Weed Biology: a foundation for weed management

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Abstract

Information on the biology of weeds is an important component in the development of integrated control strategies. While a complete understanding of their ecology would be ideal, obtaining the answers to just some key ecological questions will help substantially. In an attempt to gain a better understanding of a weed problem and its solution, land managers frequently ask questions about the weed's ecology, including: How long do individual plants live?; How long does it take young plants to become reproductive?; How long will it take for the seedbank to be depleted once adult plants are removed from a site?; How and how far is the seed dispersed?; and What is the frequency and scale of seedling recruitment? Controlling weeds is an expensive business. A better understanding of their biology will help improve control techniques and ease the financial burden on land managers.

Introduction

An understanding of the biology of the weeds invading our grasslands and woodlands is essential if effective control strategies are to be developed. Unfortunately, our current knowledge of the ecology of these weeds is limited. While some knowledge of exotic weeds can be obtained from the countries to which they are native, weeds often change their behaviour under the environmental conditions of their new home. In part, this is because the pests and diseases from their country of origin are not present in Australia, allowing the weeds to thrive to a greater extent. A complete understanding of the life cycle (Figure 1) of any weed would be ideal along with information on the influence of environmental factors. Limited resources preclude this for all but a few weeds.

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Comprehensive reviews of some of the key weeds affecting grasslands in Queensland, including rubber vine (*Cryptostegia grandiflora*) (Tomley 1995), prickly acacia (*Acacia nilotica*) (Mackey 1998), parthenium (*Parthenium hysterophorus*) (Navie *et al.* 1996) and Noogoora burr (*Xanthium pungens*) (Hocking and Liddle 1995), have highlighted important information gaps. Groves *et al.* (1995) and Panetta *et al.* (1998) compiled reviews on the biology of 33 Australian weeds including those that affect waterways, urban areas, cropping lands, rainforests and grasslands.

This paper identifies and discusses some ecological questions frequently asked by land managers trying to gain a better understanding of the weeds they are attempting to control. Where applicable, information on the ecology of exotic weeds currently threatening Queensland's grazing lands is presented to illustrate the implications for management.

Frequently asked ecological questions

How long do individual plants live?

This takes into consideration whether the weeds are annuals, ephemerals or perennials. Longevity is relatively easy to determine for ephemerals and annuals because of their short life cycles. For example, parthenium plants live for a maximum of only 6–8 months (Navie *et al.* 1996). On the other hand, the life-spans of perennials such as many of the woody weeds, are much harder to quantify, and in many instances anecdotal evidence provided by landholders and other members of the community is the best source of information. Generally, most research projects are not conducted for long enough to determine the longevity of perennial weeds.

Estimates for two of our worst exotic woody weeds, prickly acacia and algaroba mesquite (*Prosopis pallida*), show the problems facing landholders when these plants invade grasslands. Prickly acacia has been estimated to survive for 30–60 years (Carter 1994) and long-term residents at Hughenden have suggested that some algaroba mesquite plants growing around the township are at least 40 years old. In the United States where honey mesquite (*Prosopis glandulosa*) is native, some plants growing in rangelands are estimated to be over 150 years old (Archer 1989). If no control techniques are implemented, individual plants will be present for a long time. Furthermore, there will be continual input into the seedbank when environmental conditions become conducive to flowering and seed set.

How long does it take young plants to become reproductive?

Land managers who diligently control all existing plants of a weed species need to know

