

Modelling integrated weed management of an invasive shrub in tropical Australia

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Summary

1. Where biocontrol programmes for invasive plants are in place, only one-third are fully successful. Integrated weed management (IWM) emphasizes the use of several complementary control measures.

2. We used models of increasing complexity to determine which parameters affect site occupancy of an invasive shrub, *Mimosa pigra*, in tropical Australia. Two introduced biocontrol agents have spatial effects on both plant fecundity and the probability of recolonization after senescence. We incorporated biocontrol effects into IWM models with small-scale disturbance, such as grazing and pig-rooting, and large-scale disturbance, such as mechanical control, herbicide and fire. The models were parameterized from experimental and field data.

3. The models indicated that reduction in fecundity is not the most important impact of biocontrol; rather it is defoliation at the edges of stands, allowing grasses to out-compete *M. pigra* seedlings. We demonstrated that biocontrol alone is only successful at low levels of small-scale disturbance and seedling survival and, even then, current biocontrol agents would take decades to reduce a stand to < 5% site occupancy.

4. Our model predicts the most successful IWM strategy to be an application of herbicide in year 1, mechanical control + fire in year 2 and herbicide in year 3, with reduction of small-scale disturbance where possible. The addition of biocontrol improves the success of this strategy.

5. *Synthesis and applications.* Ascertaining how control measures, including biological methods, will influence persistence of an invasive requires models of the target species' dynamics and its ecosystem. As in previous applications of this model, disturbance is the most important regulator of population size in *M. pigra*; moderate to high levels of small-scale disturbance promotes *M. pigra* occupancy. We have shown that IWM can control *M. pigra* and that biocontrol is an effective part of this strategy. Reductions in fecundity alone are unlikely to control invasive leguminous shrubs. However, biocontrol agents affect the probability of recolonization after senescence and enhance control. Our recommended 3-year treatment programme (herbicide : mechanical control + fire : herbicide, with biocontrol) is justifiable in terms of the biology of the system, making it more likely to be acted upon by risk-averse farmers and land managers.

Key-words: biological control of weeds, feral mammals, fire, herbicide, spatial modelling

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Introduction

Invasive plant species pose an increasing threat to global biodiversity (Walker & Steffen 1997). Complete success of biocontrol, where no other control methods

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are required, accounts for approximately one-third of all completed biological control programmes (Fowler, Syrett & Hill 2000). Other management options are therefore required for well over half the weeds targeted by biological control programmes. In this context, it seems remarkable how few documented examples exist where integration of biocontrol with other management options has been demonstrated to result in improved weed management (Trumble & Kok 1980; Charudattan 1986; Briese 1996; Hoffman, Moran & Zeller 1998). The challenge for ecologists is to predict what combination of management strategies will be most effective, what consequences management will have on weed populations and their ability to recover, and how other components of the ecosystem respond.

Attributes of the invader and invaded community both contribute to successful invasions (Crawley 1987; Sakai *et al.* 2001), so sustainable management of invaders may involve the manipulation of invaded communities and disturbance regimes as well as direct control of the target species. For successful control, it may be necessary to change disturbance regimes or the succession trajectory of the community by creating favourable establishment opportunities for native competitors and unfavourable opportunities for weed regeneration. Empirical evidence supports the importance of land management and disturbance regimes in combination with herbivory for determining the abundance and persistence of invasive leguminous shrubs (Paynter *et al.* 2000; Bellingham & Coomes 2003).

In Australia, one of the worst weeds to threaten natural areas is *Mimosa pigra* L. (Mimosaceae). This species is native to tropical America and is now a pantropical weed that poses the most serious of all invasive threats to tropical wetlands (Cronk & Fuller 1995). In Australia, *M. pigra* forms impenetrable, nearly monospecific thickets (Lonsdale 1992) over an area of more than 800 km², where it reduces the diversity of native plants and animals (Braithwaite, Lonsdale & Estbergs 1989). Due to difficult access to stands, which may remain flooded for much of the year, and the cost of chemical control, herbicide treatments were considered a short-term solution and biological control the most promising long-term control strategy for *M. pigra* control (Forno 1992). However, Miller *et al.* (1992) suggested an integrated weed management (IWM) approach would be most effective, as biocontrol, fire, herbicide or sowing of grasses alone could not control dense infestations although combinations of these techniques showed promise. Recent experiments by Q. Paynter & G.J. Flanagan (unpublished data; Paynter & Flanagan 2002) addressed how biocontrol agents are affected by herbicide, use of bulldozers and fire.

A range of models has recently been used to predict the effect of introduced biocontrol agents and other management regimes on weed population size (Lonsdale, Farrell & Wilson 1995), time to infestation density (Buckley, Briese & Rees 2003) and the area occupied by the weed (Rees & Paynter 1997). The model developed

by Rees & Paynter (1997) was particularly suited to exploring the effect of integrating various management strategies for *M. pigra*, because of the spatial nature of the biocontrol insects' attack and the similarity of *M. pigra* to the species for which this model was originally developed. In order to predict the outcome of complex interacting control strategies with a dynamic weed population under different disturbance regimes, we used a series of models of increasing complexity. Analytical results of a tractable model were used to explain the behaviour of the more complex simulation models. The models were parameterized using published field and experimental data and recent experimental evidence (Paynter & Flanagan, in press) was used to inform integrated control models.

