

Biology and Management of *Genista monspessulana* (L.) L.A.S.

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December, 2000

DECLARATION

I hereby declare that the work in the thesis has been carried out by myself and does not incorporate any material previously submitted for a degree or diploma in any university. To the best of my knowledge, it does not contain any material previously written or published by another person, except where due reference is made in the text.

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Acknowledgments

My heartfelt thanks and gratitude go to:

Dr Christopher Preston for his positive attitude, support, encouragement, willingness to clamber across steep slopes with spraying apparatus, academic guidance and patience.

Dr Richard Roush for his enthusiasm, academic guidance, support, slashing the 'wretched' plant. To both Anne Frodsham and Rick for providing the steep slope to clamber across, allowing several fires, fire-fighting and making sure I hadn't slipped down the steep slope to weedy oblivion.

Dr Andy Sheppard for teaching me how to drive on the other side of the road, ensuring my work and stay in France was pleasant and productive. Credit is also due for his assistance with collecting density, seed production and seedbank data.

Dr Richard Groves for editing, advice and encouragement.

Dr Stephen Powles for spotting my talent and getting me involved in weeds.

The Co-operative Research Centre for Weed Management Systems for a scholarship, cooperation and numerous opportunities for travel.

To "The Weedies"; Craig, Gwen, Natalie, Chris, Kirsty, Debbie, Kathy, Jill, Anuja, Peter, Midori, Kelly, Jan and other members of the Department of Applied and Molecular Ecology for making the working environment pleasant and inspiring.

Terry Feckner and Dr Gary Taylor for their excellent management and organisation of essential facilities and resources. They also provided cryptic crosswords, the occasional answer to a clue and general good humour.

National Parks and Wildlife Service Staff and members of the Country Fire Service. With particular thanks to Stuart Paul, Bob Gooch and Volka Schultz, for unhindered access to Belair National Park, Cleland and Deep Creek Conservation Parks.

Dr Vivien Vanstone and Michelle Russ for friendship and support.

Dr Kerrie Davies for humour, friendship, advice, support, encouragement, jumping on *G. monspessulana* in a most frivolous manner to get it into the trailer. One of my fondest memories of Waite is laughing so hard we nearly fell off our stools.

Dr Mary and James Rieger for friendship and support. Counting and sifting became a delightful pastime when it involved chatting with Mary.

Dr Nicholas McClure for his support, companionship and consent to be dragged straight from a long haul flight to set up a field experiment on a cold, drizzly autumn day.

Sharyn Taylor because we'd be millionaires if we'd been given a dollar for every giggling fit!

My parents, Stephanie and Rowan, for their love, encouragement, support, finding rainfall and geographical data, editing and tracking down references.

Rebecca, Stephen and Guy for help and jolly good company.

Finally to Dr Quentin Paynter for his love, support, advice, patience and confidence in me.

Abstract

Genista monspessulana, a perennial, leguminous shrub, native to the Mediterranean region, is a major weed in native and forest ecosystems in South Australia. It is also considered a major weed in other parts of the world. This study examined the biology of *G. monspessulana* in its native and exotic ranges and investigated the outcomes of potential management strategies involving fire, herbicide and competition.

Seed production, seedbanks, density and ages of *G. monspessulana* population were examined at four sites in South Australia within the exotic range and four sites in France or Spain within the native range. Density of *G. monspessulana* stands, seedbank density and maximum age of plants were lower in its native Mediterranean habitats than in South Australia. Seed production reached a maximum in plants at about 7 years old in both habitats. There were no significant differences in seed production by plants of equivalent age between Australian and European populations.

Large, dormant seedbanks of up to 100,000 seeds m⁻² enable stands of *G. monspessulana* to persist following removal of mature plants. In experiments conducted to determine the potential reduction of *G. monspessulana* seedbanks using controlled burning, 80–90% of the seedbank was killed or stimulated to germinate by fire. A herbicide treatment, closely following burning (within 6 months) is required to remove the dense flush of germinating seedlings.

South Australian perennial, leguminous shrubs were considerably out-numbered by *G. monspessulana* in the seedbank. In addition, the percent of successful emergence of seeds of native legumes was lower. *Acacia melanoxylon*, grown in a replacement series with *G. monspessulana*, was the slower of the two species and less plants survived. In contrast, *Eucalyptus leucoxylon* seedlings, grown with *G. monspessulana*, were able to grow taller than *G. monspessulana*. Several of the *G. monspessulana* shaded by *E. leucoxylon* saplings were dead or dying at the culmination of the experiment. *Microlaena stipoides*, a native grass,

accumulated a similar biomass whether grown in pots with *G. monspessulana* or without. *M. stipoides* also reduced the proportion of *G. monspessulana* successfully emerging from the seedbank.

Native seedlings comprised no more than half of the seedbank under mature *G. monspessulana* stands, and less than 20% at all but one site in South Australia. Heating of the seeds before germination did not significantly influence the emergence of exotic or native seedlings other than *G. monspessulana*. Revegetation with native plants following removal of *G. monspessulana* is very important however, other than grasses, no significant reductions in *G. monspessulana* survival or growth were caused by the native species examined. Therefore, follow-up management after a fire will be required in addition to revegetation.

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Chapter 1. General Introduction and Literature Review

Genista monspessulana is a perennial, leguminous shrub, native to the Mediterranean region that has become established, and is considered a persistent and deleterious plant, in several other regions of the world including the Americas, Australia and New Zealand. It is considered deleterious because of its ability to form dense almost mono-cultural stands, which replace and suppress desirable native flora and economically valuable timber plants. Two species, *Cytisus scoparius* and *Ulex europaeus*, related to *G. monspessulana*, are also considered serious invasive weed problems in the Americas, Australia and New Zealand. The biology of these two species is better understood than that of *G. monspessulana*.

G. monspessulana populations are considered a threat to biodiversity if they are unmanaged. Management strategies are being developed for environmental weeds including *G. monspessulana*. Fire is considered as a management option for *G. monspessulana* in Australia. However, fire can cause large changes to a community or ecosystem. In addition, given the biology of related legumes, fire on its own is unlikely to be sufficient to manage *G. monspessulana* populations. Fire, or controlled burning, has several parameters which can be manipulated to produce different effects within a community or ecosystem. In this case it is the reduction or removal of *G. monspessulana* populations. Following a fire or controlled burn, competition is probably going to be an important factor affecting composition of the community or ecosystem.

Although *G. monspessulana* is a problem in two different types of systems (natural and commercial forest) and several countries throughout the world, the scope of this thesis is limited to natural ecosystems. The focus of the experimental work on *G. monspessulana* populations is invaded dry sclerophyll (low open) forest in South Australia and its original community in the Mediterranean.

The broad aim of this thesis is to investigate the biology of *G. monspessulana*; establish how it is likely to respond to fire and changed fire parameters, what other species are likely to occur in South Australian dry sclerophyll, low open-forest infested by *G. monspessulana* and how they respond to fire and the presence of *G. monspessulana*.

This literature review considers what is known about how *G. monspessulana* and related plants deleteriously affect natural ecosystems and thereby the reason why they are a priority for management in their exotic habitats. The review then discusses the general desired outcome of managing weeds in natural ecosystems. Various types of management tools are available for management of weeds of natural ecosystems, the review summarises them and states their strengths and weaknesses. Two tools, fire and competition are considered in detail. Finally, population biology of *G. monspessulana* and response to fire is the other main key to deciding how useful fire will be as a management tool. The biology of *G. monspessulana* is discussed. The two related legumes, *C. scoparius* and *Ulex europaeus*, are also discussed to provide more comprehensive information on the population biology of weedy legumes.

1.1 Effects of legumes on invaded ecosystems

There is growing evidence that nitrogen-fixing invaders and in some cases nitrogen-fixing residents of invaded communities change the nutrient dynamics of a community resulting in reduced species richness and an enhanced susceptibility to weed invasion (Vitousek 1990, 1994, Maron & Connors 1996, Mack & D'Antonio 1998). When sunlight and water are plentiful, productivity or community composition are determined by nutrient levels, the most important being nitrogen (Bray 1983). Most of the earth's nitrogen is present as gaseous N_2 . Plants are unable to use the gaseous form and require an oxidised (NO_3^- , NO_2^-) or reduced (NH_3^+) form. Micro-organisms in the soil or in symbiosis with plants convert gaseous nitrogen to oxidised and reduced ions. There are also micro-organisms that convert ionic soil nitrogen to gaseous nitrogen. Although ionic nitrogen is taken up and recycled by plants and animals, there is a net loss of nitrogen from the soil to the atmosphere (Bray 1983). One important factor

affecting the loss of ionic nitrogen and hence the level of nitrogen in a given ecosystem depends on the parameters of the nitrogen-fixing plant microbe symbioses. Another important factor determining the level of nitrogen in an ecosystem is the rate at which ionic nitrogen is recycled by the most abundant plant species in the system. Some plants have an 'open' nitrogen cycle in which nitrogen is taken up rapidly by the plant, used and relatively rapidly returned to the soil. Other plants may sequester nitrogen, and nitrogen taken up from the soil will remain on the plant for a long time before release (Tilman 1992). Ecosystems containing plants with an 'open' nitrogen cycle will probably have higher levels of available nitrogen than those with nitrogen sequestering plants.

The first example of a nitrogen-fixing species altering the ecosystem was discovered in Hawaii Volcanoes National Park. No native nitrogen-fixing plants occur in this area. An extremely successful invader, *Myrica faya*, has nitrogen-fixing actinorrhizal symbionts. Vitousek *et al.* (1987) demonstrated that *M. faya* significantly altered the availability of nitrogen in the system. A change in the amount of nitrogen available provides other exotic weeds with a chance to invade when normally low nitrogen levels would prevent their growth (Vitousek *et al.* 1987).

The second example of a nitrogen-fixing plant making the community more susceptible to invasion, through the increase of available nitrogen, is bush lupine (*Lupinus arboreus*) a native component of California coastal prairie. Maron & Connors (1996) examined the nutrient dynamics under and around bush lupine. There was a dramatic decline in richness of native species as samples were taken closer to bush lupine. Exotic thistles were larger and formed higher density populations near *L. arboreus* (Maron & Connors 1996).

The effect of invading nitrogen-fixing legumes in Australian forest or woodland soils may not be as marked because these communities have a rich indigenous, nitrogen-fixing flora. Rates of nitrogen production by Australian legumes have been estimated (Lawrie 1981, Adams & Attiwill 1984, Grove & Malajczuk 1992) using acetylene reduction. Amounts ranged from 1.10 – 7.1 $\mu\text{mol C}_2\text{H}_2$ reduced g^{-1} fresh weight nodules h^{-1} . These rates are generally low compared with rates for

northern hemisphere ecosystems (Grove & Malajczuk 1992). Hence, the possibility of nitrogen cycle alterations by northern hemisphere species is still possible. Brooms are recognised as having an 'open' nitrogen cycle and communities with brooms are amongst those having the highest inputs of nitrogen for non-agricultural ecosystems (Nilsen pers comm).

Legumes have the potential to alter a supporting cycle for a natural ecosystem. They also have the potential to maintain a population unlikely to be limited by nitrogen and finally they may exacerbate weed problems by making conditions more favourable for invasion. Management of weeds in natural ecosystems is important to prevent large-scale and continuing alterations to the ecosystem and requires a special approach.

1.2 Management of weeds of natural ecosystems

Management of weeds in natural ecosystems has a different purpose to management of weeds in agricultural systems where the desired result of management is the formation and maintenance of a virtual monoculture. The long-term aim of management of weeds of natural ecosystems is the maintenance or regeneration of diversity. Hence, control strategies must be closely linked with rehabilitation of endemic communities of plants or cause minimal disturbance of existing endemic communities. Disturbance, particularly that of human origin, such as alteration of fire regimes, vegetation clearance, grazing by introduced animals and eutrophication, generally, enhances weed invasion (Burke & Grime 1996, Cook & Setterfield 1996, Fox 1991, Berendse & Elberse 1990, Hobbs 1989). Rehabilitation of areas must occur after or during control because control by itself will result in under-utilised resources such as light, nutrients, and water, which are more likely to benefit weeds.

Various techniques exist for control of environmental weeds, *i.e.* weeds of natural ecosystems. They can be divided into physical and chemical methods, biological control, fire and competition or suppression with endemic plants.

1.3 Physical and chemical control

Physical methods include mowing (use of tractor or other vehicle), slashing, cutting, pulling or digging out by hand. Mowing or slashing is generally non-selective, although the height to which the vegetation is slashed relative to different heights of plants will select between different stages or species. Mowing and slashing do not usually kill the weed. Mowing is also restricted to flat and even terrain, whereas many natural ecosystems invaded by weeds are often boggy, rocky or steep. Hand-pulling of weeds is generally the best option in areas of high conservation concern with a low resilience to human disturbance. It is selective and if well-organised can lead to good re-generation of native vegetation such as with the Bradley method (Bradley 1971). The Bradley method involves systematic removal of all invasive weeds from small areas at a time, with the removal beginning in areas where endemic plant density is the highest. An alternative to hand-pulling is the specific application of herbicides to stems that have been cut or drilled (Gillespie 1991). This may be preferable due to less soil disturbance and hence less subsequent weed germination but it is more expensive due to the cost of herbicide. Both pulling and selective herbicide application are labour-intensive and rely on a dedicated group of volunteers or a large portion of a park or reserve's management budget. In addition, if weeds have been growing for some time and the seeds are long-lived, then a substantial seedbank may have already accumulated. This is the case with *C. scoparius* (Allen *et al.* 1995, Bossard 1993). The re-generation potential of the seedbank may exceed the enthusiasm of volunteers or the park's available funds.

Spraying of herbicides may be useful in the management of environmental weeds, especially if incorporated into an ecological control strategy (Groves 1989). Herbicides are not usually selective enough to spray in areas with a mixture of weeds and indigenous plants, although many Australian plants are somewhat resistant to certain herbicides when compared with associated exotic weeds, especially at certain times of the year (Groves 1991). Spraying areas with high densities of weeds will leave gaps and unless follow-up planting with endemic plants is carried out there will be rapid re-invasion by the target or another weed. Cessation of a spraying programme at Barrington Tops, N.S.W., resulted in re-

growth of the target weed, *C. scoparius*, and subsequent invasion of the surrounding eucalypt woodland (Groves 1989).

1.4 Biological control

Biological control uses the planned release of insects or microbes to control a target weed. The biological control agent is usually imported from the native country of the target weed. Selection and testing of biological control agents is an expensive, time-consuming task, especially when the target weed is related to a plant of economic value or to an indigenous plant of the invaded habitat. There have been some remarkable successes of biological control but more often (75% of releases) there are failures (Julien 1989). The difference between success and failure may depend on the agent being effectively incorporated into an integrated management strategy. In order to do this, biological information on the agent, the target weed and the invaded community is required. One example of a combined strategy is use of fire in combination with biological control agents for *Hypericum perforatum*, *Chrysolina quadrigemina* (beetle) and *Aphis chloris* (aphid). Fire favoured population increase of the agents due to higher plant nutrient levels and fresh re-growth (Briese 1996).

Three control agents for *C. scoparius* have been released in Australia. They are the twig-mining moth, *Leucoptera spartifoliella*, a broom psyllid, *Arytainilla spartifoliella*, and a seed bruchid, *Bruchidosis villosus* (Hosking *et al.* 1996). More agents are undergoing host-specificity testing. It is too early to assess the effectiveness of the three agents already released.

1.5 Fire

Fire affects many facets of ecosystems and is itself a complex, variable phenomenon. This makes it difficult to use for land management, including weed management, and be precise about how it will change the ecosystem. However, periodic fires are an integral component of many Australian ecosystems including dry sclerophyll forest in South Australia. Hence it is seriously considered as a potential tool for managing *G. monspessulana* in sclerophyll forest. In addition,

because fires are likely to occur in areas invaded by *G. monspessulana*, it is prudent to be aware of how this species responds to fires. A lot of information is available about the effects of fire on ecosystems and their components throughout the world.

1.6 Fire characteristics and behaviour

Vegetation is the source of fuel for fires of natural ecosystems. The composition of the vegetation will have a large influence on fire characteristics such as flame height, intensity, spatial variation and soil temperatures (Walker 1981, Hobbs *et al.* 1984, Hobbs & Atkins 1988). For example, soil temperatures during a fire under *Eucalyptus* stands were found to be higher deeper in the soil, frequently 60-120°C to 5 cm depth, than under a grass (*Triodia irritans*) or an *Acacia* overstorey, with temperatures of 60-120°C only to 2 cm depth (Bradstock *et al.* 1992). Fine fuels (particles <6 mm thick) on the ground have significantly greater influences on soil temperature during a fire than coarse (6-25 mm thick) or above-ground (canopy) fuel (Bradstock & Auld 1995). Weather, climate and topography are also important factors determining the nature of fires. Wind speed is the most changeable factor affecting fire behaviour and the most difficult to relate to patterns of fire behaviour (Cheney 1981). Topography influences fire behaviour directly. For example, an experiment conducted in *Quercus* communities (Franklin *et al.* 1997) found the influence of fuel biomass on soil temperature decreased as slope increased. Topography also determines wind speed and direction thereby affecting fire behaviour (Cheney 1981). Soil structure and type has an indirect influence on fire because it often determines the composition and spatial patterns of vegetation, hence fuel distribution.

1.7 Fire-induced changes in soil

Australian soils are generally low in nutrients and fire significantly alters nutrient availability (Walker *et al.* 1986). Changes to the soil properties during fire depend mainly on the amount of soil heating. Factors that affect soil heating are initial soil temperature, moisture content, bulk density, pore size, soil heat

capacity and thermal conductivity (Walker *et al.* 1986). Changes that occur as a result of different levels of soil heating are summarised in Table 1.

Table 1. Changes in soil and plant material as soil temperature increases (from Walker *et al.* 1986).

Temperature (°C)	Changes occurring
> 1200	Volatilisation of calcium
950	Clay minerals converted to different phase
600	Maximum loss of potassium and phosphorus, fine ash produced, organically bound cations form oxides
540	Little residual nitrogen and carbon left
420	Hydroxyl water from clay minerals lost
400	Organic matter carbonised, maximum amino acid nitrogen released
300	Loss of sulphur and phosphorus begins, distillation and carbonisation of organic residues, organic matter charred
200	Hydrophobicity caused by distillation volatiles, loss of nitrogen commences
125	Soil sterilisation
110	Sorbed water lost
100	Soil ammonium production starts
70	High nitrate mineralisation
60	Proteins denatured
50	Mild sterilisation owing to water loss
37	Maximum stimulation of soil micro-organisms
<25	Usual soil temperatures

Litter and vegetative cover are removed to different degrees depending on the characteristics of the fire. Removal of cover reduces the amount of habitat and food sources for litter and soil fauna. Decreasing litter and soil fauna reduce the infiltration of water and the rate of litter decomposition. Subsequent increased water run-off increases the risk of erosion (Walker *et al.* 1986).

High temperatures (200-300°C) cause volatilisation of carbon, nitrogen and sulphur. Nitrogen and carbon contents of surface soils are also reduced by lower litter input, increased respiration and leaching after a fire (Walker *et al.* 1986). However, an 'ash bed' effect has been demonstrated, in which plant growth is improved for a limited time following fire. This phenomenon results from a combination of destruction of plant toxins, reduction in plant competition, increased solubility of surface soil organic matter and subsequent accumulation of ammonium nitrogen (Walker *et al.* 1986). Under ash-beds within burnt *Eucalyptus pauciflora* forest there was increased mobilisation of cations (Ca^{2+} ,

Mg²⁺, K⁺, NH₄⁺) and anions (Cl⁻, SO₄⁻) (Khanna & Raison 1986). These changes in nutrient regime following a fire may increase nutrient availability to plants in the first year after the fire. Losses of organic matter due to the fire would then result in lower nutrient availability in later post-fire years (Khanna & Raison 1986).

Heating of the soil above 60°C for several minutes kills most soil organisms. The soil may be partially or wholly sterilised to various depths depending on fire intensity (Warcup 1981). Greater mycorrhizal development occurs at sites with lower fire frequency (Walker *et al.* 1986). Different types of mycorrhiza are affected differently by heating (Warcup 1981). Ectomycorrhizas (external) associated with *Eucalyptus camaldulensis* in a pot experiment survived heating. Endomycorrhizas (internal) associated with *Dodonaea cuneata* did not survive (Warcup 1981). As mycorrhizas have been identified as determinants of plant community structure (van der Heijden *et al.* 1998), the different responses of different mycorrhizas may lead to changes in plant community.

1.8 Effects of fire on vertebrates

Catling & Newsome (1981) reviewed the response of vertebrate fauna to fire based on a post-fire vegetation model. Within recently burnt areas there is a dramatic reduction in shelter available for mammals and birds. Six months to 1 year post-fire there is a provision of new, nutritious growth providing there is sufficient protection, for vertebrates, from predators. Vertebrates exploiting the grass and herb layer would have optimum conditions in the first 2-3 years following the fire. Vertebrates exploiting the heath layer would have optimum conditions in 5-15 years following the fire. Animals exploiting trees would do best 10 years following the fire. For animals requiring senescent trees for nesting there would not be suitable sites for 25-50 years.

Studies of vertebrates in tropical savannas found variable responses between different classes of vertebrates. Frillneck lizard (*Chlamydosaurus kingii*) populations significantly increased in areas subjected to frequent dry season fires (Griffiths 2000). Populations of three species of small mammal, northern brown

bandicoot (*Isodon macrourus*), grassland melomys (*Melomys burtoni*) and northern brushtail possums (*Trichosurus vulpecula*) continuously declined over a six-year period in areas subjected to annual fires. Populations in adjacent unburnt areas had oscillated over the six years (Griffiths 2000).

1.9 Effects of fire on invertebrates

An early study of the effect of fire on invertebrates (Springett 1979) suggested a dramatic impact of fire on soil and litter invertebrates. A subsequent study (Campbell & Tanton 1981) found the community of soil and litter invertebrates in areas burnt in autumn or winter to be within the variation found in communities of the soil and litter invertebrate community at similar unburnt sites. Neumann & Tolhurst (1991) found short-term reductions of up to one year, in Collembola, Diptera, Opilionida (harvestmen spiders), Lepidoptera and Apocrita (parasitic wasps). Longer term reductions were recorded in Annelida (earthworms) for three years, after a spring burn. An autumn burn had less influence, earthworms were not affected and arthropod taxa recovered within 10 months.

1.10 Characteristics of plants enabling them to survive certain fire regimes

Fire survival mechanisms can be divided into two broad groups, vegetative or reproductive. Vegetative mechanisms include subterranean (buried) buds or storage organs or aerial buds protected by bark, older tissue or placement above the bulk of the fuel load. Lignotubers, underground storage structures that facilitate resprouting after fire, are found in the majority of *Eucalyptus* species. Only twelve *Eucalyptus* species lack lignotubers (Gill 1981). Many herbaceous plants have corms, rhizomes or bulbs within the soil and are protected from lethal temperatures by the insulating properties of soil (Gill 1981, Walker *et al.* 1986, Bond & van Wilgen 1996). *Eucalyptus regnans* (mountain ash) and several species of North American pine (Ashton & Martin 1996, Bond & van Wilgen 1996) have foliage well separated from the ground by tall trunks (20 m) and are thereby protected from surface fires. Protected seedbanks form the basis of most reproductive survival mechanisms. *E. regnans* (Attiwill 1994), many species of Proteaceae (Bond & van Wilgen 1996, Gill 1981), Casuarinaceae, and a few other

families have canopy-stored seeds that require fire for release and to overcome dormancy. Hard coated, soil-stored seed is another common reproductive survival strategy. Fabaceae has many members with such a mechanism.

1.11 Response of plant populations to fire

A number of studies of individual species' response to fire reveal an intolerance (reduction in populations or potential extinction) to changes or variations in fire regime in most species. Optimum fire regimes can be very different depending on the particular species. Plant reproductive strategies fall into two broad groups with respect to fire, namely those that depend on fire for recruitment and those that survive fire but do not depend on it for reproduction. Responses of populations of sclerophyll species to fire is generally well understood (Auld 1986a, Auld 1986b, Bradstock 1990, Whelan & Muston 1991, Enright *et al.* 1996) and some examples follow.

Banksia hookeriana is dependent on fire for recruitment of juveniles. The optimum fire interval is 16-17 years (Enright *et al.* 1996). The species reaches reproductive maturity (produces viable seeds) at 5 years after which it gradually increases production to a fluctuating maximum at about 15 years. The seeds are stored in cones on the plants throughout the plant's lifetime. A proportion of these seeds is lost through predation, fungal decay and sporadic opening of cones. Losses of seed become significant usually only after 12-13 years. Seedlings germinating in the absence of fire die within one year, therefore there is no recruitment in the absence of fire. Fires occurring before 16 years, and certainly before 5 years limit the reproductive potential of *B. hookeriana*. Mature *B. hookeriana* do not resprout following a fire (Enright *et al.* 1996).

Another species of *Banksia*, *B. serrata*, is able to resprout in addition to having canopy stored seed that is released from dormancy following a fire. This species is described as a facultative resprouter. *Isopogon anemonifolius* from the same community as *B. serrata* is also a facultative resprouter. A study of this community (Bradstock 1990) found a fire interval greater than 9 years, if the fire intensity was high (12-13 years for low intensity fires), would result in a stable *B.*

serrata population. *I. anemonifolius* required a longer interval of 14 years with high intensity fires or 16 years with low intensity fires. *B. serrata* and *I. anemonifolius* have potential life-spans of 50 years in the absence of fire. Unlike *B. hookeriana*, the release of seeds from cones of *B. serrata* increases with increasing time since fire (Bradstock 1990). Seedling recruitment in *B. serrata* in the absence of fire is restricted by plant cover and seedling predators but does occur occasionally.

Another life history strategy enabling population persistence post-fire is that of *Acacia suaveolens*. Unlike the above examples populations of *A. suaveolens* survive by producing a hard-coated, dormant seed stored in the soil. The predicted viable half-life of *A. suaveolens* seeds in the soil is 10.7 years in the absence of a dormancy-breaking event such as fire (Auld 1986a). Dormancy is broken by heating the seeds to temperatures $>60^{\circ}\text{C}$ (Auld 1986b). These temperatures usually occur only in the event of a fire. Minimal germination and survival of *A. suaveolens* seedlings occurs in the absence of fire. Therefore, populations tend to be even-aged (Auld & Myerscough 1986) and depend on fire for perpetuation of mature plants. *Acacia* seeds have elaisomes which attract and provide a food source for ants (Auld 1986a). Considerable quantities of *A. suaveolens* seeds (40%) end up in ant nests buried deeper than 10cm (Auld 1986a). Seeds buried at these depths require a very high intensity fire and possibly soil disturbance in order to germinate successfully.

Conditions for breaking dormancy and stimulating germination of seeds from fire-prone environments has received considerable attention (Hodgkinson & Oxley 1990, Portlock *et al.* 1990, Auld & O'Connell 1991, Keeley 1991, Roy & Sonié 1992, Bell 1994, Bell *et al.* 1995, Dixon *et al.* 1995, Mucunguzi & Oryem-Origa 1996, Trabaud *et al.* 1997, Bell & Williams 1998, Keeley & Fotheringham 1998, Roche *et al.* 1998). A few general trends emerge from the results of these studies. Seeds with dormancy in fire-prone environments cease dormancy with exposure to either heat or smoke-related chemicals. A temperature range of $70-90^{\circ}\text{C}$ will break dormancy of most species requiring heat. Temperatures above 100°C will kill most seeds, although there are often individuals within most species that have an exceptionally good tolerance of high temperatures. Cool temperatures ($15-$

17°C) are generally required for subsequent germination of Australian forest species (Bell *et al.* 1995). Dominant tree species within the study by Bell *et al.* (1995) are the exception; they germinated readily over the range of conditions tested.

1.12 Temporal and spatial effects of fire on plant communities

1.12.1 Temporal patterns

The mixture of plants occupying any particular space may change with time. This process is called succession. One important factor driving succession is disturbance which provides potential for change by removing the incumbent plants from the space. Disturbances can include fires, flooding, grazing/herbivory, landslides, large plants dying or collapsing, clearing and a number of other processes. The space created can then be occupied by the same or a different species. Other important factors driving succession are competition, resource fluctuation and changing physical or edaphic factors.

The earliest, most popular model describing succession emerged in the 1920's and is attributable to Clements (cited by Noble & Slatyer 1981, Gitay & Wilson 1995, Inchausti 1995, Bond & van Wilgen 1996). The process of succession begins with uninhabited space. A particular set of species colonise the uninhabited space. These colonisers change the conditions and a new set of plants begin to occupy the space, mainly because they are stronger competitors than the previous colonising species. The process continues until the most competitive species occupy the space. The community is then considered "climax" and will continue to exist in equilibrium unless there is disturbance.

This basic model is no longer considered appropriate and a number of other models of succession have been developed (Noble & Slatyer 1981, Watson *et al.* 1997, Bond & van Wilgen 1996, Gitay & Wilson 1995, Inchausti 1995, Berendse & Elberse 1990). These other models vary depending on the perceived relative contributions of factors such as disturbance, competition, herbivory and resources to succession.

Fire ecologists have generally considered the influence of competition to be negligible and instead focus on the interplay between disturbance (fire) and timing of essential life-history events. Egler conceived such a model that was subsequently modified by Noble and Slatyer (1981); it is called the “initial floristic composition model”. This model proposes that following a fire there is a maximum diversity of plants after which, depending on life-history and life-span of the components, various species disappear from the standing vegetation with time following the fire.

Fire studies reviewed by Bond & van Wilgen (1996) support the initial floristic model. At climax, chemise chaparral in California is dominated by a single species, *Adenostoma fasciculatum* (chemise). In the first year following a fire all the components of the “climax” community are present and colonisation by new species is rare (Hanes 1971 cited by Bond & van Wilgen 1996). Likewise, in the French garrigue, dominated by scrub oak, *Quercus coccifera*, maximum diversity occurred within two years following the fire and declined thereafter (Trabaud 1994). There was no marked difference between communities 10-15 years post-fire and mature communities in the area. In contrast, post-fire regeneration in red fir (*Abies magnifica*) forest (Chappell & Agee 1996) did not fit the initial floristic composition model because red fir seedling survival is better 3-4 years post-fire rather than immediately following the fire.