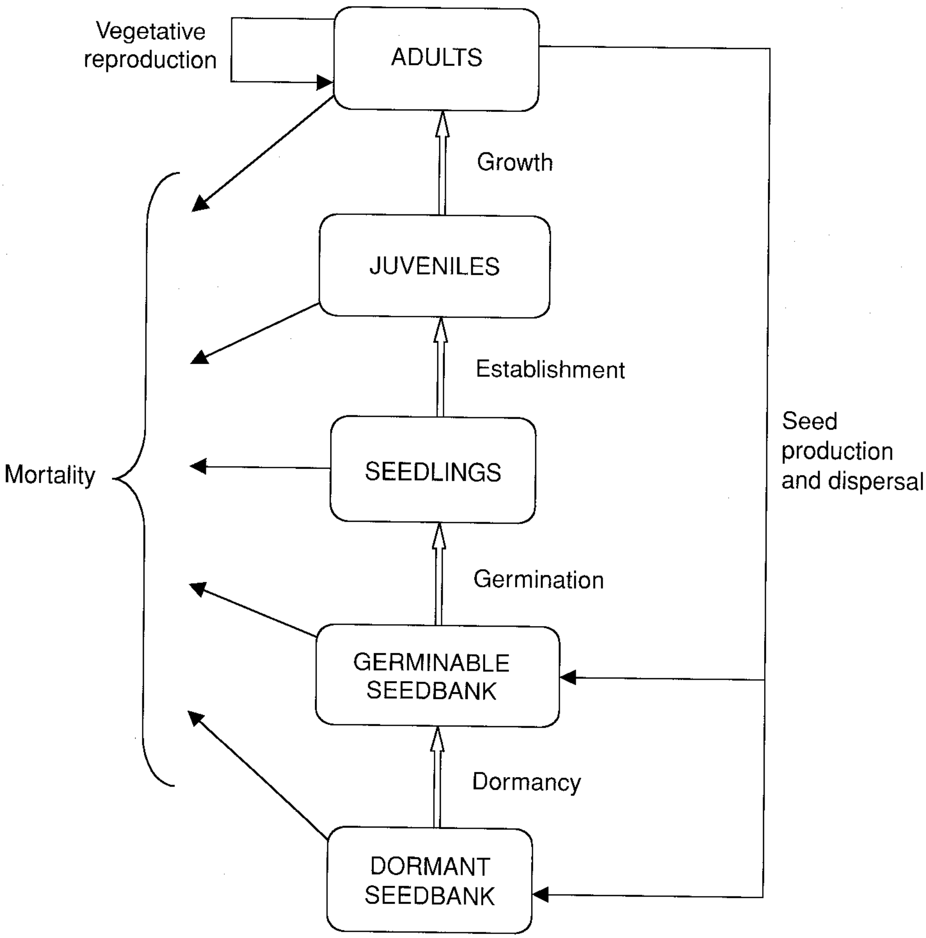

Figure 1. A generalised plant life cycle (T. Grice, unpublished data).

how long it will take before seedlings become reproductive and start replenishing the seedbank. The timeframe will vary between species and can be relatively short to extremely long (Table 1). The longer the time to reproductive maturity, the higher the natural mortality and the greater the opportunities for secondary control activities. Obviously, environmental conditions will influence how long seedlings take to become reproductive, but if land managers can make a reasonable estimate, particularly of the shortest periods, they can develop appropriate control strategies. It is a wasted opportunity if an excellent kill of original plants is followed by rapid regrowth. Delaying follow-up control efforts until just before plants become reproductive will maximise the natural mortality of seedlings and juveniles and could markedly reduce the cost of control. However, the efficacy of some treatments may be reduced as seedlings get older and more established. This is particularly the case with fire and with any chemical or mechanical control method where treatment cost is increased by plant size.

Short-lived species quickly grow from germination to reproductive maturity. The seeds they produce provide next year's infestation. Perennials, on the other hand, can often take much longer. Consequently, flowering can occur literally within months for some annuals such as parthenium but take many years for perennials such as chinee apple (*Ziziphus mauritiana*).

How long will it take for the seedbank to be depleted once adult plants are removed from a site?

The length of time that viable seeds of a weed remain in the seedbank provides an indication of how long seedlings can be expected to appear once adults have been killed. Knowing this allows secondary control strategies to be planned and implemented for the necessary duration.

Predicting the longevity of a seedbank is not a straightforward process as a combination of seed characteristics and environmental factors interact to influence how long seeds will be present, in the absence of any further seed input (Figure 2). The key factor is whether seeds can remain dormant. Dormancy is a survival mechanism that ensures the plant's continued existence in an area. Mass germination of seed in just one event is prevented and germination is spread over a number of occasions (Richards and Beardsell 1987). A number of dormancy mechanisms have been identified and can be divided into two basic types: coat-imposed dormancy — where one or other of the tissues surrounding the embryo is responsible; and embryo dormancy — where the block to germination occurs within the embryo itself (Richards and Beardsell 1987). Irrespective of the mechanism, seeds that have dormancy potential add an extra dimension of difficulty to control efforts. By ensuring that not all seeds germinate at once, the longevity of the seedbank is extended.

Table 1. Estimated time taken for young plants of some weed species to reach reproductive maturity.