The model described by Rees & Paynter (1997) incorporates small-scale disturbance, germination, seed bank decay, survival, minimum age for reproduction, longevity, fecundity, seed dispersal and the probability a site remains suitable for regeneration after the original stand dies. We used this model, modified and parameterized for *M. pigra*, to explore how these aspects of the biology interact to control weed occupancy of a site. As for Rees & Paynter (1997), disturbance in the *M. pigra* model is assumed to be on a relatively small (plant-sized) scale. Unlike in Rees & Paynter (1997), we assumed the probability of disturbance varied between unsuitable sites and those with *M. pigra*. We also expanded on the Rees & Paynter (1997) approach by explicitly modelling combinations of management strategies, in order to assess which combinations are most effective at reducing *M. pigra* populations.

Aspects of *M. pigra* performance are lower in its native range and we therefore ran the models for fecundity recorded in the native range of *M. pigra* and in Australia, to see whether this difference accounted for the invasive nature of *M. pigra* in Australia. Lower fecundity in the native range might give an indication of the potential for biological control. Introduced biocontrol agents for *M. pigra* attack the edges of stands more than the interior, reducing fecundity and changing recruitment opportunities underneath established *M. pigra*. We were particularly interested in using the model to assess the spatial effects of biocontrol within an IWM system.

Mimosa pigra control

DISTURBANCE

Competing vegetation reduces germination and reduces seedling survival by an order of magnitude (Lonsdale & Farrell 1998), supporting our model assumption that sites occupied by other vegetation are unsuitable for *M. pigra* establishment, only becoming suitable when disturbed. Like many other hard-seeded woody shrubs, disturbance that temporarily eliminates competing vegetation is the key to successful *M. pigra* establishment (Holmes, Macdonald & Juritz 1987; Paynter *et al.* 1998). Indeed, overgrazing and disturbance by feral water

buffalo *Bubalus bubalis* has been blamed for assisting the rapid expansion of *M. pigra* in the Northern Territory of Australia during the 1970s (Lonsdale & Abrecht 1988; Cook, Setterfield & Maddison 1996). Furthermore, Lonsdale (1993) provided evidence that the rate of expansion of *M. pigra* has declined following a water buffalo eradication campaign in north Australia. Other sources of disturbance, such as grazing by other invasive and native species and fires, may be harder to control.

PHYSICAL AND CHEMICAL CONTROL

Small satellite infestations can be eradicated by hand-pulling, cutting, burning and herbicides (Cook, Setterfield & Maddison 1996). Cook, Setterfield & Maddison (1996) showed that small infestations in Kakadu National Park, Australia, were eradicated within 1 year. However, 20% of outbreaks required sustained control for 7 years or more. For larger stands, which may measure thousands of hectares in Australia, a variety of less labour-intensive management strategies has been tried.

Herbicide

Several herbicides (Dicamba, Ethidimuron, Fluroxypyr, Glyphosate, Hexazinone, Metsulphuron methyl, Tebutiuron, Triclopyr, 2, 4-D, Imazapyr) have been tested against *M. pigra* (Miller & Siriworakul 1992). However, spraying may not achieve 100% kill, as treated plants can regrow from the base of the plant or stems.

Mechanical control

Various methods of mechanical control are outlined in Siriworakul & Schultz (1992). They found that even if above-ground parts are destroyed, regrowth will occur unless treatments are used in combination with herbicides. Furthermore, there is a risk that machines, contaminated with seed, will move *M. pigra* to new areas.

Fire

Untreated *M. pigra* is difficult to burn, and burnt plants often regrow from the base or stems (Miller & Lonsdale 1992). Fires were hottest where the *M. pigra* had been flattened with a bulldozer prior to burning, and were hot enough to kill seeds at the soil surface. However, many buried seeds survived and seeds heated to sub-lethal temperatures became germinable, indicating that follow-up control may be necessary.

Revegetation

The efficacy of artificial revegetation has yet to be demonstrated. However, the negative effect of competing vegetation on both seedling emergence rates and subsequent survival (Lonsdale & Farrell 1998) suggests sowing competitive native vegetation could inhibit regeneration after stand clearance.