Australian wet-sclerophyll *Eucalyptus* forests also support the initial floristic composition model (Ashton 1981). Species richness is high in the first year following fire (Ashton & Martin 1996, Bond & van Wilgen 1996) then declines. The types of species disappearing from the community will depend on fire characteristics. Hence, different fire characteristics will lead to different species mixtures from a similar initial pre-fire community. This example supports the initial floristic composition model but with potential variations in the climax community. Bond & van Wilgen (1996) state that fire return time is the primary regulator of alternative states of sclerophyll forest. For example, short fire interval will favour a more herbaceous, scrub community (Ashton & Martin 1996, Bond & van Wilgen 1996) and will kill *Eucalyptus regnans* before an adequate seedbank is established. A long fire interval will favour replacement of the wet-

sclerophyll forest by temperate rainforest. Bond & van Wilgen (1996) also stated that there is little evidence for competitively driven replacement sequences. This leaves open the question of what then causes the change from *Eucalyptus* sclerophyll forest to temperate forest if it is not competition or disturbance? It seems the role of competition in this case (Bond & van Wilgen 1996) has been overlooked because fire frequency, inappropriately, is given as the reason for a change of community because it's not a mechanism for change of the plant community *per se*. It is more appropriate to identify other processes such as competition, herbivory, different types of disturbance or combinations of these that play a bigger role due to the absence of fire.

1.12.2 Spatial Patterns

Fire research may be considered at two main scales. Firstly it may be considered at a broad scale such as patterns of regions with similar topography, dominant plants and climate. At this scale the ecosystem is given a title such as Florida scrub, dry sclerophyll forest, grassy woodland, neotropical savanna. Within each ecosystem there may be different communities or groups of commonly associated species that are recognised. This scale must be considered because different communities may have varying responses to the use of controlled burning for weed management. In addition different communities may affect how a weed responds to fire. Considering a finer scale, vegetation patches of about five metres or less, is also important for land management (Ludwig *et al.* 1999, Tongway & Ludwig 1996). In the case of a fire for managing weeds the finer scale variations may result in patchy reduction of the seedbank. Patchy reduction of the seedbank reduces the benefits of fire because the presence of more remaining seeds increase the probability of re-invasion of the area. Alternatively fine scale variations may provide refuges for fire-sensitive species and this will reduce the overall negative impact of a fire.

1.12.2.1 Broad scale

At a broad scale Menges & Hawkes (1998) describe six different communities (sandhill, turkey oak barrens, sand pine scrub, rosemary scrub, scrubby flatwoods and xeric hammocks) that arise as a result of different fire frequencies within areas of Florida scrub. Likewise, a study of fire history and vegetation patterns in

an area of Yellowstone National Park that had relatively uniform topography and geology revealed a correlation between community types and fire history (Romme 1982 cited by Bond & van Wilgen 1996). Composition of red fir forests in Oregon was also found to vary as a result of fire intensity (Chappell & Agee 1996). The post-fire stand structure was markedly different from that pre-fire in the event of a moderately intense fire but not for a low intensity fire. Following a high severity fire there was likely to be a short period (3-4 years) of shrub dominance before red fir regrew.

Broad scale patterns in vegetation will also depend on topography. Valleys may provide shelter by disrupting wind flow and because they accumulate moisture (Cheney 1981, Bond & van Wilgen 1996, Franklin *et al.* 1997) and will provide a refuge for fire intolerant species.

1.12.2.2 Fine scale

Patterns on a finer scale (<5 m) occur with uneven vertical and horizontal distribution of fuel loads and consequently gradients of fire intensity in most fire-prone vegetation (Hobbs *et al.* 1984, Hobbs & Atkins 1988, Bradstock *et al.* 1992, Bradstock & Auld 1995, Bond & van Wilgen 1996,). Benwell (1998) and Schimmel & Granström (1996) demonstrate how fuel loads and associated differences in fire intensity can determine fine scale patterns of vegetation. Significant differences in composition of Boreal Swedish forest were detectable 5 years following a controlled burn as part of an experiment to compare different fuel loads and therefore intensities and depth of heating (Schimmel & Granström 1996). Higher intensity fire, caused by a thicker layer of fuel, tended to favour seed regenerating species over rhizomatous species. However, this does not seem to be a general trend. In a study of post-fire regeneration strategies in Australian coastal heathland (Benwell 1998) survival of five out of six potential resprouting species was improved by low-intensity fires. They resprouted where fire intensity was high. Benwell (1998) suggests, based on his examination of around 150 species from two sites, that fire regeneration strategy varies with site quality and increasing stress. The sites could be divided into three habitats (wet, moist and dry heath) at one site and one (headland heath) at the other. Better site quality and

productivity may favour obligate seed regeneration whereas increasing environmental stress favours obligate resprouting.

Post-fire conditions for example, herbivory and availability of nutrients and moisture, will influence patterns of emergence and survival (Jianmin & Sinclair 1993, Tyler 1996). These conditions may vary across small scales such as 5 metres or less (Ludwig *et al.* 1999). Four dry sclerophyll species, *Eucalyptus fasciculosa*, *Pultanaea daphnoides*, *Platylobium obtusangulum* and *Acacia myrtifolia*, growing in both a burnt area and an adjacent unburnt area responded differently to differences in moisture availability in the two areas (Jianmin & Sinclair 1993). *P. daphnoides* and *E. fasciculosa* showed no significant differences in moisture stress, whereas *P. obtusangulum* and *A. myrtifolia* demonstrated considerable moisture stress in the burnt area (Jianmin & Sinclair 1993). Dry conditions following a fire will favour species better able to cope with moisture stress. Alternatively, moister patches within a burnt area that might be caused by clumps of unburnt wood or tree trunks reducing evaporation or holding run-off (Tongway & Ludwig 1996), may favour more competitive but drought-intolerant species.

Herbivores may be patchy in their distribution within fine and broad scales (Andrewartha & Birch 1954). Selective herbivores often favour one species over another (Crawley 1997, Harper 1977) and can change community composition. Tyler (1996) compared composition of maritime chaparral following a burn and herbivore presence or exclusion. In the absence of herbivores the density of perennial herbs increased.

1.13 Use of fire to manage weeds

Fire was used extensively throughout Australia by the aborigines to improve forage for hunted species, access and plant food species (Nicholson 1981). Throughout the world fire has often been used to prevent succession of grassland to scrub and forest and thereby maintain grazing for domestic or wild herds, and easier access (Bond & van Wilgen 1996). Programs of regular controlled burning have been carried out to maintain fuel loads below purported hazardous levels in

United States and Australia. More recently, fire has been used for weed management and maintenance of fire dependent plants (Agee 1996, Bond & van Wilgen 1996).

The effectiveness of fire for management has been examined for two legumes, *Mimosa pigra* (Lonsdale & Miller 1993) in northern Australia and *G. monspessulana* in California (Bossard unpublished). Field experiments and small-scale fires in containers demonstrated that fire significantly reduced the seed bank of *M. pigra* through death and germination. Erosion of top soil is a low risk following burning of *Mimosa pigra* because invaded areas are mostly flat floodplain. Integration of controlled burning with biological control and spraying programs is being investigated in the Northern Territory (Paynter pers comm). High intensity burns are possible due to isolation of *M. pigra* infestations from urban areas.

Treatments chosen in a trial conducted by the California Exotic Pest Plant Council from 1993-1996, were those considered most likely to impact *G. monspessulana* based on observations by land managers and studies of *Cytisus scoparius* (Bossard unpublished). Cutting combined with a herbicide treatment followed by a pre-rain (autumn) fire then a spray treatment of post-fire seedlings provided the most effective *G. monspessulana* control in trials. Seed bank density was reduced by 90% (Bossard unpublished). There was no discussion by Bossard (unpublished) about potential erosion risk or composition of post-fire vegetation with respect to conservation or land management objectives.

Other invasive weeds for which fire is likely to be a valuable management tool are *Cryptostegia grandiflora* (Grice 1997), an invader of tropical woodland in northern Australia, and *Pittosporum undulatum* (Mullett & Simmons 1995), an invader of southern Australian sclerophyll forest.

Disadvantages associated with use of fire for weed management and fuel reduction have been discussed by some authors (Morrison *et al.* 1996, Milberg & Lamont 1995, Hobbs 1991, Hobbs 1989). The combined study of fuel load accumulation and the effects of fire interval and time since fire on floristic

composition in dry sclerophyll forest or woodland by Morrison *et al.* (1996) demonstrated clear conflicts between burning for fire hazard reduction and for species conservation. One hundred and forty species were examined from 24 dry sclerophyll scrub or woodland sites with different mean fire intervals and times since fire. Fuel load accumulation was examined at 12 sites. Fine fuel loads accumulated to hazardous levels within 2-4 years. Species conservation was compromised at fire intervals shorter than 7 years. This was mainly due to five long-lived woody shrubs with canopy stored seedbanks; *Banksia ericifolia*, *Hakea sericea*, *Hakea teretifolia*, *Lambertia formosa* and *Petrophile pulchella*.

That disturbance enhances weed invasion is a common assumption (Milberg & Lamont 1995, Hobbs 1989, Fox & Fox 1986). Hobbs (1989) examined soil disturbance and nutrient addition in five different Western Australian plant communities, *Casuarina* scrub, heathland dominated by Proteaceae, open scrubland, woodland dominated by *Acacia acuminata* and *Eucalyptus monogyna*, and woodland dominated by wandoo (*Eucalyptus wandoo*). There were three treatments, turning the soil to a depth of 5cm, fertilising with slow release fertiliser and combining soil turning and fertiliser addition. Two species of weed seeds (*Avena fatua* and *Ursinia anthemoides*) were added to the plots, and any additional weed species germinating were scored. The number of and average biomass of individual plants were assessed after four months. There were significantly higher numbers of *A. fatua* in both treatments with soil disturbance but not with fertiliser addition in four of the five communities. There was only one significant difference in numbers of *U. anthemoides* and it was in the *Eucalyptus wandoo* community. Soil turning combined with fertiliser significantly increased the biomass of the weed, *U. anthemoides*.

Milberg & Lamont (1995) compared abundance and cover of weeds in three burnt roadside sites (previously unburnt for 22-25 years) with that in three unburnt sites. The fires were low intensity because no change in density of mature shrubs (*Banksia* spp., *Acacia blakelyi*) was recorded. There was a significant increase in the numbers of weeds and in the numbers of weed species. The dynamics of native species following the fire compared to unburnt sites was unclear in this study. Hobbs (1991) in contrast to Milberg & Lamont (1995) found no effect of

fire on the abundance of weeds in a heath community, despite also recording post-fire increases of soil phosphorus and nitrate. Hobbs (1991) states that results from a single fire event can be misleading in that an autumn fire resulted in invasion whereas a spring fire did not. Hobbs (1991) also reported that weed invasion declined very quickly as samples were taken at increasing distances from the edge of remnant vegetation.

1.14 Competition

Along with herbivory, inter-specific competition may be considered one of the most important biotic factors contributing to plant community composition. In order to manipulate plant community composition for example, to reduce the proportion of weeds, then it is important to understand the nature of competitive interactions within that community.

Competition with respect to plant ecology is defined by Tilman (1997) as an ability of one or several plants to inhibit the survival or growth of other individuals or populations. It is similarly, but more narrowly defined by Begon *et al.* (1986) as “an interaction between individuals brought about by a shared requirement for a resource in limited supply, and leading to a reduction in the survivorship, growth and/or reproduction of the individuals concerned”. Tilman’s (1997) definition is broader because it incorporates other processes, such as production of toxic chemicals by one plant that may inhibit another plant. Harper (1977) is broader still and lists many ways that plants influence their neighbours. These include the definitions above as well as producing chemicals that inhibit the germination and growth of other plants, providing refuges for herbivores, or attracting more herbivores. There may also be positive effects such as providing shelter, diverting herbivores or capturing organic material which will improve the soil structure and water holding ability. Several studies document cases where beneficial effects of neighbours are more important than the depletion of nutrients (Callaway *et al.* 1996, Buckley *et al.* 1998).

In the case of weed invasion of natural ecosystems it is important to identify those species which are likely to be out-competed by *G. monspessulana* and whether or

not there are “safer” populations of vulnerable species in areas uninvaded by *G. monspessulana*. A priority for weed management can then be assigned to the invaded area. For example, Belair National Park in South Australia contains the only known large populations of the leafy green-hood orchid, *Pterostylis cucullata* (Davies 1992). Weed invasion, including *G. monspessulana*, is identified as a threat to these populations of *P. cucullata* (Davies 1995). Competition between *C. scoparius* and three species native to invaded habitats in the Mount Lofty Ranges was investigated by Fogarty & Facelli (1999). The biomass of two species of *Acacia* (*A. verniciflua* and *A. myrtifolia*), nitrogen-fixing legumes, was not affected by competition with *C. scoparius*. The biomass of a non-nitrogen-fixing shrub, *Hakea rostrata*, was reduced by competition with *C. scoparius* (Fogarty & Facelli 1999).

In addition to species threatened by *G. monspessulana* there is also interest in any locally endemic species capable of reducing resources, such as water, nutrients and light available to *G. monspessulana* or in those that produce substances toxic to *G. monspessulana*. Nurturing potential sources of competition for invasive weeds may reduce resources such as nutrients and water available to invading weeds, thereby reducing weed vigour and survival. In this way competition could have an important role in an integrated management strategy for *Genista monspessulana*. For example, in the event of biological control agents being introduced, there may be multiplicative effects of competition and herbivory as has been recorded in other systems (Kok *et al.* 1986, McEvoy *et al.* 1993, Maron 1997).

This section of Chapter 1 has two main components: Firstly, it explores the nature of competition, in particular, what makes certain plants better competitors and how the outcomes of a competitive interaction change depending on different circumstances; secondly, it examines the different approaches to studying competition and their advantages and disadvantages.

1.15 The nature of competition

When plants of the same species compete with each other this is described as intra-specific competition. Intra-specific competition was extensively studied in the 50's and 60's by Kira, Hozumi, Shirozaki and Yoda (Firbank and Watkinson 1990). The outcome of several detailed studies was some generalisations about plant growth in mono-cultures. Firstly, there is a "law of constant final yield". As the density of the monoculture increases the biomass per individual plant decreases but the overall biomass will remain more or less constant. There are, obviously, lower densities of plants at which the maximum yield per plant is reached but the combined yield remains lower than the potential combined maximum yield (Harper 1977). Secondly, "self-thinning" or density dependant mortality occurs as plants grow older. Once a population of plants has reached a maximum density then, as time passes, individuals die and the remaining plants increase in weight and size. The increase in weight is considered to be reasonably consistent and is described by the equation:

$$\text{weight per plant} = (\text{constant} \times \text{maximum density})^{-3/2}$$

where the constant depends on the particular species studied (Firbank & Watkinson 1990, Harper 1977). Thirdly, variation in individual plant size follows a pattern (Firbank & Watkinson 1990). There is initially a normal distribution of plant weights. The distribution of plant weights then becomes skewed as the plants get older. It becomes a bimodal distribution of weights or heights because some plants become large and others much smaller. Eventually the smaller plants die and the distribution returns towards normal.

Therefore, even within the same species there is a potential ranking of competitive potential. Size inequality provides an advantage for the larger plant, it has more biomass with which to gather resources. The reasons for size inequality can range from intrinsic plant factors *e. g.* seed size, rate of growth and emergence time to external factors such as herbivores, pathogens, seed depth, and proximity to neighbours (Firbank & Watkinson 1990). These factors will also be important in determining the outcomes of inter-specific competition.

Herbivory and disturbance have the potential to alter the outcome of competition. However, the effect is not consistent across different associations or environments

that have been studied. Norris (1997) found the outcome of competition between a weed, *Portulaca oleracea* and a crop species, *Beta vulgaris* was different when herbivores were removed with insecticide. This occurred in a pot experiment however and a longer term field experiment did not show the same reversal of competitive outcome in three out of four years. McEvoy *et al.* (1993) found that the combination of herbivory by the ragwort flea beetle (*Longitarsus jacobaeae*) and inter-specific competition resulted in elimination of the normally abundant weed, *Senecio jacobaea*, at the spatial scale studied. However, competition and herbivory by a ragwort feeding moth did not significantly alter the ragwort population.

1.16 Studying competition

There are many different approaches to studying competition. However, it is not always clear which is the most appropriate approach for assessing suitable competitive native species for an integrated management strategy and the effect of a weed on endemic species. Experiments investigating competition fall into four main groups. They are: 1) Neighbourhood analysis, 2) Removal (presence/absence) experiments, 3) Addition, replacement and response-surface designs and 4) Comparative growth under a variety of conditions.

Neighbourhood analysis, as described by Campbell *et al.* (1991), is an observational study of the spatial distribution of species and local edaphic or climatic conditions. The result sought in this type of analysis is evidence of groups of plants that usually occur together or usually apart. These may or may not then also be compared with certain physical or edaphic conditions. Mullett & Simmons (1995) and Weiss & Noble (1984) used neighbourhood analysis to demonstrate that two invasive weed species, *Pittosporum undulatum* and *Chrysanthemoides monilifera* ssp. *rotundata* were displacing native vegetation. In both cases there were strong negative correlations between many native species and the invasive weed. However, any evidence of competitive displacement gleaned from this type of study will always be circumstantial as opposed to definitive. A particular regime of disturbance favouring the weeds over the

natives may have been responsible for the negative association rather than competition *per se*.

Removal experiments involve manipulation of the environment and are more likely to yield definitive results. In this type of experiment, the response of one or more species to the removal of another is measured. Removal experiments can be applied to a large size and age range of plants. Campbell *et al.* (1991) have criticised these experiments on the basis that they are generally only applicable to areas where mixtures currently exist and cannot be applied to areas where there is a mono-specific stand that has probably arisen as a result of a prior competition event. This criticism is somewhat trivial and possibly wrong because real monocultures are highly unlikely in nature as although plants may not be present as adults there may be several species of plants occupying the space as seeds. Two other limitations of removal experiments discussed in Campbell *et al.* (1991) are important. Varying seasonal patterns in resource use and allocation by different species mean that timing and duration of removal experiments is critical. Removing vegetation may also lead to an alteration of resource availability in ways additional to the simple removal of competition. This may be particularly important in environments with intrinsically low nutrient levels. It is impossible to remove all traces of plants, especially extensive fine roots, underground storage organs and mycorrhizal networks, without major disturbance.

Removal experiments are unlikely to be useful for selecting suitable native species for a weed management strategy. Removing weeds from an area and monitoring the response will merely identify those plants that are least competitive. Removing various native plants from the vicinity of weeds or weed seeds may be a more useful technique. However it is likely to be time consuming with only one species or group being tested in any one experiment.

The third category of experiments including replacement series, addition series and response-surface designs are manipulated experiments involving small numbers of different species, usually two. There has been copious debate surrounding these types of experiments. The debate ranges from questioning the validity of using replacement series under any circumstances (Connolly 1986) to a

defence of their validity based on the particular question to be answered (Cousens 1991).

These experimental designs have been used exhaustively for studies of small herbs, grasses and crop weeds (Bonser & Reader 1995, Berendse & Elberse 1990, Roush *et al.* 1989, Connolly 1986, Firbank & Watkinson 1985, Joliffe *et al.* 1984, Tilman 1984, Watkinson 1981). A replacement series, despite much criticism, currently remains the most popular design for studying competition in glasshouses (Gibson *et al.* 1999). They are difficult to apply to studies of competition in woodland or forest ecosystems with many plants being large and long-lived. However, they may be applied to seedlings of shrubs and trees. For example, Weiss (1984) used a replacement series design to study competitive interactions between seedlings of a native species, *Acacia longifolia*, and an invasive weed, *Chrysanthemoides monilifera*.

In replacement series designs two species or biotypes are grown together in different proportions but with the same overall density. In addition series designs the density of one plant is kept constant and the density of a second plant is increased. This design is useful because it closely represents the increase in weed populations in a crop environment. A response-surface design is the term used when the more basic replacement series is replicated at a number of total densities (Cousens 1991). There are weaknesses of the basic replacement series design. For example, there is the assumption that one plant of one species is equivalent to one plant of the other tested species. The larger the size difference between the plants the less likely it is that this assumption is valid (Connolly 1986, 1997, Grace *et al.* 1992). The assumption may be valid with similar sized plants. These experiments cannot distinguish between the relative influences of intra- and inter-specific competition. Growing a mono-culture series along with the mixtures can solve this problem (Cousens 1991, Rejmánek *et al.* 1989, Joliffe *et al.* 1984). Finally the results of replacement series designs need to be used cautiously to predict the effects of competition on community structure (Gibson *et al.* 1999). Removal experiments are better for this.

The final type of experiment for studying competition is to compare different aspects of plant growth between different species. For example, Campbell *et al.* (1991) investigated root and shoot foraging potential. Patches of a particular resource, light or nutrients, were provided for a plant. The ability of the plant to colonise the patch was then assessed by measuring the biomass allocated to the patch compared to other plants. The results of this experiment were then compared to a conventional competition experiment. There was good correlation between the results. However, Campbell *et al.* (1991) consider the comparative growth experiment as technically demanding, difficult to apply on a large scale, and producing large error terms. Aplet & Laven (1993) conducted a comparative growth experiment on four Hawaiian shrubby plants in an attempt to determine explanations for the relative rarity of two of the four shrubs. Common species outperformed rare species in height growth, biomass gain and shoot:root ratio. However, the two rare species (one rated as extremely rare and the other as very rare) had similar results for the various aspects of growth so other indicators of competitive ability such as seed production could be considered. Either that or factors other than relative competitive ability determine abundance.

Tilman (1997) describes a method that can be used to predict the outcome of competition for a single limited resource between two or more species based on a single summary value, R^* . This value, R^* , is the sum of all inputs and outputs of one resource (*e.g.* nitrogen) to and from the plant. The inputs and outputs include all types of nutrient and tissue loss, nutrient dependence of photosynthesis and respiration and the pattern of allocation of resources to root, stem, leaves and seeds. The plant with the lowest R^* will be the winner. Unfortunately measuring all the components of R^* would be exceptionally time consuming and difficult.

Some aspects of the biology of *G. monspessulana* such as establishment, growth, seed production and seedbank density will provide a basis for gauging outcomes of competition between *G. monspessulana* and native species. Current knowledge of the biology of *G. monspessulana* and related species follows.

1.17 *Genista monspessulana*

G. monspessulana is relatively rare throughout its native Mediterranean range compared to other brooms such as *C. scoparius* and *Spartium junceum* (pers obs). However, it is a widespread weed throughout sclerophyll forests in Victoria (Adams & Simmons 1991), Blue Mountains National Park in New South Wales (Groves pers comm), in forests in California (Bossard unpublished) and throughout the Mt Lofty Ranges and Fleurieu Peninsula in South Australia. Botanical details are provided in Appendix 1.

1.17.1 Seed production and dispersal

Flowering and seed production begin in *G. monspessulana* plants at about two years old. There are no records of annual seed production in the literature for *G. monspessulana* in its native or exotic ranges. Dispersal is primarily by explosive dehiscence then secondarily by ants (Zeven 1992) and in mud attached to animals or vehicles (Parsons & Cuthbertson 1992).

1.17.2 Seedbank dynamics

An average of 3774 seeds m⁻² in soil under *G. monspessulana* stands in Victoria, Australia was recorded by Adams & Simmons (1991). Mean seedbanks in California were about 350 seeds m⁻² (Bossard unpublished). Most of the seeds require heat or scarification to break seed dormancy, although 18% of seeds were capable of germinating without scarification or heat treatment. This small proportion of seeds without dormancy is likely to maintain recruitment (germination) in the absence of fire. González-Andres & Ortiz (1996) tested seed germination success and seedling survival in a number of broom species (Genistae). *G. monspessulana* stood out because it had significantly higher germination success, 70-100% at 16°C; exceptional winter foliage health, 100% survival and was the tallest plant at the end of the first growing season.

1.17.3 Establishment and growth of *G. monspessulana*

Data available for describing biology of *G. monspessulana* is considerably smaller than that available for *C. scoparius* and *Ulex europaeus*. Mature *G. monspessulana* in its native range is extremely variable in height. Mature plants on an exposed hillside in France were, at most, 30-50 cm tall. Plants at other sites

in Europe ranged from 1-3 m tall. In its exotic ranges mature *G. monspessulana* tends to be consistently tall, 2-3 m with a maximum height of 5 m recorded in California (Bossard unpublished). *G. monspessulana* tends to be limited to acidic soils (González-Andrés & Ortiz 1996) and grows well under a *Pinus radiata* canopy which is often too acidic for many other plants.

1.17.4 Herbivores

Surveys of herbivores on *G. monspessulana* in its native range have been conducted in recent years (Sheppard pers comm). Little has been recorded on *G. monspessulana* in its exotic range, more as a result of a lack of surveys rather than an absence of herbivores. In North America, a native moth species, *Uresiphita reversalis*, is most commonly found on *G. monspessulana* and is able to sequester alkaloids produced by the plant (Montllor *et al.* 1990). In South Australia, *G. monspessulana* is a known host of the cosmopolitan seed lucerne pest *Etiella behrii* (Austin *et al.* 1993).

1.18 *Cytisus scoparius*

The native range of *C. scoparius* covers much of Western Europe, from southern Scandinavia to the Azores and from Hungary and Ukraine to the Europe's Atlantic coast (Smith 2000). It is considered a weed in some areas of its native range (Rousseau & Loiseau 1982). *C. scoparius* occurs in and is considered a weed in New Zealand, North America and Australia (Memmott *et al.* 1993, Isaacson 2000). *C. scoparius* has also become naturalised in South Africa, Hawaii, Iran, Japan and India (Smith 2000). Botanical details are provided in Appendix 1.

1.18.1 Seed production and dispersal

Seed production, based on a study in Australia (Smith & Harlen 1991) begins when plants are 3 years old. Seed production by *C. scoparius* in its native habitat (UK and France) ranges from 72-5600 seeds per plant per annum (Rees & Paynter 1997). Production in exotic habitats is generally higher; Bossard & Rejmánek (1994) found numbers of seeds per plant in California ranged from 324 – 26,055; Williams (1981) found numbers of seeds per plant could reach 14,212. Initial

dispersal of the seeds is by explosive dehiscence from pods (Hosking *et al.* 1996). Most of the seeds fall within one metre of the parent canopy with maximum distances of four metres from the parent canopy recorded (Bossard 1991, Smith & Harlen 1991, Paynter *et al.* 1996). Secondary movement of seeds occurs due to ants (Bossard 1991), movement of water (Smith & Harlen 1991) and due to seeds in dirt or mud being picked up by vehicles or animals (Hosking *et al.* 1996).

1.18.2 Seedbank dynamics

Post-dispersal predation of seeds on the soil surface can be very high (>90%) in the native habitat of *C. scoparius* (Paynter *et al.* 1996). Levels of post-dispersal predation were lower, 50-70%, in Australia and New Zealand (Paynter *et al.* 1996).

Seedbanks of *C. scoparius* are very variable. Seedbanks below *C. scoparius* in its native habitat vary from 430 – 19,664 seeds m⁻² (Paynter *et al.* 1996, 1998). A six year old stand of *C. scoparius* in New Zealand is capable of accumulating 400 – 1200 seeds m⁻² per year (Allen *et al.* 1995). Recorded seedbank densities in Australia can be very high, ranging from 190 – 27,000 seeds m⁻² (Rees & Paynter 1997). Rates of annual seedbank decline range from 97% over three years (70% per year) in California (Bossard 1993), 50% per year in southern France (Paynter *et al.* 1998) to 20% (5% per year) over 4 years (Smith & Harlen 1991) and 36% per year (Sheppard *et al.* in press) in Australia. The large range of values may be explained to some extent by different techniques, burial of mesh bags versus a seedbank estimate based on soil cores but there is no consistent trend. The two most varying figures, 97% over three years versus 20% over four years, were obtained by use of bags.

A large proportion of *C. scoparius* seeds are dormant (Smith & Harlen 1991, Tarrega *et al.* 1992, Bossard 1993). Bossard (1993) examined breaking of dormancy, germination and survival of *C. scoparius* seeds. Seed was unable to emerge successfully from depths greater than 8 cm, a result similar to that observed by Tarrega *et al.* (1992). The temperature range within which *C. scoparius* will germinate is 4 to 22°C, with the optimum being from 18 to 22°C. Bossard (1993) also examined the temperature required to break dormancy in

conjunction with susceptibility to fungal infection and found that 65°C was the optimum temperature. A higher temperature (100°C) resulted in higher germination rates, but mortality due to fungal infection increased.

1.18.3 Establishment and growth of *C. scoparius*

Bossard (1991) examined several factors that may influence the establishment of *C. scoparius* in California; habitat disturbance, seed predation, ant dispersal and finally abiotic factors. The experiments were carried out at two different sites, Eldorado and Redwood National Parks, with contrasting biological properties. Disturbance was the only factor at the Eldorado site that significantly enhanced germination and establishment of *C. scoparius*. There was no significant difference between disturbance treatments at the Redwood site. This was partly due to the exposure and predation of seed in all plots at Redwood by quail and grouse, effectively changing all plots to disturbance treatments. The quail and grouse also preferentially foraged for *C. scoparius* seed. The only abiotic factor having a significant effect on establishment was soil moisture.

Subsequently, disturbance has been found to significantly increase germination and establishment of *C. scoparius* in Canada (Ussery 1996), Australia (Sheppard *et al.* in press) and France (Paynter *et al.* 1998). In addition, a spatial model of *C. scoparius* population dynamics reveals that probability of disturbance is one of only three parameters that influence the abundance of *C. scoparius* (Rees & Paynter 1997). The other two parameters are the probability that a site becomes suitable for *C. scoparius* establishment following senescence of a mature plant and the maximum longevity of *C. scoparius*. The probability that a site becomes suitable for establishment following senescence is probably closely linked to or the same as the probability of disturbance. Disturbances range from small scale turning of the soil by pigs, gophers, quails (Bossard 1991, Sheppard *et al.* 2000) to larger scale disturbances such as fires, mowing, grazing and cultivation.

Williams (1981) conducted a series of experiments on *C. scoparius* ecology in New Zealand, the results of which help to determine the limits of, or potential sites for, *C. scoparius* invasion. Growth of *C. scoparius* under different light intensities was assessed; seedling dry weight was still high under 30%

transmittance, but was low under 10% transmittance. Thus, light does not seem to be a crucial factor limiting growth in Williams's (1981) study except at very low light intensities. However, studies in Australia and France (Sheppard *et al.* in press, Paynter *et al.* 1998) demonstrate that seedlings of *C. scoparius* are unable to survive beyond 1-2 years under a parent canopy. *C. scoparius* grew significantly better in slightly acid soil with a moderate amount of iron- and aluminium-bound phosphorus. It also grew very well on strongly acid soil when a super-phosphate supplement was applied. Soil with calcium-bound phosphorus and low organic matter was less favourable for *C. scoparius* growth (Williams 1981).

