x 10\(^{-3}\) m\(^3\). The depth of this amount of water in each plant's soil cell of known area can be calculated from the equation for the volume of any shape with parallel sides, e.g. a cylinder

\[
v = dr^2
\]

Equation 4.3

and therefore

\[
d = \frac{v}{\pi r^2}
\]

Equation 4.4

where \(v\) is the volume of the cylinder, \(d\) is its depth and \(r\) is its radius. The radius of a circle of 33.3 x 10\(^{-3}\) m\(^2\) in area can be calculated by rearrangement of the equation for
the area of a circle \((a = \pi r^2)\), and is 0.329 m. Therefore the depth of 494 ml of water in a cylindrical soil cell of surface area \(33.3 \times 10^{-2} \text{ m}^2\) is 14.5 mm. So, at a density of 30 plants \(\text{m}^{-2}\), a crude estimate is that 14.5 mm of rain is required for transpiration up to a stage of minimal reproductive output during summer in the Victorian mallee.

From field data and models of soil water transport (SWEAT, see Chapter 5), it is known that in a soil surface devoid of vegetation, evaporation from deeper layers of soil is limited after the surface layers become dry and form a layer of hydraulic insulation. Consequently it is reasonable to assume that the soil water in the top 50 mm of soil following rainfall is completely lost to evaporation, the remainder being available for plant transpiration. Assuming soil bulk density of 1.3 Mg m\(^{-3}\), a drained volumetric water capacity of 20 % and air-dry volumetric water capacity of 5%, the top 50 mm of this soil will hold 7.5 mm of rainfall (Dalgliesh and Foale 1998). Therefore, the total amount of rainfall required for common heliotrope to reach a minimum reproductive stage is the sum of the above values of transpiration (14.5 mm) and evaporation (7.5 mm), and is equal to 22 mm.

### 4.3.4. Discussion

The estimate of 22 mm as the amount of rainfall required for minimal reproductive output by plants of common heliotrope corresponds well with the finding that 24 mm of rain is the minimum amount required for successful emergence of common heliotrope in the field. As mentioned in Section 4.2, the estimate of 24 mm as the minimum threshold amount rain for germination is likely to be slightly high. This is due to the shape of the fitted curve from which the value was estimated, problems associated with mimicking rainfall, and the time of year at which the experiment was conducted. Consequently, the two figures may be viewed as being in very good agreement.

Obviously, the amount of rainfall required for minimal reproductive output will vary with soil type and evaporative conditions. This experiment was conducted during late January and early February, which is when evaporation in the region is highest for the year (a pan evaporation of 9.1 mm day\(^{-1}\) is the long term average for the month of January at Walpeup (Anon. 2004), and as a result, the estimate of 22 mm will be at the upper end of the range of actual amounts of rainfall required for minimal reproductive output. Plants that germinate in late spring when evaporation is less (6.9 mm day\(^{-1}\) for
November at Walpeup) will theoretically require less water to achieve minimal reproductive output. Further evidence that the minimum amount of rainfall required for germination and the amount of rainfall required to achieve minimum reproductive output are linked is provided by the cyclic behaviour of common heliotrope's germination requirements, as elucidated in Chapter 2. Less fastidious water requirements for germination in late spring will result in emergence after smaller rainfall events and in greater equivalent densities than in late summer when these requirements become more fastidious.

These results support the hypothesis that common heliotrope possesses predictive germination essentially capable of detecting when conditions are suitable for the achievement of minimal reproductive output. It would benefit our understanding of arid germination ecology if the relationship between germination requirements, minimum amount of rainfall required for emergence and the amount of water required for minimal reproductive output was investigated in other arid summer ephemerals. For example, it would be of tremendous interest to quantify the amount of rainfall required for minimal reproductive output of *Tribulus terrestris*, which requires significantly less rainfall for emergence than common heliotrope (Ernst and Tolsma 1988; Squires 1969). To date, only fragments of information exist for any given species, making the existence of predictive germination purely speculative at this point. Although the minimum rainfall required for emergence has been quantified for many arid summer annuals (Section 4.2), there has not been a corresponding interest in minimum amounts of rainfall required for reproductive output. The only value given in the literature is by Keya (1997), who reported that the perennial grass *Leptothrium senegalense* emerged and reproduced successfully after 31.9 mm rain fell in 34 days in the arid savannah region of Kenya. Even this is not a quantified minimum, merely an observed value. In addition, studies must think in terms of soil moisture duration rather than rainfall amount if they are to have application beyond the soil type on which the experiment was conducted (see Chapter 5 for a discussion of this).

An important biological attribute of common heliotrope that compliments its apparent predictive germination is its indeterminate growth and flowering. As mentioned in Chapter 1, flowering commences in common heliotrope three weeks after germination and continues until death by drought or senescence (Moore 1956). Consequently, whilst
minimal reproductive output is virtually guaranteed by germination requirements, common heliotrope can respond to more water becoming available (through further rainfall or roots reaching sub-soil reserves) by massively increasing growth and reproductive output. This will be dealt with in the next section.

4.4. Root growth in common heliotrope

4.4.1. Introduction

Moore (1956) and Dellow (1987) suggested that the rapid growth of a strong tap-root with which to access sub-soil moisture is an important biological attribute of common heliotrope. The findings of Section 4.3 indicate that sub-soil moisture may not be as important to the survival of common heliotrope as thought. If plants are able to reproduce entirely on the water available from the rainfall event that allowed them to emerge, which can be as little as 24 mm (Section 4.3), all this water can be available in the top 0.2 m of most soil profiles. Further to this, at the time common heliotrope is emerging, soil profiles in the region are frequently very dry. This is particularly the case beneath crop stubbles and senesced pastures that will have had all available moisture transpired by the crop or pasture. Consequently, there are layers of dry soil through which plant roots cannot grow (Passioura 2002), between the moist upper layers following a germinating rainfall event and any moist subsoil. Subsoil moisture will only be a potential resource for common heliotrope if the rainfall causing emergence (or subsequent rain) is of sufficient magnitude to wet the soil profile down to any previously existing moisture. Given these considerations, it is more likely that common heliotrope will present a pattern of root growth indicative of methodical exploitation of the moist layers of soil available to it, and not necessarily a rapid downward growth to the subsoil as hypothesised by earlier authors. This section will describe post-emergence root growth and structure of common heliotrope in order to further understand water use in the species. As common heliotrope primarily acts as a weed by depriving subsequent crops of water, an understanding of where common heliotrope obtains water for its growth is very important.

The survival and reproduction of plants in arid environments is dependent, in part, on their ability to respond quickly to short term increases in water and nutrients
Increased water acquisition in response to rainfall may occur through new root growth, elongation of existing roots and stimulation of uptake capacity of existing roots (Ivans, Leffler et al. 2003). This section also describes opportunistic observations made in the field indicating that common heliotrope increases water acquisition through rapid new root growth.

4.4.2. Methods

Rate of root growth in a controlled environment

Sandy loam soil (an Endohypersodic and Vertic Pedal Hypercalcic Calcarosol; Isbell 1996) taken from near Walpeup (S 35° 54' 24" E 141° 59' 53", 99 m above sea level) was sieved and pasteurised before being packed to original bulk density (1.3 Mg m$^{-3}$) into pots made from 90 mm diameter storm water pipe cut into 0.4 m lengths. The bottom ends of the pots were covered with fine plastic mesh in order to allow them to drain and prevent the soil from falling out. Twenty pre-germinated seeds were sown at a depth of 10 mm in each pot and the pots saturated with water and allowed to drain.

Four controlled temperature rooms provided four different temperature treatments. The temperature in each room was recorded using four Dataflow 906 temperature sensors placed among the pots and connected to a Dataflow DS93 data logger (Dataflow Systems, Caboolture, Australia). The mean temperatures and standard errors (in brackets) of the different rooms over the duration of the experiment was 17.1 (0.3), 20.3 (0.1), 26.5 (0.2) and 31.8 (0.7) °C. The lighting in each room was provided by 32 fluorescent tubes with a light/dark periodicity of 14/10 hours.

Thirty-five pots were then allocated to each temperature treatment, allowing for seven destructive harvests to be made on five replicates at each harvest. At each harvest, five pots from each treatment were selected at random, and the plant roots in each pot were carefully washed from the soil. The distance from the root/shoot interface to the root tip was measured with digital callipers while plants were suspended in water, and the root not stretched. This meant that what was being measured was effectively root depth in
the soil. The first harvest took place two days after sowing, and harvests were repeated every two days subsequently, for a total of 7 harvests over 14 days.

Field observation of post-emergent root growth

Following emergence of common heliotrope at the Jil Jil field site (see Section 1.4.2 for a location description) in January 2002, observations and measurements of root growth were made regularly over a period of weeks. For each measurement, a large ditch was dug around a group of plants at each of the ten permanent quadrats (see Chapter 1), and the soil surrounding each plant's root system was carefully washed away using a pressurised water sprayer. The maximum depth to which roots had penetrated, depth of branching, and root length were measured with digital callipers.

Field observation of growth of new roots in response to a small rainfall event

During a field trip to Normanville (see Section 2.4.2 for location description) on 20 March 2001, it was noticed that mature plants that had emerged following rain on 21 December 2000 had a profusion of new lateral roots around the main taproot immediately below the soil surface. It was hypothesised that this was an opportunistic response to 6 mm of rain that fell on 16 March 2001. This hypothesis was supported by the observation that plants growing under the rain shelters used for the experiment outlined in Section 4.2 did not have any roots growing from the main tap root near the soil surface (Figure 4.6). It was further hypothesised that the architecture of the aboveground parts of common heliotrope was such that water falling on plants would run down the plant's branches to the main stem, concentrating water in the zone where the opportunistic roots emerge. On 21 March 2001, a further 9 mm of rain fell. In order to test the second hypothesis, the volumetric water content (VWC) of the soil at increasing distances surrounding 7 mature plants approximately 0.3 m diameter was measured using a time-domain reflectometry probe connected to a Hydrosense™ display unit (Decagon Devices, Pullman, U.S.A.).
4.4.3. Results

Rate of root growth in a controlled environment

Maximum root depth elongation at different temperatures following germination is presented in Figure 4.4. Root elongation was approximately linear in behaviour, and the rate of elongation increased with temperature, with the highest rate being observed in the 31.8°C treatment. A linear function was fitted to describe growth at each temperature, with the gradient of the function being equivalent to the growth rate of the roots at each temperature (Table 4.3). An analysis of parallelism using Genstat 5 (Genstat 5.0, Rothamsted U.K.) found that the growth rates at different temperatures were significantly different (p<0.05) from each other, except for the 20.3 and 25.5°C treatments (Table 4.3).