BIOLOGICAL CONTROL

Mimosa pigra is the subject of biocontrol programmes in Australia, Thailand, Vietnam and Malaysia (Harley *et al.* 1995). Six insect species are currently confirmed to have established and are widespread through much of the introduced range of *M. pigra*. Here we consider the two currently most effective species, the stem-mining moths *Neurostrotta gunniella* Busck and *Carmenta mimosa* Eichlin & Passoa. *Neurostrotta gunniella* has reduced fecundity of *M. pigra* by up to 60% and stunted growth of both mature plants and seedlings (Lonsdale & Farrell 1998; Paynter & Hennecke 2001). Recent work indicates *C. mimosa* is locally very damaging, causing defoliation and reducing fecundity (Paynter & Flanagan 2002). *Carmenta mimosa* and *N. gunniella* also affect the probability of recolonization of senescent *M. pigra* sites (which we term self-replacement) by defoliating adult plants and reducing shading on the ground below. Percentage cover of competing vegetation is significantly higher in plots containing *C. mimosa* compared with those where *C. mimosa* is absent (Q. Paynter, unpublished data). Lonsdale & Abrecht (1988) showed that artificial shading increased *M. pigra* seedling survival, and competing vegetation reduced seedling survival by an order of magnitude (Lonsdale & Farrell 1998). The effect of shade on germination was not investigated but the presence of competing vegetation reduced germination (Lonsdale & Farrell 1998). Therefore, we would expect *M. pigra* seedlings to survive under an intact *M. pigra* canopy, but at the edges of stands, where biocontrol agents are abundant, *M. pigra* will have a lower probability of recolonization of senescent sites. This is due to increased competition with grasses.

M. pigra population dynamics

SEED PRODUCTION

Seed production of *M. pigra* in Australia can be as high as *c.* 38 000–220 000 seeds year⁻¹ for the largest plants growing in dry and wet sites, respectively; typical plants produce *c.* 9000 seeds year⁻¹ in Australia (Lonsdale 1992). In Mexico, plants were less than half the size of plants growing in Australia (Lonsdale & Segura 1987), producing less than half as many pods and two-thirds as many seeds pod⁻¹. We therefore expect the seed production of a typical Mexican plant to be *c.* 13% that of a typical Australian plant (Table 1).

GERMINATION

Mimosa pigra seeds are hard-coated and may remain dormant for several years (Table 1). In Australia, germination is enhanced by diurnal heating and cooling of soils (surface temperatures can fluctuate between 19.9 °C and 67 °C in September), which breaks down the seed coat (Lonsdale 1992). Two weeks after sowing at the end of the wet season (when most annual germination takes place), seedling emergence averaged 29% in plots

Table 1. Population parameters recorded for *Mimosa pigra* in both native and exotic populations

Parameter	Site/comments	Country	Reference
Seed production			
9103 seeds m ⁻²	Adelaide River floodplain pre-biocontrol, edge and interior similar	Australia	1
Up to 220 000 seeds plant ⁻¹	Adelaide River floodplain	Australia	1
3946 seeds m ⁻²	Adelaide River floodplain, <i>N. gunniella</i> (low levels)		2
2117 seeds m ⁻²	Adelaide River floodplain, <i>Neurostrotia</i> (high levels)		2
2870 seeds m ⁻²	Edge of stand attacked by <i>Neurostrotia/Carmentia</i>	Australia	3
6090 seeds m ⁻²	Interior of stand attacked by <i>Neurostrotia/Carmentia</i>	Australia	3
1171 seeds m ⁻²	Estimate	Mexico	4
Germination probability			
0.29	Site with competing vegetation	Australia	2
0.42	Competing vegetation removed	Australia	2
0.8	After fire	Australia	5
Seed banks			
Native range			
117.5 m ⁻²	Near Acapulco	Mexico	4
Exotic range			
8500–c. 12 000 m ⁻²	Near Darwin	Australia	6
12 380 m ⁻²	Near Darwin	Australia	4
12 610 m ⁻²	Near Chiang Mai	Thailand	4
Seed bank half-life			
8.5 weeks	Kakadu National Park	Australia	7
9.4 weeks	Surface of black cracking clay	Australia	7
99 weeks	Buried at 10 cm in sandy clay	Australia	7
Seed dispersal			
Up to 2000 m; mean distances 14–195 m year ⁻¹	Adelaide River floodplain	Australia	8
Seedling survival probability			
0.16	Disturbed plots	Australia	3
0	Undisturbed plots	Australia	3
Longevity			
Seedling half life of 28 months	Black cracking clay	Australia	1
Half life of 21.4 months	'Heavy' soil	Australia	1
Half-life of 13.3 months	'Light' Soil	Australia	1
Senescence after 5 years		Australia	9
Time to reproduction			
6–8 months	Under 'ideal conditions'	Australia	1

¹Lonsdale (1992); ²Lonsdale & Farrell (1998); ³Q. Paynter (unpublished data); ⁴Lonsdale & Segura (1987); ⁵Lonsdale & Miller (1993); ⁶Lonsdale (1988); ⁷Lonsdale, Harley & Gillet (1988); ⁸Lonsdale (1993); ⁹Miller (1988).

with competing vegetation and increased to 42% where competing vegetation was removed (Lonsdale & Farrell 1998). Lonsdale & Miller (1993) showed that fire also enhances germination of *M. pigra* seedlings, with immediate germination rates of up to 80% recorded for seeds heated between 100 °C and 105 °C.