Weed	Estimated times to reach reproductive maturity	Source
Parthenium	— Can flower within 4–6 weeks.	Navie *et al.* (1996)
Noogoora burr	— The mean number of days to flowering for plants grown under a wide range of conditions has been estimated as 117 days. Plants germinating late in the season will produce burrs at a very early age.	Moran *et al.* (1981)
Rubber vine	— In Queensland, first flowering has been reported within 250 days of germination. More commonly it takes 400–450 days.	Mackey (1996)
Lantana	— Can be reproductive within 12 months.	Swarbrick *et al.* (1995)
Chinee apple	— Estimated to take approximately 6 years to reach reproductive maturity.	Grice *et al.* (1999)
Prickly acacia	— Estimated to be as early as 18 months under favourable conditions, but more likely around 5 years under average conditions.	Mackey (1998)
Mesquite	— Earliest time taken to reach reproductive potential in the field was 30 months.	Grice *et al.* (1999)

Seeds of parthenium can last for as long as 7 years in the field (Navie *et al.* 1996). This means that a degree of diligence will be needed if replenishment of the seedbank is to be prevented. With parthenium plants capable of taking less than 8 weeks from germination to seed production, regular monitoring will be necessary to locate and control plants before they set seed. Noogoora burr is another good example. If no new burrs are introduced into an area, and seeding by existing plants is prevented, it will take at least 6 years for the viable seed population of noogoora burr to decline to less than 1% of the original (Martin 1981 cited by Hocking and Liddle 1995; Pitt 1991). Nevertheless, even 1% of an initial seedbank of 1160 burrs per m^2 still equates to 11 seeds per m^2 (Hocking and Liddle 1995), probably enough for reinvasion of a site if environmental conditions favour seedling establishment.

The time that many leguminous woody weed seeds will remain viable depends on the conditions to which seeds are exposed. Many species have a hard seed coat which is impermeable to water (referred to as hard seeds) and prevents germination. Temperature fluctuations, mechanical disturbance and fire are just some of the factors that can stimulate germination by either rupturing the coat or allowing water to pass through a specialised region known as the strophiole (Richards and Beardsell 1987).

If seeds of some species of mesquite are kept in a dry environment and exposed to moderate temperatures, they will remain viable indefinitely (Tschirley and Martin 1960). Seeds of velvet mesquite (*Prosopis velutina*) stored in a laboratory at the Herbarium of Tucson, Arizona retained 60% viability for at least 50 years (Glendening and Paulsen 1955). In the field, seeds of another mesquite species (*Prosopis juliflora*) were buried, with samples recovered 2, 5 and 10 years after burial. Most seed germinated within a year after planting following suitable rainfall, but 8% of seeds remained dormant and viable after 10 years of burial even when soil moisture had been adequate for germination (Tschirley and Martin 1960). These seeds could provide a reservoir for reinfestation after a decade of controlling the weed.

Seed dormancy is particularly important for annual weeds as one failed germination event could result in total depletion of the seed bank. This would be ideal for weed control, but unfortunately it rarely happens. It may, however, happen for some perennial weeds, such as rubber vine. Freshly fallen seed of rubber vine is highly germinable and, if favourable environmental conditions (prolonged rainfall and warm temperatures) prevail, germination will occur. Consequently, the seedbank may be markedly depleted and, if adult plants have been previously controlled, rubber vine may be greatly reduced at

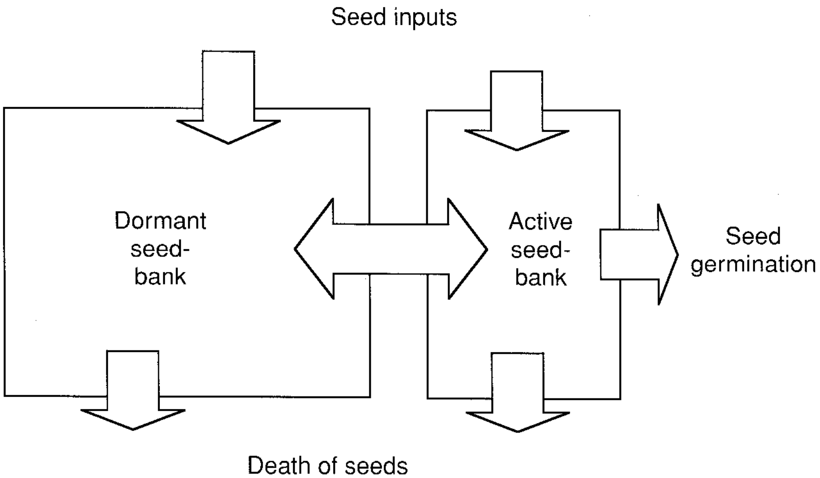

Figure 2. Model of seed-bank dynamics. Adapted from Whelan (1995).

a site. The only source of reinfestation would be from external sources or possibly from seed that was located too deep in the soil to allow germination. Seed at depth may sit there waiting for a disturbance to bring it closer to the surface where conditions for germination are more favourable. Mechanical techniques such as bulldozing, stick-raking and chain pulling could possibly do this.