![Figure 4.4](image)

**Figure 4.4.** Root depth growth of pre-germinated seeds of common heliotrope over time at 17.1 (○), 20.3 (■), 26.5 (●) and 31.8°C (□) and regression lines for each temperature (—). Error bars are ± the standard error of the mean.

**Table 4.3.** Growth rate of common heliotrope root depth at different temperatures estimated by linear regression for each temperature. Growth rates with a different letter are significantly different (p<0.05) as determined by analysis of parallelism.

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Growth Rate (mm day⁻¹)</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>17.1</td>
<td>2.1        a</td>
<td>0.96</td>
</tr>
<tr>
<td>20.3</td>
<td>3.9        b</td>
<td>0.96</td>
</tr>
<tr>
<td>26.5</td>
<td>4.2        b</td>
<td>0.90</td>
</tr>
<tr>
<td>31.8</td>
<td>5.6        c</td>
<td>0.94</td>
</tr>
</tbody>
</table>
Field observation of post-emergent root growth

Figure 4.5 shows the maximum root depth of plants of common heliotrope in the field at Birchip following a germinating rainfall of 28 mm on 22 January 2002. A linear function was fitted to the data ($R^2 = 0.98$); the gradient of this function provides an estimate of root depth growth rate, which was $5.9$ mm day$^{-1}$. Observations of the position and structure of common heliotrope root systems as they appeared in the field on 20 February are synthesised in Figure 4.6.

![Figure 4.5](image.png)

**Figure 4.5.** Root depth growth of common heliotrope (●) over time in the field at Birchip following a germinating rainfall of 28 mm on the 22 January 2002. Error bars are $\pm$ the standard error of the mean. Linear equation is $y = 5.9x + 7.6$ ($R^2 = 0.98$).
Figure 4.6. A scale drawing of plant development, root position and structure of common heliotrope plants in the field over 26 days following emergence.
Field observation of growth of new roots in response to a small rainfall event

Figure 4.7 shows photographs of common heliotrope plants dug up on 20 March 2001. These plants were growing in the open, had germinated after rainfall on 21 December 2000 and had received a further 6 mm of rainfall on 16 March 2001 (a), and plants that were growing under a rain shelter and did not receive this rain (b). There is an obvious profusion of new lateral roots surrounding the root collar of the plants exposed to the rain, but none on those that were under the rain shelter. Maximum root growth rate observed in common heliotrope is 5.9 mm day\(^{-1}\) (Figure 4.5), and the roots surrounding the main stem were observed to be 15-20 mm in length, indicating that the growth was recent.

![Figure 4.7](image)

**Figure 4.7.** Plants of common heliotrope growing in the open (a) and under a rain shelter (b). There is a profusion of new roots below the root collar in the plants growing in the open, but not in those growing under a rain shelter.

Figure 4.8 shows the mean volumetric water content (VWC) of soil surrounding mature plants of common heliotrope at increasing distances from the plant stem approximately 12 hours after 9 mm of rain fell. There was a significant negative effect of distance on volumetric water content (p<0.05). A Tukey comparison showed that the VWC at 0 m was significantly greater than the VWC at all other distances (p<0.05), but that the VWC at all other distances were not significantly different from each other (p>0.05).
4.4.4 Discussion

The rates of root depth growth of common heliotrope recorded in pots under constant temperatures and the rate of root depth growth recorded in the field are comparatively slow compared with other weeds. The maximum rate of root depth growth recorded at a constant temperature was 5.6 mm day\(^{-1}\) at 31.8 °C, a value comparable to the rate of root depth growth in the field, which was 5.9 mm day\(^{-1}\). The rate of root elongation in many other weed species is much greater. Roman, Thomas \textit{et al.} (1999) found that radicle elongation in the temperate annual \textit{Chenopodium album} was 9.1 mm day\(^{-1}\) at 27.5°C. Shrestha, Roman \textit{et al.} (1999) found that radicle elongation in \textit{Ambrosia artemisiifolia} was 21.6 mm day\(^{-1}\) at 32.5 °C, a rate nearly quadruple that of common heliotrope. It is then reasonable to conclude from this experiment that the rapid growth of a strong tap root hypothesised by Moore (1956) and Dellow (1987) does not occur in common heliotrope. From the observation of root growth and structure in the field, it appears more likely that plants of common heliotrope methodically exploit the regions of soil moisture available to them by producing a highly branched root system. In most cases in the Victorian mallee, this will only be to the depth reached by the wetting front of the rainfall event that caused emergence. A similar root growth strategy was observed in arid ephemeral species in the southern Egyptian desert by Springuel (1990), in comparison to perennials in the same region that rapidly developed a long tap root.
the case of common heliotrope, if moisture exists in the subsoil (i.e. on a fallow paddock as described in Chapter 1), provided layers of dry soil do not block their progress, it is likely that the roots will grow to considerable depth and exploit this resource.

The root growth and water use of common heliotrope observed here has implications for control: if a cohort of common heliotrope establishes following a small germinating rainfall (e.g. 20-25 mm) in a paddock with no existing sub-soil moisture, the only water that the plants would use would be from the germinating rainfall. Such an amount of rain will only penetrate to a depth of around 120 - 150 mm and even in the absence of transpiring plants is likely to have evaporated prior to sowing. In such a circumstance, it would not be economically viable to control common heliotrope for water conservation. However, there would be benefits from reducing the seed-bank, preventing tie-up of nutrients and allowing storage of further rainfall.

The observations of root growth in response to small amounts of summer rain illustrated by Figure 4.7 indicate that rapid development of lateral roots in regions of soil where moisture has become available may be an important attribute of common heliotrope. Rapid growth of such roots would allow exploitation of water resources located near the soil surface that would otherwise be lost to evaporation. Growth of new roots in arid species in response to small amounts of rain has been observed within hours in desert succulents by Noble (1984) and within days in the tussock-grass *Agropyron desertorum* by Cui (1997). The speed with which the lateral roots of common heliotrope grew is unknown, but as Figure 4.7 shows, they were certainly well developed just four days after a rainfall event of 6 mm.

The amount of water available to new roots growing in response to summer rain from beneath the main stem appears to be increased by the above ground parts of the plant funnelling water down the main stem. Funnelling of water by above ground parts of plants has been observed in arid species such as mulga (*Acacia aneura*: Williams 1982), and it is possible that it is an important attribute allowing plants growing in arid regions to make the most of limited water resources. However, it may merely be the inevitable effect of a branching system and will happen for all branched species in any environment. Further experimentation comparing species of different architecture and ecologies would further elucidate this, and two interesting subjects of comparison may
exist in the *Heliotropium* genus. Creeping heliotrope (*H. supinum* L.) is morphologically very similar to common heliotrope, except that as its name suggests, it grows closely to the ground. It co-occurs with common heliotrope during late spring and summer in the Victorian Mallee, but is not considered a weed of importance. This is principally because its occurrence is limited to areas recently occupied by ephemeral water bodies that have evaporated during the warmer months e.g. deep puddles left by heavy summer rain, dry lake beds and agricultural dams. It may be worthy of note that common heliotrope, which is dependent on rainfall, as opposed to collected bodies of water, has upright, bushy architecture with the only point of contact with the earth being the main stem. This architecture appears capable of concentrating rainfall to the region of soil surrounding its stem. Prostrate heliotrope, which relies on the large amounts of sub-soil moisture remaining after the evaporation of collected ephemeral water, has a supine architecture that is unlikely to be able to concentrate water around its main stem, where opportunistic roots could then grow and access it. Further study into the ecology of these two species may be beneficial in increasing understanding of the importance of plant architecture in water harvesting in arid environments.

4.5 References


Guterman Y (1993) 'Seed Germination in Desert Plants.' (Springer-Verlag: Berlin)

Isbell RF (1996) 'The Australian Soil Classification.' (CSIRO Publishing: Collingwood)


4.6 Appendices

Appendix 1. ANOVA table - effect of distance from the main stem of plants of common heliotrope on volumetric water content 12 hours after 9 mm of rain.

<table>
<thead>
<tr>
<th></th>
<th>Df</th>
<th>Sum of Sq</th>
<th>Mean Sq</th>
<th>F Value</th>
<th>Pr(&gt;F)</th>
</tr>
</thead>
<tbody>
<tr>
<td>distance</td>
<td>6</td>
<td>920.53</td>
<td>153.42</td>
<td>13.14</td>
<td>2.59e-8</td>
</tr>
<tr>
<td>Residuals</td>
<td>42</td>
<td>490.29</td>
<td>11.67</td>
<td>11.67</td>
<td></td>
</tr>
</tbody>
</table>
Chapter 5. Modelling the Effect of Edaphic Variation on Soil Moisture Persistence

5.1. Introduction

According to the literature, common heliotrope does not appear to show any marked preference for soil type (Moore 1956; Sheppard, Brun et al. 1996). It grows on a wide range of soil types, principally loams but ranging from sands to clays (Cunningham, Mulham et al. 1981; Parsons and Cuthbertson 2001; Sheppard, Brun et al. 1996). However, casual observations to the contrary have been made throughout this study. On a paddock scale, common heliotrope infestations were consistently more prevalent on lighter, sandier soils in preference to heavier clays and clay loams. On a regional scale, common heliotrope is far more prevalent in the Victorian Mallee than it is in the grain-growing region immediately to the south, known as the Wimmera. In the Wimmera, common heliotrope only becomes a problem in years with massive summer rainfall events.