SEED BANKS

Seed banks can be very high where *M. pigra* is an exotic weed, but seed densities recorded in Mexico, where *M. pigra* is native, are much lower (Table 1). Seeds can remain viable for more than 5 years under laboratory conditions (Wara-Aswapati 1983). Experiments revealed that the half-life of seeds varied from just 9.4 weeks on the surface of black cracking clay to 99 weeks when buried at a depth of 10 cm in light sandy clay (Lonsdale & Abrecht 1988). Counts of emerging seedlings suggested a half-life of 8.5 weeks in Kakadu National Park (Lonsdale & Abrecht 1988). Because seed banks can be so high

beneath stands and the rate of loss is lower for buried seed, seed banks may persist for at least two decades in Australia (Lonsdale 1992).

SEED DISPERSAL

Although fallen stems can become established by suckering, by far the most important means of dispersal is by seed. Pods are covered with bristles that facilitate floating, enabling dispersal along rivers and during seasonal flooding. Lonsdale (1993) measured mean annual rates of spread of up to 195 m year⁻¹ (with a maximum value of greater than 2000 m) from 1980 to 1986. Yearly dispersal distances were strongly correlated with the wet-season rainfall.

SEEDLING SURVIVAL

Lonsdale & Farrell (1998) noted that both inter- and intraspecific competition affected seedling growth and

survival. For an initial seedling density of *c.* 10 seedlings m^{-2} , approximately 5% of seedlings survived for 10 months in plots where competing plants were excluded, compared with just 0.5% of seedlings in plots where competing plants were not excluded. In plots where the initial density of *M. pigra* seedlings was *c.* 1000 seedlings m^{-2} , the equivalent figures for survival were *c.* 1.5% and 0.15%, respectively.

LONGEVITY

In their home range, *M. pigra* plants live for 3–5 years (Rea 1998). It is not clear how long *M. pigra* plants survive in Australia. Mortality rates vary on different soil types, the half-lives of tagged plants in Australia being 28 and 22 months on heavy and sandy clay soils, respectively (Lonsdale 1992). However, these figures are probably biased by high death rates due to self-thinning in smaller plants (Lonsdale 1992) and are therefore unlikely to be a reliable indication of how long a stand can survive. Miller (1988) noted that deaths of plants reaching maturity occur from about 5 years of age. However, the size of some individuals and the persistence of some populations suggest that plants can live for 15 years or more in Australia (Rea 1998).

TIME TO REPRODUCTION

Reproduction is by seed. Under ideal conditions, plants can set seed 6–8 months after germination (Lonsdale 1992).

Description of the model

We first describe an analytical model and solve this for equilibrium under the simplifying assumptions of saturated local colonization and probabilities of recolonization of senescent sites of 0 and 1. We then go on to explore more complex situations with a simulation model, incorporating edge effects of biocontrol and multiyear IWM strategies with and without biocontrol. The simulation model is described in Rees & Paynter (1997).

We assume there are a large number of identical sites, each 1×1 m, the typical area occupied by a plant in Australia (Lonsdale 1992). Numerical quantities estimated from the simulation model are, unless otherwise stated, arithmetic means of the last 200 years of a 500-year simulation. Each site can be in one of three states, either occupied by *M. pigra*, unsuitable for colonization by *M. pigra*, or open and so suitable for colonization by *M. pigra*. Sites that are unsuitable for *M. pigra* colonization are assumed to contain native vegetation that excludes *M. pigra* recruits. Sites are further classified as edge sites, if they have at least one neighbouring cell unoccupied by *M. pigra*, or interior cells, if all eight neighbouring cells are occupied. In each year, events occur in the same order as that outlined in Rees & Paynter (1997), with the additions that different disturbance rates operate on sites occupied by *M. pigra* (p_{distM}) or

unsuitable sites (p_{distU}). Also, in models incorporating edge effects, fecundity and the probability of a senescent site being recolonized, depend on whether the plant is in an interior ($F_{int}, p_{so,i}$) or edge ($F_{edge}, p_{so,e}$) site.

Analytical descriptions of the simulator

See Appendix 1 for an index of all notation used. Here we derive the age structure of the sites occupied by *M. pigra*. If sites containing *M. pigra* are disturbed, then the age structure of the *M. pigra* population will follow a truncated geometric distribution (Rees & Paynter 1997), with z_i given by:

$$z_i = \frac{p_{distM}(1 - p_{distM})^i}{1 - (1 - p_{distM})^{A_{max}+1}} \quad i = 0, 1, 2, \dots, A_{max} \quad \text{eqn 1}$$