Even if seed is highly germinable and located at a position in the soil profile where germination can occur, environmental conditions may limit germination. In tropical regions, the lack of rainfall will be the most common limiting factor. The longevity of the seedbank under these circumstances will therefore be dependent on the length of time before sufficient rainfall is received to promote germination. During this period, some natural attrition of seeds will occur. It is sometimes recommended that control strategies be implemented after prolonged drought. For example, mechanical control of prickly acacia is recommended following periods of drought in order to minimise the number of seedlings that will need to be treated (Mackey 1998). This is based on the hypothesis that the seedbank should be at a low level as adults would not have produced much seed during the drought and a large portion of the seed will have died. This may be true for some weeds but not all.

How and how far is the seed dispersed?

There are numerous dispersal mechanisms and agents that can introduce new weeds into an area or cause existing infestations to expand. Understanding how a weed is dispersed will suggest management practices to reduce the risk.

New weeds can be transported into an area via flooding, wind, animals and human intervention, with the mode of spread largely dependent on characteristics of the seed. Humans have the capacity to spread seeds the furthest distance from the initial source (Cousins and Mortimer 1995). This may be through movement of vehicles and machinery or in infested fodder, crop and pasture seed, and stock feed or in and on animals. Parthenium and the ever-increasing giant rat's tail grass (*Sporobolus pyramidalis*) are good examples of weeds that can be spread widely by human activity. Preventing them from establishing on a previously clean property will require a great deal of diligence. An example of the comprehensive procedures that should be implemented to reduce the risk of dispersal are those given for giant rat's tail grass as part of "Best Practice Management" recommendations (Table 2) (McIntosh *et al.* 1999). A strong emphasis is placed on good property hygiene. This is relevant to all weeds where human activity plays a major role in their spread. The important measures to prevent weeds establishing on a property in the first place are: to ensure vehicles and machinery entering the property are clean of weed seeds; to try not to bring in seed through infested produce; and to regularly monitor entrance roads, around homesteads, water points, stock yards and other frequently visited areas. This will enable early identification and eradication and eliminate the need for expensive control of large infestations.

Movement of water cannot be controlled as easily as human activity, so prevention of spread by water is harder to implement (on an individual basis) and will require more co-ordinated efforts. Parkinsonia (*Parkinsonia aculeata*) is a good example of a weed spread in water. Many areas containing uniformly aged juvenile parkinsonia plants can be observed on flood plains in central and northern Queensland. Seeds have clearly been deposited there during flooding as there are no mature reproductive trees present. Regular inspection of flood-prone areas is advised so that new infestations can be treated as early as possible. However, this becomes a demoralising task if the source of the seed is not controlled and reinfestation occurs after each flood. This is where integrated control activities on a catchment basis come into their own, with the problem being tackled at the top of the catchment first to prevent reinfestation of controlled areas.

Most seeds fall close to parent plants, although how closely will be dependent on whether fruits are dehiscent or indehiscent. Seeds contained within indehiscent fruits will usually fall directly to the ground while still contained within the fruit. Dehiscent fruits, on the other hand, may burst or split open at maturity while attached to the plant and disperse seeds some distance. For example, seeds of bellyache bush (*Jatropha gossypifolia*) can be propelled for up to 14 m (F. Bebawi, personal communication). Movement over greater distances may occur through wind and water and the activities of humans, native, feral and domestic animals and insects such as ants. Domestic animals such as cattle, sheep and horses play a significant role in spreading seeds of some weed species. Many leguminous shrubs, including prickly acacia and mesquite, are readily spread by domestic animals. Stock are the main agent of dispersal for prickly acacia and cattle are generally regarded as causing greater spread than sheep. Cattle pass about 80% of ingested prickly acacia seeds in their faeces and about 40% of these seeds are viable (Harvey 1981). The faeces also provide an ideal environment for germination (Harvey 1981). Sheep pass few viable seeds in their faeces, but spit out about 35% of seed during ingestion and regurgitate about a further 15% as viable seed (Carter and Cowan 1988). Since seeds take about 6 days to pass through livestock, stock moved by road transport can disperse viable seeds over large distances (Mackey 1998).