Dancer *et al.* (1977) found that a *C. scoparius* stand was able to accumulate 63 kg N hectare⁻¹ year⁻¹ in an initially 'harsh', nutrient-poor, sandy, drought-affected soil. This rate of accumulation was compared to a site initially invaded by a non-leguminous woody shrub where nitrogen accumulation was only 15 kg N hectare⁻¹ year⁻¹. In the United Kingdom, *C. scoparius* and other leguminous shrubs are generally primary colonisers of disturbed environments. *C. scoparius* and other legumes are then succeeded by more competitive non-leguminous woody shrubs and climax vegetation, or if a fire occurs, by a community of grasses or bracken (Dancer *et al.* 1977).

In addition to its ability to tolerate a wide range of light and nutrient conditions, *C. scoparius* can tolerate drought. A comparative study of water potential and drought resistance of various New Zealand shrubs and the introduced brooms, *C. scoparius* and *G. monspessulana*, revealed that both broom species developed very high water potential and either did not wilt or recovered with minimal damage (Bannister 1986). The capacity of these brooms to withstand dry conditions was greater than most of the native New Zealand species examined.

1.18.4 Herbivores

Waloff (1968) investigated the insect fauna associated with *C. scoparius* in the United Kingdom. Thirty-five species of phytophagous insects occupying several different niches were found to be supported by *C. scoparius* in the United Kingdom. The niches include seed-feeding, pod-feeding, gall-forming, foliivore,

sap feeding, stem mining and bark mining guilds. A further aspect of Waloff's (1968) study comparing *C. scoparius* sprayed with insecticide versus unsprayed plants showed that insect herbivores had a significant effect on *C. scoparius* growth and reproduction in its native range. The maximum life span of *C. scoparius* in its original habitat is 10-12 years. Growth of unsprayed *C. scoparius*, as measured by height, was slower than for sprayed bushes and unsprayed bushes failed to reach the same maximum height. Mortality was significantly greater in unsprayed plots (49.2%) than in sprayed plots (25%). Seed production of unsprayed bushes over a ten year period was 75% lower than seed production of sprayed bushes.

Seed and pod feeding insects do not seem to have a considerable impact on *C. scoparius* seedbanks in some parts of Europe (Hosking 1992). Significant impacts are recorded in other areas of the native range of *C. scoparius* (Paynter *et al.* 1996).

Invertebrate fauna found on *C. scoparius* in its exotic ranges are a combination of native species transferring to *C. scoparius*, and introductions, intentional and accidental, of species from the native range of *C. scoparius*. North America has the largest range of predators, vertebrate and invertebrate, compared to other exotic habitats of *C. scoparius* (Bossard & Rejmánek 1994, Syrett *et al.* 1999). Fauna on *C. scoparius* in all its exotic ranges is considerably poorer than that within its native range (Syrett 1993, Hosking *et al.* 1996, Syrett *et al.* 1999).

1.18.5 Effects of *C. scoparius* in exotic habitats

Waterhouse (1988) investigated native plant diversity in areas infested with *C. scoparius* compared to uninfested areas. *C. scoparius* substantially reduced diversity of native understorey species. Shading by *C. scoparius* was considered the major cause of reduced native cover and native species richness. Waterhouse (1988) also speculated that *C. scoparius* modifies the soil so that the soil is less suitable for native species. There is also evidence that *C. scoparius* produces chemicals that reduce survival of other plants in its vicinity (Horie *et al.* 1990, Shibuya *et al.* 1994).

Work by Smith (1994) extended the impact assessment by Waterhouse (1988) by considering the changing impact of *C. scoparius* as the population matures. Smith (1994) identified four major stages in the growth of *C. scoparius*. Stage one is the seedling stage which lasts two years and the plant grows to between 20-30 cm. Stage one seedlings are vulnerable to grazing, but in the absence of grazing or severe dry conditions the seedlings survive to stage two. In stage two the plants have vigorous upright growth and there is little light below the canopy. By stage four the canopy begins to collapse and eventually becomes prostrate. This process allows more light to penetrate the canopy. At this stage there is some recovery of species richness. Several native plant species are more common under stage four *C. scoparius* than they were prior to invasion. The change in flora composition is reflected by a change in fauna (Smith 1994); reptile diversity decreases compared to the pre-invasion condition while bird diversity increases.

1.19 *Ulex europaeus*

The native range of *U. europaeus* is Europe with populations most common along the western European seaboard from northern France to Portugal (Rees & Hill In press, Parsons & Cuthbertson 1992). It is regarded as a serious weed of pastures in New Zealand, Chile, Hawaii, North America and Australia (Richardson & Hill 1998). Botanical details are provided in Appendix 1.

1.19.1 Seed production and dispersal

Plants begin producing seed from 1.5 years onwards (Parsons & Cuthbertson 1992). Annual seed production for stands of gorse in New Zealand varied from 442 - >36,741 seeds m⁻² (Rees & Hill In press). Unlike *C. scoparius* and *G. monspessulana*, which have one main flowering period per year, *Ulex europaeus* has two main flowering periods but is capable of flowering all year (Parsons & Cuthbertson 1992). Dispersal is very similar to *C. scoparius* with an initial explosive dehiscence from the plant sending seeds up to 5 m from the plant but most seeds land within 1 m of the centre of bushes (Rees & Hill In press). Longer distance dispersal, as with *C. scoparius*, is by water and in mud on animals and vehicles (Parsons & Cuthbertson 1992). Birds and ants also move the seeds (Parsons & Cuthbertson 1992).

1.19.2 Seedbank dynamics

Large, hard-coated seedbanks (133 – 20,742 seeds m⁻²) accumulate under mature stands of *U. europaeus* (Zabkiewicz & Gaskin 1978). Estimates for decline of the seedbank range from 1 to 50% per annum (Popay & Adams 1990, Rees & Hill In press). The higher figure (50%) is for sites disturbed by cultivation and spraying. Losses from the seedbank are mainly caused by germination of the seeds (Rees & Hill In press).

1.19.3 Establishment and growth of *Ulex europaeus*

Burning promotes recruitment of *U. europaeus* seedlings but the presence of grasses, forbs and a litter layer increase mortality of seedlings (Partridge *et al.* in press). Grazing when combined with competition from grasses also increases seedling mortality (Rees & Hill In press). Seedlings of *U. europaeus* are very susceptible to drought (Rees & Hill In press). Gorse is able to grow in a wide range of soil types and grows well on poor soils (Parsons & Cuthbertson 1992). Senescence of gorse plants normally occurs when plants are between 25-30 years old (Rees & Hill In press).

1.19.4 Herbivores

There has been some progress on use of herbivores for biological control of gorse. In Hawaii four agents have been released and can be considered established and a fifth agent was scheduled for release in 1996 (Markin *et al.* 1996). The agents are; a seed weevil (*Apion ulicis* also previously referred to as *Exapion ulicis*), a defoliating moth (*Agonopterix ulicetella*), a thrip (*Sericothrips staphylinus*), a mite (*Tetranychus lintearius*) and a moth (*Pempelia genistella*) (Markin *et al.* 1996). The weevil, originally from the United Kingdom, has also been introduced in New Zealand, Australia, the United States and Chile (Parsons & Cuthbertson 1992). The impact of the seed weevil on seed production is variable (Parsons & Cuthbertson 1992, Rees & Hill In press). In Hawaii the weevil may damage up to 85% of pods (Markin *et al.* 1996). In New Zealand, at one site, seed production in one year was reduced by 96% (Rees & Hill In press).

1.20 Biology of invasive legumes

Firstly, being legumes and able to fix nitrogen, *G. monspessulana* and its relatives are able to survive on low nitrogen soils better than a number of other plants. Low nitrogen soils are common throughout Australia (Walker *et al.* 1986). Seed production is generally high within 4 to 5 years of germination and the seeds are hard-coated, and will survive one year or more in the soil. Seedbanks accumulate under undisturbed stands because there is limited recruitment and therefore minimal seedbank.

Recruitment of *C. scoparius* and *U. europaeus* is minimal in the absence of soil disturbance or death of mature plants. Requirements for recruitment of *G. monspessulana* are largely unknown. However the data available (Adams & Simmons 1991) suggest that some seeds do not require heating (fire) for germination, but that most seeds do require heat.

Invasive legumes are excellent exploiters of disturbance because they accumulate large seedbanks. Once disturbed the seedlings grow rapidly and are unlikely to be limited by nitrogen. Seed production begins in two years and for *C. scoparius* reaches maximum in 4 to 5 years. *C. scoparius* populations, once established, shade a number of other native species and reduce the diversity of native species.

1.21 Summary of literature review

The potential of populations to increase with minimal limitations and subsequently reduce diversity of native species means they need to be managed. Preservation of diversity is considered a global priority.

Use of fire for management of *G. monspessulana* at first glance appears to be contradictory to the general rule of managing weeds of natural ecosystem, that is minimising disturbance. Brooms also benefit from disturbance, it improves recruitment probability. Burning, injudiciously applied, may also negatively impact vertebrates, invertebrates, the soil structure and diversity of plants. Why should fire be considered? Fire should be considered because large seedbanks of *C. scoparius* and *Ulex europaeus* have accumulated and it is probable that there

are many large seedbanks of *G. monspessulana*. Disturbance can be minimised by reducing access by fencing areas from grazing animals, not burning indiscriminately and carefully planning weed removal. However, it can not be prevented as fires in South Australian dry sclerophyll forest are regular. Soil movement on slopes and flooding of creek banks are inevitable. Where there are large seedbanks of *G. monspessulana*, populations will persist and are likely to increase. Reduction of the seedbank, by killing seeds and stimulating them to germinate is possible using fire. Fire can be manipulated in a number of ways to minimise negative impacts on the ecosystem.

The biology of a number of dry sclerophyll species and their response to fire is well known and there are fire regimes that have minimal or low impacts on plants. Spatial variation of vegetation may provide refuges of lower soil temperatures or pockets of higher temperature to favour certain species and perhaps increase the diversity of an area. The numbers and diversity of native species within an area infested with *G. monspessulana* will probably be different depending on the density of *G. monspessulana*. The relative impact of fire may change depending on the specific components of the ecosystem.

Post-fire responses of vegetation are likely to be very important in determining community composition. How do seedlings of native species interact with *G. monspessulana*? *G. monspessulana* is implicated as out-competing native vegetation without supporting experimental data. Design of experiments to study competition is complicated and remains controversial. Competitive outcomes between two or more species will often vary in response to other factors such as disturbance and herbivory. Use of competitive species within an integrated management strategy is largely unexplored.

The aims of this thesis are:

- To confirm that fire can effectively reduce the seedbank of *G. monspessulana*.
- To investigate the affect of changing fire parameters such as season and intensity on *G. monspessulana* and native vegetation associated with *G. monspessulana* infestations.
- To identify methods of reducing possible impacts of fire and follow-up control on native vegetation.
- To identify native species that occur in the seedbank associated with *G. monspessulana* seedbanks.
- To assess the contribution that competition between *G. monspessulana* and native species can make to management of the former.

Chapter 2. Population age structure, seed production and seedbanks of *G monspessulana* in its native range and South Australia

2.1 Introduction

Comparing the biology of invasive plants in their native habitat with their biology in exotic habitats identifies stages of the plant's life-cycle that are susceptible to common ecological processes such as herbivory and competition. Once the effective processes and susceptible stages are identified, similar processes can be incorporated into a management strategy for the plant in its exotic habitat.

Models play a fundamental role in understanding ecological processes (Gillman & Hails 1997, Hilborn & Mangel 1997). Good models are useful to weed management because they can be used to study the outcomes of management strategies and enhance diversity of endemic species before large investments of time and resources are made (Jones & Medd 1999, Smith *et al.* 1999, Shea & Possingham 2000). Models can be tested and hence rated good or inappropriate. Hillborn & Mangel (1997) describe a range of techniques for testing models. In addition to prediction, models can also be used to determine which parameters are the most influential within a given system and provide an objective method of determining the most important empirical data to collect (Higgins *et al.* 1996).

Rees & Paynter (1997) and Rees & Hill (In press) have developed models simulating the dynamics of populations of *Cytisus scoparius* and *Ulex europaeus*. The *C. scoparius* model was used to predict the parameters having the greatest influence on how much space *C. scoparius* occupies. The influence of herbivores, hence potential biological control agents, was one of the parameters examined. The model suggests that biological control will have the greatest impact if disturbance is high, seedling survival is low and plant fecundity is low (Rees & Paynter 1997). Similar predictions were obtained with the model developed for *Ulex europaeus* (Rees & Hill In press).

Development of both models for *C. scoparius* and *Ulex europaeus* was based on realistic parameter estimates obtained from biological data on seed production, seedbank density, emergence and age structure of both species. Similar data were not available for development of a model for *G. monspessulana*. Therefore, biological data were obtained in order to compare *G. monspessulana* in its native and exotic habitats and provide information with which to build a model *G. monspessulana* population dynamics.

2.2 Study Sites

2.2.1 Australia

2.2.1.1 Deep Creek

The Deep Creek site in Deep Creek Conservation Park (35°36'S, 138°16'E) comprises mainly a creek-line and flanking *E. obliqua* sclerophyll forest. The major disturbances in the last fifty years have been construction of a walking trail, subsequent disturbances by walkers and seasonal flooding in the immediate vicinity of the creek. The estimated mean annual rainfall is 700 mm.

2.2.1.2 Henschke

Henschke, the most northern site in Australia (latitude 34°31'S, longitude 139°09'E, altitude 390 m above sea level), was a roadside infestation of *G. monspessulana*, near Keyneton, South Australia, with minimal remaining native vegetation apart from an overstorey of *Eucalyptus leucoxylon*. The road verge is flanked by pasture, wood-lots and cropping land. The mean annual rainfall is 546 mm.

2.2.1.3 Lenswood

This site at the Lenswood Research Centre (latitude 34°95'S, longitude 138°81', 452 m above sea level) was located in between remnant *E. obliqua* sclerophyll forest and mown grass that flanks an experimental apple orchard. There is no *E. obliqua* cover over the *G. monspessulana*. The mean annual rainfall is 1017 mm. There is a gentle slope of 25° with a southern aspect.

2.2.1.4 Upper Sturt

This Upper Sturt site (35°02'S, 138°41'E, 460 m above sea level) was located within remnant roadside vegetation that adjoins Belair National Park. The vegetation is *E. obliqua* sclerophyll forest. The estimated mean annual rainfall is 900 mm. A walking trail meanders through the vegetation. The slope is approximately 30° and has a north–northwestern aspect.

2.2.1.5 Willunga Hill

This population of *G. monspessulana* was part of a small patch of remnant *E. obliqua* dry sclerophyll forest along a roadside (Willunga to Meadows road at 35°17'S, 138°37'E, 334 m above sea level). Native species present in the understorey included *Xanthorrhoea* sp., *Acacia paradoxa*, *Platylobium obtusangulum*, *Hakea* sp., *Pultanaea daphnoides*, *Banksia* sp., *Poa* sp. and *Microlaena stipoides*.

2.2.2 Europe

2.2.2.1 Corse – Site 1

Two sites were studied on Corse. Seedbank data were obtained from a site at 400 m above sea level, 1 km along road D84 from Porto heading towards Evisa (latitude 41°57'N, longitude 08°39'E). These soils were granitic. Understorey vegetation comprised *Arbutus unedo*, *Erica arborea*, *Cistus salvifolius*, *Calicotome spinosa* and *Cytisus villosus*. The overstorey was Corsican pine.

2.2.2.2 Corse – Site 2

Seed production and age data were obtained from *G. monspessulana* growing at a disused roadside (D48, near Sartene) quarry site. The site was 200 m above sea level on granitic soils (latitude 41°37'N, longitude 08°56'E). Other Genistae species occurring at the site were *Cytisus villosus*, *Calicotome villosa* and *Spartium junceum*.

2.2.2.3 Font Josepa

This site in north eastern Spain was near Romaña de la Selva in the Sierra de Gavarres mountain range (250 m above sea level, latitude 41°90'N, longitude 02°75'E). It had been burnt within the last 5 years. The soil type is schist based.

Vegetation comprised *Quercus suber*, *Q. coccifera* with an understorey of *Arbutus unedo*, *Erica arborea*, *Cistus salvifolius*, *Calicotome spinosa*, *Cytisus arborea*, *Cytisus villosus*, *Spartium junceum* and *Pistacia lentiscus*.

2.2.2.4 Forca Real (Chappelle de Notre Dame)

This site in southern France on schist soil over limestone was at 500 m above sea level at a latitude of 42°44'N and longitude of 02°42'E. Overstorey vegetation consisted of *Quercus coccifera* and *Q. ilex*. Understorey vegetation consisted of *Rubus* sp., *Arbutus unedo*, *Erica arborea*, *Ulex parviflorus*, *Juniperus oxycedrus*, *Cistus monspeliensis* and *Calicotome spinosa*. The site had been burnt in the last 10 years.

2.2.2.5 Gratteloup

This population of *G. monspessulana* was situated in the Arboretum du Gratteloup, north of Bormes les Mimosas by route D41 (latitude 43°7'N, longitude 05°55'E). The area had been partially cleared of *Quercus suber*, *Pinus halepensis*, *Pinus pinaster* forest for planting of *Castanea sativa*. The scrub community included, *Cistus salvifolius*, *C. monspeliensis*, *Calicotome spinosa*, *Cytisus villosus*, *Erica arborea*, *Inula viscosa*, *Lavendula staechas*, *Lonicera* sp., *Pteridium aquilinum*, *Quercus coccifera*, *Rubus* sp. and *Smilax aspera*. The soils were schist based.

2.2.2.6 Lunel de Viel

This site was an old river gravel quarry with scattered *G. monspessulana* amongst a *Spartium juncaum* infestation at Petit bois de la Devège (GR653, latitude 43°41'N, longitude 04°06'E). Other flora at the site included scattered *Quercus pubescens*, *Q. ilex*, a euphorb and *Rubus* sp.

2.3 Materials & Methods

2.3.1 Estimation of *G. monspessulana* age

The field sites within South Australia receive consistent seasonal, winter rainfall. *G. monspessulana* has a notable annual growth spurt around August each year coinciding with high soil moisture as a result of this winter rainfall. One annual

growth spurt and consequent annual ring patterns in *G. monspessulana* are consistent with those in *Cytisus scoparius* (Williams 1983).

Basal stem sections were obtained by cutting desired *G. monspessulana* stems as close to the soil as possible with a pruning saw. The whole plant or 30 cm of basal stem were brought to the laboratory and sectioned. Most annual ring patterns were immediately clear. Those that were more difficult to determine were sanded and/or ground to improve the contrast.

Thirty dead plants, without stem rot, were collected from Gratteloup in France and Henschke in South Australia. The age at death was determined by taking stem sections and used to estimate an average age at death.

2.3.2 Seedbank

Twenty soil samples were taken from four sites prior to dehiscence of the annual seed crop. Each sample consisted of eight cores (2 cm diameter and 10 cm depth) from within an area of 0.25 m².

Seeds were separated from the soil by washing the pooled cores through a 6 mm mesh sieve followed by a 2 mm mesh sieve. This separation protocol was sufficient to allow counting of seeds in a white tray.

2.3.3 Seed Production

The numbers of seeds on individual plants were estimated by counting (Australian plants) or weighing (European plants) pods from each plant. Samples of 30 pods from each site were dissected and the number of seeds was counted to obtain an average number of seeds per pod. Samples from bushes at the same site were counted and weighed to determine an average weight per pod. This enabled an estimation of seed production per plant.

2.3.4 Seed rain

Twenty traps (Figure 2.1) were placed throughout broom infestations at six sites in 1997 (Deep Creek, Upper Sturt, Willunga Hill - Meadows Road, Lenswood, Crafers and Henschke) and four (Deep Creek, Lenswood, Henschke, Upper Sturt)

in 1998. Twenty traps were placed at one site in Spain (Font Josepa). The traps were 10 cm in diameter, about 20 cm tall and buried a minimum of halfway into the soil.



Figure 2.1 Seed trap viewed from side and top (left). Seed trap as placed in the field (right).

The effectiveness of the seed traps was tested prior to use. Seeds were thrown at a trap from different angles and the proportion of seeds bouncing out compared to those falling in the trap was around 10%.

The traps were collected following dehiscence, which occurred any time between December and March depending on the site. The seeds were separated from other incidental contents of the traps, insects, leaves and gum nuts, using a 4 mm mesh sieve. The number of swollen seeds within the seed traps was recorded along with the total number of seeds. Swelling of the seeds indicates mortality or ability to germinate immediately without temperature treatment.

2.3.5 Obtaining plant samples for determination of ages and seed production

Transects of 40 metres were established in four (Deep Creek, Lenswood, Upper Sturt and Henschke) infestations of *G. monspessulana* in South Australia. At random distances along the transect, plots of 1 m² were marked out and all the *G. monspessulana* within that plot was harvested, or counted (seedlings < 1 year). High densities of plants limited the number of quadrats that were eventually sampled.

2.3.6 Data analysis

Estimates of seed number for each plant were transformed using the following formula

$$\log_{10}(x + 1)$$

where x is the number of pods multiplied by the average number of seeds per pod for the appropriate site. This transformation reduces multiplicative effects and therefore reduces the difference between the actual distribution and an expected normal distribution of the data. Three regression analyses were performed on the data from the two different continents. First, the data from each continent were compared separately, *i.e.* South Australian sites only, European sites only. Then the sites were combined and analysed to compare seed production in the native versus the exotic range, *i.e.* Europe and Australia. Genstat (v.5) for Windows was used to perform the analyses.

Mean soil seedbanks were calculated for each site. Seedbanks in Europe were compared to seedbanks in Australia using a non-parametric Mann-Whitney test using ranks of the mean seedbank estimates instead of the actual values (Zar 1984).

Age structure at seven sites was compared using linear regression of $\log_{10}(\text{density})$ against $\log_{10}(\text{age})$. Genstat (v.5) for Windows was used for the analysis. Age structure of *G. monspessulana* in its native range was also compared with its age structure in South Australia, an exotic habitat.

2.4 Results

2.4.1 Seed Production

Satisfactory regression coefficients were obtained by fitting separate models for each site for both the South Australian and European data. Seed production begins once the plants are two years old and maximum seed production occurs at 6 or 7 years. Mean numbers of seeds per pod (\pm standard deviation) were 4 ± 1 for all sites except Lenswood (5 ± 1) and Font Josepa (3 ± 1).

There was a considerable range in potential seed production per plant at different sites in South Australia (Figure 2.2). Maximum seed production occurred at Lenswood and Deep Creek and is about 5000-6000 seeds per plant, for plants between 6-8 years old. The lowest maximum seed production occurred at Henschke with only 600 seeds per plant. The trends in South Australia correlate with moisture availability as measured by rainfall. The infestation at Deep Creek was along a watercourse that had permanent water throughout the year. Lenswood had comparatively high rainfall, 1017 mm, Upper Sturt slightly lower rainfall, 900 mm and Henschke had the lowest rainfall, 546 mm, of the four South Australian sites.

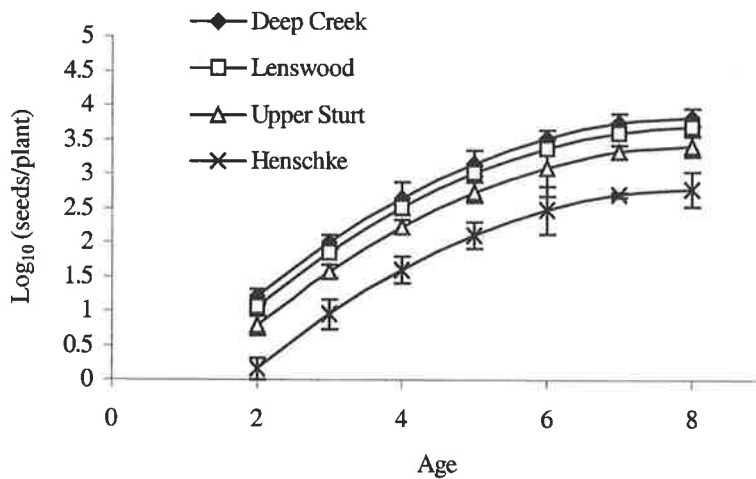


Figure 2.2. Relationship between age and seed production per plant for four sites in South Australia.

The range of maximum potential seed production at European sites was larger than that of South Australia. Seed production related to age is shown for four sites in Europe (Figure 2.3). The outstanding site was Corse having a maximum seed production at 7 years of 12,000 seeds per plant. The lowest seed production per 6-8 year old plant occurred at Gratteloup (1000 seeds per plant).

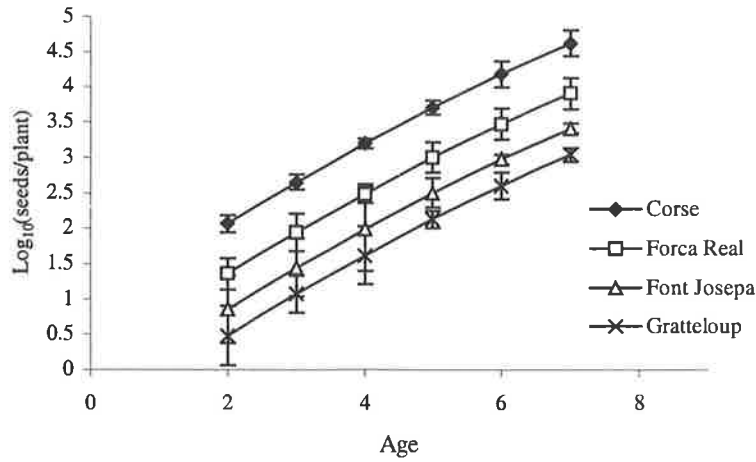


Figure 2.3. Relationship between age and seed production for four sites in Europe.

When seed production data for the four sites in each continent were combined the relationship between age and seed production was similar for the two continents (Figure 2.4).

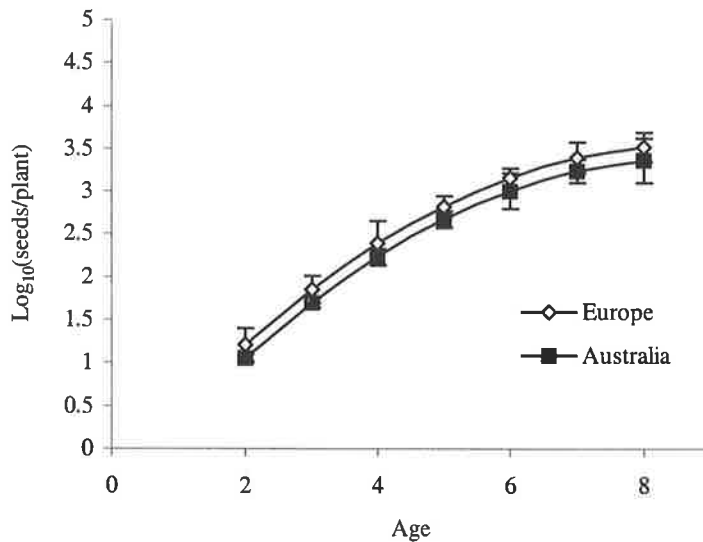


Figure 2.4. Relationship between age and seed production per plant in Europe and Australia.

2.4.2 Densities of *G. monspessulana* in its native and exotic ranges

Numbers of plants were counted at four sites in South Australia and four sites in Europe. Density of *G. monspessulana* was very variable and much higher in South Australia. The sites with the highest *G. monspessulana* densities in Australia and Europe, Lenswood and Forca Real (Table 2.1), had no overstorey.

The site on Corse was exceptional because there was little or no overstorey but instead there was a thicker cover of other understorey shrubs of similar height to *G. monspessulana*. Densities of *G. monspessulana* in Australia were consistently higher than in Europe.

Table 2.1. Densities of *G. monspessulana* in Australia and Europe. * This site was difficult to reach (steep climb) and move through (thick shrubs with large spines) and density was estimated by eye. ** Rather than dividing the site into several small quadrats the whole site at Gratteloup was counted as one quadrat (36m x 10m).

Continent	Site	Plants m ⁻² ± Standard Deviation
Australia	Deep Creek	14 ± 3
	Lenswood	59 ± 41
	Upper Sturt	15 ± 8
	Henschke	16 ± 8
Europe	Corse 1	Approximately 2*
	Forca Real	6 ± 9
	Font Josepa	4 ± 5
	Gratteloup	< 1 (0.15) **

2.4.3 Seed Rain

Seed traps were placed at four sites in South Australia and one site in Europe. Data from Europe is unavailable because the seeds did not dehisce before the end of the study period. Seed rain at different sites throughout South Australia was variable between site and at the same sites over two years (Table 2.2). The highest estimate for seed rain, 4893 seeds m⁻² was at Lenswood in 1998. Other sites with substantial seed rain were Crafers, Upper Sturt and Deep Creek. However lower rainfall sites had lower seed rain.

Table 2.2. Estimates of *G. monspessulana* seed rain m⁻² at sites in South Australia for two consecutive years based on numbers of seeds falling into seed traps.

Site	1998		1999	
	n	Seeds m ⁻² ± SD	n	Seeds m ⁻² ± SD
Deep Creek	20	451 ± 480	19	1491 ± 1922
Lenswood	19	4893 ± 4834	20	991 ± 1066
Upper Sturt	20	559 ± 642	19	1196 ± 742
Henschke	20	457 ± 923	19	628 ± 476
Crafers	19	1330 ± 717	-	-
Willunga Hill	20	450 ± 343	-	-

Estimates of seed production using the two methods were different (Table 2.3). Seed rain estimated using traps on the ground were consistently lower. Differences in the estimates are in the order of 50-90%.

Table 2.3. Comparison of estimates of seeds m^{-2} using two methods in 1999. The two methods were counting pods on all the plants within $1 m^2$ or within seed traps at ground level.

Site	Seeds on Plants		Seed Traps	
	Seeds/ m^2	SD	Seeds/ m^2	SD
Deep Creek	8804	5939	1491	1922
Lenswood	13430	8928	991	1066
Upper Sturt	2518	2362	1196	742
Henschke	5998	4805	628	476

2.4.4 Seed Production

Soil seedbanks of *G. monspessulana* in Australia are significantly higher than seedbanks in Europe ($U(20) > U_{crit} (\alpha=0.05)(18)$). The highest seedbank occurred at Henschke (Table 2.4) in South Australia. The lowest occurred at Lunel de Viel in France. Soil seedbanks in Australia were up to 3,000 times greater than soil seedbanks in Europe.