We will assume a site can be in one of three states: M_i , occupied by *M. pigra*; U_i , unsuitable for colonization by *M. pigra*; O_i , open for colonization. In addition to these state variables, we will also derive an equation for the average density of seeds in a site, S_i . If a site is open then the probability it becomes colonized, P_c , is given by:

$$p_c = 1 - \exp(-gsS_i) \quad \text{eqn 2}$$

where S_i is the average density of seeds in a site. Equation 2 is used below to couple seed bank dynamics with site fate. The dynamics of the system are described by the following set of equations:

$$U_{t+1} = (1 - p_{distU})U_t + (1 - p_{distM})(1 - p_{so})z_{max}M_t + p_{distU}(1 - p_c)U_t + p_{distM}(1 - p_c)M_t + (1 - p_c)O_t \quad \text{eqn 3}$$

$$M_{t+1} = (1 - p_{distM})(1 - z_{max})M_t + p_{distU}P_cU_t + p_{distM}P_cM_t + p_cO_t$$

$$O_{t+1} = p_{so}z_{max}(1 - p_{distM})M_t$$

$$S_{t+1} = (1 - d)S_t + FM_t f_r$$

where z_{max} is the proportion of plants aged A_{max} , and f_r is the fraction of plants that are of reproductive age. Figure 1 is a flow chart representing all possible fates of sites, analogous to equation 3 except that the seed bank is not represented in Fig. 1. We can solve this system of equations for the equilibrium fraction of sites occupied by *M. pigra* (M^*) by making some simplifying assumptions. If open sites are colonized with probability one (i.e. $p_c = 1$), then the equilibrium fraction of sites occupied by *M. pigra*, M^* , is given by:

$$M^* = \frac{p_{distU}}{p_{distU} + z_{max}(1 - p_{distM})(1 - p_{so}(1 - p_{distU}))}. \quad \text{eqn 4}$$

So, providing local colonization is saturated, the proportion of sites occupied is determined by just four parameters: the probability of disturbance of both unsuitable sites p_{distU} , and sites containing *M. pigra*, p_{distM} ; z_{max} , itself a function of A_{max} and p_{distU} , equation 1; and p_{so} , the probability a site becomes open following senescence. There are two special cases of equation 4

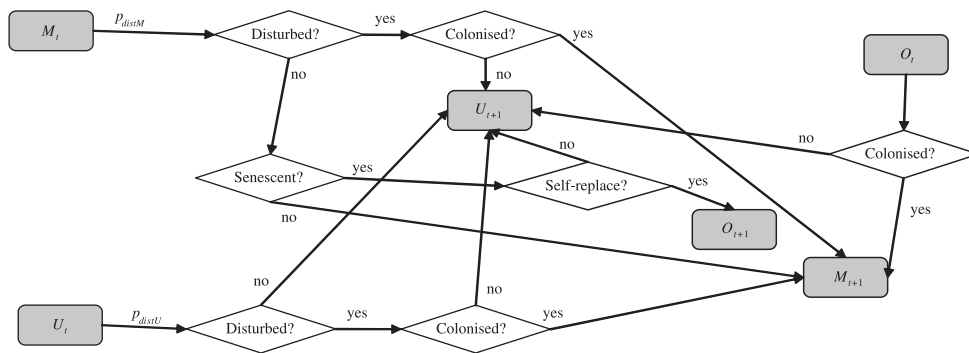


Fig. 1. Flow chart showing the possible fates of *M. pigra* occupied (M), unsuitable (U) and open (O) sites. The grey boxes are start and end points and this diagram corresponds to equation 3 (excluding S).

that are of interest. First, assuming all sites become suitable for colonization following *M. pigra* senescence (i.e. $p_{so} = 1$), then equation 4 simplifies to:

$$M^* = \frac{1}{1 + z_{\max}(1 - p_{\text{dist}M})}, \quad \text{eqn 5}$$

Increasing the probability that a site containing *M. pigra* is disturbed, $p_{\text{dist}M}$, or maximum plant longevity, A_{\max} , will decrease z_{\max} (equation 1), leading to an increase in M^* . If $p_{\text{dist}M} > 0$, *M. pigra* will spread until the only sites left open are those in which *M. pigra* has senesced and left open; these sites will then be recaptured the following year.

The second case of interest is when all sites become unsuitable for colonization following *M. pigra* senescence (i.e. $p_{so} = 0$), then equation 4 simplifies to:

$$M^* = \frac{1}{1 + z_{\max}(1 - p_{\text{dist}M})/p_{\text{dist}U}}. \quad \text{eqn 6}$$

In this case both the probabilities of disturbance, $p_{\text{dist}M}$ and $p_{\text{dist}U}$, and maximum plant age are important. As z_{\max} decreases rapidly with increasing $p_{\text{dist}M}$ (equation 1), increasing $p_{\text{dist}M}$ (i.e. death of plants not attributable to senescence at A_{\max}) can result in the proportion of sites occupied by *M. pigra* increasing. This is because when an *M. pigra* plant senesces without disturbance, the site becomes unsuitable for recolonization by *M. pigra*, and if $p_{\text{dist}U}$ is small then the unsuitable site created will not be suitable for colonization for a long time (the average time required for an unsuitable site to become suitable being $1/p_{\text{dist}U}$). In contrast, if a site containing *M. pigra* is disturbed, it becomes suitable for colonization immediately.