Giant rat's tail grass can be transported by cattle, be it in dung, stuck to their coats or in the mud on their hooves. A controlled feeding study

Table 2. Suggested recommendations with regards vehicles and machinery, livestock and hay and pasture seed if spread of giant rat's tail grass (GRT) is to be prevented.

Must	Must not
Vehicles and Machinery	
i. Clean machinery suspected of carrying GRT seed.	i. Do not indiscriminately drive machinery through paddocks infested with GRT.
ii. Provide a specific wash-down area and regularly check for GRT.	ii. Do not slash GRT-infested pastures.
iii. Work clean areas first.	iii. Do not carry GRT specimens loose in the cabin or in the tray of a ute.
iv. Preferably work GRT-sensitive areas separately.	iv. Do not allow off-farm vehicles to drive around your property without first knowing their GRT status.
v. Maintain 10 m wide GRT-free buffer strip.	
Livestock	
(a) Cattle	
i. Quarantine cattle for at least 5 days when moving from infested paddocks to clean paddocks.	i. Do not muster on rainy days.
ii. Cattle purchased from suspect areas should be quarantined for at least 5 days.	ii. Do not muster in mornings when dew is present.
iii. Muster GRT-infested paddocks with horses or on foot to prevent contamination of motorbikes and vehicles.	iii. Do not shift livestock directly from a contaminated to a clean paddock.
iv. Muster in the afternoon when pasture is dry.	
	iv. Do not walk cattle from infested paddocks through clean paddocks.
	v. Do not purchase livestock without attempting to locate their property of origin.
(b) Other livestock	
i. Treat horses, goats etc. similar to cattle, as similar quarantine strategies apply.	i. Do not allow horses into clean paddocks if there is a possibility they are carrying seed.
ii. Avoid working horses or dogs in GRT pastures under wet conditions.	ii. Do not allow your dogs to roam GRT paddocks during wet weather or on dewy mornings.
iii. Wash horses or dogs following their use in GRT-infested pastures.	
Hay and pasture seed	
i. Determine the origin of hay and treat as suspicious any hay from known GRT areas.	i. Do not knowingly purchase hay contaminated with GRT.
ii. Feed hay in a yard, feedlot or small holding paddock. Maintain a vigilant watch for any strange weeds or grasses.	ii. Do not buy seed that has *Sporobolus* spp. listed as a contaminant.
iii. Check that pastures that are to be baled do not contain GRT.	iii. Do not buy seed without knowing its origin.
iv. Purchase seed only from a reputable seed merchant.	
v. Sow the recommended competitive pasture grasses when replanting GRT-infested pastures.	

(Adapted from McIntosh *et al.* 1999)

found that 28% of seed fed to cattle survived passage through the digestive tract and was excreted as live seed (Bray 1999). Most seeds were excreted 2–3 days after being consumed with only a few excreted after Day 4. Manure was also collected from cattle grazing infested paddocks. From this, it was estimated that up to 150 000 seeds/beast/day were excreted in summer and 3000 seeds/beast/day in winter, of which approximately 25% were viable (Bray 1999).

Management can be adjusted to minimise the risk of weed spread through domestic animals. Table 2 outlines some recommendations on what must and must not be done with livestock handling if spread of existing infestations of giant rat's tail grass on a property is to be minimised. These points are appropriate for most weeds spread by domestic animals, including exotic woody weeds. Steps such as fencing of dense areas, restricting livestock movement in infested paddocks when plants are seeding/fruiting and quarantining of stock in yards or small holding paddocks until seed is excreted (hold for approximately 5–7 days depending on the weed) if they are suspected of coming from weed-infested areas will minimise both the risk of spread and the subsequent cost of control.

What is the frequency and scale of seedling recruitment?

Whether recruitment of new seedlings of a weed occurs on a regular basis or sporadically plays a major role in determining the pattern of invasion, how much effort will be needed to keep it under control and when control is most urgent. A number of aspects need to be considered, including seed production, the conditions needed for germination to occur and the survival of seedlings in subsequent years. Reproduction of the majority of grassland weeds is through seed, although for some, such as bellyache bush, vegetative reproduction can be important.