The climates and agricultural practices of these two regions are not markedly different, but the soil types dominating them are (Figure 5.1). Broadacre cropping in the Victorian Mallee principally takes place on Calcarosols (Isbell 1996; Victorian Department of Primary Industries 2004). Calcarosols are defined as soils that are calcareous throughout, or at least below the A horizon, and lack a clear or abrupt textural B horizon (Isbell 1996). The Calcarosols in the Mallee region vary quite considerably in terms of surface soil texture, ranging from those dominated by sands to those that are clayey throughout. Light textured Calcarosols predominate in the north of the region, and heavy textured Calcarosols predominate in the south (Victorian Department of Primary Industries 2004). Vertosols are the dominant soil on which broadacre cropping is conducted in the Wimmera (Victorian Department of Primary Industries 2004). Vertosols are clay soils with shrink-swell properties that exhibit strong cracking when dry, and are often called cracking clay soils. Based on colour of the upper 0.5 m of the soil profile, Vertosols can be grouped into various Suborders (Isbell 1996). Grey Vertosols are the most common in the Wimmera (Victorian Department of Primary Industries 2004). Vertosols may be further distinguished by surface soil structure (i.e. Self-Mulching, Epipedal and Massive). Both Self-Mulching and Epipedal Vertosols are common throughout much of the Wimmera region, Self-Mulching having a more friable
Moisture availability is the primary environmental factor limiting heliotrope occurrence (Moore 1956 and Chapter 1 and 2). The amount of water available to a plant or seed is not purely a function of rainfall, but also soil texture, atmospheric moisture, and soil and air temperature (Wester, Dahl et al. 1986). Soil texture determines the water potential that will be experienced by a plant or seed at a given soil water content, and also impacts on how quickly water will drain and evaporate. Atmospheric moisture and air and soil temperature dictate how quickly water evaporates, and hence influence the amount of water to which plants or seeds are exposed.

As mentioned above, soil texture and temperature (due to differences in albedo) are the only two factors that differ significantly between the Mallee and the Wimmera. Because of common heliotrope's finely tuned germination ecology (Chapters 2, 3 and 4), it is hypothesised that soil texture and albedo and resultant hydraulic properties could potentially explain the difference in prevalence of common heliotrope between dark, heavy textured and light coloured and textured soils, and in the Mallee and the
Wimmera. In order to test this hypothesis, the amount of soil water available to seeds of common heliotrope in soils representative of the three main soil types of the Wimmera and Mallee following a typical summer rainfall event (and subsequent climatic conditions) were predicted using the soil water, energy, and transpiration (SWEAT) model (Daamen and Simmonds 1996). The amount of plant available soil moisture that persisted at depth was also modelled, as this has implications for the continued survival and reproductive success of common heliotrope once emerged (Daamen and Simmonds 1996).

5.2. Model description

SWEAT is a one-dimensional model of soil water and temperature based on the numerical approach of Campbell (1985) and Philip (1957). It simulates a one-dimensional soil profile by considering it to consist of a series of homogeneous layers with variable thicknesses ranging from 1 mm at the surface to 200 mm at depth. Fluxes in the soil profile are simulated on an hourly time-step between points within each layer. Water potential and temperature are assumed constant within each layer and time-step. The model can be specified for a given soil by changing the parameters in the governing equations (see Daamen and Simmonds 1996), which are listed in Table 5.1, and it requires hourly meteorological data (net radiation, air temperature, humidity, wind speed and rainfall) as inputs. SWEAT does not take into account all known water and heat flow processes. Soil hydraulic properties are assumed homogenous with depth, and run-off, run-on and ponded conditions are assumed not to occur. Flow in macropores (e.g. cracks, old root holes) is also not simulated. These limitations do not present a problem for this study, as although the soils being studied exhibit heterogeneity with depth, only the top 150 mm of profile is being considered, which on the soils in question is of uniform soil type. Run-off and run-on rarely occur during summer in the study region, although cracks are certainly a consideration in Vertosols and their effect on water balance is discussed further in Section 5.6.

SWEAT was accessed through the EMERGE (Mullins, Townsend et al. 1996) user interface.
5.3. Soil description and parameterisation of SWEAT

5.3.1. Calcarosol with light textured (sandy to loamy) surface soil

SWEAT was parameterised for a soil typical of the Calcarosols with light textured surface soil of the northern Victorian Mallee. The soil that was chosen as representative of this type was from the Walpeup site described in Chapter 4. This site is a plain landform in the central Mallee land system (Rowan and Downes 1963), and the soil is described by Newell (1961) as a mid-Mallee sandy loam, and its Australian soil classification is: Endohypersodic (and Vertic) Pedal Hypercalcic Calcarosol (Isbell 1996; O'Connell, Connor et al. 2002). The parameter values for this soil used as input by SWEAT and the sources from which they were obtained are listed in Table 5.1.

5.3.2. Calcarosol with heavier textured (clay loamy-clay) surface soil

Soil from the Jil Jil field site described in Chapter 1 was chosen as a soil typical of the Calcarosols with heavier textured surface soil of the southern Victorian Mallee. This site is a level plain within the Culgoa land system (Rowan and Downes 1963); the surface soil is described by Department of Primary Industries (2004) as a hard-setting and massive clay loam, and its Australian soil classification is an Epihypersodic, Pedal, Hypercalcic Calcarosol (Isbell 1996; Victorian Department of Primary Industries 2004). The parameters for this soil required by SWEAT and the sources from which they were obtained are also listed in Table 5.1.

5.3.3. Self-mulching grey Vertosol

Soil from the Longerenong field site described in Chapter 2 was selected as a soil typical of the Grey Self-Mulching Vertosols of the Wimmera. This site is described by Martin et al. (1996) as a level plain dominated by Kalkee Clay, which is an Epicalcareous-Endohypersodic, Self-mulching, Grey Vertosol (Isbell 1996; Martin, Imhof et al. 1996) under the Australian soil classification. The parameters for this soil required by SWEAT and the sources from which they were obtained are again listed in Table 5.1.
Table 5.1. The SWEAT parameters and the sources from which their values were obtained for the three different soils.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Calcarosol with light textured surface soil</th>
<th>Source</th>
<th>Calcarosol with heavier textured surface soil</th>
<th>Source</th>
<th>Self-mulching grey Vertosol</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil air entry potential (kPa)</td>
<td>-0.54</td>
<td>O'Connell (2002)</td>
<td>-0.87</td>
<td>Martin, Imhof et al. (2002)</td>
<td>-0.33</td>
<td>Martin, Imhof et al. (2002)</td>
</tr>
<tr>
<td>Soil saturated hydraulic conductivity (m s(^{-1}))</td>
<td>2.08 x 10(^{-5})</td>
<td>J. G. Nuttall, pers. comm.</td>
<td>8.30 x 10(^{-6})</td>
<td>J. G. Nuttall, pers. comm.</td>
<td>2.70 x 10(^{-6})</td>
<td>J. G. Nuttall, pers. comm.</td>
</tr>
<tr>
<td>Soil bulk density g cm(^{-3})</td>
<td>1.4</td>
<td>O'Connell (2002)</td>
<td>1.3</td>
<td>J. G. Nuttall, pers. comm.</td>
<td>1.1</td>
<td>J. G. Nuttall, pers. comm.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Newell (1961)</td>
<td>0.3</td>
<td>Martin, Imhof et al. (2002)</td>
<td>0.5</td>
<td>J. G. Nuttall, pers. comm.</td>
</tr>
<tr>
<td>Soil clay fraction (g g(^{-1}))</td>
<td>0.11</td>
<td>Newell (1961)</td>
<td>0.5</td>
<td>Martin, Imhof et al. (2002)</td>
<td>0.36</td>
<td>Martin, Imhof et al. (2002)</td>
</tr>
<tr>
<td>Soil quartz fraction (g g(^{-1}))</td>
<td>0.77</td>
<td>Newell (1961)</td>
<td>0.16</td>
<td>Martin, Imhof et al. (2002)</td>
<td>0.02</td>
<td>Martin, Imhof et al. (2002)</td>
</tr>
<tr>
<td>Soil albedo value</td>
<td>0.3</td>
<td>Newell (1961)</td>
<td>0.16</td>
<td>Post, Fimbres et al. (2000)</td>
<td>0.02</td>
<td>Post, Fimbres et al. (2000)</td>
</tr>
<tr>
<td>Soil emissivity</td>
<td>0.92</td>
<td>Default</td>
<td>0.92</td>
<td>Default</td>
<td>0.92</td>
<td>Default</td>
</tr>
</tbody>
</table>
5.4. Model validation

In order to validate the outputs of the SWEAT model for the soils and conditions of the Victorian Mallee, it was first parameterised for the soil of the Jil Jil field site (Table 5.1). A meteorological data file was created using air temperature and rainfall data that had been recorded hourly at the Jil Jil site, hourly net radiation for Mildura (34.2° S, 142.1° E, 52 m above sea-level) and hourly wind-speed and relative humidity for Swan Hill (35.4° S, 43.5° E, 67 m above sea-level) from the Commonwealth Bureau of Meteorology.

SWEAT assumes a bare soil surface, whereas the Jil Jil field site had a sparse layer of litter (approx 10% cover). Mullins et al. (1996) recommended that the effect of mulch can be simulated by reducing the amount of radiation reaching the soil, and increasing the soil roughness, which in turn increases width of the soil surface boundary layer. Therefore, in order to simulate the effect of this layer of mulch, the radiation from the input file was multiplied by 0.9 to simulate the cover provided by the mulch, and the soil roughness was increased to 20 mm.

Using these inputs, the model was run from 21 January 2002 to 5 February 2002. This time period was chosen as it included a rainfall event of 28 mm during 21 and 22 January 2002, following which soil temperatures at 20 and 50 mm depth had been recorded hourly, and soil moisture from 0 to 50 mm depth had been recorded daily at the site up to 28 January (this is the germinating rainfall event described in Chapter 1).