Once M^* is known, the equilibrium seed bank density is given by:

$$S^* = \frac{f_r FM^*}{d} \quad \text{eqn 7}$$

In order to determine if *M. pigra* will invade a habitat, we consider the initial stages of an invasion. We calculate the condition for *M. pigra* to increase from one year to the next (see Appendix 2). This gives the condition:

$$(1 - p_{\text{dist}M})(1 - z_{\max}) + \frac{p_{\text{dist}U}gsFf_r}{d} > 1 \quad \text{eqn 8}$$

Note that the total number of seeds that become seedlings from the F seeds produced is given by:

$$\begin{aligned} \text{total number of seedlings} &= \sum_{x=0}^{\infty} gF(1 - d)^x \\ &= \frac{gF}{d} \end{aligned}$$

$(1 - p_{\text{dist}M})(1 - z_{\max})$ is the proportion of *M. pigra* plants surviving from one year to the next and each plant colonizes $p_{\text{dist}U}gsFf_r/d$ sites. Using equation 8 we can derive the critical proportion of seeds that must be destroyed to eliminate *M. pigra*, given by:

$$\theta = 1 - \frac{1 - (1 - p_{\text{dist}M})(1 - z_{\max})}{Ff_r p_{\text{dist}U}gs/d} \quad \text{eqn 9}$$

From this equation, if the number of recruits produced by a single *M. pigra* plant is large (i.e. $Ff_r p_{\text{dist}U}gs/d \gg 1$), then the likelihood of eliminating *M. pigra* using seed-feeding insects is low.

Control scenarios examined

DISTURBANCE

In all simulations $p_{\text{dist}M}$ was set to 0.05; we assume that just 5% of *M. pigra*-occupied sites get disturbed each year. This assumption is supported, as the main sources of disturbance, grazing and fire, do not affect green *M. pigra* thickets. The effect of disturbance on unsuitable sites was extensively explored by running all simulations with $p_{\text{dist}U}$ taking values between 0 and 0.95.

PHYSICAL AND CHEMICAL CONTROL

Herbicide and mechanical control were assumed to have the same effects in the model, i.e. $p_{\text{dist}M} = 1$: all adult *M. pigra* plants are killed. Selective herbicides kill *M. pigra*, but not floodplain grasses. Therefore, *M. pigra* germination rates and seedling survival will depend on how quickly grass recovers, once shading from *M. pigra* is removed. Lonsdale & Miller (1993) measured the impact of temperature on seed survival and germinability: up to 80% of seeds become germinable immediately after a fire; however, this peak is for a rather

narrow temperature range (100–105 °C). Fire alone kills *M. pigra* adults (10%) and seedlings (50%) but does not affect the seed bank, as the fire is not hot enough to kill seeds or make them germinable.

BIOCONTROL

The potentially best biocontrol scenario in Australia was modelled assuming seed-feeding insects reduce fecundity from 9000 to 1171 seeds m⁻²: the average seed production observed in the native range. The outcome of biocontrol observed in the field in Australia was explored using the maximum pre-biocontrol fecundities (9000 seeds m⁻²) for both the edge and interior of a stand, and contrasting this with reductions in fecundity to 6000 seeds m⁻² in the interior of stands and 2000 seeds m⁻² at the edges of stands. High and low values of A_{\max} (10 and 5 years) and high, medium and low values of s (0.16, 0.05 and 0.005) were also used. We ran the simulations under three scenarios for colonization after *M. pigra* senescence. First we assumed that *M. pigra* could not recolonize after senescence ($p_{so} = 0$), secondly that it could recolonize after senescence ($p_{so} = 1$) and finally that $p_{so} = 0$ at the edges of stands ($p_{so,e}$) and $p_{so} = 1$ at sites in the interior ($p_{so,i}$). For the latter scenario it was assumed that the biocontrol agents *C. mimos*a and *N. gunniella*, which are most active at the edges of stands, reduced shade at ground level at the edges of *M. pigra* stands, so that grasses could invade and out-compete regenerating *M. pigra* seedlings. We calculated the numerical solution of equation 3 for global biocontrol and no biocontrol scenarios, and for the edge biocontrol scenario S_{t+1} was calculated as:

$$S_{t+1} = (1 - d)S_t + (M_t^8 F_{int} + (1 - M_t^8) F_{edge}) M_t f_r \quad \text{eqn 10}$$

Given that biocontrol alone can control *M. pigra* populations under certain parameter values (see the Results), we explored how long it would take for a *M. pigra* population covering 90% of the area to be reduced to a population covering < 5% of the area. This gives a best case scenario for how long it would take for biocontrol to be seen to be successful. This time is likely to be an underestimate, as it assumes that the biocontrol agents are established and attack stands every year to the same maximum level. The time taken to reduce stands to < 5% was determined for the following sets of parameters. Global biocontrol: $F = 2000$, $p_{so} = 0$, $A_{\max} = 5, 10$, $s = 0.005, 0.05$, $p_{distU} = 0.01, 0.05$. Edge biocontrol: $F_{edge} = 2000$, $F_{int} = 6000$, $p_{so,i} = 1$, $p_{so,e} = 0$, $A_{\max} = 5, 10$, $s = 0.005, 0.05$, $p_{di} = 0.01, 0.05$. Mean time to < 5% cover was calculated as the average of 20 runs.