Table 2.4. Estimated soil seedbank at 5 sites in Europe and 4 in South Australia. n is the number of individual cores taken at each site.

Continent	Site	Mean seeds $m^{-2} \pm SD$	n
Europe	Lunel de Viel	10.7 ± 35	12
	Font Josepa	613 ± 982	10
	Forca Real	47.2 ± 49	5
	Corse	1138 ± 2123	10
	Gratteloup	926 ± 578	10
Australia	Deep Creek	4803 ± 3959	20
	Lenswood	6498 ± 4436	20
	Upper Sturt	9389 ± 6763	20
	Henschke	30297 ± 19586	19

2.4.5 Age Structure

Systematically searching through stands for old plants yielded a maximum age of plants in Australia of 13 years old. In Europe, the oldest plant sampled was 9 years, although more plants were sampled in Australia. Old plants were upright and not collapsed like old, stage four *C. scoparius* (Smith 1994). The average age of death in South Australia (Henschke) was 5 ± 2 years and in Europe was 4 ± 3 years. Three of the South Australian sites (Deep Creek, Lenswood and Upper Sturt) were similar (Fig 2.5) and had a higher proportion of younger plants at the time of sampling. The Henschke population had a higher proportion of older plants and had a considerably higher seedbank (Table 2.4). The chance of death

increased considerably for a plant of 5 years old. No single age group dominated (more than 60%) the populations examined in South Australia.

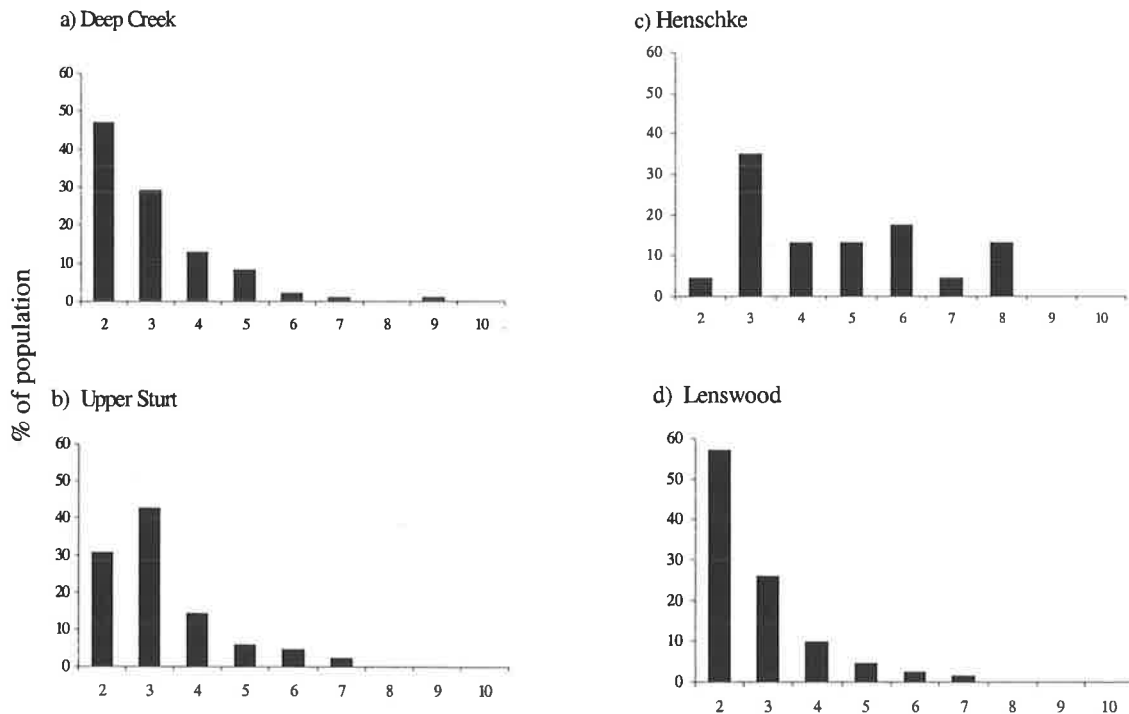


Figure 2.5. Estimation of age structure (percentage plants of each age group within the population) of *G. monspessulana* at four sites in South Australia based on a random sample of the populations taken during October - January 1998/1999.

European populations (Fig 2.6) differed from Australian populations in that recruits (1 & 2 years) were a smaller proportion of the population. Younger plants, 1 to 2 year made up a greater proportion (40-60%) of South Australian populations, with the exception of Henschke, than 1 to 2 year old plants in Europe (< 30%).

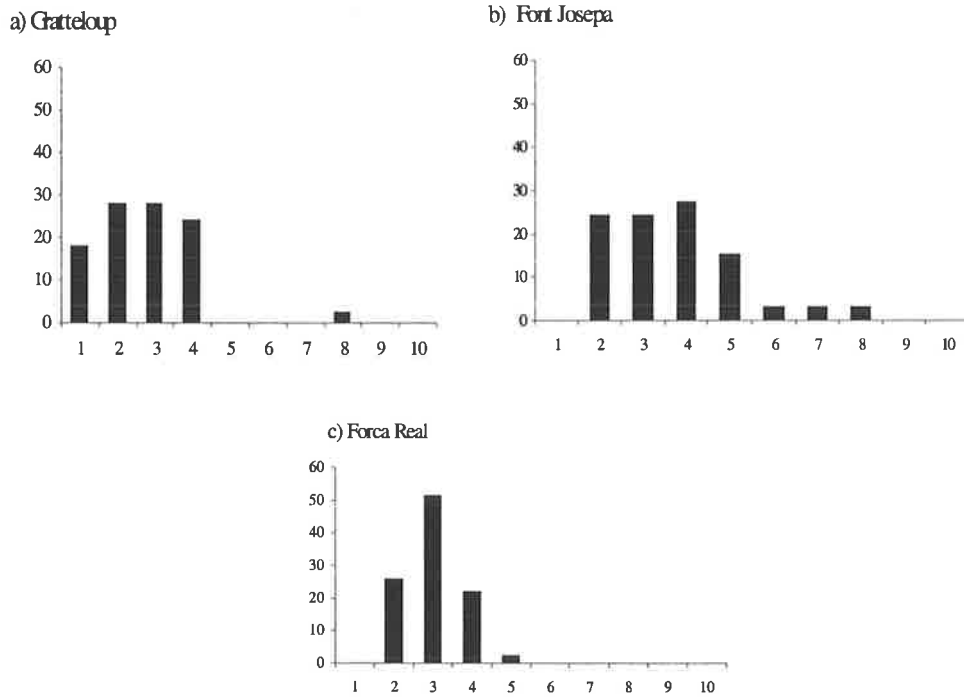


Figure 2.6. Estimation of age structure (percentage plants of each age group within the population) of *G. monspessulana* at three sites in Europe based on a random samples of the populations taken during May - June 1999.

Age structure of populations of *G. monspessulana* in South Australia were considerably different from European populations because there was a large difference (Fig 2.7) in the numbers of younger plants and recruits in exotic habitats. Densities of young plants in South Australia were; 1 year - 111 ± 131 , 2 years - 44 ± 62 and 3 years - 8 ± 5 plants m^{-2} . Densities of young plants in Europe were; 1 year - 3 ± 5 , 2 years - 1 ± 1 and 3 years - 1 ± 1 plants m^{-2} .

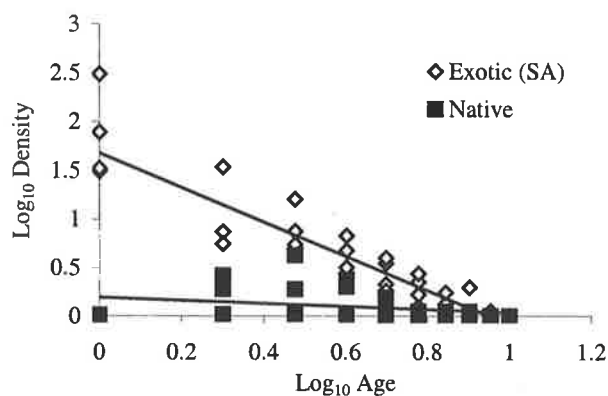


Figure 2.7. Regression lines fitted to data for age (fixed) against density (response). The variance accounted for with two separate lines (exotic habitat or native habitat) is 82.5%.

2.5 Discussion

2.5.1 Seed production

Production of seeds of *G. monspessulana* in its native range and exotic ranges begins at two years old. Maximum numbers of seeds produced per plant (600-6000 seeds m⁻² depending on the site) are reached when plants are 6-8 years old. Whether the population of *G. monspessulana* is in a native or exotic habitat does not influence maximal seed production. In contrast, *C. scoparius* plants are capable of producing more seed in their exotic habitats (Rees & Paynter 1997, Bossard & Rejmánek 1994, Williams 1981). Specific site features such as density, rainfall or moisture availability and cover all appear to influence seed production per plant. Seed production per m² by *G. monspessulana* does not reach the same level as that reached by *U. europaeus*. The highest estimate of seed production by *G. monspessulana* was 13,000 seeds m⁻² whereas >36,741 seeds m⁻² has been recorded for *U. europaeus* in New Zealand (Rees & Hill In press).

Differences in estimates of annual seed production in South Australia between seed traps and harvesting were likely to have arisen due to a combination of factors. Firstly, a small proportion of seeds probably bounced out of the traps. However, if the density of the seedbank is predicted using the recorded annual seed production m⁻² for each site over three years and modified by an estimate of annual decline (*e.g.* 40%) then the predicted seedbank density is twice as high as the actual seedbank density for all sites except Henschke. Therefore other pre-dispersal losses of seed must occur. Pods and seeds failing to complete development and dehiscence were observed on plants when the traps were collected. Also there may have been some pre-dispersal predation of seeds by generalist insects, birds or introduced rodents. For example *G. monspessulana* has been recorded as a host for lucerne seed web moth, *Etiella behrii* (Austin *et al.* 1993), which was found in pods of *G. monspessulana*.

2.5.2 Seedbanks

Seedbanks of *G. monspessulana* are greater in South Australia compared to its native range (Table 2.4). The difference in seedbank is not due to an inherent potential of plants in South Australia to produce more seeds. There was no

difference in age related seed production between Australia and Europe (Fig 2.4). The difference in density can be attributed to seed predation or herbivory, greater inter-specific competition or harsher edaphic factors such as colder winter temperatures and possible frosts in Europe. In contrast, there is not such an obvious difference in seedbanks between continents in *C. scoparius* (Rees & Paynter 1998).

2.5.3 Density and age structure

Recruitment and survival of seedlings of *G. monspessulana* was higher in its exotic range. This is consistent with larger seedbanks in the exotic range. Stands of *G. monspessulana* are multi-aged in Australia which indicates that while they are likely to benefit from disturbance they do not require disturbance for recruitment. Limiting or reducing disturbance alone will not be an adequate strategy to prevent expansion and persistence of weedy populations of *G. monspessulana*.

Age structure data, average age of death and the presence of older plants in South Australian populations suggest that *G. monspessulana* lives slightly longer (2-3 years) in Australia than Europe. However, these observations of older plants in South Australia may be the result of a higher number of recruits rather than an inherent difference in the probability of death or age of senescence between Europe and South Australia.

2.6 Conclusion

The outstanding differences between populations of *G. monspessulana* in its native range compared to an exotic range are higher densities of seedlings, 1 to 2 years old in South Australia and much higher seedbanks. So a distinct difference between the populations in their different ranges has been identified. The acquisition of this data prompts further questions relevant to development of management strategies. Does the lower seedbank limit population sizes of *G. monspessulana* in its native range and will reducing the seedbank limit the population in the event that recruitment opportunities in exotic habitats are not limiting.

Biological data collected in this study have been used to modify (Pareja *et al.* In preparation) a spatial model (Rees & Paynter 1997) designed to predict population dynamics of *C. scoparius*. The model incorporates age-related seed production and age structure of *G. monspessulana* and data from fire experiments described in a later chapter. The model suggests two important but mutually exclusive approaches to management. Firstly, it predicts *G. monspessulana* populations will be limited by reducing recruitment opportunities. Recruitment opportunities are disturbances and this concurs with the general “rule of thumb” discussed previously. However the model also predicts that biological control of *G. monspessulana* will be more effective when combined with control methods that keep populations of *G. monspessulana* younger and hence seed production lower. Keeping the populations young requires regular disturbances that could include fire, herbicide, pulling or mowing. While the two broom models (Rees & Paynter 1997, Pareja 2000) predict the seedbank does not limit populations of *C. scoparius* or *G. monspessulana* it would be both worthwhile and feasible to test this hypothesis and the model’s predictions empirically within three years.

Chapter 3. Interactions between *G. monspessulana* and a Number of Australian Species of Eucalypts, Legumes and Grasses

3.1 Introduction

There is very little experimental data on the nature of competition or comparative growth between Australian native species and *G. monspessulana*. Records of plant associations, be they negative or positive, are available in the form of surveys and databases maintained by state government environment departments. Hence, surveys of vegetation associated with *G. monspessulana* were not considered a priority for this project. In any case, the majority of land managers, including park rangers, pest control officers, and Landcare volunteers, state that *G. monspessulana* out-competes native vegetation with or without major disturbance.

A number of different competition experiments were conducted in order to determine whether or not *G. monspessulana* out-competes native vegetation. Additional experiments were conducted to determine whether or not there were native species with potential to be used as part of an integrated management strategy for *G. monspessulana*.

3.1.1 Choice of experimental design

Removal experiments, replacement and addition series experiments were chosen to examine competition between native species and *G. monspessulana*. Removal experiments were chosen because they were the most practical method of manipulating plant populations to achieve consistency. Replacement and addition series experiments were set up in relatively homogenous environments. The rationale for using these contrived experiments in relatively homogenous conditions was to minimise edaphic and biotic influences and distil any effects of competition. Replacement and addition series experiments also provide a defined template which can be modified to examine how herbivory and changing nutrient conditions influence competition.

3.1.2 Choice of plants for competition experiments with *G. monspessulana*

Significant differences in soil water potential were detected between stands of *Eucalyptus viminalis* with or without a *G. monspessulana* infested understorey (Burns, unpublished). Removal experiments were conducted to determine whether or not *G. monspessulana* was capable of out-competing another important overstorey species, *E. obliqua* for water. *Eucalyptus leucoxyton* was also chosen for one study because it is a dominant overstorey species occurring in some areas invaded by *G. monspessulana*.

Four locally common native, perennial leguminous species were chosen because of their similarity to *G. monspessulana* in terms of ability to obtain nitrogen and their size. The four species were *Acacia melanoxylon*, *A. pycnantha*, *A. paradoxa* and *Pultanaea daphnoides*.

Two locally common native grasses, *Microlaena stipoides* and *Themeda triandra*, were chosen for a few reasons. Grasses are considered to be effective at suppressing weeds in orchards (Harrington 1995). Grasses establish and grow relatively rapidly and are also capable of producing large numbers of seeds. *Microlaena stipoides* was frequently observed surviving under canopies of *G. monspessulana* throughout the Mt Lofty Ranges. Finally, selective herbicides are available that kill broad-leaved plants, such as *G. monspessulana*, and not grasses.

3.2 Materials & Methods

3.2.1 Competition for water between a dominant overstorey species, *Eucalyptus obliqua* and *G. monspessulana*

This experiment was conducted at the Crafers (see Chapter 5) site. The overstorey species was *Eucalyptus obliqua*, the understorey consisted of dense, fairly even *G. monspessulana* with very few other understorey species except *Microlaena stipoides*, *Acrotriche fasciculiflora* and *Rubus discolor*. Sixteen trees with diameter at breast height (dbh) between 10-20 cm with no other *E. obliqua* within 7 m were selected and labelled from one to sixteen. The sap pressure of each tree was measured early one morning in spring (October 1996). A Scholander Pressure Bomb (Scholander *et al.* 1965) was used to obtain the sap

pressure. Following the spring measurements, an area with a five metre radius around eight randomly selected trees was cleared of *G. monspessulana* by slashing. The sap pressure of all trees was measured again on an early morning in late summer (March 1997).

Trees undergoing more competition for water from *G. monspessulana* are expected to have lower water potential. However, in order to reduce variation expected due to differences between trees, the change in potential between spring and summer was compared using a t-test.

3.2.2 Competition and comparative growth of two perennial legumes, *G. monspessulana* and *Acacia melanoxylon* in the field

A replacement series competition experiment between *Genista monspessulana* and *Acacia melanoxylon* was set up in 1996 at Wild Dog Glen, near Waite Campus, University of Adelaide. This site was gently sloped (20°) with a northern aspect. The land had been previously cleared and used for grazing sheep but more recently was made part of a reserve (Waite Conservation Reserve). The existing vegetation, mainly introduced herbs and grasses, was cleared from an area of 12 m by 12 m. Two weeks prior to planting, this area was sprayed with glyphosate to kill plants that had germinated following clearing. Each plot was 0.5 m by 0.5 m.

Seeds of *A. melanoxylon* and *G. monspessulana*, for planting at Wild Dog Glen, were pre-treated with boiling water, planted in seedling trays and kept in a glasshouse until planting. Seeds of both species were collected from pods in the last fruiting season prior to the experiment (November/December 1995). Six blocks were planted over three months May to July, one every two weeks. The first height measurements were taken in July, then once every month until October.

A randomised block design was used with eight treatment plots within each block. The eight treatments were; 25 *A. melanoxylon*, 25 *G. monspessulana*, 17 *A. melanoxylon*, 17 *G. monspessulana*, 8 *A. melanoxylon*, 8 *G. monspessulana*, 17 *G. monspessulana* plus 8 *A. melanoxylon*, 8 *G. monspessulana* plus 17 *A.*

melanoxylon. Plots of lower densities of each species alone were included to detect any effects of intra-specific competition.

A two way analysis of variance was used to compare the change in height of plants relative to their initial height ((final height – initial height)/initial height) and the transformed proportion ($x' = \arcsin (x^{0.5})$) of plants dying in each treatment. To avoid an unbalanced design and pseudo-replication inherent in each treatment due to the different densities, the mean relative change in height for each plot was calculated and used in the analysis. Least significant difference (LSD) was used to select those treatments with significant variation in the event that the null hypothesis (no significant difference between means due to different treatments) was rejected.

3.2.3 Competition between *G. monspessulana*, *Eucalyptus leucoxylon*, *Acacia pycnantha* and *Themeda triandra* in a raised soil bed

Three densities of *G. monspessulana* (2, 4 & 9 m⁻²) and two arrangements of the native species were replicated four times in a randomised block design (Figure 3.1 and 3.2). The positions of the *G. monspessulana* are indicated by an x in Fig 3.3) The experiment is based on addition series experiments of Firbank & Watkinson (1985).

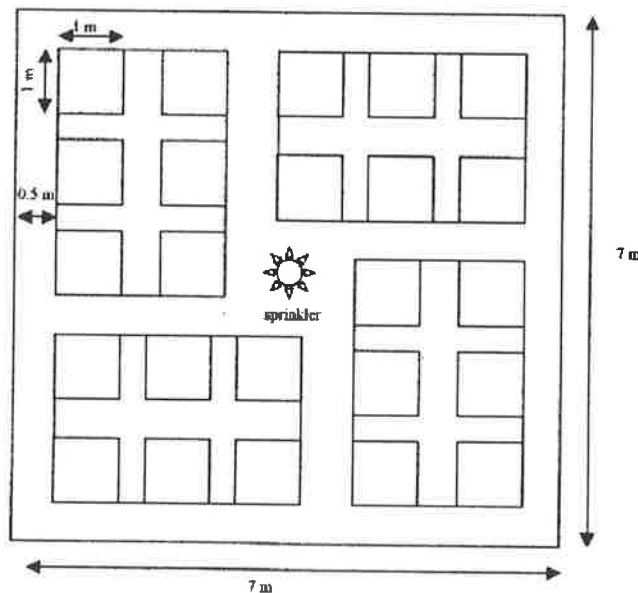


Figure 3.1. Layout and dimensions of blocks and plots within the raised soil bed at Waite campus, University of Adelaide.

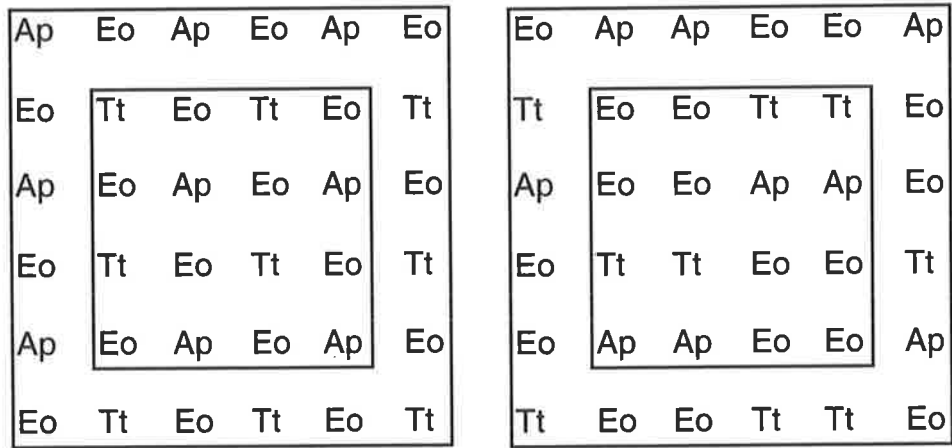


Figure 3.2. Two different arrangements of native species tested in the raised soil bed at Waite campus. The left-hand side is the spread arrangement and the right-hand side is the clumped arrangement. Ap = *A. pycnantha*, Eo = *E. obliqua*, Tt = *T. triandra*. The plants in the centre square were harvested and the plants in the outer area were unharvested buffer plants.

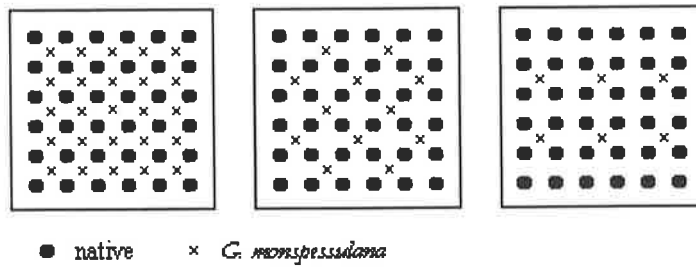


Figure 3.3. Three densities of *G. monspessulana* used showing the positions of the weeds relative to native species.

Hot (100°C) water was poured on seeds of *G. monspessulana* and *Acacia pycnantha* prior to planting in seedling trays. *Eucalyptus leucoxylon* and *Themeda triandra* seeds were planted without treatment into seedling trays. The seedlings were transplanted to the experimental plot two weeks after emergence.

Any plants failing to establish within two weeks of planting were replaced with new seedlings. A large proportion of *A. pycnantha* died after two months and all remaining *A. pycnantha* were removed from the experiment. Throughout the growing period the area was weeded regularly and watered once weekly during late spring and summer. Symptoms of fungal infection appeared two months following planting and the site was treated with fungicide.

At harvest (March 1999), plants were cut off at the base, placed in calico or paper bags and dried for 24 hours. Following drying, plant material was weighed. Plants on the outer edge were not harvested to avoid edge effects.

Predictions of the treatment and random effects in the experiment were made using a residual maximum likelihood model (REML) following a power transformation (0.2) of dry weight.

3.2.4 Competition between *Eucalyptus obliqua*, *Microlaena stipoides* and *Pultanaea daphnoides* and *G. monspessulana* in pots

Replacement series experiments were established between *G. monspessulana* and *Eucalyptus obliqua*, *Pultanaea daphnoides* and *Microlaena stipoides*. These three native species are common components of forests in the Mt. Lofty Ranges invaded by *G. monspessulana*. Four total densities, 2, 4, 6 and 8 in 20 cm pots were examined. The mixture treatments contained equal numbers of two species, *G. monspessulana* and either *Eucalyptus obliqua*, *Microlaena stipoides* or *Pultanaea daphnoides*. There were another two corresponding pots of the same density with a single species per pot. Three blocked replicates were set up in different locations, two blocks in glasshouses and one block was outside under shade-cloth. No one location provided sufficient space for more than 28 pots.

Each pot was initially planted with surplus seeds to ensure emergence of the correct number of plants. Seedlings germinating in excess of requirements were immediately removed. The plants were watered and monitored for pests over four months. After this time each plant was cut off at the base, placed in a paper bag and dried for 24 hours. Once dried the plants were weighed to determine final dry weight.

A two way analysis of variance was used to compare the final \log_{10} biomass in each treatment. To avoid an unbalanced design and pseudo-replication inherent in each treatment due to the different densities, the average biomass for each pot was calculated and used in the analysis. Scheffé's test (Day & Quinn 1989) was used to select those treatments with significant variation in the event that the null

hypothesis (no significant difference between means due to different treatments) was rejected.

3.2.5 Suppression of *G. monspessulana* by established grasses

In June (early winter) 1998, an area (20 m by 20 m) of mature *G. monspessulana* was slashed and the severed tops were cleared from the area. Forty-six plots (50 cm by 50 cm) were marked out within the area. There was a thin, consistent cover of introduced and native (*Microlaena stipoides*) grass species across most of the area. The plots were randomly assigned to be either cleared or remain grassy. All vegetation was removed, by hand from plots assigned a clear treatment, in June and December 1998.

Seed counts of *G. monspessulana* were made by collecting three soil cores (2 cm diameter) from each plot. The cores were combined and seeds were separated from the soil by washing the pooled cores through a 6 mm followed by 2 mm mesh sieve.

The number of *G. monspessulana* seedlings germinating in each plot was recorded in December 1998 and September 1999. The percent cover by grass in each plot was also estimated when the last census of seedlings was conducted in December.

3.3 Results

3.3.1 Competition for water between a dominant overstorey species, *Eucalyptus obliqua* and *G. monspessulana*.

There was no significant difference in the change of water potential (Fig 3.4) between trees in the two different areas. The change in potential was slightly lower for trees within uncleared areas. The power of the t-test was low, 0.30, meaning there was only a 30% chance of detecting a significant difference.

3.3.2 Competition and comparative growth of two perennial legumes, *G. monspessulana* and *Acacia melanoxylon* in the field

Emergence of *G. monspessulana* in the seedlings trays was considerably more successful than *A. melanoxylon* with 80-90% emergence for *G. monspessulana*

and 30-50% emergence for *A. melanoxyton*. Rainfall at Waite campus in October 1996 (23.4 mm) was half the mean rainfall for October (52.2 mm).

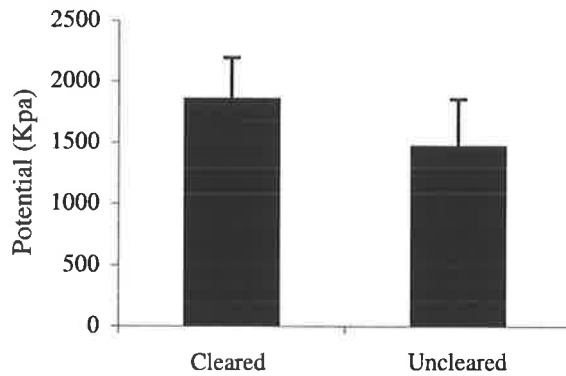


Figure 3.4. Difference between spring and late summer water potential comparing trees in areas cleared of *G. monspessulana* and uncleared areas.

G. monspessulana had a significantly faster relative change ($F_{\text{prob}} < 0.001$) in height and lower mortality than *A. melanoxyton* (Figure 3.5). There is a trend of decreasing relative change in height with increased density for *G. monspessulana* but not for *A. melanoxyton*. Relative change in height $((H_2 - H_1) / H_1)$ of *G. monspessulana* ranged from 1.5 – 2.0 cm in four months whereas for *A. melanoxyton* it ranged from 1.0 – 1.5 cm in four months. There were no significant effects of the treatments, density or mixture on either species (treatment $F_{\text{prob}} = 0.704$, species.treatment $F_{\text{prob}} = 0.532$). There were no symptoms of insufficient light such as etiolation) in seedlings of either species.

At least one or two plants in each plot died between the September and October measurements and by November many plants had died. The proportion of *A. melanoxyton* dead by October was significantly higher ($F_{\text{prob}} < 0.001$) than the proportion of dead *G. monspessulana* (Fig 3.5). Different densities and mixtures had no significant influence on the proportion of either species dying.

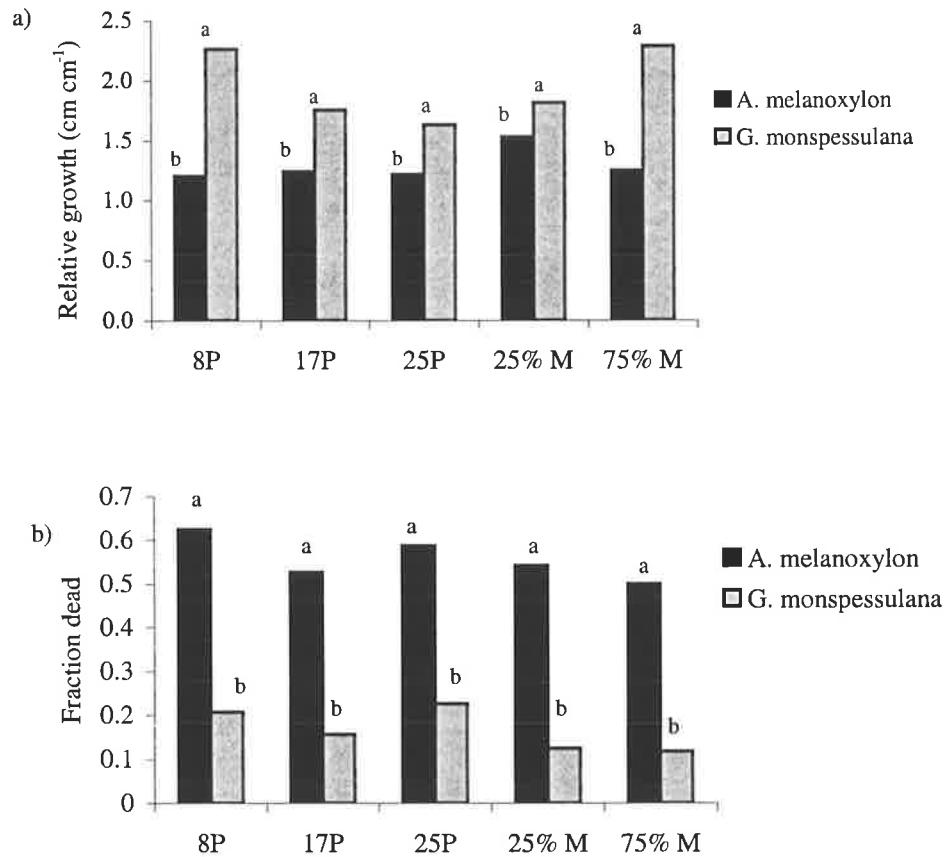


Figure 3.5. Comparison of relative growth a) (over three months) and mortality b) of *A. melanoxylon* and *G. monspessulana* with five different treatments. The different treatments were different densities of a single species (8P, 17P & 25P) and two different mixtures of the two species (25%M, 75%M). Treatment 25%M for *A. melanoxylon* indicates there were 8 *A. melanoxylon* plants and 17 *G. monspessulana* plants in the treatment. Treatment 25%M for *G. monspessulana* indicates there were 8 *G. monspessulana* and 17 *A. melanoxylon*. Different letters (a or b) above the columns indicate significantly different means.