The SWEAT simulated soil temperatures for this period are plotted against the recorded values in Figures 5.2. Figure 5.3 shows the deviation of the SWEAT simulated temperature from the recorded temperature. Deviations were defined as differences between simulated and measured values divided by measured values and expressed as a percentage (Mitchell 1997). The model predicts actual soil temperature at 20 mm very accurately, maximum deviations of the simulated in comparison to observed temperatures are commonly within 10% (Figure 5.3). Although large deviations do occur during the middle of the day on 26 January and 2 and 3 February, this is due not to model inaccuracy, but the radiation input data. Simulated temperature in SWEAT is very sensitive to radiation (Mullins, Townsend et al. 1996), and the radiation data was recorded at Mildura - which is 300 km to the north of the Jil Jil field site. It is obvious
from studying the actual soil temperatures on those days that the weather became overcast at Jil Jil (the soil temperatures dip and waver and do not peak as they do on days such as 29 January), but did not do so at Mildura.

The SWEAT simulated soil water potentials at 10 and 20 mm depth for this period are plotted against the recorded values in Figures 5.4 and 5.5. In order to determine how well SWEAT simulated soil water potential, 95% confidence intervals for the measured soil water potentials were calculated from adjusted standard errors calculated by the S-PLUS 2000 statistical package (MathSoft Inc., Seattle, U.S.A.) and 2-tailed t-statistic for 9 degrees of freedom. Table 5.2 shows that the SWEAT simulated soil water potentials were within the confidence intervals of the observed values at both 10 and 20 mm depth.

In summary, Figures 5.2 to 5.5 show that the SWEAT model provides a good prediction of actual soil temperatures and water potentials for the purposes of comparing the hydraulic properties of the three different soil types.
Figure 5.2. Recorded soil temperature (—) and soil temperature simulated by SWEAT (—) at 20 mm depth for the Jil Jil field site from midnight 21 January 2002 to midnight 5 February 2002.

Figure 5.3. Deviation of simulated from observed temperatures at 20 mm depth at the Jil Jil field site from midnight 21 January 2002 to midnight 5 February 2002.
Figure 5.4. Recorded soil water potential at 0-10 mm depth (■) and soil water potential at 10 mm depth simulated by SWEAT (●) for the Jil Jil field site from midnight 21 January 2002 to midnight 28 January 2002. Soil water measurements were taken at approximately 9:00am on each day, and the SWEAT output corresponding to 9:00 am are shown here. Error bars are ± the standard error of the mean for the recorded values.

Figure 5.5. Recorded soil water potential at 10-20 mm depth (■) and soil water potential at 20 mm depth simulated by SWEAT (●) for the Jil Jil field site from midnight 21 January 2002 to midnight 5 February 2002. Soil water measurements were taken at approximately 9:00am on each day, and the SWEAT output corresponding to 9:00 am are shown here. Error bars are ± the standard error of the mean for the recorded values.

Table 5.2. 95 % Confidence intervals for the recorded soil water potentials at 0-10 and 10-20 mm depth.

<table>
<thead>
<tr>
<th>Date</th>
<th>Soil Water Potential at 0-10 mm (kPa)</th>
<th>Soil Water Potential at 10-20 mm (kPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Upper confidence interval</td>
<td>Lower confidence interval</td>
</tr>
<tr>
<td>23/01/2002</td>
<td>1121</td>
<td>-1145</td>
</tr>
<tr>
<td>24/01/2002</td>
<td>659</td>
<td>-1607</td>
</tr>
<tr>
<td>25/01/2002</td>
<td>103</td>
<td>-2431</td>
</tr>
<tr>
<td>26/01/2002</td>
<td>-904</td>
<td>-3438</td>
</tr>
<tr>
<td>28/01/2002</td>
<td>-1916</td>
<td>-4450</td>
</tr>
</tbody>
</table>
5.5. Model simulations

In order to compare the soil water fluxes of the three different soils, some assumptions were made about the common environment under which the simulations were to take place. A hypothetical paddock is assumed to have been subjected to management typical of the region, which results in the creation of ideal habitat for common heliotrope, i.e. devoid of living plants and plant residue, air-dry on the surface but with some subsoil moisture at depth. A typical scenario resulting in the creation of such habitat would be a paddock on which a legume crop or medic pasture was grown during the winter, but which was harvested or senesced in spring, leaving the sub-soil water potential at the lower extractable limit of the crop or pasture, assumed to be -1500 kPa. If the paddock received no more rain after the crop was harvested or the pasture senesced, the top-soil would become air-dry on the surface, and between -1500 kPa and air-dry at depth. The paddock was assumed to have been grazed heavily and was consequently devoid of living plants and has little or no plant residue. This scenario is reflected in the starting conditions provided to SWEAT, which are outlined in Table 5.3. The values of air-dry and partially air-dry soil were taken from actual measurements made at the Jil Jil field site approximately 30 days after the last rainfall.

Table 5.3. The starting conditions provided to SWEAT for the simulations, which commenced at midnight on 30 December 2002.

<table>
<thead>
<tr>
<th>Soil depth (m)</th>
<th>Temperature (°C)</th>
<th>Water Potential (kPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>24°C</td>
<td>-10000</td>
</tr>
<tr>
<td>0.05</td>
<td>24°C</td>
<td>-4500</td>
</tr>
<tr>
<td>0.15</td>
<td>24°C</td>
<td>-1500</td>
</tr>
<tr>
<td>1</td>
<td>20°C</td>
<td>-1500</td>
</tr>
</tbody>
</table>

In order to compare the hydrothermal properties of the three different soils, a meteorological data file was created describing a summer rainfall event typical of the region, and the subsequent climatic conditions. The meteorological file was based around a 26.6 mm rainfall event that occurred at Swan Hill on 30 and 31 December 2002, and ran from 30 December 2002 to 30 January 2003. Hourly air temperature, relative humidity, rainfall and wind-speed data for the file were taken from the Commonwealth Bureau of Meteorology automatic weather station at Swan Hill (S 35.4°, E 143.5°, 67 m above sea-level), and hourly radiation data were taken from the Commonwealth Bureau of Meteorology station at Mildura (S 34.2°, E 142.1°, 52 m above sea-level).
The SWEAT model was parameterised and run for each of the three soils using these meteorological data as input. The output of the SWEAT simulation pertinent to the biology of common heliotrope (soil water potential at 10, 20, 100 and 150 mm depth) was analysed for differences between the three soils that may favour the establishment or survival of common heliotrope.

Figure 5.6 shows the simulated soil water potential at 10 and 20 mm in the Vertosol and two Calcarosols. It shows that soil water potential remains at levels more conducive to germination (> -800 kPa, see Chapter 4) for significantly longer in the two Calcarosols in comparison to the Vertosol. Soil water potential remained at levels more conducive to germination for longer in the lighter Calcarosol in comparison to the heavier Calcarosol. From the results of Chapter 4, this indicates that a Vertosol would have a higher threshold value of rainfall that results in germination, and that if all three soil types containing seeds of common heliotrope were subjected to a rainfall event of equal magnitude, a greater proportion of the seed population would germinate in the Calcarosols than in the Vertosol, with even more germinating in the lighter Calcarosol compared to the heavy.

In addition to this, Figure 5.7 shows that more soil water becomes available at depth in the lighter Calcarosol compared to the heavier Calcarosol and Vertosol. This would result in plants growing on the lighter Calcarosol potentially being able to grow faster and for longer, and having greater reproductive output as a consequence.
Figure 5.6. Simulated soil water potential for Vertosol at 10 (---) and 20 (---) mm, heavy Calcarosol at 10 (---) and 20 (---) mm and light Calcarosol 10 (---) and 20 (---) mm.

Figure 5.7. Simulated soil water potential for Vertosol at 100 (---) and 150 (---) mm, heavy Calcarosol at 100 (---) and 150 (---) mm and light Calcarosol 100 (---) and 150 (---) mm.
5.6. Discussion

The results from the SWEAT simulation of soil water potential indicate that soil type is likely to have a significant impact on the germination and subsequent growth of common heliotrope. Soils of lighter texture and colour (e.g. the Calcarosols predominant in the Mallee) provide more available moisture in the germination zone (5 to 15 mm depth, Chapter 2) for longer (Figure 5.6). Given the hypothesis put forward in Chapter 4 relating to a physiological process required for germination taking longer to reach completion at more negative water potentials, and being more rapid at less negative water potentials, this means seeds of common heliotrope in lighter soils will be able to germinate on smaller rainfall events than those in heavier soils. It also means that a greater proportion of the seed population of common heliotrope in lighter soils will be able to germinate (Chapters 2, 3 and 4) in comparison to those in heavier soils. This would result in denser populations of common heliotrope emerging on lighter soils more often. This is substantial evidence to support the hypothesis that the difference in prevalence of common heliotrope observed between the Wimmera and the Mallee can be explained by the soil types dominant in each region. This effect may be further exacerbated by the shrink-swell properties of the Vertosols dominant in the Wimmera, which result in large cracks appearing as they dry out over summer. Theoretically, this could mean more rainfall would be lost down cracks and thus not available to seeds of common heliotrope to germinate, and the sub-soil moisture which common heliotrope may use for subsequent growth to be lost faster.

However, differences in prevalence of common heliotrope due to soil type will only be observed following reasonably marginal germinating rainfall events such as the one used for the simulation above (26.6 mm of rain over two days). Under such circumstances, soil type plays a critical role in determining whether seeds are exposed to hydraulic conditions above or below their threshold for germination or not. Germinating rainfall events of greater amount and duration will result in seeds being exposed to adequate moisture for germination regardless of soil type, and this has probably led to the observations made by Moore (1956) and Sheppard (1996) to the indifference of common heliotrope to soil type. This is also supported by the observation that common
heliotrope does occur in the Wimmera often at high densities, but only after large amounts of summer rain.

Regardless of rainfall amount and duration, soil type may still play an important role in determining how much water is then available to a plant for the remainder of its life cycle. Figure 5.7 shows that there is more water available to plant roots at depth on the lighter textured and coloured Calcarosols than on the darker, heavier Vertosol. This is due to the lower air-filled porosity of soils with higher clay content, which results in the wetting front not moving as far down the soil profile, and as a consequence water is more rapidly lost to evaporation (Dalgliesh and Foale 1998). Observation at both the Walpeup and Jil Jil field sites in 2001 and 2003 respectively indicated that plants on lighter textured soils were able to stay alive and reproductive for longer than those that were on heavier soils.