INTEGRATED WEED MANAGEMENT

We ran more than 25 different single and combination treatments involving biocontrol, herbicide application, mechanical control and fire. We ran all combination

treatments with and without edge biocontrol and with and without recolonization after senescence in interior and edge sites by varying the parameters $p_{so,i}$ and $p_{so,e}$. We present results of the most effective combination strategies and strategies for comparison with combinations. Simulations were first run for 500 generations to ensure equilibrium had been reached, with or without biocontrol, after which the other control methods were applied over 1–3 years. Following treatment the population parameters within the model reverted to those that existed before the treatment, to investigate whether treatment permanently removes *M. pigra* stands or, if not, how long they take to recover.

Lonsdale & Miller (1993) measured the temperature at and below the soil surface during a fire on a herbicide-treated patch of *M. pigra* with and without mechanical crushing. Lonsdale, Harley & Gillet (1988) measured the proportion of seeds in the seed bank found at the soil surface or buried. By combining these sources of information we were able to estimate the effects of fire on the seed bank in the different treatment combinations. Either herbicide or mechanical control in combination with fire kills all adults ($p_{distM} = 1$) and the fire results in immediate mortality of seeds in the seed bank (34%) and immediate germinability of the survivors of 32%. In the simulation, fire induced seed mortality and germination to occur before normal seed bank decay and germination. The hottest fires were achieved after both herbicide and mechanical control were applied, with more than 60% of seed killed; of the survivors, 14% were immediately germinable.

Mimosa pigra regeneration can be rapid. Under ideal conditions seedlings can reach flowering age within just 1 year of germinating (Lonsdale 1992). For this reason, we tested follow up treatments, performed within one year of the initial stand clearance. We explored 1-year, 2-year and 3-year treatment combinations. For the 2-year treatments, herbicide was applied in year 1 and fire (with or without mechanical control) in year 2. Three-year treatments were similar to the 2-year treatments but with an additional herbicide application in year 3.

Results

DISTURBANCE

From both the analytical results (equations 4, 5, 6, 8 and 9) and simulations (Fig. 2), it is apparent that decreasing disturbance of occupied and unsuitable sites decreases *M. pigra* site occupancy. However, decreasing disturbance alone will be ineffective unless it can be maintained at a very low level (< 10% of unsuitable sites disturbed each year).

PHYSICAL AND CHEMICAL CONTROL

Due to persistent seed banks, 1-year treatments of fire, mechanical control or herbicide application with or without biocontrol do not reduce *M. pigra* site

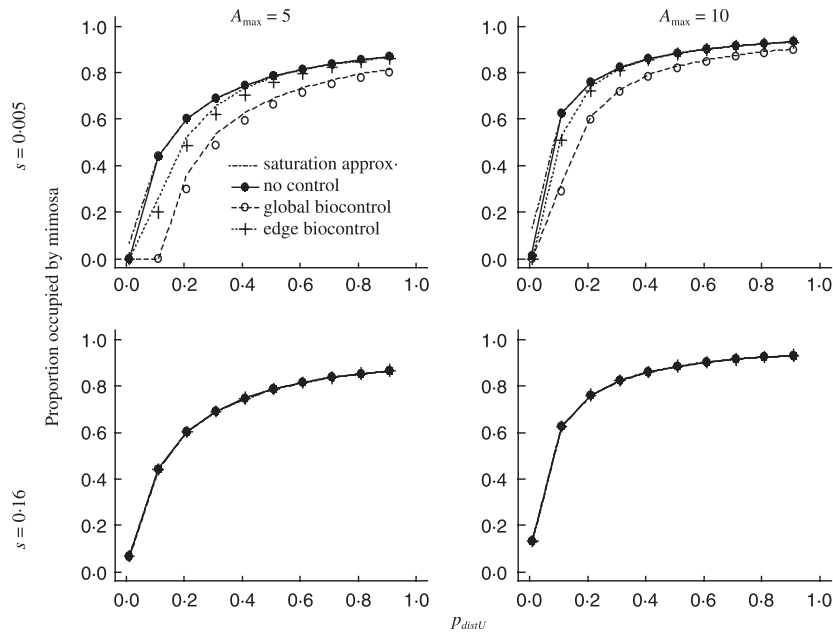


Fig. 2. Proportion of sites occupied by *M. pigra* assuming $p_{distM} = 0.05$, $A_{min} = 1$, $p_{so} = 0$, $A_{max} = 5$ or 10 and $s = 0.005$ or 0.16 . At $A_{max} = 10$ all biocontrol scenarios converge on the saturation approximation at full fecundity ($F = 9000$). The points are from simulations, the lines are from either the saturation approximation (equation 6) or numerical solutions of equation 6 at the three different fecundity scenarios ($F = 9000$ for no control, $F = 1171$ for global biocontrol control and $F_{int} = 6000$, $F_{edge} = 2000$ for edge biocontrol).

occupancy, either immediately or within the 10-year recovery period at $p_{distU} > 0$ (data not shown).