3.3.3 Competition between *G. monspessulana*, *Eucalyptus leucoxylon*, *Acacia pycnantha* and *Themeda triandra* in a raised soil bed

G. monspessulana was initially the fastest growing species. Throughout July and August it grew vigorously and was the tallest plant for three months. *E. leucoxylon* and *T. triandra* grew very slowly until September. With warmer temperatures and longer daylight *E. leucoxylon* grew very quickly and overtook *G. monspessulana*. *T. triandra* formed thicker tussocks in September and October and most plants flowered. In the two weeks preceding harvest several *G. monspessulana* died or were close to death. Neither the *T. triandra* or *E. leucoxylon* showed similar signs of stress (Fig 3.6).

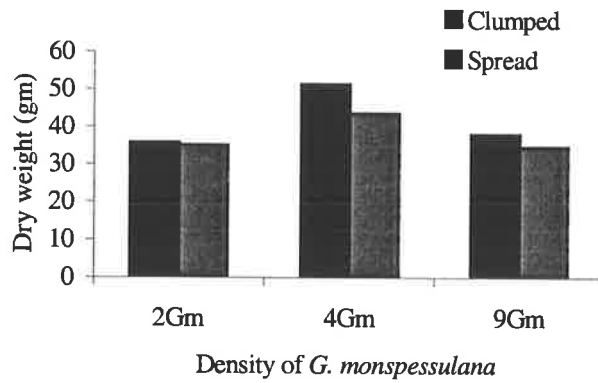


Figure 3.6. *Eucalyptus leucoxylon*, *G. monspessulana* and *Themeda triandra* growth after 8 months. The dead plant on the right side of the photos (arrow) is *G. monspessulana*. The dashed arrow points to *T. triandra*.

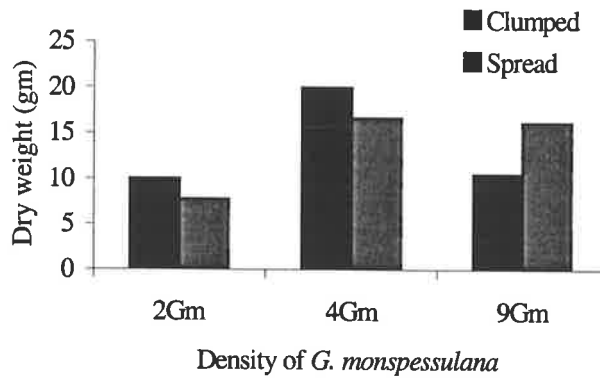
Final biomass of all three species is shown in Fig. 3.7. There were no significant effects of, or interactions between, density of *G. monspessulana* and arrangement (clumped or spread) of the native species. The biomass of *E. leucoxylon* was considerably greater than *T. triandra* and *G. monspessulana*.

Differences between blocks were significant so block was left as a term in the statistical model. This contributed to more variance and reduced the power of the experiment. One obvious cause of variation between blocks was the proximity of a pepper tree to the experimental area. All plants within the block closest to the pepper tree were smaller than plants in other blocks.

a) *Eucalyptus leucoxylon*



b) *Genista monspessulana*



c) *Themeda triandra*

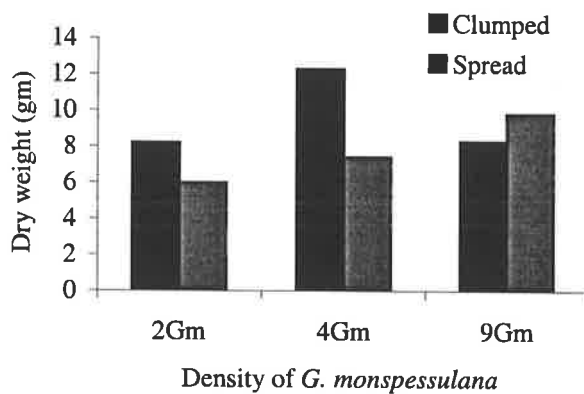


Figure 3.7. a) The mean final biomass of *E. leucoxylon*. in each different treatment. b) The mean final biomass of *G. monspessulana* in each different treatment. c) The mean final biomass of *T. triandra* in each different treatment. Standard errors were very large and no differences between biomass in these graphs are significant.

3.3.4 Competition between *Eucalyptus obliqua*, *Microlaena stipoides* and *Pultanaea daphnoides* and *G. monspessulana* in pots

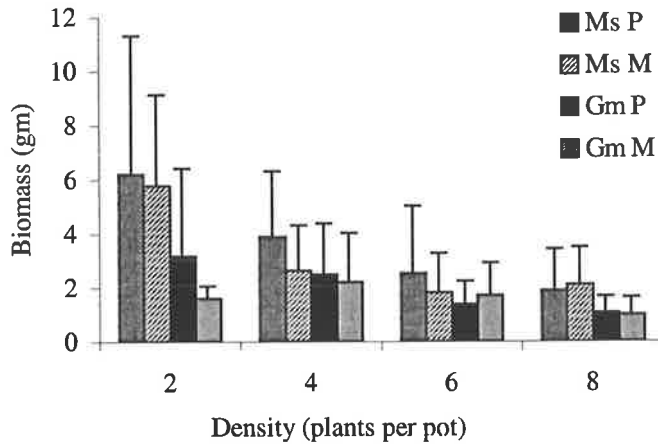
At the lowest density (2 plants) *E. obliqua* growth was inhibited (Table 3.1, Fig 3.8) by the presence of *G. monspessulana* compared to growth with another *E. obliqua*. Increasing density had a significant effect (Table 3.1, Fig 3.8) on all species except *P. daphnoides* which grew very slowly in both mixture and pure treatments relative to the three other species.

Table 3.1. Results of two-way analysis of variance using transformed ($x' = \log_{10}x$) data (biomass) comparing the effects of density and composition (mixture or monoculture).

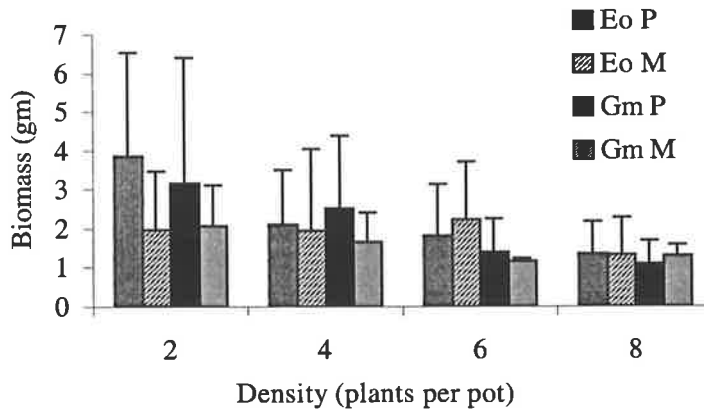
Species	Variable	df	F probability
<i>E. obliqua</i>	Density	3	0.002
	Treatment (Mixture or Pure)	1	0.077
	Density.Treatment	3	0.026
<i>G. monspessulana</i>	Density	3	0.039
	Treatment (Mixture or Pure)	1	0.447
	Density.Treatment	3	0.675
<i>M. stipoides</i>	Density	3	<0.001
	Treatment (Mixture or Pure)	1	0.308
	Density.Treatment	3	0.365
<i>G. monspessulana</i>	Density	3	0.003
	Treatment (Mixture or Pure)	1	0.260
	Density.Treatment	3	0.352
<i>P. daphnoides</i>	Density	3	0.152
	Treatment (Mixture or Pure)	1	0.871
	Density.Treatment	3	0.709
<i>G. monspessulana</i>	Density	3	0.002
	Treatment (Mixture or Pure)	1	0.198
	Density.Treatment	3	0.789

At each plant density, each species, with the exception of *E. obliqua* accumulated a similar amount of biomass regardless of whether competition was intraspecific or interspecific. *M. stipoides* accumulated the highest mean biomass (6 g), but it was not significantly higher than the other species. *P. daphnoides* final biomass was much lower, 0.5-1 g, than the other species.

a) *M. stipoides* & *G. monspessulana*



b) *E. obliqua* & *G. monspessulana*



c) *P. daphnoides* & *G. monspessulana*

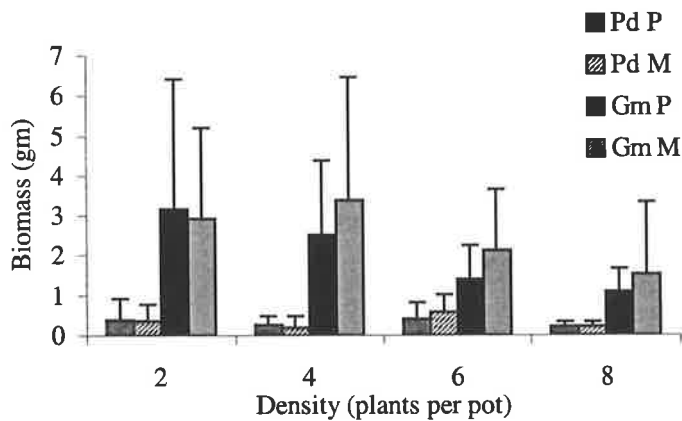


Figure 3.8. Final biomass, after four months, of native species and weed grown in a monoculture (P) or mixture (M). a) *M. stipoides* and *G. monspessulana*. b) *E. obliqua* and *G. monspessulana* and c) *P. daphnoides* and *G. monspessulana*. The bars indicate standard errors.

3.3.5 Suppression of *G. monspessulana* emergence by established grasses

The bulk of the seedlings emerged in autumn 1999. The proportion of the seedbank germinating under grass cover was consistently low compared with cleared areas (Fig 3.9). The actual numbers of seedlings emerging in either treatment was extremely low, less than 1% of the total seedbank. The actual number of seedlings germinating was very variable, ranging from 4-300 seedlings m^{-2} (Fig 3.10).

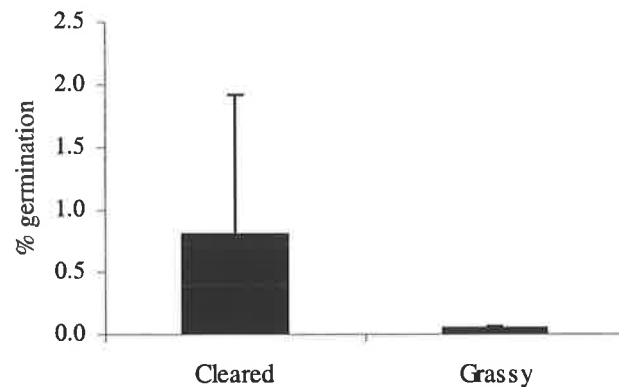


Figure 3.9. Comparison of the percent of seedbank germinating within two different treatments, cleared or covered with grass. The bars indicate 95% confidence intervals based on the t_{crit} for unequal variances. There is a significant difference between the treatments ($P = 0.017$).

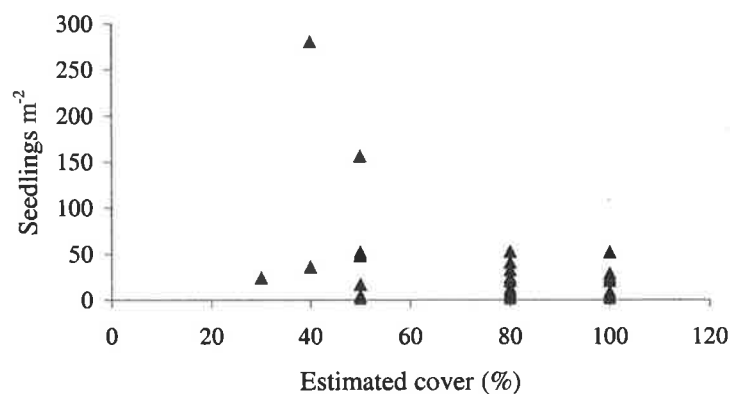


Figure 3.10. Estimated % cover of grass at the end of the experiment at Crafers plotted with respective densities of emerged seedlings.

3.4 Discussion

G. monspessulana has features of a coloniser or early successional species. These features include an ability to fix nitrogen (Crawley 1997), hard-coated seeds

enabling broad scale (10 years) dispersal in time and a relatively short time (2 years) until seed production. *G. monspessulana* did not emerge as a superior competitor at the densities and over the times examined in this thesis. This is consistent with *G. monspessulana* being a coloniser or early successional species and requiring disturbance with stronger competitors removed, for successful recruitment (Dancer *et al.* 1977, Noble & Slatyer 1981, Crawley 1997). It is also consistent with studies of competition between *C. scoparius* or *Ulex europaeus* and other species (Paynter *et al.* 1998, Fogarty & Facelli 1999, Partridge In press, Rees & Hill In press).

The existence of dense, almost mono-cultural stands of *G. monspessulana* is not necessarily a consequence of it out-competing native species for resources. Seed production of *G. monspessulana* is high compared to similar native shrub species. Collecting seeds of native shrub species involved harvesting from more trees and, unlike *G. monspessulana*, a high proportion of mature plants lacked seed due to bud and flower gall formation. Mean seed production per plant for an Australian legume, *A. suaveolens* was 11-90 seeds per plant (Auld & Myerscough 1986) which is much lower than seed production for *G. monspessulana* ~ 2000 (Chapter 2). Reproductive maturity was not reached until 4 to 8 years in a number of Hawkesbury sandstone shrub species (Whelan & Muston 1989). Dense stands of *G. monspessulana* with low numbers of native species could be the result of a higher probability, through higher numbers, of *G. monspessulana* being in a site conducive to emergence and recruitment rather than competitive ability.

Leguminous native shrubs, while having an apparent similar niche to *G. monspessulana*, had a lower probability of germination, grew more slowly, and had lower probability of survival. Poor survival of *A. melanoxylon* (replacement series in the field), *A. pycnantha* (raised soil bed) and *P. daphnoides* (pots) compared to survival of *G. monspessulana* could be because *G. monspessulana* is less fastidious with respect to types of symbiotic, nodule-forming, nitrogen-fixing bacteria (Thrall 2000). In addition, soil types may not have been suitable for the natives. This fastidiousness of the legumes compared to *G. monspessulana* being adaptable means the leguminous shrubs are difficult to use as competitors because of the uncertainty about their suitability for any one particular area. Many areas

infested by *G. monspessulana* have no remnant leguminous shrubs to indicate whether or not it was a suitable habitat for them.

These experiments indicate two possible options for use of competitive plants in an integrated management strategy. *M. stipoides* tended to accumulate more biomass, under the same conditions, than *G. monspessulana* (Fig 3.8). In addition, established *M. stipoides* reduced emergence of *G. monspessulana* (Fig 3.9). More research is required to firmly establish the benefits of grasses such as *M. stipoides* because, firstly, established *M. stipoides* may be removed in the event of a disturbance such as fire. This is a time when substantial *G. monspessulana* germination and recruitment is likely to occur. In this situation selective herbicides such as triclopyr which, applied at the recommended rate, will kill *G. monspessulana* and not *M. stipoides* should be used. Secondly, subsequent survival to reproductive maturity of the few *G. monspessulana* seedlings emerging through *M. stipoides* may be higher in grassy areas. More seedlings may germinate in cleared areas but the density of reproductive *G. monspessulana* may eventually be the same due to self-thinning (Firbank & Watkinson 1990).

The second possibility for management of *G. monspessulana* may be to follow-up removal of mature *G. monspessulana* with a reasonably dense planting (20 seedlings m⁻²) of an endemic, dominant *Eucalyptus* sp. seedlings. Where *G. monspessulana* was grown in competition with *E. leucoxylon* most of the *G. monspessulana* seedlings were dead or dying by the time the plots were harvested (Fig 3.6). *Eucalyptus* seedlings could be germinated and grown to seedling stage and planted following a fire and herbicide treatment of the first flush of *G. monspessulana* seedlings. The *Eucalyptus* seedlings would then have an initial height advantage.

3.5 Conclusion

Negative effects of competition between *G. monspessulana* and native species were not clearly identified in the pot, field and raised soil bed experiments. Densities of *G. monspessulana*, and in some cases numbers of replicates, may have been too low. However features of *G. monspessulana* were identified that

are likely to increase its chance of monopolising limited resources. These features were rapid emergence relative to native legumes, rapid vertical growth and growth in winter. Native species tended to be fairly static throughout colder months.

Competing natives can be incorporated into an integrated management strategy for *G. monspessulana*. Native grasses and eucalypts are useful because they are fast growing and produce high numbers of seeds. The high numbers of seeds is required to put the plants on a par with the high numbers of *G. monspessulana* seeds. Grasses are largely unaffected by broad-leaf selective herbicides that may be used to control *G. monspessulana*. However, the affect of competition is not sufficient to remove the requirement for follow-up treatments of herbicide or physical methods because the density of germinating *G. monspessulana* is too high following a disturbance.

Chapter 4. Seedbanks of Native and Introduced Species under *G. monspessulana* Infestations

4.2 Introduction

Managing a weed population, particularly weeds of natural ecosystems, constitutes a disturbance and seedbanks and immigrants have an opportunity to benefit from management or disturbance (Cavers & Benoit 1989, Parker *et al.* 1989). Some disturbances such as fire, cultivation and flooding can dramatically alter the seedbank and the structure of the plant community (Graham & Hopkins 1990, Harper 1994, Crawley 1997). Therefore, the nature of the seedbank under a weed population is crucial for making management decisions. Whether or not to outlay time or finance to manage weeds in a particular area depends partially on the potential of the seedbank to provide a more desirable community following control of the weed. Given that the seedbank could provide a desirable community, the composition of the seedbank will determine both the choice of the initial weed control method and what else might need to be done to distil a desirable community from the existing seedbank. It is possible for the seedbank to be altered. For example, seeds of desirable species can be added.

Composition of seedbanks in a number of non-agricultural ecosystems, ranging from sand-dunes and meadows to rainforests, throughout the world have been examined recently. Some of the studies (Looney *et al.* 1995, Tsuyuzaki & Kanda 1996, Pérez *et al.* 1998, Falinska 1999) have been conducted in order to understand the contribution of the seedbank to secondary succession. Other studies have examined the seedbank from a more applied conservation perspective and examined the soil seedbank as a reserve of species otherwise lost by clearing, agriculture or pollution (Vlahos & Bell 1986, Partridge 1989, Graham & Hopkins 1990, Komulainen *et al.* 1994, Teketay & Granström 1995, Bakker *et al.* 1996, Bekker *et al.* 1997, Carrington 1997, Drake 1998, Morgan 1998). Two studies have examined the seedbank with particular attention to the potential changes to the ratio of introduced and native species in the event of disturbance and subsequent seedbank germination.

Two main methods were used to detect seeds in the soil. One method involves sieving of soil that may be followed by flotation of seeds. Tsuyuzaki & Kanda (1996) floated the seeds in a potassium carbonate (K_2CO_3) solution to separate them from the soil sample. Seeds were then germinated in an incubator and grown, in order to identify the species. Coarse sieving followed by spreading the soil samples in a thin 1 to 2 cm layer, over an inert layer of sand or vermiculite, and waiting for 6 to 12 months for seeds to germinate was the technique used in most studies (Vlahos & Bell 1986, Partridge 1989, Graham & Hopkins 1990, Looney & Gibson 1995, Teketay & Granström 1995, Bakker *et al.* 1996, Bekker *et al.* 1997, Carrington 1997, Drake 1998, Morgan 1998). The germination technique was sometimes modified with a treatment of the soil samples, appropriate to the type of seeds likely to be in the seedbank, in order to stimulate dormant seeds. Vlahos & Bell (1986) heated their soil samples. Bekker *et al.* (1997) treated the samples with gibberellic acid solution. Three studies used both techniques (Komulainen *et al.* 1994, Pérez *et al.* 1998, Falinska 1999).

Gross (1990) and Falinska (1999) both found that estimates of seedbank density were higher when sieving was used to separate seeds from soil. However, predictions of viability of seeds using this method may be inaccurate because the sieving and subsequent drying can kill seeds (Gross 1990). Gross (1990) detected more species using the germination method. Falinska (1999) detected 41 species using sieving and sorting using a microscope compared to 36 species by germination. The germination method is less time consuming while being comparable in determination of composition of seedbanks.

The germination method was used to determine the composition of seedbanks present under areas of South Australian dry sclerophyll forests invaded by *G. monspessulana*. The focus was native versus exotic content and was also characterised in terms of the potential response of the seedbank to fire by applying a heating treatment to sub-samples of soil.

4.2 Materials & Methods

Twenty soil samples were collected from each of four sites. The sites were Deep Creek, Lenswood, Upper Sturt and Henschke. Details of these sites, such as density and average age of *G. monspessulana* are provided in chapter 2. Collections of soil were done in early spring (September-October). Each sample consisted of two adjacent cores (1 cm apart) 10 cm diameter by 10 cm depth. The two cores were pooled.

4.2.1 Preparation and treatment of the soil

Rocks and twigs were brushed (to keep as much soil in the samples as possible) and removed from each sample. The soil was then mixed and halved. One half of the soil was heated at 80°C for 15 minutes. Both halves of the soil were then spread out as a 1.5 cm layer onto pots containing steam-sterilised potting mix and placed outside, on a flat area. Ten pots containing only potting soil were interspersed amongst the soil from field sites. These enabled identification of soil and airborne seeds likely to contaminate the samples. The pots were watered when required.

4.2.2 Detection and identification of emerging seedlings.

Pots were examined for emergent seedlings each month for the first six months then once every two months for another six months. Seedlings that were immediately recognised were recorded and removed. Unidentifiable seedlings were transferred to larger pots (1 seedling per pot), and were grouped based on similarity. Once all emerged plants were removed the soil was turned, being careful not to go deeper than the sample, and patted down.

Plants were identified using keys in Flora of South Australia and Crop Weeds of Australia. Dr David Cooke, Dr Chris Preston and Richard Davies identified ambiguous specimens.

Some grasses had not flowered by the end of the project. These were identified to genus or considered native or weed based on Dr Cooke or Dr Preston's knowledge of local grass weeds.

4.2.3 Data Analysis

Species emerging from the control pots were removed prior to analysis of the data. An angular transformation ($x' = \arcsine(x^{1/2})$) was applied to the proportion of natives before a two-way analysis of variance. A logarithmic transformation ($x' = \log_{10}(x+1)$) was applied to the abundance of weeds (total number of weeds), abundance of weeds excluding *G. monspessulana* and abundance of natives per replicate before a two-way analysis of variance. Significantly different means were identified using Scheffé's critical value (Day & Quinn 1989). Finally the seedlings emerging were classified into six categories; native shrub/tree, native herb, native grass, introduced shrub/tree, introduced herb and introduced grass. The total number of seedlings in each category, for each site are presented as a percent of the total number of seedlings at each site.

4.3 Results

Most seedlings emerged within the first three months following collection of the soil. *G. monspessulana* continued to emerge throughout year and "contaminating" species increased in the final six months. *G. monspessulana* dominated the number of emerging seedlings only at Henschke (Table 4.1). The mean number of different species emerging from each replicate soil sample was 5.1 ± 2.8 . Native species made up 10-15% (Fig 4.4) of the total number of species at three out of the four sites infested with *G. monspessulana*. The seedbank under the infestation at Deep Creek was significantly richer in native species with 40-50% of emerged seedlings being natives. Heating the soil did not significantly affect the proportion of native species emerging (Table 4.2). One species, *Stellaria palustris*, emerging from one Deep Creek sample, is considered uncommon (Black 1986) but there is some doubt about its status as a native species. The remaining native species emerging and surviving were classified as common.

Table 4.1. Summary of total numbers of species and seedlings emerging at each site.

Site	Deep Creek	Henschke	Lenswood	Upper Sturt
Number of Native Species	24	8	11	12
Number of Introduced Species	29	30	31	15
Seedlings m ⁻² emerged	4692	8394	5928	3702
<i>G. monspessulana</i> seedlings (% of total seedlings)	28	89	31	48

Table 4.2. Table of ANOVA's for seedbank survey data. The effects of site and heat treatment on three variables; proportion of natives, abundance of introduced species and abundance of native species, are compared.

Variable	Interaction	Variance ratio	Fprob
Proportion of species that are native	Site	22.99	<0.001
	Treatment	0.32	0.570
	Site.Treatment	1.32	0.272
Total number of introduced species	Site	8.97	<0.001
	Treatment	3.91	0.050
	Site.Treatment	0.70	0.552
Total number of introduced species (excluding <i>G. monspessulana</i>)	Site	35.33	<0.001
	Treatment	1.35	0.248
	Site.Treatment	0.95	0.417
Total number of natives	Site	61.30	<0.001
	Treatment	1.56	0.213
	Site.Treatment	0.48	0.699

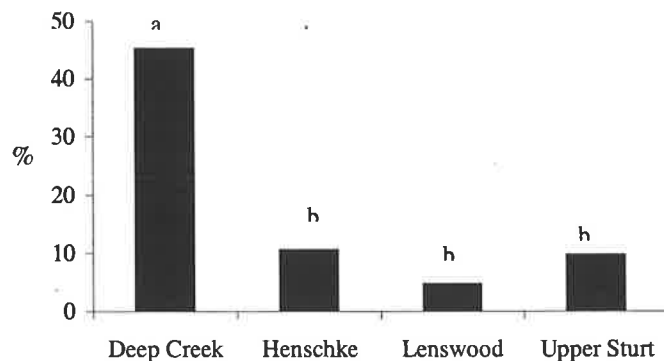


Figure 4.1. Back-transformed mean percent of native species emerging at the four different sites. Different letters indicate significantly different means identified using Scheffé's test.

Heating the soil samples (Table 4.2) did not significantly affect the abundance of native or introduced (excluding *G. monspessulana*) seedlings. Heating the soil only caused a significant change in the number of introduced species seedlings emerging when *G. monspessulana* was included in the analysis. Numbers of native species seedlings emerging ranged from 0-3683 seeds m⁻². Samples from Deep Creek yielded a significantly greater number (Fig 4.2) of native seedlings.

Numbers of introduced species seedlings (Fig 4.3), other than *G. monspessulana*, ranged from 0-5969 seeds m^{-2} . Mean abundance of introduced seedlings varied considerably between sites.

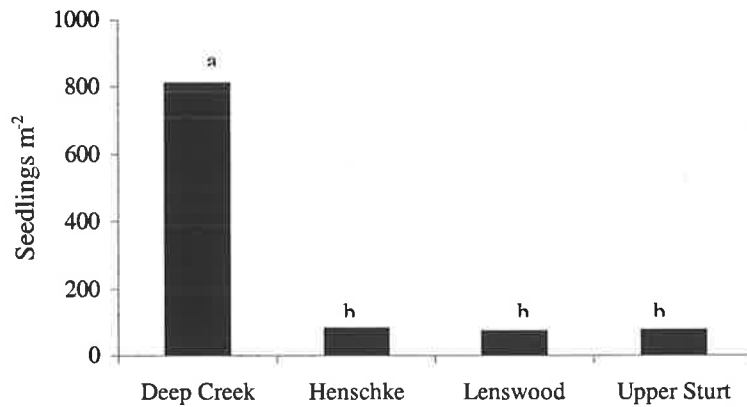


Figure 4.2. Back-transformed mean abundance (converted to an estimate of seedlings m^{-2}) of native seedlings emerging at each site. Different letters indicate significantly different means identified using Scheffé's test.

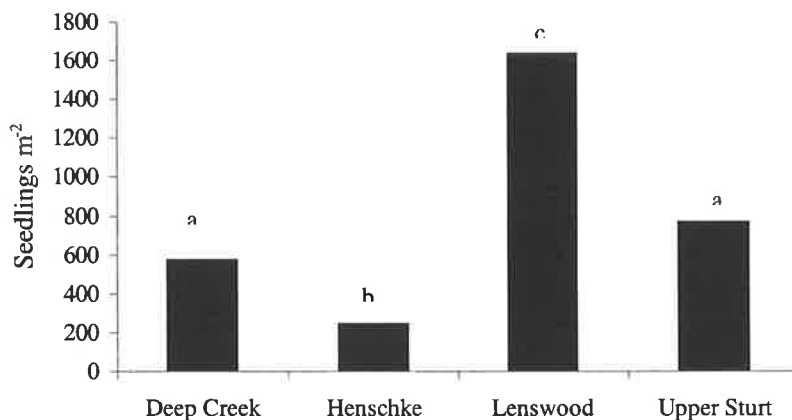


Figure 4.3. Back-transformed mean abundance (converted to an estimate of seedlings m^{-2}) of introduced seedlings, excluding *G. monspessulana* at each site. Different letters indicate significantly different means identified using Scheffé's test.

Introduced shrub species, excluding *G. monspessulana* were generally poorly represented in the samples (Fig 4.4). Introduced herbs formed the second largest component of the samples from Henschke and Upper Sturt. The introduced herbs formed the bulk of the seedlings emerging at Lenswood. The soil from Henschke

had large numbers of *G. monspessulana* seedlings emerge. This site also had the largest seedbank and the highest proportion of older plants (Chapter 2).