Germination and hence occurrence of common heliotrope is not limited purely by rainfall amount, but by soil water amount and duration. Soil water amount and duration are a function of rainfall amount, soil type and prevailing climatic conditions (Wester, Dahl et al. 1986). Consequently, soil type will have an impact on the prevalence and distribution of common heliotrope, and this may be observed by the differences in prevalence of the weed in the Wimmera and Mallee. This will also be true of all arid ephemeral species that rely on discrete rainfall events for initiation of their life cycle. Soil water amount and duration are the parameters that will drive emergence events, and attention should be paid to them rather than rainfall alone in studies of emergence of arid ephemerals.

5.7. References


Isbell RF (1996) 'The Australian Soil Classification.' (CSIRO Publishing: Collingwood)


Rowan JN, Downes RG (1963) 'A Study of the Land in North West Victoria.' Soil Conservation Authority Technical Communication No. 12, Kew.


Chapter 6. Implications for Control

6.1. Introduction

As discussed in Chapter 1, the primary methods utilised for control of common heliotrope in the Victorian Mallee are cultivation and spraying with post-emergent herbicides such as glyphosate. Both of these methods have serious disadvantages associated with them. Cultivation is detrimental to the fragile soil structures of the region, and is a primary contributor to wind erosion, which is a significant environmental problem (Ridge 1986). It also requires large inputs of fossil fuels. Control with glyphosate can be difficult due to the region's hot, dry and dusty summer conditions. Frequently, humidity is so low and temperatures are so high that the droplets from spray nozzles evaporate before they settle on foliage, reducing the efficacy of the active constituents; drought-stressed plants do not translocate glyphosate, and the clay particles in dust neutralise it (Subramaniam and Hoggard 1988). Also, glyphosate is only effective on very young common heliotrope plants (Jackman 2001). Control of common heliotrope with both cultivation and glyphosate can potentially be very costly, as they need to be repeated each time a cohort of common heliotrope emerges. Additionally, if the germinating rainfall does not meet up with subsoil reserves, common heliotrope will only use water that would otherwise be lost to evaporation (Chapter 4).

Jackman (2001) and van Rees (2000) have demonstrated that emergence of common heliotrope can be greatly reduced by the pre-emergent application of the sulfonylurea herbicides chlorsulfuron and metsulfuron-methyl and the triazine herbicide atrazine. When sprayed prior to rainfall at the beginning of the common heliotrope growing season (October/November), common heliotrope emergence was prevented for the remainder of the season (Jackman 2001). Such pre-emergent control has several distinct advantages over post-emergent controls. Firstly, it only requires a single application of the herbicide to prevent the potential emergence of many separate cohorts of common heliotrope. Secondly, pre-emergent herbicides are much cheaper to apply per hectare than glyphosate or cultivation. The major disadvantages of such pre-emergent herbicides are that they do not control summer grass weeds, which may also infest paddocks (e.g. Panicum capillare, Eragrostis cilianensis), and that they can have a significant detrimental effect on legume crop and pasture growth in the following
season, particularly if the summer is dry (Black, Pederson et al. 1999). The active ingredient in these herbicides can also blow away with soil, which can result in off-site damage in following years. Also, no return is made on the cost of application if a summer rainfall event of sufficient magnitude to allow common heliotrope emergence does not occur.

Control of common heliotrope with a pre-emergent herbicide is currently not a common commercial practice in the region. However, it has the potential to be a much more cost-effective method of control in comparison to cultivation and post-emergent herbicides. The aim of this chapter is to analyse the risks and likely benefits associated with pre- and post-emergent control methods using historical summer rainfall data from the Victorian Mallee. Summer rainfall is not only the primary cause of common heliotrope germination, but also an important source of water for use by subsequent crops (Cooke, MacLennan et al. 1989; Fischer 1987; O'Leary and Connor 1997; Ridge 1986). The costs associated with control need to be balanced against the likelihood of achieving a benefit in the form of subsequent crop yield by preserving existing soil moisture and ‘harvesting’ summer rainfall.

6.2. Methods

Daily rainfall data for November-February for the 27 years from 1976 to 2002 were obtained from the Commonwealth Bureau of Meteorology for 20 rainfall stations spread geographically across the Victorian Mallee (Figure 6.1).

These data were searched manually for rainfall events that, given the findings of Chapter 4, were likely to have resulted in the emergence of common heliotrope. Criteria for a rainfall 'event' were that it was a day, or sequence of days, on which rain fell. A sequence could contain a maximum of one day without rain. If days of rainfall were separated by two or more days without rain, then the events were considered to be separate (Figure 6.2).

Rainfall events were classified into different categories according to the amount of rain falling and the consequent likelihood of them resulting in emergence of common heliotrope. Rainfall events of less than 15 mm were assumed to result in no emergence
of common heliotrope. Rainfall events between 15 and 20 mm were assumed to have 'possibly' resulted in emergence, and rainfall events greater than 20 mm were assumed to have 'probably' resulted in emergence (see Chapter 4 for a validation of these figures). The number of times each of these categories of rainfall event occurred over the 27 years was counted, and this figure divided by 27 to give the frequency of occurrence of each category.

Figure 6.1. The locations of rainfall stations within the Victorian Mallee used in this study. The shaded areas indicate regions in which broadacre dry-land cropping is the dominant land use (Victorian Department of Primary Industries 2004).

<table>
<thead>
<tr>
<th>Date</th>
<th>Rainfall (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>1</td>
</tr>
<tr>
<td>Rainfall (mm)</td>
<td>0</td>
</tr>
</tbody>
</table>

Event 1 = 21.5 mm  
Event 2 = 7.5 mm  
Event 3 = 27.5 mm

Figure 6.2. Example rainfall data showing the classification scheme used to define discrete rainfall events. The series of dates that are underlined each constitute a discrete event, and their magnitudes are taken as the sum of the rain falling within them. Note that Event 1 includes a day without rainfall.

Rainfall events greater than 20 mm were also assumed to be 'water harvest' events, where the amount falling in excess of 20 mm is stored in the soil for potential use by subsequent crops. This assumes that 20 mm of rain falling in an event larger than 20
mm is lost to evaporation, and the remainder is stored in the soil. Subsequent rainfall events in excess of 20 mm are assumed to add cumulatively to the stored soil water. The number of years in which harvest events occurred was divided by 27 to give the frequency of water harvest years. The mean amount of water harvested at each location across all years was also calculated.

The number of years in which multiple predicted emergence events occurred was counted and divided by 27 to give the frequency of multiple event years. The frequency of multiple event years is an important statistic with regard to control, as the incidence of multiple rainfall events in the one season economically favours control with pre-emergent herbicide. Likewise, the number of years in which no emergence rainfall events occurred (nil years) was also counted, as these are years in which application of a residual herbicide would have been wasted.

The Southern Oscillation Index (SOI) is frequently used as a seasonal forecasting tool in Australia. The SOI is calculated from the air pressure difference between Tahiti and Darwin. Positive values of the SOI are associated with stronger Pacific trade winds, warmer sea temperatures to the north of Australia, and waters in the central and eastern tropical Pacific Ocean becoming cooler. This gives an increased probability that eastern and northern Australia will be wetter than normal. Negative values of the SOI are associated with extensive warming of the central and eastern Pacific and weak trade winds, which increase the probability of drier conditions in Australia. The fluctuation in the mean monthly SOI (SOI phase) between the two months prior to the period of forecasting interest is often used to infer probabilities of rainfall. SOI phase between two monthly means can be positive, rising, neutral, falling or negative (Allan, Lindesay et al. 1996). In order to determine if there was a relationship between phases of the SOI and frequency of emergence events or amount of water harvest from November to February, the average frequency and mean water harvest was averaged across all locations, and categorised according the phase of the September-October SOI observed in each year.

A comparison of the mean economic return from two different control methods across all years and locations was made using the number of germination events and the amount of water harvested in each year at each location. The two control methods were;
1. Obligatory application of chlorsulfuron prior to the emergence of the first cohort of common heliotrope in late spring

2. Application of glyphosate (with appropriate adjuvant and surfactant) in response to all emerging cohorts of common heliotrope

These two control methods are representative of the cost and likely returns from other pre- and post-emergent control options. The cost per hectare of applying other pre-emergent herbicides such as metsulfuron-methyl and atrazine is similar to that of chlorsulfuron, and the cost of cultivation is similar to that of applying glyphosate (Harris 2002; Jackman 2001). The mean costs of each of these methods are presented in Table 6.1; all currency figures are in Australian dollars. The cost per hectare of each control method ($P_c$) was assumed constant for all years (Table 6.1). The number of applications of each method required to control all cohorts of common heliotrope emerging in a given year ($a$) was assumed to be one for chlorsulfuron and equal to the sum of all emergence rainfall events ('possible' and 'probable') occurring in that year for glyphosate.

The return from a given control method is calculated using the likely portion of yield of a wheat (*Triticum aestivum*) crop attributable to water harvested during November, December, January and February of a given year i.e.

$$R_c = \sum \left( (h \times WUE \times P_w) - P_c \times a \right)$$

Equation 6.1

where $R_c$ is the mean annual net return ($\$ \text{ha}^{-1}$) of a given control method for $n$ years at a specific location, $h$ is the amount of water harvested in a given year at a specific location and $WUE$ is the water use efficiency of wheat, which is assumed constant at 20 kg ha$^{-1}$ mm$^{-1}$ (French and Schulz 1984). The price of wheat ($P_w$) was assumed constant at $0.15 \$ \text{kg}^{-1}$.