How much seed a plant produces provides a good indication of the maximum possible rate of infestation that may occur and the difficulty that will be encountered when trying to eliminate it. Prolific seeders can spread rapidly, particularly if environmental conditions are conducive to seedling survival. Giant rat's tail grass and parthenium certainly fit this category. Seed production of giant rat's tail grass ranges from 1885 seeds/m^2 in light infestations to 80 000 seeds/m^2 in heavily infested areas (Vogler 1999). Similarly, parthenium has been reported to produce some 300 000 seeds/m^2. If only 0.5% of giant rat's tail grass seed germinates and reaches the adult stage, 9 new plants per m^2 will arise even from a light infestation.

When plants produce more than one cohort annually, there is an increased chance of seedlings establishing because the risks of establishment are spread over a number of occasions. The chance of some seedlings receiving favourable environmental conditions is therefore increased. For example, parthenium is capable of producing 4 or more cohorts of seedlings during a good growing season (Pandey and Dubey 1989). Giant rat's tail grass can produce seedlings throughout the year given adequate moisture and temperature (W. Vogler, personal communication).

Significant changes in the population dynamics of woody weeds generally occur at the seedling stage. The number of cohorts (distinct groups of seedlings of the same age) produced and subsequent number of surviving seedlings that reach the juvenile stage will determine whether populations remain at equilibrium or increase over time. As mentioned earlier, mature plants tend to be extremely resilient to adverse environmental conditions and are long-lived; consequently, only minor reductions in adult populations occur, unless control is effected. A number of scenarios may arise as a consequence. Firstly, the initial population may reach an equilibrium and not change much over time. Secondly, the population may gradually increase as a result of intermittent recruitment of new plants following periods where environmental conditions are conducive to seed germination and establishment. Thirdly, the population may remain relatively constant until some episodic event causes a population explosion through mass recruitment. This third scenario is commonly associated with consecutive years of above-average rainfall.

Slow-spreading weeds that have been around for a long time can lull people into a false sense of security, with the extent of the problem being realised only once it is too late. Chinee apple is one such weed. It has been present in many regions, particularly those that have a mining background, for a number of years, yet has not been widely regarded as 'that big a problem'. Populations have built up slowly and it is only in recent years that genuine concern regarding this plant has been expressed. It is important to remember that small infestations are much cheaper to control than large infestations.

The invasion of the mitchell grass plains of northern and western Queensland by prickly acacia has been attributed to a combination of Scenarios 2 and 3. For this weed, a stepwise pattern of increase has occurred with some spread in many years but with most occurring in very wet years (Mackey 1998). Algaroba mesquite appears to behave in a similar fashion. A study undertaken in northern Queensland to understand its seedling dynamics followed 11 different groups of seedlings (cohorts), based on the distinct rainfall events on which they germinated. There were 3 germination events in both the first and second years and 5 in the third year even though rainfall for each of the 3 wet seasons was less than the long-term mean. Seedling emergence varied from 1180 seedlings per ha during the first wet season in an infestation density of 67 reproductive trees per ha, to 58 500 seedlings per ha during the third wet season in an infestation density of 1280 reproductive trees per ha. Survival up to 12 months averaged 4% and ranged from no seedlings surviving to as many as 16% remaining alive (M. Keir, personal communication). Cohorts that exhibited high survival tended to receive high initial rainfall on which germination occurred and good subsequent rainfall soon after germination. The ability of algaroba mesquite to have at least 3 germination events every year for 3 consecutive years of below-average wet season rainfall demonstrates the invasive potential of this plant. Even with an average survival rate after 12 months of 4%, reinvasion of cleared areas or thickening up of scattered infestations can take place. However, it will be in the above-average rainfall years when survival is higher that the invasiveness of mesquite will be fully realised (Grice *et al.* 1999).

It will be extremely important following high rainfall years that seedling populations are monitored regularly, particularly in areas where control of adults has been undertaken. If a large proportion of these seedlings remain alive 6 months after emerging and look well established, consideration must be given to how they can be controlled before they become reproductive. If they are widespread such as over a whole paddock, some broadscale method will need to be implemented, perhaps the use of fire or aerial application of a foliar herbicide. In the case of algaroba mesquite, a fire-susceptible species, burning will keep the population in check provided there is sufficient fuel to carry a fire evenly across the whole area.

Conclusion

Development of control techniques and ecological research need to go hand in hand if effective weed management strategies are to be developed. The ecological questions that have been outlined are by no means all that need to be answered for a full understanding of a weed. They do, however, illustrate the role ecological knowledge can play in weed management.

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