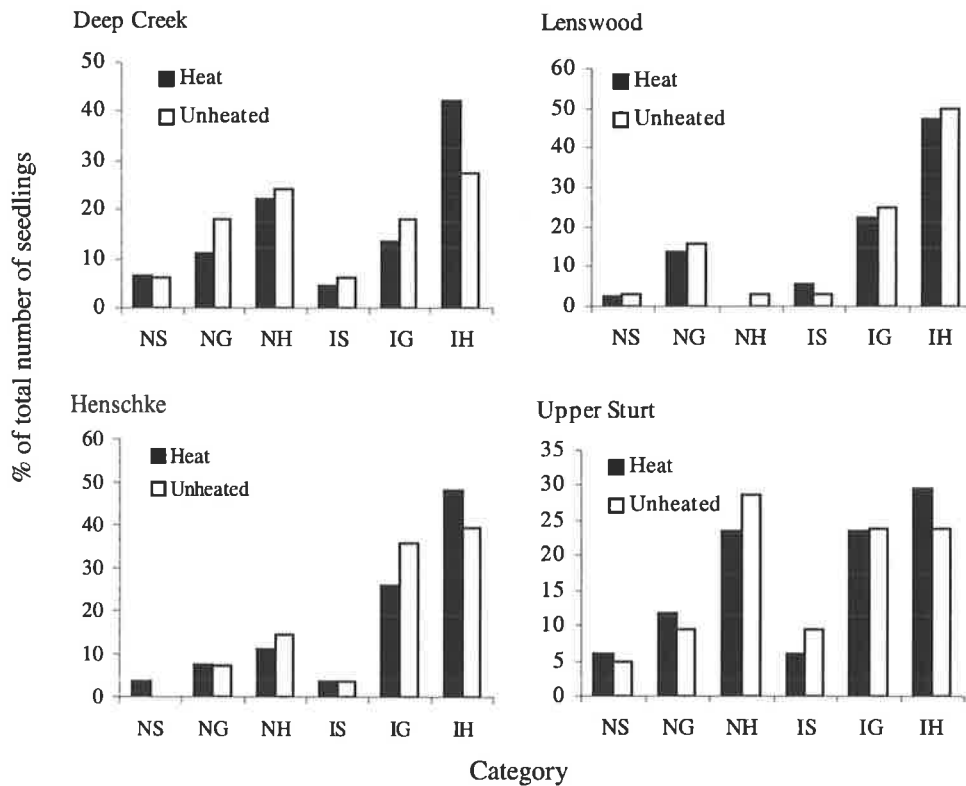


Figure 4.4 Seedlings were divided into six categories; native shrub/tree (NS), native grass (NG), native herb (NH), introduced shrub/tree excluding *G. monspessulana* (IS), introduced grass (IG) and introduced herb (IH). The percent each category contributes to the total number of seedlings is shown for each site and heated and unheated samples.

4.4 Discussion

This seedbank survey demonstrates the efficiency of *G. monspessulana* to regenerate following removal of mature plants. Domination of the seedbank by *G. monspessulana* in comparison to other species was expected given the huge size of *G. monspessulana* seedbanks (Chapter 2).

Seedbanks below the four established *G. monspessulana* stands were fairly consistent with respect to richness (number of different species) with the exception of Deep Creek. Proximity to remnant vegetation is not necessarily an indicator of a richer seedbank. Deep Creek, only one out of three sites close to remnant vegetation, had a reasonable native component. However, less disturbance is characteristic for the Deep Creek site. The populations at Deep Creek, Lenswood and Upper Sturt are all young populations relative to the

population at Henschke (see Chapter 2). This helps to explain the significantly lower value for abundance of introduced species, excluding *G. monspessulana*, at Henschke.

Differences in the abundance of weeds could be the result of a number of factors. Other than the site at Deep Creek, the different abundances in introduced species reflects the difference in rainfall patterns. The site history will also have an important influence on the abundance of weeds along with the length of time *G. monspessulana* has been present at the site. The likely large range of seed sizes and only one standard sample size may affect the accuracy of estimates of abundance for some components of the seedbank (Ambrosio *et al.* 1997). Smaller seeds with clumped distributions were probably underestimated in this study. Finally, there were differences in composition between sites and how well each particular species present in the sample responds to the particular conditions set up for germination will influence the estimate of abundance.

The abundance of seedlings emerging is within the broad range (990-12,304 seeds m⁻², Carroll & Ashton 1965) of seedling emergence from Victorian sclerophyll forest soils. The richness for all four sites is comparable to jarrah forest soil seedbanks (20-45 species) examined by Vlahos & Bell (1986) using the germination method, although only a limited number of the species which emerged in the study by Vlahos & Bell (1986) were introduced species. Weed seeds were also very low in proportion (0.6-4.0%) in soil samples studied from unlogged and logged rainforest in north Queensland (Graham & Hopkins 1990). The greater number of introduced species at sites studied here reflect significantly greater and more sustained disturbance patterns.

The application of this survey is limited by being based on a single set of samples within one season and one year. A series of samples taken over the period of a year would be better to detect more transient residents of the seedbank. In addition, smoke water (Bell *et al.* 1995) could have been applied to the sample to encourage those species requiring a chemical trigger to break dormancy. Identification of immature plants to species, particularly long-lived perennial species, will always be problematic for studies limited to a few years.

Grasses, introduced and native, are relatively common at all sites and the use of a broad-leaf selective herbicide, following a fire will kill most germinating *G. monspessulana* and a number of introduced herbs leaving the ground protected by grasses. Lack of a significant difference in the proportion and abundance of native species indicates that fire could be considered a tool for management at three of the four sites. There may be benefits of using fire to reduce the seedbank of *G. monspessulana* while not dramatically reducing the diversity of native species. For example, frequent burning did not appear to influence the richness or abundance of weeds in *Themeda triandra* grassland, although a sustained history of burning at these sites may have already brought the richness and abundance to a steady state with respect to response to burning (Morgan 1998). A slightly higher abundance of native seedlings at Deep Creek suggests management strategies without fire may be more appropriate for Deep Creek and similar areas. Burning should still be considered a management option at the three other sites given that all other conditions are amenable.

4.5 Conclusion

The densities of native species at sites with thick infestations of *G. monspessulana* were low at three out of four sites (Fig 4.2). Given the large seedbanks of *G. monspessulana* this was an expected result. There was little relationship between general proximity to native vegetation and the size of native species seedbanks. Instead age of *G. monspessulana* and disturbance patterns appeared to have more influence on seedbank composition. Heating the soil did not significantly alter the proportion or abundance of native species (Fig 4.1). Clearly the nature of the seedbank needs to be considered when management decisions for *G. monspessulana* infestations are made.

Chapter 5. Use of Fire for the Reduction of *G. monspessulana* Seedbanks

5.1 Introduction

G. monspessulana has a large, long-lived seedbank. This seedbank enables *G. monspessulana* to regenerate for 7 years or more following removal of mature plants. Fire has the potential to reduce the seedbank by killing seeds or stimulating them to germinate but accurate information about how the seedbank of *G. monspessulana* responds to fire is needed. Fire can also have dramatic, possibly detrimental effects, on an ecosystem. Fire will be useful for managing *G. monspessulana* only if its effectiveness outweighs any negative outcomes.

The aim for this chapter is to obtain accurate information on the response of the *G. monspessulana* seedbank to fire. In addition, experiments were conducted to determine the potential of fire to reduce the seedbank of *G. monspessulana* and assess the relative contributions of seed death and seed germination to the reduction. Fuel levels, distribution and season of burn were varied to provide information about how *G. monspessulana* responds to changing these factors. The response to burning, of a number of native species which occur in areas infested with *G. monspessulana* was examined in order to identify soil temperatures and herbicide treatments which provide management of *G. monspessulana* while benefiting native species.

5.2 Study sites

5.2.1 Belair

This site, in Belair National Park (latitude 35°00'S, 138°38.5'E), was located near the lower waterfall. Vegetation consisted of *E. obliqua* with a dense understorey of *G. monspessulana* and a very sparse ground level layer of *Microlaena stipoides*. On the riparian edge of the plot there was *Rubus* sp. and two native grass species, *Microlaena stipoides* and *Poa* sp. This moderately sloped site had a western aspect.

5.2.2 Cleland

This site, in Cleland Conservation Park (latitude 34°58'S, longitude 138°48'E, altitude 580 m above sea level), was approximately two hectares of *E. obliqua* (stringybark) forest, moderately sloped (about 45°), with a western aspect and a depression/ drainage course roughly dividing the site into two areas each with a different level of *C. scoparius* infestation. One area was predominantly broom (>80%) *C. scoparius*, with scattered *G. monspessulana* and a sparse ground layer of *Microlaena stipoides* and *Acrotriche fasciculiflora*. The second area had a more indigenous and diverse understorey of *P. daphnoides*, *Scaevola* sp., *Acrotriche fasciculiflora*, *Poa* sp., *Microlaena stipoides*, *D. leptophylla* with scattered weeds, blackberry, *G. monspessulana* and *C. scoparius*.

5.2.3 Crafers

The vegetation at Charlick Rd, Crafers (35°00'S, 138°41'E, 520 m above sea level) consisted of *E. obliqua* forest with an understorey composed almost entirely of *G. monspessulana*. Other understorey plants that were present in low density were *Acrotriche*, *Hibbertia* sp., *Adiantum aethopicum*, *Microlaena stipoides*, *Olea europaea*, *Rosa canina* and *Rubus discolor*. An area of remnant vegetation further east along Charlick's Road with minimal weed infestation comprised an overstorey of *E. obliqua*, an understorey of *Pultenaea daphnoides*, *Davesia* sp., *Acacia pycnantha*, *Bursaria* and ground-cover of *Hibbertia*, *Acrotriche*, *Microlaena*, *Poa* sp. The experimental site was steeply sloped with a south-south west aspect.

5.2.4 Marble Hill

The study site at Marble Hill (34°55'S, 138°46'E, 610 m above sea level) had an overstorey of *E. obliqua* and an understorey of *G. monspessulana*. Towards the top of the slope, the density of *G. monspessulana* decreased and more endemic species such as *P. daphnoides*, *Xanthorrhoea* sp., *Poa* sp., *Microlaena stipoides*, *Acrotriche fasciculiflora* and *Hibbertia* sp. were present.

5.2.5 Roseworthy

The Roseworthy campus, University of Adelaide site (latitude 34°51'S, longitude 138°68'E, altitude 65 m above sea level) was located on and comprised a level area of pasture which had been fenced and subsequently ungrazed for about one year. The vegetation was predominantly introduced legumes and grasses.

5.3 Materials and Methods

5.3.1 Collection and treatment of soil cores to estimate seedbank density

Soil cores, where required, were collected with an auger or corer. The dimensions of the auger and corer were 10 cm diameter by 10 cm depth and 2 cm diameter by 10 cm depth respectively. Although the depth of the auger and corer was 10 cm, soil cores were sometimes shorter due to shallow soil on rock or compact clay subsoil. Once collected, soil cores were placed in plastic press seal bags, labelled and processed in the laboratory. Soil cores were air-dried, crushed and shaken through two sieves, the first with an 8 mm mesh and the second with a 2 mm mesh. Separation of the seeds from the soil using the 2 mm mesh sieve was aided by washing with water. Remaining organic material was separated from the *G. monspessulana* seeds by flotation. It was then easy to count seeds in a white tray.

5.3.2 Determination of fuel load

The approximate fuel load was determined by collecting all plants, twigs and leaf litter from six semi-randomly located quadrats (25 cm x 25 cm) within the experimental site. Three positions along the bottom edge of the plot were selected and 2 random distances, upwards through the experimental area, were chosen from each position for the location of the quadrat. The different materials were weighed (fresh weights) then weights were combined for each quadrat. This value for fuel load does not incorporate trees, trunks or branches with diameters >2 cm.

5.3.3 Datalogger, thermocouples and temperature sensors

Measurements of soil temperatures at Crafers, Cleland Conservation Park and Roseworthy were made using a Micropower Datalogger (Tain Electronics Pty Ltd) with 16 data input channels. Temperature measurements close to the surface

were made with chrome-alumel (Type "K") thermocouple wire with a temperature range of 0°C-1200°C. Deeper temperature measurements were made with AD590 temperature transducers which had a temperature range of 41°C-130°C. An ambient temperature probe was also fitted to the data-logger. Calibration and testing of the data-logger and temperature sensors was done 3 days prior to each burn, using a laboratory oven.

Thermax™ 10 level strips of three temperature ranges A (40-71°C), B (77-127°C) and C (132-182°C) were used to measure soil temperatures during burns at Roseworthy, Marble Hill, Crafers and Belair National Park. The temperature scale is on adhesive paper with a scale in Celsius and Fahrenheit. The actual temperature indicator is a series of white boxes that change to black when the adjacent scale temperature is reached.

5.3.4 Gravimetric water content of soil samples

Soil samples (about 3-7 g) were collected and placed in press seal plastic bags (Marble Hill) or 10 ml screw top vials (Belair). The soil was weighed, placed on glass petri dishes and dried at 100°C for 24 hours. The samples were removed from the oven and weighed again.

5.3.5 Comparison of the effects of different management strategies, slashing & fire, fire and herbicide on *G. monspessulana*

An area of approximately 80 m by 80 m, within a dense stand of *G. monspessulana* was divided into 16 plots of 10 m by 10 m each separated by slashed and cleared 2 m paths around each plot. Twenty five soil cores (10 cm diameter and 10 cm depth) were taken diagonally across the experimental area to check for a marked gradient in soil seedbank density. Each plot was randomly assigned one of four treatments; cut and burn, burn, herbicide and unburnt control (Figure 5.1). The cut and burn treatment was included to dry and distribute the fuel more evenly and closer to the ground. Cutting was done with a rotary slasher one week prior to burning. The herbicide treatment was a basal bark application of 25% triclopyr (Garlon®™) in diesel. Temperatures in the soil were measured using the Tain electronics data-logger placed 10 m from the thermocouple tips. Plots were burnt individually in October 1996.

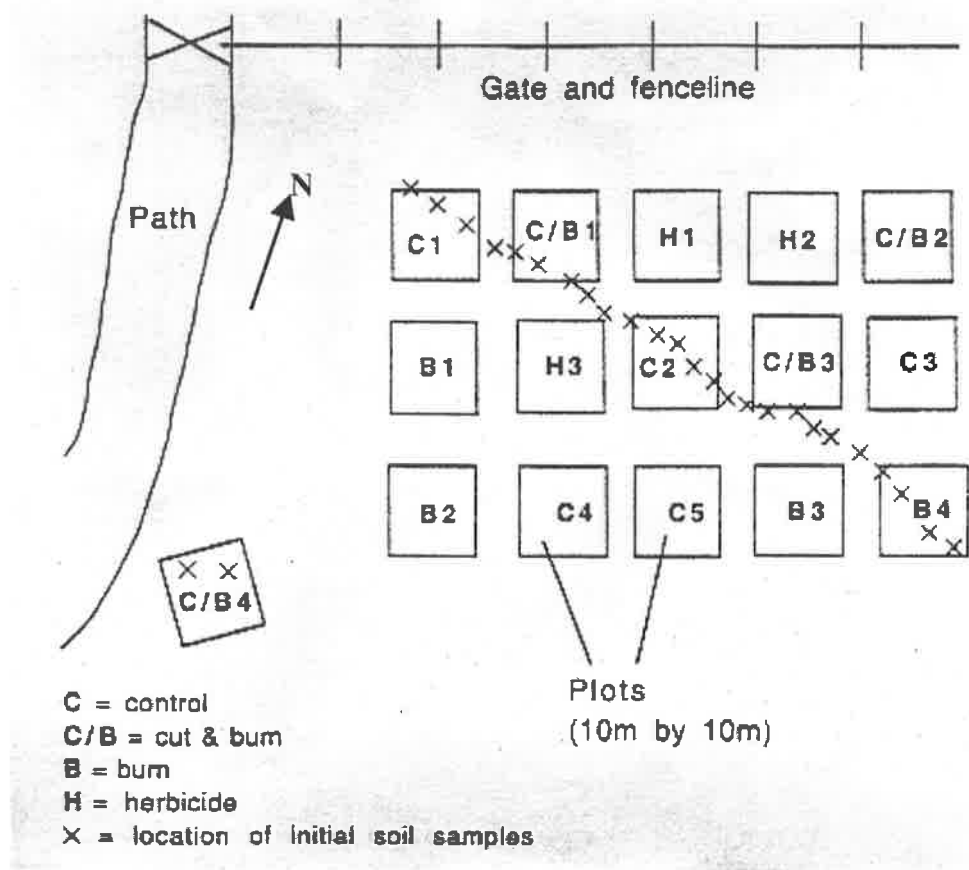


Figure 5.1 Arrangement of treatments and plots at Crafers.

The following autumn, burnt and herbicide treated plots were split and the emerging seedlings in each half-plot were treated with glyphosate in order to examine the effects of glyphosate on emerging native flora. Emerging seedlings were counted and three soil cores (10 cm diameter and 10 cm depth) were taken from each plot in autumn (April) of the two successive years following the burn. Numbers of seedlings per m² were also estimated at these times by counting seedlings in 10 randomly placed quadrats, 10 cm by 10 cm, in each plot. The placement of quadrats was determined by using a random number table to select two distances from the uphill and western edges of each plot.

Seedbank estimates obtained from soil cores were compared using a one-way analysis of variance; the significantly different means were identified using the least significant difference (LSD) and Scheffé's test (Day & Quinn 1989). A non-

parametric analysis of variance (Kruskal-Wallis) was used to compare the seedling densities resulting from different treatments. Seedlings emerging in 1998 were considered as a proportion of the 1997 seedbank. Arcsine transformed proportions were then compared using a one-way analysis of variance and least significant differences.

5.3.6 Comparison of response to post-fire herbicide treatments in areas heavily or lightly infested with *C. scoparius* and *G. monspessulana*

Sixteen quadrats of 3 m x 2 m were marked throughout the site with star droppers (Fig 5.2). Three soil cores (10 cm diameter, 10 cm deep) were collected from each quadrat before the area was burnt. In addition, pre-burn numbers of introduced and native species within the quadrats were recorded. Three thermocouples were placed at 1cm in the soil, 10 metres from the edge of the burn site. Location of a safe site for the data-logger and the length of the thermocouple wire (10 m) limited their placement to areas with predominantly *C. scoparius*. No temperature measurements were recorded for the area with mostly native vegetation. The burn was conducted in late spring (November 30th), 1997. A strip of about 1 m was burnt along the upper boundary of the site as an additional firebreak to the road.

Four quadrats within each vegetation type (predominant broom versus predominant indigenous flora) were randomly assigned a spray treatment (glyphosate). The spray treatment was applied 6 months after the burn (June 1998). Eleven months following the spray treatment, the number of introduced and native species within the quadrats was recorded.

Post-fire proportion of native plants was arcsine transformed and plots within the two different areas, low broom or high broom, were analysed separately using t-tests assuming equal variances.

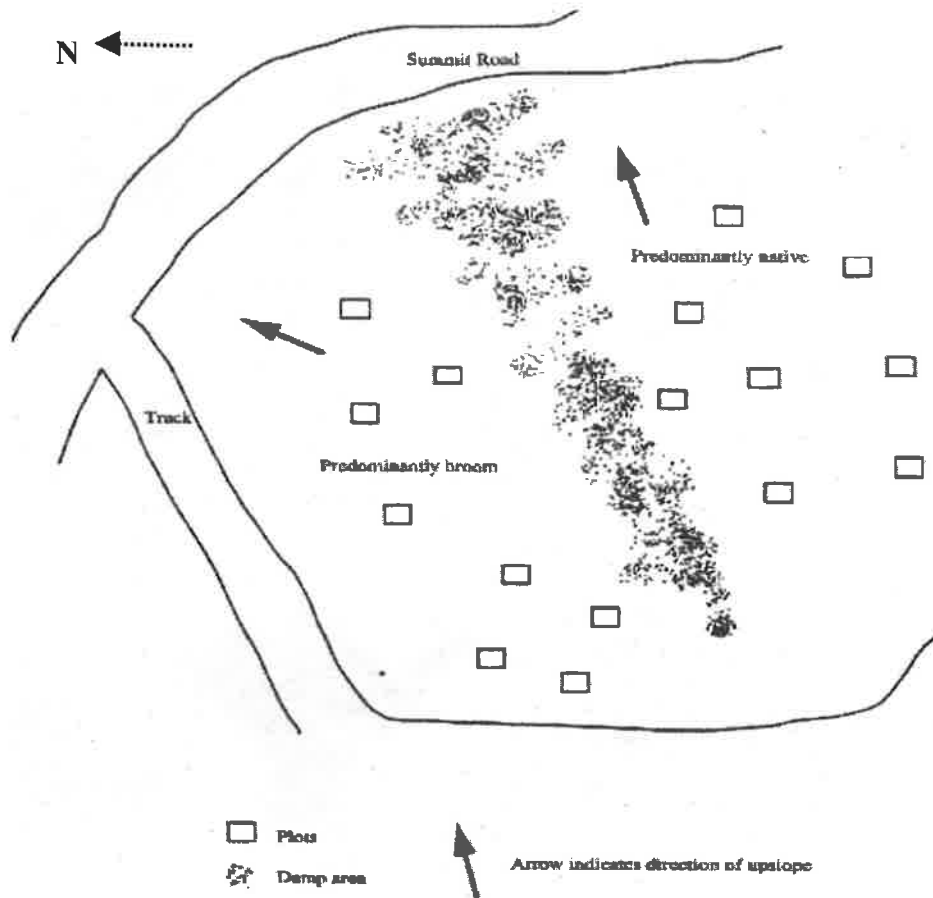


Figure 5.2. Location of plots at Cleland Conservation Park. Dashed arrow indicates direction.

5.3.7 Determination of the effect of fuel load on soil temperature and subsequent germination of native and exotic species

Controlled burns conducted at Crafers and Cleland were heterogeneous with respect to fuel load, seedbank density, variable depth of seed and intensity during the burns. In addition the terrain made use of the data-logger difficult. For these reasons, a level site at Roseworthy was chosen for a third burn in which fuel load was imported. Measured amounts of seeds, weeds and native, were buried at specific depths under the contrived fuel loads. The dimensions of each plot were 3 m x 3 m. There were three replicates of three fuel levels plus unburnt controls. The treatments were randomised across the plots. Within each plot, four sub-plots (18 cm x 18 cm) of 1 cm or 3 cm depth were dug. A temperature sensitive strip was placed in the hole along with a calico bag with 30 seeds of each species or 30 loose seeds of each species. The hole was then filled and marked with a tent peg.

The species used in this experiment were *G. monspessulana*, *C. scoparius*, *Acacia melanoxylon*, *A. pycnantha*, *A. paradoxa*, *Pultenaea daphnoides*, *Microleana stipoides* and *Themeda triandra*.

Fuel loads on the plots were based on estimates of fuel load at Crafers. The different fuel load treatments were about 1000 g m⁻² (low), 2500 g m⁻² (medium) and 4000 g m⁻² (high). The fuel load was measured when establishing the experimental plots by sampling broom from the same source to be used for the experiment; basal stem diameter and weight per plant were measured to determine an approximate relationship between stem diameter (which could be estimated by eye) and weight. Stems 1.5 cm or greater were given an average weight of 1250 g and stems less than 1.5 cm in diameter were allocated an average weight of 300 g. Plants were counted onto the plots until the appropriate weight was reached.

G. monspessulana fuel was collected from a roadside near Keyneton. It was cut with a rotary slasher and transported in a caged trailer. On the day prior to burning, the plants were counted onto the appropriate plots.

Following the fire, the calico bags were retrieved from the appropriate holes and taken to the laboratory. The seeds were removed from the calico bags and placed in seedling trays, kept outside, and seedlings were removed and recorded as they germinated.

5.3.8 Estimation of the proportion of seedbank germinating versus seed death following burning at Marble Hill

Five quadrats each of 3 m x 3 m were established in areas of dense broom infestation. In each of these quadrats 5 soil cores (10 cm x 10 cm) were taken to estimate pre-burn seedbank density and gravimetric water content. A temperature sensitive strip was buried at 1 cm in the soil within each quadrat one day prior to the burn. The controlled burning was conducted by staff of NP&WS (National Parks & Wildlife Service) and CFS (Country Fire Service) volunteers in early summer (December 1997). Six months after the burn (June 1998) 5 soil cores were taken to estimate seedbank density. Numbers of *G. monspessulana* seedlings were also counted.

5.3.9 Investigation of the relationship between soil temperature during a fire and seedbank reduction due to germination and death at Belair

Fifty sampling points were marked throughout an area of 80 m by 80 m with star droppers (Fig 5.3). Eight soil cores (2 cm diameter and 10 cm length) were taken at each point to determine the number of *G. monspessulana* seeds in the soil prior to the burn. One day prior to the burn, temperature sensitive strips were placed at each sample point in the soil at a depth of 1 cm and five soil samples were taken to determine gravimetric soil moisture content. Eight soil cores at each sampling point (2 cm by 10 cm) were taken after the burn in June 1998 when substantial numbers of *G. monspessulana* seedlings had germinated, and in March 1999, 11 months following the burn. The six cores from each site were combined then processed, as described previously, to obtain estimates of seedbank density. Seedling numbers were also estimated at these times. The relationship between temperature and seedbank loss was examined by fitting a logarithmic regression.

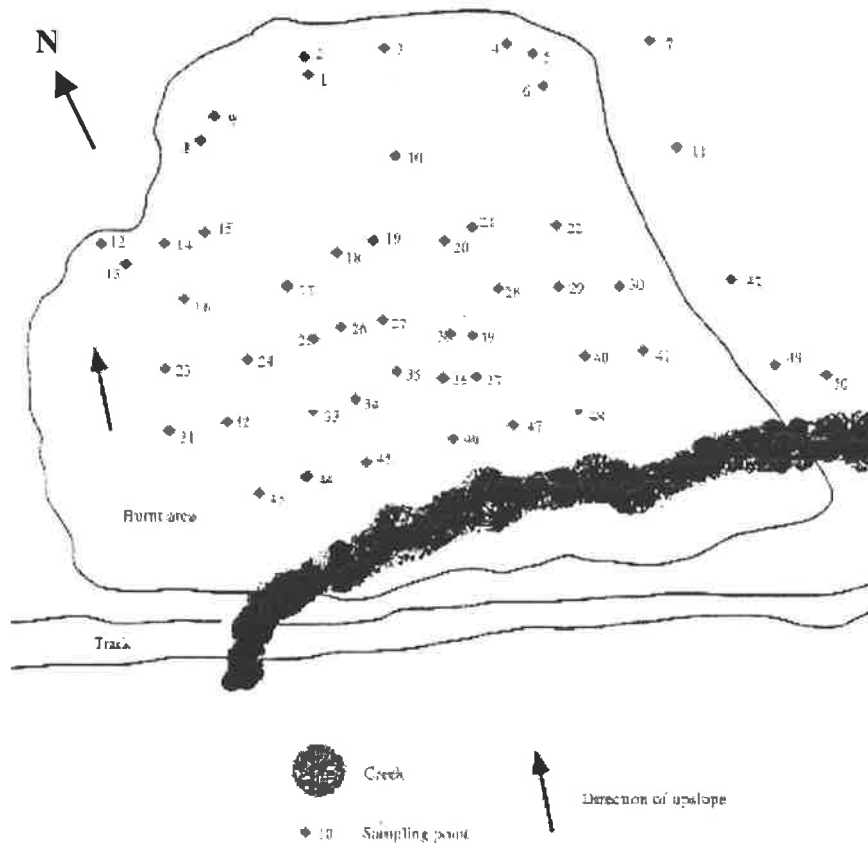


Figure 5.3. Layout of sampling points and extent of burn in Belair National Park. Dashed arrow indicates direction.

5.3.10 Investigation of germination and *G. monspessulana* survival following clearing or burning followed by an early or late spray treatment

Twenty three plots within the burnt area at Belair were sprayed in August 1998 when the height of the *G. monspessulana* seedlings was about 1 to 5 cm. Sixteen plots within the burnt area were sprayed in November 1998 when the *G. monspessulana* was 20 to 50 cm tall.

Seven plots nearby but outside the burnt area at Belair were cleared of all vegetation (mainly *G. monspessulana*) and coarse leaf litter (leaves & twigs) before the date of burning. Five plots outside the burnt area that remained unburnt and uncleared were similarly measured. Seedling density was measured in May 1998 and January 1999. Germination relative to seedbank density and survival of seedlings were compared between differently treated areas using a Kruskal-Wallis non-parametric analysis of variance (Zar 1984).

5.3.11 Determination of optimum temperatures required to break dormancy, with or without smoke derived chemicals, of *G. monspessulana* and five native species.

Seeds of *G. monspessulana*, *A. pycnantha*, *Davesia leptophylla*, *Microlaena stipoides*, and *Themeda triandra* were surface sterilised by soaking in 75% ethanol for one minute followed by 1% hypochlorite solution (Milton) for one minute then rinsed three times in sterile distilled water.

The seeds were heated in 10 ml tissue culture vials with screw top lids for 10 minutes. Sand (30 g) was placed into each vial, followed by 4 g of either sterile distilled water or sterile smoke water. This resembled the gravimetric moisture content of soils from Marble Hill and Belair. The seeds were added last and mixed into the sand by shaking the vials vigorously. One replicate consisted of all species of seeds heated to one of eight temperatures (40, 50, 60, 70, 80, 90, 100 or 110°C). The oven temperature in the vicinity of seeds was confirmed with a thermometer.

Smoke water was obtained from Richgro Garden Products in Western Australia. The smoke water was produced by passing air, under pressure, through two

drums. The first drum contained burning vegetation and smoke. The smoky air from the first drum was bubbled through water in the second drum.

Following heating, the seeds were left in the vials for three days then separated from the sand and transferred to petri dishes containing moistened sterile filter paper. Benlate (1 g L⁻¹) and pimarinic acid (0.4 µl ml⁻¹) were added to the sterile water used to moisten the filter paper in order to minimise fungal and bacterial infection. The plates were wrapped in alfoil, except *M. stipoides*, and incubated in a cabinet set to provide a cycle of 14 hours at 20°C followed by 10 hours at 15°C. The plates were examined every 3-4 days for germinated seeds.

The response to increasing temperature and smoke chemicals was compared using a two-way analysis of variance of numbers of seeds germinating.