For the purposes of comparison, it is assumed that if common heliotrope is allowed to grow un-checked in years of potential water harvest, then no water is actually harvested and made available to the subsequent crop i.e. it is all transpired by common heliotrope. This makes the net return from no control always $0 \$ \text{ha}^{-1}$. This is a conservative assumption, as there are data to suggest that in regions with sub-soil constraints (e.g.
salinity, prevalent throughout much of the region), common heliotrope can extract water unavailable to wheat plants (up to 30 mm over 1m depth of soil), which leaves the soil profile in water deficit to wheat at the start of the planting season (D. Roget pers. comm.).

Table 6.1. The costs per hectare of the two different control methods

<table>
<thead>
<tr>
<th></th>
<th>Chlorsulfuron</th>
<th>Glyphosate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Application Rate</td>
<td>10g ha(^{-1})</td>
<td>1.5 L ha(^{-1}) (with 2% (NH(_4)(_2))_2SO(_4) and 0.2% surfactant)</td>
</tr>
<tr>
<td>Chemical cost ($ ha(^{-1}))</td>
<td>2.4</td>
<td>13.25</td>
</tr>
<tr>
<td>Method of application</td>
<td>Linkage boomspray with light FWA tractor</td>
<td>Linkage boomspray with light FWA tractor</td>
</tr>
<tr>
<td>Application cost ($ ha(^{-1}))</td>
<td>6.25</td>
<td>6.25</td>
</tr>
<tr>
<td>Total cost of each application ($ ha(^{-1}))</td>
<td><strong>8.65</strong></td>
<td><strong>19.5</strong></td>
</tr>
</tbody>
</table>

Analysis of variance using the S-PLUS 2000 statistical package (MathSoft Inc., Seattle, U.S.A.) was used to test for significant effects of location on mean water harvest with the main effect of year removed, and September-October SOI phase on mean emergence event frequency and water harvest averaged across all locations. A paired t-test was used to test for differences between mean return from the two control methods across all locations and years. Analysis of variance was also used to test for significant effects of control method on net return at each location, with the main effect of year removed. Confidence intervals were calculated to determine if mean net return for each control method at each location was significantly different from $0 ha\(^{-1}\), the assumed net return from not controlling common heliotrope.

### 6.3. Results

Estimated mean summer water harvest in the region varied from 17.9 mm at Lake Cullulleraine to 31.3 mm at Robinvale with a regional mean of 24.1 mm (Table 6.2). There was no significant difference (p>0.05) between location in mean water harvest (see Appendix 6.1 for ANOVA table), although the effect was only marginally non-significant. Thus we can consider the regional mean November-February water harvest to be 24 mm. Figure 6.3 shows the mean water harvest averaged across all locations over the 27 years of data used.
There was no significant effect of September-October SOI phase (p>0.05) on mean emergence event frequency or mean water harvest (see Appendix 6.2 for ANOVA table).

Table 6.3 shows the selected rainfall stations and the mean economic return from each of the two control methods calculated using Equation 6.1. The estimated net return from chlorsulfuron is significantly greater (p<0.05, t = 24.45, df = 537) than that from glyphosate when averaged across all locations and years. Calculation of confidence intervals (Appendix 6.3) shows that the regional mean returns from chlorsulfuron and glyphosate are significantly greater (p<0.05) than $0 ha^{-1}. There is no significant effect (p>0.05) of location on mean return from each control method averaged across all years (see Appendix 6.4 for ANOVA tables), although again the results for chlorsulfuron were only marginally non-significant.

Figure 6.3. Mean regional water harvest during the study period.
Table 6.2. Analysis of summer rainfall patterns for the last 26 years from 20 locations across the Victorian Mallee.

<table>
<thead>
<tr>
<th>Location</th>
<th>Frequency of occurrence of possible events</th>
<th>Frequency of occurrence of probable events</th>
<th>Frequency of multiple event years</th>
<th>Frequency of nil event years</th>
<th>Frequency of water harvest years</th>
<th>Mean summer water harvest (mm)</th>
<th>S.E. of mean summer water harvest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barraport North</td>
<td>0.69</td>
<td>1.88</td>
<td>0.73</td>
<td>0.08</td>
<td>0.81</td>
<td>28.7</td>
<td>5.7</td>
</tr>
<tr>
<td>Beulah</td>
<td>0.69</td>
<td>1.23</td>
<td>0.58</td>
<td>0.12</td>
<td>0.69</td>
<td>18.0</td>
<td>4.6</td>
</tr>
<tr>
<td>Birchip</td>
<td>0.38</td>
<td>1.85</td>
<td>0.85</td>
<td>0.12</td>
<td>0.88</td>
<td>30.4</td>
<td>5.7</td>
</tr>
<tr>
<td>Boundary Bend</td>
<td>0.46</td>
<td>1.77</td>
<td>0.69</td>
<td>0.19</td>
<td>0.77</td>
<td>30.5</td>
<td>6.4</td>
</tr>
<tr>
<td>Culgoa</td>
<td>0.54</td>
<td>1.42</td>
<td>0.65</td>
<td>0.27</td>
<td>0.69</td>
<td>23.7</td>
<td>5.3</td>
</tr>
<tr>
<td>Lake Boga</td>
<td>0.38</td>
<td>1.27</td>
<td>0.54</td>
<td>0.27</td>
<td>0.73</td>
<td>18.8</td>
<td>4.5</td>
</tr>
<tr>
<td>Lake Cullulleraine</td>
<td>0.65</td>
<td>1.19</td>
<td>0.58</td>
<td>0.15</td>
<td>0.65</td>
<td>17.9</td>
<td>4.9</td>
</tr>
<tr>
<td>Lascelles</td>
<td>0.38</td>
<td>1.62</td>
<td>0.58</td>
<td>0.15</td>
<td>0.81</td>
<td>30.7</td>
<td>5.5</td>
</tr>
<tr>
<td>Manangatang</td>
<td>0.52</td>
<td>1.16</td>
<td>0.52</td>
<td>0.16</td>
<td>0.60</td>
<td>25.4</td>
<td>5.8</td>
</tr>
<tr>
<td>Meringur</td>
<td>0.35</td>
<td>1.31</td>
<td>0.54</td>
<td>0.27</td>
<td>0.73</td>
<td>20.7</td>
<td>5.7</td>
</tr>
<tr>
<td>Murrayville</td>
<td>0.58</td>
<td>1.38</td>
<td>0.62</td>
<td>0.15</td>
<td>0.85</td>
<td>19.4</td>
<td>5.1</td>
</tr>
<tr>
<td>Nyah</td>
<td>0.54</td>
<td>1.27</td>
<td>0.58</td>
<td>0.23</td>
<td>0.65</td>
<td>28.1</td>
<td>6.6</td>
</tr>
<tr>
<td>Ouyen</td>
<td>0.31</td>
<td>1.54</td>
<td>0.65</td>
<td>0.19</td>
<td>0.73</td>
<td>25.7</td>
<td>5.2</td>
</tr>
<tr>
<td>Patchewollock</td>
<td>0.42</td>
<td>1.19</td>
<td>0.42</td>
<td>0.15</td>
<td>0.77</td>
<td>18.1</td>
<td>5.0</td>
</tr>
<tr>
<td>Quambatook</td>
<td>0.85</td>
<td>1.46</td>
<td>0.73</td>
<td>0.12</td>
<td>0.69</td>
<td>22.2</td>
<td>5.1</td>
</tr>
<tr>
<td>Rainbow</td>
<td>0.54</td>
<td>1.27</td>
<td>0.58</td>
<td>0.12</td>
<td>0.77</td>
<td>20.5</td>
<td>5.2</td>
</tr>
<tr>
<td>Red Cliffs</td>
<td>0.50</td>
<td>1.54</td>
<td>0.62</td>
<td>0.12</td>
<td>0.77</td>
<td>26.7</td>
<td>6.8</td>
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<tr>
<td>Robinvale</td>
<td>0.39</td>
<td>1.57</td>
<td>0.55</td>
<td>0.24</td>
<td>0.71</td>
<td>31.3</td>
<td>7.4</td>
</tr>
<tr>
<td>Sea Lake</td>
<td>0.27</td>
<td>1.42</td>
<td>0.50</td>
<td>0.19</td>
<td>0.77</td>
<td>21.8</td>
<td>5.1</td>
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<tr>
<td>Walpeup</td>
<td>0.46</td>
<td>1.38</td>
<td>0.69</td>
<td>0.15</td>
<td>0.81</td>
<td>23.8</td>
<td>7.1</td>
</tr>
<tr>
<td>Mean</td>
<td>0.50</td>
<td>1.44</td>
<td>0.61</td>
<td>0.17</td>
<td>0.74</td>
<td>24.1</td>
<td>-</td>
</tr>
<tr>
<td>S.E.</td>
<td>0.03</td>
<td>0.05</td>
<td>0.02</td>
<td>0.01</td>
<td>0.02</td>
<td>1.1</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 6.3. Estimated mean net returns for control of common heliotrope using chlorsulfuron and glyphosate.