5.4 Results

5.4.1 Comparison of the effects of different management strategies, slashing & fire, fire and herbicide on *G. monspessulana*

Burns within cut plots were easy to ignite and maintain in early October. Burns within plots of uncut *G. monspessulana* could not be lit and self-perpetuated until late October. Successful recording of temperature using the data-logger occurred in one slashed and burned plot and one burned without slashing plot. The maximum and minimum temperatures, at 1cm depth in the soil, recorded during burning were 245°C and 30°C (Fig 5.4). The duration of maximum temperature was approximately one minute. The intensity of the fires within each plot was very variable. In patches the fire moved quickly and produced a lot of heat and in these areas there were no *G. monspessulana* stems remaining. In other patches within the same plot the fire moved slowly and did not burn stems >1 cm in diameter.

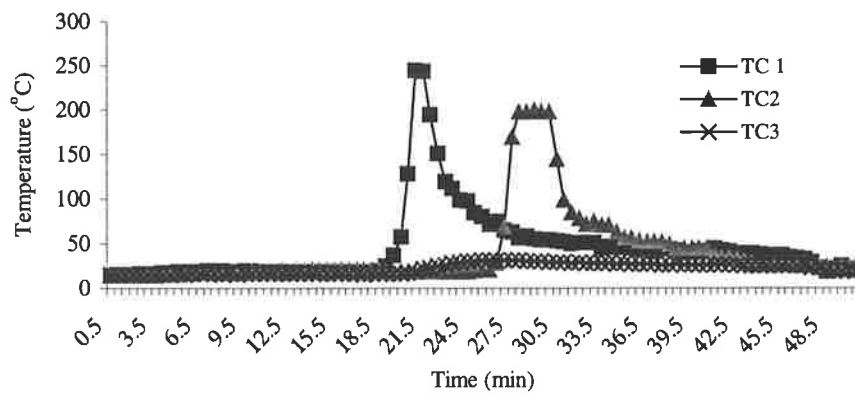


Figure 5.4. Temperature throughout burning in plot (c/b 2). TC1-TC3 indicate three thermocouples at 1 cm at different points within the plot.

There was no obvious gradient in seed densities ($53,441 \pm 36,258$ seeds m^{-2}) in any direction across the 80m by 80m experimental area, prior to burning, although variation was high (Fig 5.5). Post-fire seedbank densities following the two burning treatments were significantly different ($F_{pr} < 0.001$) from the herbicide treatment and the control (Figure 5.6). There was no significant difference in seedbank densities between the two different burning strategies. The mean reduction of the seedbank for slash/burn and burn plots combined was 86%. Numbers of seeds following burning were 3,000 - 5000 seeds m^{-2} whereas original numbers had been up to 100,000 seeds m^{-2} .

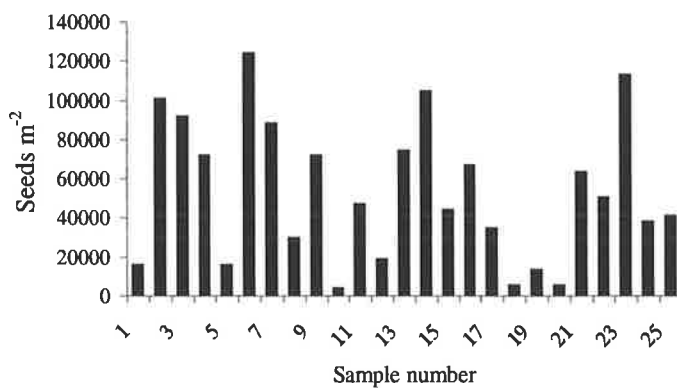


Figure 5.5. Estimates of seedbank density from pre-fire soil samples collected from Crafers plots.

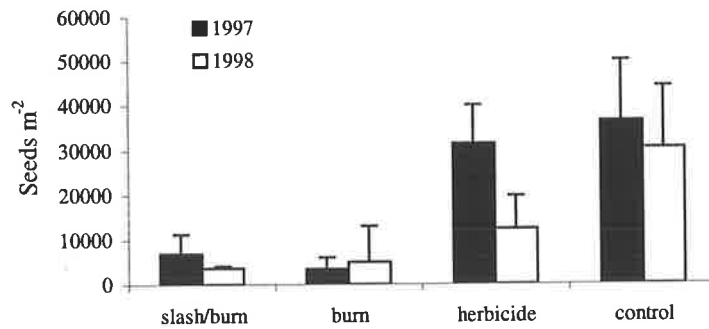


Figure 5.6. Estimates of seedbank density, with standard deviations, for two years following different treatments of plots at Crafers.

Burning increased the numbers of seedlings germinating (Fig 5.7). The non-parametric analysis of variance (Kruskal-Wallis) of seedling densities indicates a significantly higher germination of *G. monspessulana* in slash/burn and burn plots during 1997.

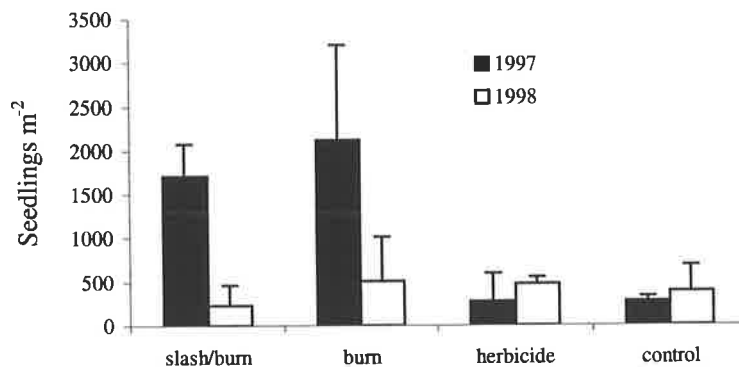


Figure 5.7. Densities of seedlings with standard deviations in 1997 and 1998.

Seedling emergence in 1998 was considered as a proportion of the previous year's seedbank because of the large difference recorded in burnt and unburnt plots in 1997. *G. monspessulana* emergence was significantly different ($F_{pr} = 0.036$) for one treatment, burnt without slashing (Fig 5.8). This difference is attributable to two outlying, higher emergences in plots B1 and B2 in the second year (1998) following the fire. Both of these plots burnt more consistently, had higher flames and less charred stems than all other plots subjected to burning treatments.

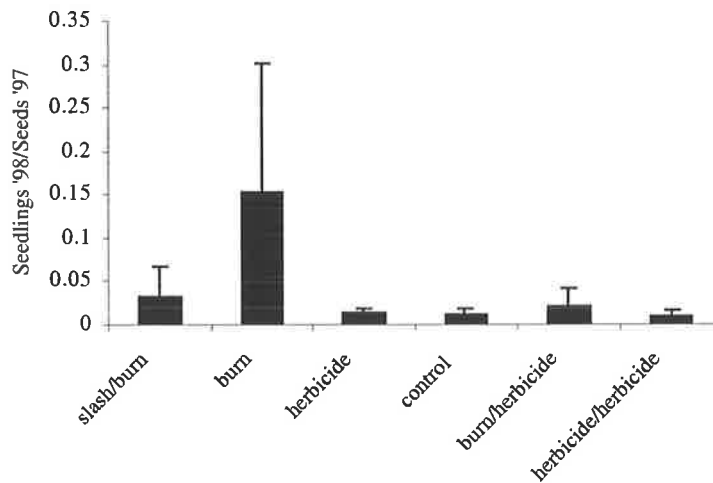


Figure 5.8. Number of seedlings germinating in 1998 as a proportion of estimated seed density in 1997.

Major (non-broom) components of regenerating vegetation following burning treatments were broad-leaf herbaceous weeds, particularly *Solanum nigrum*, *Senecio pterophorus*, *Fumaria* sp. (autumn & winter), *Rubus* sp. and *Cerastium fontanum*. Native plants regenerating in burnt plots, albeit in comparatively small densities, included *Adiantum aethopicum*, small patches of *Microlaena stipoides* and *Eucalyptus obliqua*. The herbaceous weeds, *G. monspessulana* seedlings, and small numbers of native species had covered the 80-90% of the ground in the burnt plots by the first autumn (April 1997) following the burn. Herbicide (triclopyr) treated plots had only *G. monspessulana* seedlings emerging. Split plots sprayed with herbicide (glyphosate) in April 1997 were sparsely covered (10-20%) for about a year. All plots were covered 80-90% in the third year following burning (April 1999) and after the second year since spraying with glyphosate. The amount of cover contributed by grasses increased.

5.4.2 Comparison of response to post-fire herbicide treatments in areas heavily or lightly infested with *C. scoparius* and *G. monspessulana*

The firebreak created by the road at the top of this site was extended by 3 m by a slow back burn (down the slope). The main fire was ignited with drip torches at the lower southern edge of the site. The fire progressed rapidly through the predominantly native vegetation, sometimes reaching the canopy of *E. obliqua*. Upon reaching the predominantly broom area, the fire noticeably slowed and

reduced in height until eventually it was burning only irregularly the litter layer and scorching the broom leaves and smaller stems. The thermocouples indicated very minimal soil heating at 1cm under broom (60°C). The majority of emerging broom seedlings throughout the site were *G. monspessulana*, including areas which were populated predominantly by *C. scoparius* prior to the fire.

Burning decreased the richness (number of native species) of native species within the area of low initial broom density (Table 5.1). There was a slight increase in richness of native species within the area of high initial broom density.

Table 5.1 Richness and abundance of native and abundance of introduced plants at Cleland before and after burning and a spray treatment of glyphosate. The numbers of introduced plants include *C. scoparius* and *G. monspessulana*. Numbers are means \pm standard deviation of data from four plots per treatment.

Broom level	Variable	Treatment	Pre-fire	Post-fire
Low (<30%)	Number of Native species	Unsprayed	7 \pm 1.5	3 \pm 0.5
		Sprayed	8 \pm 1	6 \pm 1
	Number of Introduced individuals	Unsprayed	3 \pm 1	615 \pm 463
		Sprayed	2 \pm 1.5	51 \pm 26
	Number of Native individuals	Unsprayed	26 \pm 2	49 \pm 25
		Sprayed	28 \pm 2	29 \pm 9
High (>70%)	Number of Native species	Unsprayed	1 \pm 1	3 \pm 3
		Sprayed	1 \pm 1	1 \pm 1
	Number of Introduced individuals	Unsprayed	18 \pm 7	214 \pm 118
		Sprayed	16 \pm 8	42 \pm 14
	Number of native individuals	Unsprayed	2 \pm 2	29 \pm 29
		Sprayed	2 \pm 1	4 \pm 6

Spraying with glyphosate following a fire within the area which initially had a low proportion of broom significantly increased the abundance of native plants relative to unsprayed, burnt plots (Fig 5.9) ($t_{crit} 2.44 < t 2.72$, $P = 0.03$). In contrast spraying had no significant effect ($t_{crit} 2.44 > t -0.34$, $P = 0.74$) on the abundance of native plants in areas with an initial high density of broom despite the survival of broom seedlings being much lower in sprayed plots. Cover by native species, in particular *M. stipoides*, in the high broom area was considerably lower in all plots following burning and spraying (Fig 5.10).

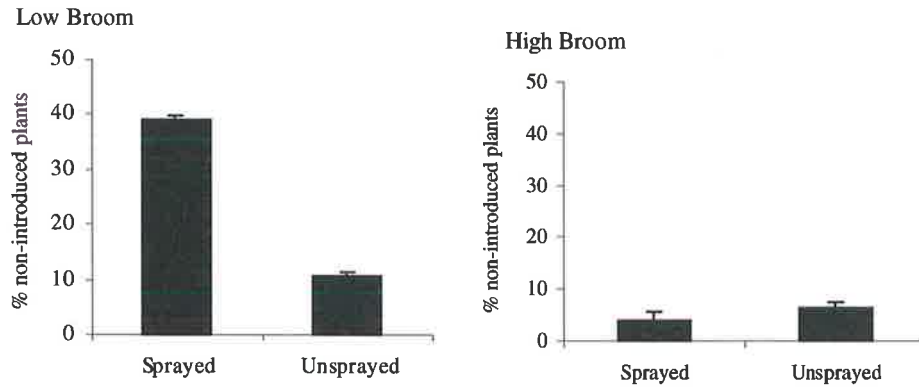


Fig 5.9 Proportion of native plants in sprayed and unsprayed plots following burning at Cleland in November 1997 showing means and standard errors.



Figure 5.10 Top; unsprayed plot at Cleland Conservation Park following a spring burn. *Microlaena stipoides* is the predominant species. Bottom; sprayed plot at Cleland Conservation Park.

5.4.3 Determination of the effect of fuel load on soil temperature and subsequent germination of a selection of native and exotic species

The burn was difficult to maintain due to gusty winds and damp *G. monspessulana*. Intensity appeared to depend more on wind speed and direction than fuel loads. This is reflected in the temperature measurements for each fuel load (Table 5.2). Of the seeds left at the experimental site only a small proportion

of the initial thirty seeds germinated successfully. The most successful was *G. monspessulana* for which there were 6 seedlings in a high fuel plot, a total of 3 within two medium fuel plots and 8 in a low fuel plot. *C. scoparius* was the second most successful with 2 in a medium fuel plot and 2 in a low fuel plot. One *A. paradoxa* emerged in a low fuel plot. These all emerged prior to June 1997. In September 1997 four *A. pycnantha* emerged from a low fuel plot. Germination of seeds removed from the site following the burn was more successful.

Table 5.2. Maximum temperature at specified depths during burning of cut *G. monspessulana* on plots at Roseworthy. One set of temperature measurements for 3 cm is missing due to a shortage of temperature sensitive strips.

Depth	Fuel Load			
	High	Medium	Low	Control
1 cm	77°C	71°C	62°C	<40°C
	54°C	71°C	<40°C	<40°C
	<40°C	46°C	75°C	<40°C
3 cm	<40°C	<40°C	<40°C	<40°C
	65°C	<40°C	<40°C	<40°C

The highest germination (Fig 5.11) of exhumed seeds for most species occurred when soil temperatures reached 60 - 80°C. The exceptions were the two grass species. The most successful germination (50%) of *M. stipoides* occurred when soil temperature was 40°C or less. Low germination (4%) of *T. triandra* occurred in plots with 54°C and 77°C. Emergence of the three *Acacia* species began in early spring (September 1997), four months after burning. *C. scoparius*, *G. monspessulana*, *M. stipoides* and *T. triandra* emerged prior to June 1997, shortly following burning of the plots.

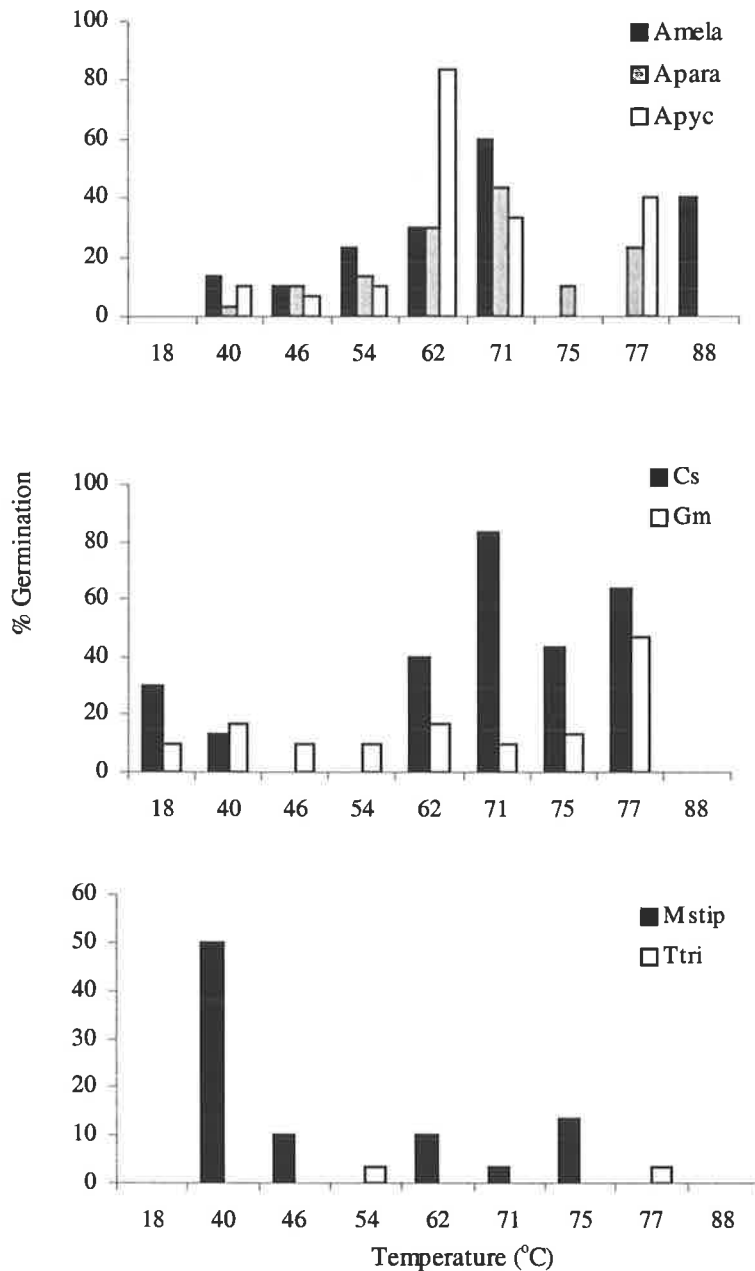


Figure 5.11 % Germination of seven species (placed in calico bags for the duration of the burn then exhumed and potted) used in Roseworthy trial at each temperature recorded in the plots. Amela – *Acacia melanoxylon*, Apara – *A. paradoxa*, Apyc – *A. pycnantha*, Cs – *Cytisus scoparius*, Gm – *G. monspessulana*, Mstip – *Microlaena stipoides*, Ttri – *Themeda triandra*. No *Pultanaea daphnoides* germinated at any temperature. The minimum temperature recorded by temperature sensitive strips is 40°C so this figure represents seeds germinating at any temperature between ambient (18°C) temperature and 40°C. 18°C is on the graphs because the control plots were assumed to remain at ambient temperature.

5.4.4 Estimation of the proportion of seedbank germinating versus seed death following burning at Marble Hill

Gravimetric soil moisture of the samples ranged from 16% to 35%. There were no significant differences in moisture content between the plots ($F_{pr} = 0.56$). The

seedbank at this site was initially low compared to other sites studied (2743 seeds m^{-2} - 7950 seeds m^{-2}). The oldest plants (estimated by counting rings as described earlier) found at this site were 10-11 years old. Across most of the site the burn was slow and cool. In some patches the *G. monspessulana* survived. Plot 4 and the surrounding area remained unburnt. This is verified by the range of temperatures (<40°C - 46°C) at 1 cm measured by temperature sensitive strips. Despite the low temperatures a substantial reduction (70-97%) in the seedbank resulted from a cool burn in four out of five plots. In three of the plots, most of the loss was attributable to seed death rather than to germination (Figure 5.12). There was also considerable germination of *Microlaena stipoides* in all plots except plot 4.

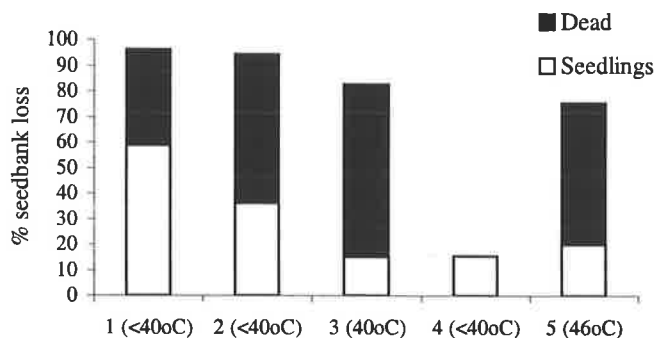


Figure 5.12 Reduction in seedbank showing death or germination of seeds for the five plots (x-axis) at Marble Hill.

5.4.5 Investigation of the relationship between soil temperature during a fire and seedbank reduction due to germination and death at Belair

The average number of seeds at the burn site in Belair National Park before the burn was 61,025 seeds m^{-2} with numbers as high as 102,000 seeds m^{-2} near the creek line. Following the burn, the average number of seeds was 6144 seeds m^{-2} . This is an overall reduction in the seedbank of 86%, across the burnt area. Where the temperature was higher than 70°C, the reduction of the seedbank was larger, 90-100% (Fig 5.13). Where the temperature in the soil at 1 cm was below 70°C the resulting seedbank reduction was variable. There was no detectable reduction in the seedbank in unburnt, cleared areas from which the mature *G. monspessulana* was removed.

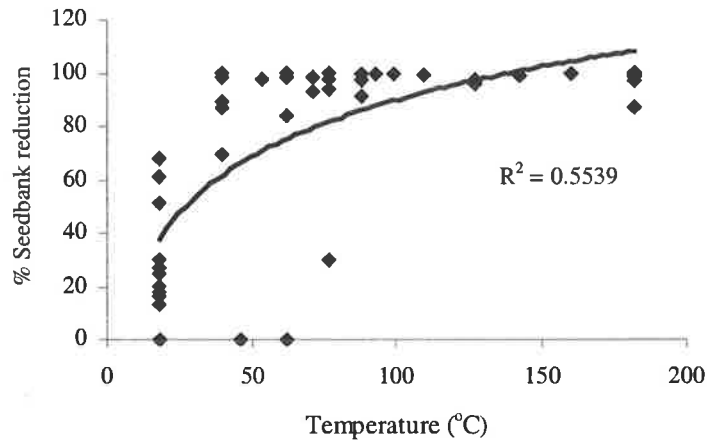


Figure 5.13. Percent of seeds lost from the seedbank through death or germination following and fire at Belair National Park relative to temperature at 1 cm in the soil. Data from burnt and unburnt, cleared plots is included. Regression equation $Y = 30.474 \ln(x) - 50.534$.

5.4.6 Investigation of recruitment and plant survival at Belair following clearing or burning followed by an early or late spray treatment

Germination rates within the burnt area were significantly higher than within cleared and untreated areas (Table 5.3). Thirty to sixty percent of the seedbank germinated within the burnt area, while rates of germination within the cleared or untreated areas remained below 10%.

Table 5.3 Germination of *G. monspessulana* following burning, clearing or no treatment in Belair National Park. Kruskal-Wallis $H = 25.1146$, $H_{crit}(\alpha=0.05) = 5.991$

Treatment	Burnt (n = 45)	Unburnt/Uncleared (n = 5)	Cleared (n = 7)
% Germination	34.7 ± 35	2.7 ± 1.6	1.4 ± 0.74

Spraying with herbicide removed a large number of seedlings germinating following the fire regardless of whether spraying was conducted three or five months following the fire (Table 5.4). However, quite a high density of seedlings remains following both burning and treatment with herbicide. Following the early spray treatment, a few seedlings survived because they were sheltered from herbicide by fallen logs or large rocks and stones. *M. stipoides* seedlings appeared following the fire and were not killed by the herbicide treatment although they were kept quite small by grazing rabbits, goats or wallabies. Seedlings that survived the later spray treatment were generally too large to be sheltered by rocks and logs, but a proportion of shorter plants appeared to have

been shielded by larger ones. The early spray treatment was more effective than the later spray treatment. The number of seedlings remaining in the unsprayed cleared plots was lower than the burnt, sprayed and untreated plots. There was more rapid establishment of introduced herbs, grasses and a small proportion of native grass (*M. stipoides*) in cleared compared to burnt and unburnt plots.

Table 5.4. Comparison of survival of *G. monspessulana* seedlings, showing percent survival following spraying or clearing and final density of seedlings after seven months in four differently treated areas at Belair National Park. Kruskal-Wallis $H = 17$, $H_{crit}(\alpha=0.05) = 7.815$.

Treatment	Early spray (n = 23)	Late Spray (n = 16)	Cleared (n = 7)	Control (n = 5)
% Survival ($\bar{x} \pm SD$)	0.94 \pm 1.7	2.11 \pm 2.9	5.6 \pm 1.7	7.1 \pm 3.8
Seedlings m ⁻² ($\bar{x} \pm SD$)	83 \pm 132	229 \pm 171	15 \pm 5	150 \pm 94

5.4.7 Determination of optimum temperatures required to break dormancy, with or without smoke derived chemicals, of *G. monspessulana* and five native species.

Seeds of *M. stipoides*, *G. monspessulana*, *A. pycnantha* and *Davesia leptophylla* germinated consistently. The majority of seeds of *T. triandra* and *A. paradoxa* failed to germinate. The responses of *G. monspessulana* and *A. pycnantha* are most similar (Fig 5.14). Temperature had a significant effect on seed germination of all species (Table 5.5). The temperature range for optimum temperature range for breaking dormancy of *G. monspessulana* was 70-90°C. The highest proportion of *A. pycnantha* seeds germinated at 90°C and 100°C. Eighty to one hundred degrees was the optimum temperature range for breaking dormancy of *D. leptophylla*.

The effects of smoke water were variable depending on both the species and temperature. Smoke chemicals significantly increased (Table 5.5) germination of *Davesia leptophylla* at most temperatures. Smoke chemicals slightly, but not significantly, decreased germination of *G. monspessulana* at most temperatures. *Microlaena stipoides* exhibited a completely different response to the three legume species. Temperature had a significant effect on germination at $\alpha = 0.05$, whereas smoke had weaker effect on germination ($F_{prob} = 0.072$). Germination of *M. stipoides* was excellent from 40-60°C, with a decline in germination success at 70°C and no successful germination above 80°C.

Table 5.5 Summary of ANOVAs from the seed heating experiment. The effects of temperature and smoke are treated on numbers of seeds germinating from a total of ten for *A. pycnantha*, *G. monspessulana*, *D. leptophylla* and *M. stipoides*.

Species	Factor	df	SS	MS	F	P
<i>A. pycnantha</i>	Temperature	5	657.67	131.55	53.12	<0.001
	Smoke	1	0.19	0.19	0.08	0.782
	Temp.Smoke	5	30.52	6.11	2.47	0.041
	Residual	72	178.29	2.48		
	Total	83	866.67			
<i>G. monspessulana</i>	Temperature	6	633.36	105.56	39.71	<0.001
	Smoke	1	0.036	0.036	0.01	0.908
	Temp.Smoke	6	124.96	20.83	7.84	<0.001
	Residual	98	260.50	2.66		
	Total	111	1018.86			
<i>D. leptophylla</i>	Temperature	5	186.77	37.35	19.99	<0.001
	Smoke	1	58.80	58.80	31.47	<0.001
	Temp.Smoke	5	42.50	8.50	4.55	<0.001
	Residual	108	201.80	1.87		
	Total	119	489.87			
<i>M. stipoides</i>	Temperature	7	930.00	132.86	49.82	<0.001
	Smoke	1	9.00	9.00	3.37	0.072
	Temp.Smoke	7	14.75	2.11	0.79	0.599
	Residual	48	128.00	2.67		
	Total	63	1081.75			

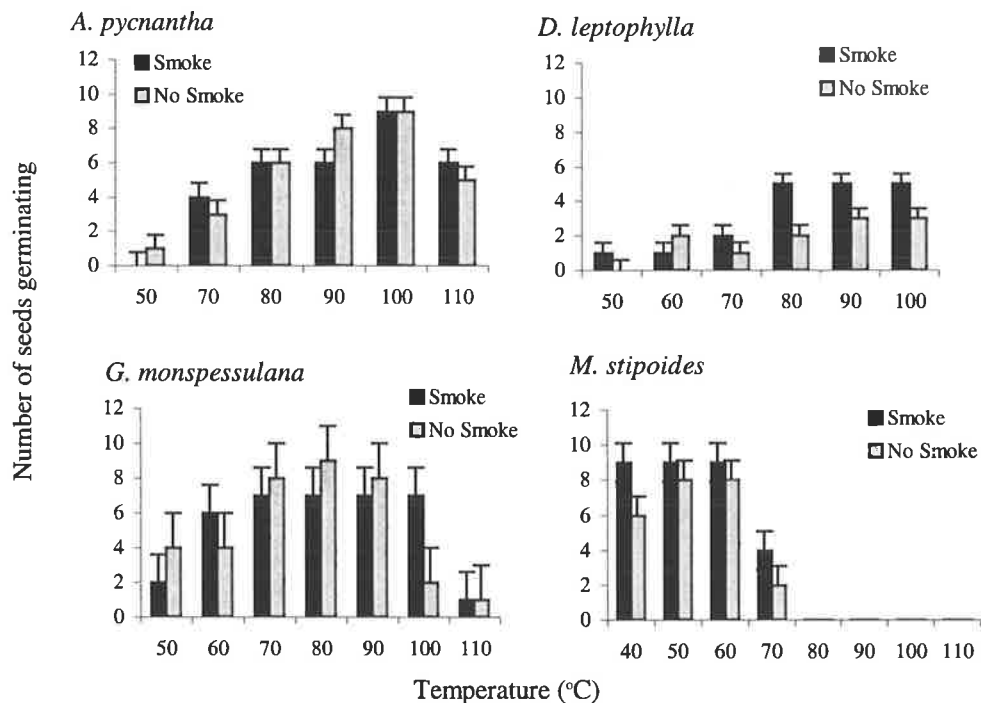


Figure 5.14. Response of seeds to increasing temperature and the presence of smoke chemicals in the water surrounding seeds during heating. The total number of seeds for each temperature and treatment was 10.

5.5 Discussion

5.5.1 Reduction of the *G. monspessulana* seedbank

Soil temperatures of $>50^{\circ}\text{C}$, achieved by controlled burns, at Crafers, Marble Hill and Belair consistently resulted in seedbank losses of 80% or higher. A substantial proportion (50% or higher) of the seedbank loss was generally attributable to seed death. Despite this at sites with very high initial seedbank densities, 5000 – 120,000 seeds m^{-2} , there are still large densities of seeds, 3000 – 9000 seeds m^{-2} , even after an 86% reduction of the seedbank.

There were two outlying higher emergences of seedlings in two burn plots in the second year following fire at Crafers. This exceptionally high germination, and hence higher seed reduction over two years rather than just the first year following fire is interesting and there are two possible explanations. The reduced number of stems combined with the proximity of these plots to a minor watercourse could have led to more erosion. This erosion could bring buried seeds, previously unable to germinate, to a depth from which more seeds can emerge successfully. Alternatively the higher intensity and consistency of the burn may have broken

the seed coat of a greater proportion of the seedbank initially although some of these seeds did not germinate until the following year due to other factors which maintained dormancy. These factors may range from a localised depletion of nutrients and water by the flush of other seedlings germinating to levels below those required to stimulate germination (Harper 1977, Rees 1997), surface seeds initially being inhibited by light then later becoming buried (Rees 1997) or inherent, genetic polymorphism between seeds with respect to timing of their response to germination cues (Harper 1977).

Results from the experiment at Belair clearly demonstrate the relationship between temperature and seedbank loss. Temperatures above 80°C in the soil can result in substantial seedbank losses of 95-100%. Cooler burns also have the potential to substantially deplete the seedbank but with less consistency. There were two low values, 0% and 30%, out of 13 between 40°C and 70°C. It is possible these were quadrats with more deeply buried seeds, perhaps as a result of ant burial. Distinctive accumulations of *G. monspessulana* seeds were observed around entrance holes to ant nests. In addition, burial of legume seeds by ants in Australia has been observed by Auld (1986a).

Death of a substantial portion of the seedbank (50-60%) was achieved with cooler burns. Remaining loss of the seedbank was due to germination. Densities of seedlings at Crafers and Belair were sometimes as high as 60,000 plants m⁻². Simultaneous emergence of large numbers of seedlings is likely to reduce any one seedling's chance of survival due to more intense competition for resources. Patches of seedlings also suffered fungal or bacterial diseases when there were high densities. However, following a controlled burn sufficient numbers of seedlings survived to re-colonise the site unless further control was implemented.

Removal of a mature stand of *G. monspessulana* by means other than fire such as herbicide, cutting and herbicide, or slashing can reduce the seedbank by 20-30% through increased germination. Sufficient seedlings emerge and survive these treatments to colonise the site (Crafers & Belair). Hence not using fire does not eliminate the need for follow-up management. However, it is likely that faster

developing and increased cover observed in unburnt, cleared areas at Belair and Crafers reduced the germination or survival of *G. monspessulana* seedlings.

Decline of the seedbank, other than as a direct result of burning, following initial control of mature vegetation, is an important factor for deciding on an appropriate method of control. The seedbanks in plots treated with herbicide had declined about 50%, from 33,000 seeds m⁻² to 13,000 seeds m⁻² in one year after the death of mature plants. Despite this reduction, the density of *G. monspessulana* seeds is still much higher than densities of native seeds. Decline of the seedbank in slash and burn plots one year following burning was also in the order of 50%, 8000 seeds m⁻² to 4000 seeds m⁻².

5.5.2 Minimising negative impacts on native species

The controlled burn conducted at Roseworthy in autumn showed that *G. monspessulana* germinates in the immediate post-fire period and there is a gap of three months before native legumes emerged in spring. Therefore it is possible to spray *G. monspessulana* seedlings before native legumes emerge. Early spraying of seedlings was also more effective than a later spray at Belair. The native grass, *Microlaena stipoides*, that most commonly occurs in *G. monspessulana* infestations, will emerge at the same time as *G. monspessulana* and cover by this species was substantially reduced by spraying with the non-selective herbicide, glyphosate, at Cleland. This problem could be overcome by use of a broad leaf selective herbicide effective against *G. monspessulana*, such as triclopyr, that won't harm grasses.

Substantial reductions (80-90%) of the seedbank occurred after a low intensity burn at Marble Hill. This was the result of germination enhancement rather than seed death at one sampling point however populations of native grass were higher at this site than at other *G. monspessulana* sites. A low intensity burn at this site was probably more appropriate because there is likely to be better survival of native grass seed. The laboratory seed heating experiment demonstrates that *M. stipoides* seeds are capable of surviving up to 60°C but rarely tolerate >70°C. In addition the site was not in the vicinity of a watercourse so is more amenable to use of the residual selective herbicide, triclopyr.

Optimum temperature for breaking dormancy of *G. monspessulana* seeds was lower (70-80°C) than for two of the native legumes tested (80-100°C). Managing conditions to achieve a cooler burn may favour survival of native legume seeds, in addition to *M. stipoides*, by stimulating only *G. monspessulana* to germinate.

Slashing *G. monspessulana* did not have a significant impact on the seedbank relative to burning without slashing. However, it was possible to burn the slashed *G. monspessulana* plots earlier in the spring than standing green *G. monspessulana*. Slashing the *G. monspessulana* so it can be burnt when ambient temperature is lower and soil moisture is higher is a way in which a more desirable cooler burn could be achieved.

5.5.3 Fire and experimental design

The two successful attempts at recording temperatures during burning indicate considerable variation of temperature between burning treatments. In addition within-plot variation was observable after the burn due to uneven fuel consumption, ash and no *G. monspessulana* stems versus singed twigs (~0.5cm diameter) and the presence of *G. monspessulana* stems. The maximum temperature (245°C) recorded at 1 cm is very high compared to 120°C at 0.4 cm measured by Bradstock & Auld (1995) in New South Wales. This may have been due to movement of soil following placement of the thermocouple, lower soil moisture, different soil composition or different fuel load. More consistency was achieved when the area burnt was larger. Most of the variation in temperature at Belair was at the boundaries of the burnt area.

These fire experiments had two important limitations. Firstly, adequate replication was difficult to achieve and is a common problem for fire research (Anderson *et al.* 1998) because of the large number of parameters (discussed in Chapter 1) that influence fire. Secondly, changes to vegetation will continue to occur in the 3 years or more following burning and spraying. Knowledge of these changes is important for management decisions and was not able to be examined here.

5.6 Conclusions

Controlled burning did substantially reduce the seedbank of *G. monspessulana*; however burning also enhanced germination of seedlings immediately providing recruitment opportunities for a new generation of the weed. Relatively high reductions of the seedbank could be achieved with a cooler burn (Fig 5.13). Triclopyr, a broad-leaf selective herbicide, can be used to remove the seedlings following fire without adverse affects to regenerating grasses.

Impacts to native vegetation can be minimised by setting up conditions to achieve a cooler burn or less soil heating. Cooler burns could be achieved by burning when soil moisture is low enough to burn but still enough to keep the temperature down. Less soil heating occurs when flames move faster over the ground. Burning in autumn stimulates immediate germination of *G. monspessulana*, whereas native legumes are unlikely to germinate before spring. This provides the opportunity to apply herbicide treatments to *G. monspessulana* in the interim. An earlier spray treatment also killed more *G. monspessulana* seedlings.

Chapter 6. General Discussion

6.1 Biology and management of *G. monspessulana*

G. monspessulana is a successful plant in South Australian dry sclerophyll forest ecosystems. A spatial population model (Pareja 2000, Pareja *et al.* In preparation) of *G. monspessulana* indicates that the main constraint to space occupied by *G. monspessulana* (spread and success of *G. monspessulana*) is the number of recruitment opportunities. Cleared native vegetation, roads, fires, disturbed slopes and watercourses have been common features of South Australian dry sclerophyll forest for the last 100 years or more. These features have probably favoured *G. monspessulana* establishment because they provide opportunities for dispersal and recruitment. The closely related perennial legume, *C. scoparius* reduces the diversity of native flora (Waterhouse 1987, Heinrich & Dowling 2000). It is probable that *G. monspessulana* has already, and will continue to, reduce diversity of native flora if not managed.

Features of *G. monspessulana* identified in Chapters 2 and 3 that favour its germination and establishment in Australia in place of similar native perennial legumes are *G. monspessulana*'s high viable seed production, early emergence and growth in winter. This high viable seed production (Figs 2.2, 2.3 & 2.4) leads to seedbanks of *G. monspessulana* that are larger, up to 100-fold, (Table 2.4) than native legumes (Auld 1986a, Vlahos & Bell 1986). *G. monspessulana* growing in South Australia does not produce significantly more seeds per plant than *G. monspessulana* plants in Europe (Fig 2.4). The difference in *G. monspessulana* seedbanks between South Australia and Europe is probably the result of a combination of higher densities of seed producing plants in South Australia (Table 2.2) than Europe and more seed predation in Europe. For example it is known that significant numbers of *C. scoparius* seeds are consumed by predators in Europe (Paynter *et al.* 1996). Whether or not the higher seedbank in South Australia is the sole cause of higher mature plant densities has not been established.

Early, rapid, vertical growth of *G. monspessulana* means it is likely to shade seedlings of slower growing species. *A. pycnantha*, *A. melanoxylon* and *P. daphnoides* were slower to increase height and tended to put resources into growing lateral stems, increasing in width, rather than increasing the height of the main stem. This rapid vertical growth also means that *G. monspessulana* is less likely to be shaded by other plants in the process of establishment. *G. monspessulana* was growing faster than *E. leucoxylon*, *A. melanoxylon* and *T. triandra* when temperatures were cooler.

Growth in winter and rapid early growth provide possibilities for selective control of *G. monspessulana*. Herbicides such as triclopyr could be used in winter to control *G. monspessulana* but not slower growing native plants. *G. monspessulana*, if it is taller than other vegetation, may also be susceptible to weed wiper application. A weed wiper is a device which applies herbicide to exposed taller plants (Kent & Preston 2000). This may be particularly useful along a riparian zone where spraying with triclopyr is not permitted.

One reason for lower densities of *G. monspessulana* in its native range may be because species present in Europe, the native habitat of *G. monspessulana* may be more competitive relative to species present in South Australia, the exotic habitat of *G. monspessulana*. European species were certainly more competitive than *C. scoparius* when there was minimal disturbance (Paynter *et al.* 1998). Sheppard *et al.* (2000) also suggests that Australian native plants were not as competitive as their European counterparts when grown in plots with *C. scoparius*. In addition, rather than being suppressed by *G. monspessulana* other species in its native habitat may be more tolerant of shade while becoming established and eventually overtake *G. monspessulana* and subsequently reduce its density. Native plants generally did not out-compete *G. monspessulana* in competition experiments conducted in this thesis (Figs 3.3 & 3.5). *M. stipoides* reduced the emergence of *G. monspessulana* but did not prevent it as 16-40 seedlings m⁻² were generally present in plots with grass cover. A single plant reaching maturity can, by itself, produce ample seeds, 600 up to 6000, to replace itself and probably increase the population.

Recruitment opportunities may also be more common in Australia than Europe. Rates and causes of disturbance in Australia and Europe, other than intentional burning in Australia, were not examined. When suitable conditions arise for recruitment in South Australia in particular space it is more likely that a *G. monspessulana* seed will be occupying a particular space as the seedbank of native species was very low in *G. monspessulana* invaded sites (Chapter 4).

An aptitude for colonising following disturbance is shared by *G. monspessulana* with the related legumes *C. scoparius* and *U. europaeus* (Sheppard *et al.* 2000, Rees & Hill In press). While this characteristic is similar between these three leguminous weeds there are important differences between *C. scoparius* and *G. monspessulana*. Firstly, *G. monspessulana* has a lower age of senescence, in Australia (13 years, Chapter 2), than *C. scoparius* (up to 22 years old) and the canopy does not collapse. When the canopy of *C. scoparius* collapses it allows more light to penetrate and the cover by grasses and herbs increases (Smith 1994). The proliferation of different and more native understorey species before removal or death of *C. scoparius* probably increases the chance of a species other than *C. scoparius* colonising the space. This opportunity for other species is not available under *G. monspessulana*. Litter levels under *G. monspessulana* are higher than those under native vegetation (Huynh 1999) and are likely to inhibit growth of other species.

The second important difference between *C. scoparius* and *G. monspessulana* is the continuing recruitment of *G. monspessulana* plants under a mature canopy (Fig 2.5). Recruitment of *C. scoparius* under a mature canopy tends not to occur until the plants reach senescence and the canopies open (Sheppard *et al.* 2000, Smith 2000). However age distributions of *G. monspessulana* populations in South Australia show a mix of young and old plants (Fig 2.5) indicating continual recruitment.

The management recommendation for *C. scoparius* based on collapse of the mature canopy at stage 4 and limited recruitment of *C. scoparius* before this stage is to wait for stage 2 and 3 stands to reach stage 4 before spraying (Sheppard *et al.* 2000). The presence of other species under the collapsed stand is likely to

improve regeneration of native species and provide more competition for *C. scoparius* seedlings. The continuing presence of new recruits and the absence of stand collapse in *G. monspessulana* means control of *G. monspessulana* should not be delayed.

Minimising disturbance is considered an important strategy for reducing invasion of remnant vegetation and natural ecosystems by weeds such as *G. monspessulana* (Bradley 1971, Hobbs & Humphries 1995). However, disturbance is an integral feature of ecosystems and there will be native species relying on disturbance for their existence. Large seedbanks of *G. monspessulana* present a dilemma because there are always going to be disturbances and hence recruitment opportunities for this weed. In addition, in the absence of a disturbance to break the dormancy of seeds Adams & Simmons (1991) found 10% of *G. monspessulana* seeds germinated in the laboratory. Experiments conducted for this thesis found 1% (equalling approximately 400 seedlings m⁻²) of the seedbank germinated in the field in undisturbed control plots (Chapter 5, Fig 5.7). Management methods which do not disturb the soil such as application of herbicide by spraying or cutting and painting do not substantially reduce the seedbank of *G. monspessulana* (Fig 5.6). Decay rates of seedbanks of native and other introduced legumes in Australia are about 30 to 50% in the absence of disturbance (Auld 1986b, Smith & Harlen 1991, Sheppard *et al.* 2000). If the decay of *G. monspessulana* seedbanks is similar, then the seedbank will remain as a persistent source of seedlings needing continued monitoring and management for 10 to 14 years at sites with large densities of accumulated seeds (Figs 2.4 & 5.5).

Fire provides a relatively inexpensive (Vranjic *et al.* 2000) means of removing a mature stand of *G. monspessulana* and significantly reducing the seedbank (Fig 5.6, Fig 5.12, Fig 5.13). The applicability of fire for management of areas with *G. monspessulana* will depend on several factors. Bond & van Wilgen (1996) outline constraints to the use of fire for management of vegetation (Table 6.1).

Table 6.1 Constraints to the use of fire as a management practice in vegetation (from Bond & van Wilgen 1996).

Constraint	Nature of constraint	Areas where constraints apply
Ecological	Fires may have undesirable effects on vegetation composition if applied at the wrong frequency, intensity or season	Areas sensitive to fire regimes, or where introduced or other undesirable species that are favoured by fire occur
Safety	The danger that prescribed burns could escape to areas which should not burn	Areas that abut on urban development, agricultural land or plantation forestry
Temporal	Seasonal or annual differences in weather result in conditions that are either too dangerous (fires become uncontrollable) or too wet (fires cannot spread)	Most areas
Legal	The application of fire may be prohibited or subject to severe restrictions	Mainly developed areas and industrialized countries
Global concerns	Increases in CO ₂ and other gases emitted that may lead to changes in the earth's atmosphere	All areas

Sites with heavy *G. monspessulana* infestation have very little native flora present above ground or in the seedbank (Table 5.1, Chapter 4). Ecological constraints at these sites are minimal with respect to vegetation composition. However some native flora (Appendix 2) is present despite the heavy infestations of *G. monspessulana*. This flora can be the basis for revegetation of the site. Impacts to these remaining species can be reduced in several ways. Firstly by correct timing of burning, in autumn, and spraying, before germination of native legumes in spring (Section 5.3.3). An early spray treatment also proved to be the most effective at controlling *G. monspessulana* populations (Section 5.3.6).

Secondly, substantial reductions to the seedbank can be achieved with cooler burns (Fig 5.12 & 5.13). Cooler burns are less likely to kill seeds of *M. stipoides* (Fig 5.14). *M. stipoides* is commonly associated with *G. monspessulana* stands (Appendix 2, Fig 5.12, Section 5.3.1, Section 5.3.4) and is important for management of *G. monspessulana*. The native grass, *M. stipoides*, is a good candidate species for post-fire revegetation because it covers the ground and gains biomass relatively quickly (Section 3.3.4, Fig 3.5) and plants can produce large amounts of seed. The selective herbicide, triclopyr can be used to kill

regenerating *G. monspessulana* seedlings without affecting *M. stipoides* (Section 5.3.6). Cooler burns are also less likely to stimulate native legume germination (Section 5.3.7, Fig 5.14, Auld & O'Connell 1989, Auld & Bradstock 1996). Ungerminated legumes will not be susceptible to follow-up herbicide treatments and may be available for revegetation once numbers of *G. monspessulana* seeds and seedlings have been reduced.

For sites with more native species, such as at Deep Creek, the value of fire to manage *G. monspessulana* will depend on the desired plant community. For example, if an endangered fire-sensitive species occurs at this particular site and few or no other sites then fire will not be an option. If areas with lower *G. monspessulana* densities are burnt then follow-up spraying is required to prevent increase of *G. monspessulana* and other weed populations (Fig 5.9). Spraying with broad-leaf selective herbicide will also reduce the density of native broad-leaf species. This is probably an undesirable outcome and burning should not be recommended for these areas unless the desired outcome is a community of introduced and native grasses (Fig 4.4).

There are likely to be other weeds at sites of *G. monspessulana* infestation. Blackberry (*Rubus discolor*) was present at all sites except Roseworthy. Bridal creeper (*Asparagus asparagoides*) and blackberry were present at Belair. Boneseed (*Chrysanthemoides monilifera* subsp. *monilifera*) occurs at other sites infested with *G. monspessulana* (pers obs). Knowledge of the response of these weeds to fire may enable use of the fire to manage more than one weed at the site. Spraying prior to burning is recommended for *R. discolor* (Bruzzeze *et al.* 2000). However, access to *R. discolor* growing amongst *G. monspessulana* is very limited (pers obs) and spraying prior to a fire would be very difficult. Following a fire, resprouting *R. discolor* are small and access is easier because *G. monspessulana* is removed. Use of triclopyr is also recommended for control of *R. discolor*. A late summer or autumn burn is recommended for *A. asparagoides* (Willis 2000) as well as *G. monspessulana* (Section 5.4.2). However triclopyr is unlikely to be effective against *A. asparagoides* and sites with this weed should be sprayed with metsulfuron methyl (Parsons 1995). *C. monilifera* subsp. *monilifera* is also susceptible to use of fire followed by application of metsulfuron methyl

(Melland *et al.* 2000). Use of fire for management is compatible with strategies for management of some other weeds commonly occurring with *G. monspessulana*.

Riparian zones are the most problematic with respect to management of *G. monspessulana* because of their inherent high probability of disturbance and good conditions for germination and recruitment of *G. monspessulana*. In addition, the selective herbicide, triclopyr, is not recommended for use near watercourses. The watercourse provides an excellent mechanism for long-distance dispersal of *G. monspessulana* seeds. However the high rate of disturbance at riparian zones may make *G. monspessulana* more amenable to biological control (Rees & Paynter 1997, Pareja 2000, Pareja *et al.* In preparation). A model of *G. monspessulana* populations dynamics developed by Pareja *et al.* (In preparation) predicts that seed predators will have the greatest impact on *G. monspessulana* when the probability of disturbance is high (Pareja *et al.* In preparation).

6.2 Research Directions

Information on the probability and nature of disturbance in areas invaded by *G. monspessulana* and, hence, the probability of recruitment opportunities for *G. monspessulana* were not obtained in these studies. Obtaining these data would be important to improve the accuracy of model predictions and to help identify factors that are increasing rates of *G. monspessulana* spread. Once the nature of important disturbances are identified, it may be possible to minimise some disturbances. Knowledge of the nature of disturbances will also help in terms of predicting where rates of spread of *G. monspessulana* are fastest and therefore where weed management resources need to be directed. There may also be certain areas of remnant vegetation for which *G. monspessulana* is less of a threat. For example, areas of lower fire risk or hill tops without roads which have lower probability of disturbance or are harder to colonise by water or soil-borne seed respectively.

Investigation of longer term rates of seedbank decline, in the absence of mature plants, will increase the criteria available to decide whether or not fire is

worthwhile in areas of lower *G. monspessulana* populations and lower density seedbanks. To some extent the rate of seedbank decline is likely to be related to rates of disturbance.

The introduction of biological control agents for *G. monspessulana* (Sheppard 2000) will require monitoring to assess the compatibility of fire and insects. It would also be useful to re-assess the effect of competition in the presence of herbivores. The combined effects of competition and herbivory may obviate the need for follow-up herbicides.

6.3 Summary

In response to the aims of this thesis:

- The seedbank of *G. monspessulana* is substantially reduced by fire.
- The season and temperature of burn can be altered to reduce negative impacts of fire on native species.
- Timing of burning and using broad-leaf selective herbicides will reduce the negative impacts of follow-up control on native species.
- Density of native species relative to weed species is generally low in seedbanks under *G. monspessulana* infestations.
- Competition between native species and *G. monspessulana* will not make a significant contribution to a management strategy based on current available management methods.

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Appendix 1. Botanical details for *G. monspessulana* and related weedy species

(from Black 1986)

Genista monspessulana (L.) L. Johnson

Tribe Genisteae, Family Fabaceae

Common names: Montpellier broom, canary broom, French broom, cape broom.

Synonyms: *Cytisus monspessulanus* L., *Teline monspessulana* (L.)C., *Cytisus canariensis*, *Genista candicans* L., *Cytisus candicans* (L.)DC.

Cytisus scoparius (L.) Link

Tribe Genisteae, Family Fabaceae

Common names: Scotch broom, English broom, common broom.

Synonyms: *Spartium scoparium* L., *Sarothamnus scoparius* (L.) Wimmer ex Koch.

Ulex europaeus L.

Tribe Genisteae, Family Fabaceae

Common names: Furze, gorse.

Synonyms: None listed

Appendix 2. List of plant species emerging from soil samples collected at four sites

Site	Origin	Heated	Unheated		
Deep Creek	Native	<i>Acacia retinodes</i>	<i>Aceana echinata</i>		
		<i>Acacia</i> sp.	<i>Adiantum</i> sp.		
		<i>Aceana echinata</i>	<i>Carex</i> sp. 1		
		<i>Adiantum</i> sp.	<i>Eucalyptus obliqua</i>		
		<i>Carex</i> sp. 1	<i>Gonocarpus</i> sp.		
		<i>Dichondra repens</i>	<i>Goodenia ovata</i>		
		<i>Eucalyptus obliqua</i>	Grass 2		
		<i>Geranium retrorsum</i>	Grass 4		
		<i>Gnaphalium involucratum</i>	<i>Juncus</i> sp.		
		<i>Gnaphalium</i> sp.	<i>Microlaena stipoides</i>		
		<i>Goodenia ovata</i>	<i>Oxalis perennans</i>		
		Grass 2	<i>Pelargonium littorale</i>		
		Grass 4	<i>Poa</i> sp. 1		
		<i>Microlaena stipoides</i>	<i>Poranthera microphylla</i>		
		<i>Opercularia ovata</i>	<i>Pultenaea daphnoides</i>		
		<i>Oxalis perennans</i>	<i>Stellaria palustris</i> (uncertain origin)		
		<i>Poa</i> sp. 1			
		<i>Poranthera microphylla</i>			
		Introduced		<i>Briza minor</i>	<i>Aira</i> sp.
				<i>Carduus pycnocephalus</i>	<i>Briza minor</i>
<i>Carthamnus lanatus</i>	<i>Bromus diandrus</i>				
<i>Cerastium fontanum</i>	<i>Conyza canadiensis</i>				
<i>Cirsium acana</i>	<i>Cerastium fontanum</i>				
<i>Cirsium vulgare</i>	<i>Epilobium ciliatum</i>				
<i>Conyza canadiensis</i>	<i>G. monspessulana</i>				
<i>Epilobium ciliatum</i>	<i>Hypochoeris radicata</i>				
<i>G. monspessulana</i>	<i>Juncus effusus</i>				
<i>Gnaphalium spicatum</i>	<i>Lactuca serriola</i>				
<i>Holcus lanatus</i>	<i>Phalaris minor</i>				
<i>Hypericum perforatum</i>	<i>Picris echoides</i>				
<i>Hypochoeris radicata</i>	<i>Poa annua</i>				
<i>Juncus effusus</i>	<i>Rubus discolor</i>				
<i>Lactuca serriola</i>	<i>Sisymbrium irio</i>				
<i>Leontodon taraxacoides</i>	<i>Solanum nigrum</i>				
<i>Medicago polymorpha</i>	<i>Sonchus asper</i>				
<i>Phalaris minor</i>					
<i>Picris echoides</i>					
<i>Poa annua</i>					
<i>Rubus discolor</i>					
<i>Rumex acetosella</i>					
<i>Senecio vulgaris</i>					
<i>Sisymbrium irio</i>					
<i>Sonchus asper</i>					
<i>Vulpia bromoides</i>					

Site	Origin	Heated	Unheated
Henschke	Native	<i>Crassula pedicellosa</i>	<i>Chloris</i> sp.
		<i>Crassula sieberana</i>	<i>Crassula sieberana</i>
		<i>Danthonia</i> sp. 1	<i>Danthonia</i> sp. 1
		<i>Eucalyptus</i> sp.	<i>Oxalis perennans</i>
		<i>Microlaena stipoides</i>	<i>Vittadinia australasica</i>
		<i>Oxalis perennans</i>	
	Introduced	<i>Anagallis arvensis</i>	<i>Avena fatua</i>
		<i>Avena fatua</i>	<i>Bromus diandrus</i>
		<i>Bromus mollis</i>	<i>Bromus rigidus</i>
		<i>Centarium erythraea</i>	<i>Chenopodium</i> sp.
		<i>G. monspessulana</i>	<i>Echium plantagineum</i>
		<i>Gallium murale</i>	<i>G. monspessulana</i>
		<i>Juncus capitatus</i>	<i>Juncus capitatus</i>
		<i>Lactuca serriola</i>	<i>Lactuca serriola</i>
		<i>Lolium rigidum</i>	<i>Lolium rigidum</i>
		<i>Medicago polymorpha</i>	<i>Medicago polymorpha</i>
		<i>Oxalis pes-caprae</i>	<i>Oxalis pes-caprae</i>
		<i>Picris echoides</i>	<i>Panicum miliaceum</i>
<i>Poa annua</i>	<i>Phalaris minor</i>		
<i>Polycarpon tetraphyllum</i>	<i>Poa annua</i>		
<i>Polygonum aviculare</i>	<i>Polygonum aviculare</i>		
<i>Romulea rosea</i>	<i>Romulea rosea</i>		
<i>Sisymbrium irio</i>	<i>Senecio pterophorus</i>		
<i>Trifolium augustifolium</i>	<i>Trifolium augustifolium</i>		
<i>Trifolium glomeratum</i>	<i>Trifolium glomeratum</i>		
<i>Vicia monantha</i>	<i>Trifolium subterraneum</i>		
<i>Vulpia bromoides</i>	<i>Trifolium tomentosum</i>		
		<i>Vulpia bromoides</i>	

Site	Origin	Heated	Unheated		
Lenswood	Native	<i>Agrostis</i> sp.	<i>Agrostis</i> sp.		
		<i>Eucalyptus</i> sp.	<i>Cyperus tenellus</i>		
		<i>Geranium retrorsum</i>	<i>Danthonia</i> sp. 1		
		Grass 3	<i>Eucalyptus</i> sp.		
		<i>Juncus planifolius</i>	<i>Eucalyptus</i> sp.		
		<i>Juncus</i> sp.	Grass 3		
		<i>Microlaena stipoides</i>	<i>Microlaena stipoides</i>		
		<i>Oxalis perennans</i>	<i>Ranunculus lappaceus</i>		
		<i>Ranunculus lappaceus</i>			
		Introduced		<i>Anagallis arvensis</i>	<i>Anagallis arvensis</i>
				<i>Avena fatua</i>	<i>Avena fatua</i>
				<i>Briza minor</i>	<i>Briza minor</i>
				<i>Bromus diandrus</i>	<i>Bromus diandrus</i>
				<i>Bromus rubens</i>	<i>Bromus mollis</i>
<i>G. monspessulana</i>	<i>G. monspessulana</i>				
<i>Hypochoeris radicata</i>	<i>Hordeum leporinum</i>				
<i>Juncus subnodulosus</i>	<i>Hypochoeris radicata</i>				
<i>Lactuca serriola</i>	<i>Lactuca serriola</i>				
<i>Lamium amplexicaule</i>	<i>Leontodon taraxacoides</i>				
<i>Leontodon taraxacoides</i>	<i>Medicago polymorpha</i>				
<i>Medicago polymorpha</i>	<i>Phalaris minor</i>				
<i>Phalaris minor</i>	<i>Plantago lanceolata</i>				
<i>Plantago lanceolata</i>	<i>Poa annua</i>				
<i>Poa annua</i>	<i>Rumex acetosella</i>				
<i>Polygonum patulum</i>	<i>Solanum nigrum</i>				
<i>Rubus discolor</i>	<i>Trifolium arvense</i>				
<i>Rumex acetosella</i>	<i>Trifolium augustifolium</i>				
<i>Sisymbrium irio</i>	<i>Trifolium glomeratum</i>				
<i>Solanum nigrum</i>	<i>Trifolium subterraneum</i>				
<i>Trifolium arvense</i>	<i>Trifolium tomentosum</i>				
<i>Trifolium augustifolium</i>	<i>Vicia monantha</i>				
<i>Trifolium glomeratum</i>	<i>Vulpia bromoides</i>				
<i>Trifolium subterraneum</i>					
<i>Trifolium tomentosum</i>					
<i>Vicia monantha</i>					
<i>Vulpia bromoides</i>					

Site	Origin	Heated	Unheated		
Upper Sturt	Native	<i>Danthonia</i> sp. 2	<i>Agrostis avanacea</i>		
		<i>Eucalyptus leucoxyton</i>	<i>Eucalyptus leucoxyton</i>		
		<i>Oxalis perennans</i>	<i>Gnaphalium gymnocephalum</i>		
		<i>Pelargonium australe</i>	<i>Gonocarpus</i> sp.		
		<i>Poa</i> sp. 2	<i>Oxalis perennans</i>		
		<i>Scaevola</i> sp.	<i>Poa</i> sp. 2		
		<i>Senecio quadridentatus</i>	<i>Senecio quadridentatus</i>		
			<i>Wahlenberghia</i> sp.		
			<i>Wahlenberghia stricta</i>		
		Introduced		<i>Anagallis arvensis</i>	<i>Agrostis capillaris</i>
				<i>Briza major</i>	<i>Anagallis arvensis</i>
				<i>G. monspessulana</i>	<i>Briza minor</i>
				<i>Hypochoeris radicata</i>	<i>Bromus diandrus</i>
				<i>Lactuca serriola</i>	<i>Centarium erythraea</i>
<i>Leontodon taraxacoides</i>	<i>G. monspessulana</i>				
<i>Phalaris minor</i>	<i>Hypochoeris radicata</i>				
<i>Poa annua</i>	<i>Phalaris minor</i>				
<i>Senecio pterophorus</i>	<i>Poa annua</i>				
	<i>Rubus discolor</i>				
	<i>Senecio pterophorus</i>				
	<i>Sonchus asper</i>				