<table>
<thead>
<tr>
<th>Location</th>
<th>Mean net return from control using chlorsulfuron ($ ha(^{-1}))</th>
<th>Mean net return from control using glyphosate ($ ha(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barraport North</td>
<td>78</td>
<td>41</td>
</tr>
<tr>
<td>Beulah</td>
<td>45</td>
<td>19</td>
</tr>
<tr>
<td>Birchip</td>
<td>83</td>
<td>49</td>
</tr>
<tr>
<td>Boundary Bend</td>
<td>83</td>
<td>50</td>
</tr>
<tr>
<td>Culgoa</td>
<td>62</td>
<td>36</td>
</tr>
<tr>
<td>Lake Boga</td>
<td>48</td>
<td>25</td>
</tr>
<tr>
<td>Lake Cullulleraine</td>
<td>45</td>
<td>21</td>
</tr>
<tr>
<td>Lascelles</td>
<td>84</td>
<td>56</td>
</tr>
<tr>
<td>Manangatang</td>
<td>68</td>
<td>45</td>
</tr>
<tr>
<td>Meringur</td>
<td>53</td>
<td>31</td>
</tr>
<tr>
<td>Murrayville</td>
<td>50</td>
<td>21</td>
</tr>
<tr>
<td>Nyah</td>
<td>76</td>
<td>50</td>
</tr>
<tr>
<td>Ouyen</td>
<td>68</td>
<td>42</td>
</tr>
<tr>
<td>Patchewollock</td>
<td>46</td>
<td>23</td>
</tr>
<tr>
<td>Quambatook</td>
<td>58</td>
<td>22</td>
</tr>
<tr>
<td>Rainbow</td>
<td>53</td>
<td>29</td>
</tr>
<tr>
<td>Red Cliffs</td>
<td>71</td>
<td>42</td>
</tr>
<tr>
<td>Robinvale</td>
<td>85</td>
<td>59</td>
</tr>
<tr>
<td>Sea Lake</td>
<td>57</td>
<td>34</td>
</tr>
<tr>
<td>Walpeup</td>
<td>63</td>
<td>37</td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td><strong>64</strong></td>
<td><strong>37</strong></td>
</tr>
<tr>
<td><strong>S.E.</strong></td>
<td><strong>3.1</strong></td>
<td><strong>2.8</strong></td>
</tr>
</tbody>
</table>

6.4. Discussion

The data presented in Table 6.2 show that across all locations, the frequency of 'possible' and 'probable' events combined varies from 1.65 per year at Meringur and Lake Boga to 2.58 at Barraport North, indicating that on the balance of probabilities, there will be around two emergence rainfall events in any given year in the region. However, the frequency of multiple event years and frequency of nil event years indicate that emergence rainfall events are not spread evenly across all years, but clustered into certain years. This pattern makes control using obligatory application pre-emergent herbicide more of a risk, as it will be an input cost without benefit in these years. However, this is mitigated somewhat by the requirement of herbicides such as chlorsulfuron, metsulfuron-methyl and atrazine to be applied shortly before rainfall i.e. application of pre-emergent herbicide need not occur until a rainfall event of a magnitude likely to cause heliotrope emergence is imminent. The risk of residual herbicide application could be further reduced if there is a correlation between the frequency and amount of summer rain events and long-term forecasting indices such as
the Southern Oscillation Index (SOI). However, this study found no effect of the different phases of the September-October SOI on emergence event frequency or mean water harvest. If likelihood of nil, single or multiple event years could be forecast, management decisions in favour of pre- or post-emergent control options could be applied or withheld accordingly.

The regional frequency of water harvest years is 0.74, but once again the temporal pattern of dispersal is clustered, increasing the risk of receiving no benefit from the obligatory application of pre-emergent herbicide. In years where water harvest does occur, the amount harvested could be of great benefit to subsequent crops. In terms of yield benefit associated with controlling common heliotrope, if a water use efficiency for wheat of 20 kg ha\(^{-1}\) mm\(^{-1}\) is assumed (French and Schulz 1984), then the mean benefit to crop yield in years in which water harvest occurs, assuming a regional mean water harvest of 24 mm, will be 480 kg ha\(^{-1}\). This represents over a quarter of the 15 year (1990-2004) average yield of wheat for the region (1782 kg ha\(^{-1}\), Martin 2005). The water use efficiency of 20 kg ha\(^{-1}\) mm\(^{-1}\) assumed here and in Equation 6.1 are supported by van Rees (2000), who found that at Charlton (located in the south east corner of the Victorian Mallee) an additional 70 mm of sub-soil water in plots in which common heliotrope had been controlled compared to those in which it had not. This translated into an extra 1510 kg ha\(^{-1}\) of wheat yield, which is equivalent to a water use efficiency of 21.6 kg ha\(^{-1}\) mm\(^{-1}\). The amount of additional stored water in the plots where common heliotrope was controlled (70 mm) also validates the water harvest assumptions made here, which calculated that in 1998-99, 79 mm of water would be harvested at Barraport North, the closest rainfall station to Charlton used in this study. O'Leary (1997) reported similar amounts of water being harvested under Mallee fallows during summer to those given in Table 6.2.

The economic analysis of the two control methods shows that across all locations in the last 26 years, obligatory application of chlorsulfuron would on average have resulted in a mean return of $63.79 ha\(^{-1}\), whilst application of glyphosate in response to all emerging cohorts of common heliotrope would have resulted in a mean return of $36.62 ha\(^{-1}\). Both of these figures are significantly greater than the assumed return from no control ($0 ha\(^{-1}\) in all years), so it can be concluded that even though the two will not result in a positive return in all years (returns from chlorsulfuron will be negative in years where there is no water harvest; return from glyphosate will be negative in years
when there are rainfall events which result in germination, but little or no water harvest), there is a statistically significant economic benefit in controlling all emerging cohorts of common heliotrope in the long term.

Across all locations, the return from chlorsulfuron was significantly greater than the return from glyphosate. Based on the last 26 years of rainfall data for the region and the assumptions of water harvest and return from control used here, obligatory application of a pre-emergent herbicide such as chlorsulfuron will give a greater economic return than controlling each cohort that emerges using post-emergent methods such as glyphosate. However, the returns from post-emergent control are also significant, and the economic difference between the two methods may be offset by increased flexibility in crop rotations allowed by non-residual post-emergent options.

The most significant conclusion from this study is that effective control of common heliotrope and other summer weeds from 1976-2002 would have resulted in a regional annual average water harvest of 24 mm, which represents over a quarter of the average wheat yield for the region. That is, if common heliotrope were not controlled, it would be responsible for reducing the wheat yield of the region by a quarter.

The economic approach adopted in this chapter is a simplistic spreadsheet comparison, and only serves as an initial investigation of the management and economic implications of the biological attributes of common heliotrope elucidated in this thesis. A more serious appraisal of the relative benefits associated with different control methods would require an approach akin to that of Pannell et al. (2004). In that study, a biophysical model of crop and weed growth was used in conjunction with dynamic programming to more realistically assess the whole-system impacts of weed management. In terms of extending results to growers, impacts of controlling or not controlling common heliotrope should be delivered in probabilistic terms. Again, a biophysical crop production model (e.g. APSIM, Keating, Carberry et al. 2003) would be ideal for this, and simulation to support economic and management decisions is recommended as an area of further research.
6.5. References


Harris G (2002) Farm machinery costs for broadacre cropping. In 'DPI PrimeNote fs0575'. (Department of Primary Industries, Queensland, Australia)


6.6. Appendices

Appendix 6.1. ANOVA table for effect of location on mean water harvest

<table>
<thead>
<tr>
<th></th>
<th>Df</th>
<th>Sum of Sq</th>
<th>Mean Sq</th>
<th>F Value</th>
<th>Pr(F)</th>
</tr>
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<tbody>
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<td>Station</td>
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<td>594.349</td>
<td>1.59560</td>
<td>0.05276573</td>
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<tr>
<td>Year</td>
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<td>9705.019</td>
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<td>0.00000000</td>
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<tr>
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</table>

Appendix 6.2. ANOVA tables for effect of SOI phases on emergence event frequency and mean water harvest

Emergence event frequency

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<tr>
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<th>F Value</th>
<th>Pr(F)</th>
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</thead>
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<td>1.318889</td>
<td>0.2940013</td>
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<td>Residuals</td>
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<td>22.02587</td>
<td>1.001176</td>
<td></td>
<td></td>
</tr>
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</table>

Mean water harvest

<table>
<thead>
<tr>
<th></th>
<th>Df</th>
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<th>Mean Sq</th>
<th>F Value</th>
<th>Pr(F)</th>
</tr>
</thead>
<tbody>
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<td>Sept.Oct.SOI.Phase</td>
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<td>2803.009</td>
<td>700.7523</td>
<td>1.552214</td>
<td>0.2221158</td>
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<tr>
<td>Residuals</td>
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Appendix 6.3. 95% Confidence intervals for the regional mean returns of the two treatments

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<tr>
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<td>69.68</td>
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<tr>
<td>Glyphosate</td>
<td>41.92</td>
<td>31.32</td>
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</table>
Appendix 6.4. ANOVA tables for effect of location on returns from chlorsulfuron and glyphosate

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<thead>
<tr>
<th></th>
<th>Df</th>
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<th>Mean Sq</th>
<th>F Value</th>
<th>Pr(&gt;F)</th>
</tr>
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<td>101591</td>
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<td>87346.55</td>
<td>26.09158</td>
</tr>
<tr>
<td></td>
<td>Residuals</td>
<td>494</td>
<td>1653760</td>
<td>3347.69</td>
<td></td>
</tr>
</tbody>
</table>

<table>
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<tr>
<th></th>
<th>Df</th>
<th>Sum of Sq</th>
<th>Mean Sq</th>
<th>F Value</th>
<th>Pr(&gt;F)</th>
</tr>
</thead>
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<td>Glyphosate</td>
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<td>79689</td>
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<td>1.33060</td>
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<td>51003.36</td>
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<td>1550822</td>
<td>3152.08</td>
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</tbody>
</table>
Chapter 7. The Ecology of Common Heliotrope

7.1. Conclusions on the ecology of common heliotrope

Germination in seeds of common heliotrope is limited entirely by temperature and water availability (Chapter 2), and the range of conditions over which a population of seeds will germinate changes cyclically over time (Chapter 3). That is, natural seed populations of common heliotrope have cyclic dormancy, which is the primary endogenous factor that determines germination. Chapter 3 also showed that geographically disparate populations of common heliotrope germinate over different ranges of temperatures and water potentials. This all indicates that it is the seed’s endogenous response to temperature and water at any given time, and the moisture and temperatures that seeds are exposed to, which form the primary determinants of occurrence of infestations of common heliotrope. The germination responses of populations of seeds of common heliotrope do not fit the assumptions of the model of hydrothermal time. The data collected in this thesis is not of sufficient breadth to allow the creation of a new model that would better allow for fractional germination at sub-optimal conditions. In terms of predicting field emergence, such a model would be of little value, as for management purposes, the knowledge that common heliotrope will emerge after discrete rainfall events in late spring and summer is sufficient.

It is the seed’s endogenous cyclic germination response to external temperature and water conditions that allows common heliotrope to detect its spatial and temporal niche. Chapter 4 demonstrated that there is a direct link between the water and temperature requirements of seeds and the likelihood of conditions favourable to continued growth and reproduction. That is, the minimum amount of rainfall required for the germination of seeds of common heliotrope in the field corresponds with the amount required for growth up until minimal reproduction. This is ‘predictive’ germination as defined in Chapter 4. The indeterminate growth and flowering of common heliotrope then allows plants to exploit opportunistically any further water reserves that become available, either in the form of subsoil moisture or subsequent rainfall. Slow but methodical root growth exploits all water resources that become available. The endogenous cyclic germination response of populations of seeds of common heliotrope to temperature and moisture conditions also allows for germination and emergence of varying plant
densities in response to conditions more or less likely to allow continued growth and reproduction.

Quantification of the germination requirements of other species with similar life histories to common heliotrope is highly recommended as an area of further study. Such a study would begin to fill the massive gaps which currently exist in the literature pertaining to the germination ecology of arid annual and ephemeral species. This information would be a valuable contribution to our collective knowledge, as it will broaden the view of germination requirements and their impact on whole-plant ecology, which is currently biased toward temperate species. This broadened context will result in a much improved understanding of the clandestine processes of germination.

Chapter 4 highlighted the possibility that the branched habit of common heliotrope is an important adaptation to an arid environment that contributes to reproductive success byfunnelling rainfall down the plants main stem where it is easily accessed by opportunistic roots. Comparative ecological studies of common heliotrope and its close relative creeping heliotrope (*H. supinum* L.) would be of interest in elucidating this, and indeed in determining more generally if a branched habit is an important attribute of plants growing in arid environments, or merely an accident of evolution.

Besides rainfall, an important component of the amount of water that is available to a seed for germination and plant for subsequent growth is soil type. Chapter 5 shows that the effect of soil type is critical; to the extent that it likely to explain differences in occurrence between two contiguous cropping regions of Victoria (the Wimmera and Mallee) with very similar climates and cultural practices. Field studies of arid annuals and ephemerals that rely on discrete rainfall events for germination and emergence should be sympathetic to the role that soil type plays in the amount of water that is available to seeds and plants.

### 7.2. Implications for Control

The farming systems endemic to the Victorian Mallee inherently create an ideal habitat for common heliotrope. They do this by leaving extensive areas devoid of living vegetation, and often organic matter, during late spring and summer, in the form of
sparse cereal and legume stubbles, senesced pastures and cultivated fallow. Common heliotrope will germinate in the Victorian Mallee in such areas from mid-spring to early autumn following rainfall events in excess of 15-20 mm. It is more likely to germinate after marginal rainfall and in greater densities earlier during its growing season (October to December).

Chapter 4 showed that common heliotrope can emerge, grow and reproduce on minimum germinating rainfall alone. This means that there will not be an economic return from controlling common heliotrope in situations where there is little existing subsoil moisture, the emergence rainfall event is too small to be stored under fallow (<20 mm), and there is not further rainfall of sufficient magnitude to be stored under fallow for the remainder of the season. However, Chapter 6 shows that on average in the Victorian Mallee, common heliotrope has the potential to remove 24 mm of subsoil moisture arriving as summer rain alone, which would otherwise be available to subsequent crops. Assuming a water-use efficiency of wheat (the region’s dominant crop) of 20 kg ha\(^{-1}\) mm\(^{-1}\), this represents over a quarter of the region’s long-term wheat yield (1782 kg ha\(^{-1}\)). Multiplying this out to the average area of land sown to grain crops in the Victorian Mallee (1,169,638 ha, 2000-04 five year average, N. Clarke pers. comm.) and assuming the price of wheat to be $150 t\(^{-1}\), on average, common heliotrope uncontrolled would potentially cost the Victorian Mallee $84 million annually in lost yield. Assuming control of all emerging cohorts by glyphosate or cultivation (cost of $19.5 ha\(^{-1}\)), on average, control of common heliotrope potentially costs the Victorian Mallee $33 million dollars annually (regional mean frequency of ‘probable’ rainfall events multiplied by area of cropped land multiplied by cost of control per unit area). The net potential return from control is therefore $51 million annually in the region.

Common heliotrope is indeed a weed of tremendous economic significance, and its control offers growers significant return on investment. However, refinements may be made in the way that control is currently achieved in the region. Owing to the longevity of seeds of common heliotrope (Vasconcelos and Sa 1988), the incredibly high soil seed bank densities found within its range in Australia (Chapter 1, Sheppard, Brun et al. 1996), and the low plant densities required for economic loss (due to indeterminate growth), there is probably little to be gained in focused reduction of common heliotrope soil seed banks. There are areas in which the efficiency of current control options may be improved or better integrated into Mallee farming systems, and these are
outlined below. The sustained management of common heliotrope will best be achieved through integration of these techniques, and they should each be given strong consideration for further agronomic research.

7.2.1. Education in decision making and development of tools.

Firstly, control of common heliotrope may not be economically viable in all situations, as outlined above. Efficiency of common heliotrope control could be greatly enhanced through education, and instruction on use of existing decision-making tools to allow growers to determine the likely economic benefits of controlling common heliotrope following emergence events. Existing tools such as HowWet, HowOften (APSRU 2005) and Yield Prophet® (Hochman, van Rees et al. 2005) could be used within the framework of understanding of common heliotrope’s life history as elucidated by this thesis to support control decisions. HowOften returns the probabilities of receiving specified amounts of rainfall over a given period using location-specific historical rainfall i.e. what are the probabilities of receiving an emergence rainfall event from now until the end of the common heliotrope growing season? HowWet calculates the plant available soil water balance of fallows given actual rainfall and generic soil types. Yield Prophet® is a web-portal for the production model APSIM (Keating, Carberry et al. 2003) designed for use by growers. It returns actual and probable future plant available soil water balances of fallows and probable impact of stored soil moisture on crop yield.

The questions that require answering for a control decision to be made, and the available decision support tools required to answer them, are outlined in Table 7.1.

To improve the accuracy of information that underlies decision making, the way in which common heliotrope uses soil water over time would be of tremendous advantage. Further quantification of common heliotrope’s development and water use is highly recommended as an area of further research. The results could be integrated into existing decision support tools to provide growers with very valuable management resources.
<table>
<thead>
<tr>
<th>Question</th>
<th>Decision support</th>
<th>Result favouring control</th>
<th>Result favouring no control</th>
</tr>
</thead>
<tbody>
<tr>
<td>What is my current soil moisture?</td>
<td>Estimation, field measurement, modelling (HowWet, Yield Prophet®)</td>
<td>High</td>
<td>Low</td>
</tr>
<tr>
<td>Do I have a high level of subsoil constraints?</td>
<td>Field measurement (electrical conductivity, boron, exchangeable sodium percentage, pH)</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Was the germinating rainfall event large enough to store water under fallow?</td>
<td>Field measurement (rainfall)</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>What are the probabilities of receiving further rainfall events large enough to store water under fallow?</td>
<td>Farm or regional rainfall records, SOI phase, HowOften, Yield Prophet®</td>
<td>High</td>
<td>Low</td>
</tr>
<tr>
<td>How much water am I likely to save, how much will control cost, and what increase in yield am I likely to get?</td>
<td>Hand or spreadsheet calculation, Yield Prophet®</td>
<td>High chance of significant return</td>
<td>Low chance of significant return</td>
</tr>
<tr>
<td>Other factors? (e.g. nutrient use and tie-up, allelopathy, toxicity to stock, disease hosting)</td>
<td>Published experimental results, past experience, field inspection</td>
<td>Significant to management</td>
<td>Not significant to management</td>
</tr>
</tbody>
</table>
7.2.2. Residual herbicides

Chapter 6 indicates that obligatory application of residual herbicide at the start of the heliotrope season will be economically advantageous in comparison to post-emergent treatments in the long term. However, there are limitations associated with this method such as deleterious effect on subsequent crops, environmental concerns, and other non-susceptible summer weed species. Obligatory application of residual herbicide prior to or early in the common heliotrope growing season should be considered on paddocks with high risk of emergence and economic loss (i.e. paddocks devoid of living vegetation and organic matter and with existing subsoil moisture) e.g. winter fallow paddocks, legume stubbles or senesced pastures. Further research is needed to determine the efficacy of different residual control treatments, and their persistence in the alkaline soils of the Victorian Mallee. There could also be issues of herbicide resistance associated with control by this method, although common heliotrope has a long lived seed bank which modelling suggests would buffer resistance with susceptible genes, resulting in resistance taking longer to appear (Jasieniuk, Brûlé-Babel et al. 1996).

7.2.3. Farming systems less prone to common heliotrope infestation

Use of triazine-tolerant canola in rotations allows in-crop application of residual herbicides that may give effective control of common heliotrope over its growing season. It has also been observed during the course of this study that common heliotrope is less prevalent on conventional canola stubbles, to which triazines would not have been applied, in comparison to other crops. It is known that canola contains glucosinolates, which hydrolyse to form compounds toxic to plants, and which have been found to significantly reduce emergence of several weed species (Haramoto and Gallandt 2005). The effect of allelopathic substances from canola on emergence of common heliotrope and the potential for it to be recognised as a method of control could certainly bear further investigation.

As recommended by Moore (1956) all those years ago, common heliotrope may be controlled by the establishment of perennial pastures of lucerne or native grass species. Whilst such pastures will not fit well into the short cropping rotations currently used in
the Mallee, they may have a place in a longer term phase system that could be
developed for the region. The economic viability of such systems, and indeed the future
of land use in the Mallee, will be determined by the relative market prices of grain and
livestock.

7.2.4. Improved efficiency of existing physical control methods

A very useful addition to the current control options available to growers would be a
low-draught, low-disturbance implement that would sever common heliotrope roots
without destroying soil structure. Examples of existing implements that achieve this
would be a rod-weeder or blade plough. Such an implement would reduce the cost of
control because of the lower draught and hence lower fuel costs required for operation.
It would also leave the soil structure largely intact, avoiding the problem of wind
erosion and loss of organic matter. Development and testing of such implements in the
Victorian Mallee is highly recommended as an area of subsequent research.

7.3. References

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