BIOCONTROL

For realistic parameter values (Table 1) and assuming that *M. pigra* cannot recolonize after senescence ($p_{so} = 0$), the proportion of seed that would need to be destroyed to eliminate *M. pigra* (equation 9) is very high and unlikely to be sustained with current biocontrol agents. Seed-eating biocontrol agents alone, even in the best case scenario where fecundities are reduced to those observed in the native range, will not eliminate *M. pigra* unless p_{distU} is very low. As disturbance increases, *M. pigra* occupancy quickly rises to dominate the area. Seed eaters alone are only effective at a low seedling survival probability (0.005) and are completely ineffective at a seedling survival probability of 0.16.

If we assume that *M. pigra* can recolonize after senescence ($p_{so} = 1$), then the impact of biocontrol can be divided into two effects: first, the reduction in fecundity from 9000 seeds m^{-2} to 6000 seeds m^{-2} in the interior of stands and to 2000 seeds m^{-2} on the edges of stands, and secondly opening up the edges of stands to light, allowing grasses to invade and exclude *M. pigra* seedlings, $p_{so,e} = 0, p_{so,i} = 1$. From Fig. 3 it can be seen that the reduction in fecundity is only effective when $s = 0.005$ and $p_{distU} = 0.01$ (where $p_{so,i} = 1$ and $p_{so,e} = 1$), whereas reductions in proportion of sites occupied by *M. pigra* over a wider range of s and p_{distU} values can be achieved by changing $p_{so,e}$ to 0. Increasing the maximum age from 5 to 10 makes the populations marginally more difficult to control (Figs 2 and 3).

Table 2. Mean \pm SE time taken to reduce the proportion of *M. pigra* in a site from 90% to < 5% through biocontrol alone. Two biocontrol scenarios are examined, global biocontrol with $F = 2000$ and $p_{so} = 0$ and edge biocontrol with $F_{int} = 6000$, $F_{edge} = 2000$, $p_{so,i} = 1$ and $p_{so,e} = 0$

Mean (years)	SE	A_{max}	s	p_{distU}
Edge biocontrol, $F_{int} = 6000$, $F_{edge} = 2000$, $p_{so,i} = 1$ and $p_{so,e} = 0$				
13	0	5	0.005	0.01
24.75	0.76	5	0.005	0.05
24.5	0.26	10	0.005	0.01
29.25	2.35	5	0.05	0.01
Global biocontrol, $F = 2000$, $p_{so} = 0$				
12	0.08	5	0.005	0.01
23.8	0.35	5	0.005	0.05
23.21	0.18	10	0.005	0.01
29	1.26	5	0.05	0.01

The time taken for biocontrol to reduce the proportion of *M. pigra* in a site from 90% to < 5% is given in Table 2. Even under the most optimistic parameter values (very low disturbance, short life time and very low seedling survival), biocontrol would take at least 12 years to be effective, and could take up to 29 years under slightly less optimistic parameter sets. Other methods of control are therefore needed to reduce the undesirable impacts of *M. pigra* stands in the short to medium term.

INTEGRATED WEED MANAGEMENT

Figure 4 gives an example of the chronology of a multiple-year treatment (the 3-year herbicide/mechanical

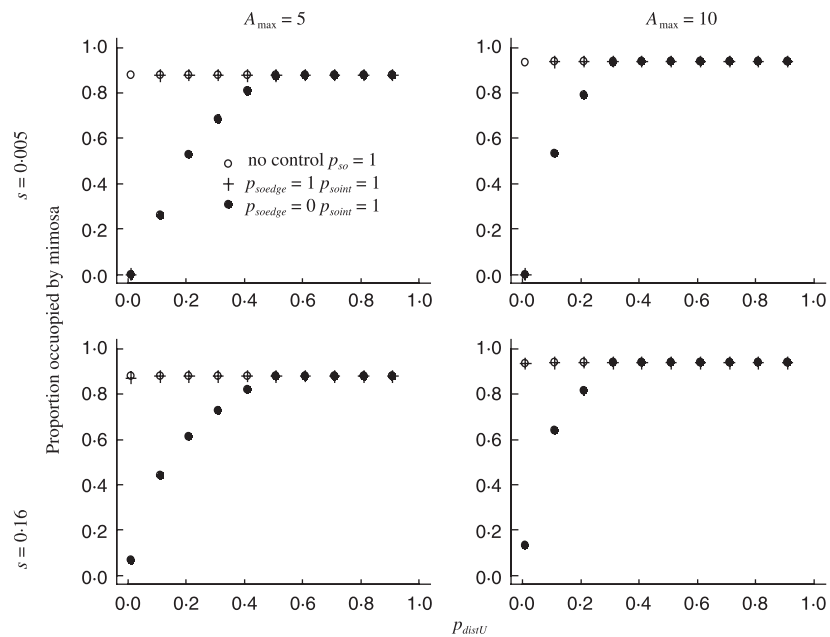


Fig. 3. Proportion of sites occupied by *M. pigra* assuming $p_{distM} = 0.05$ and $A_{min} = 1$, $A_{max} = 5$ or 10 and $s = 0.005$ or 0.16 . The points are from the following simulated scenarios: open circles, no control $F = 9000$; crosses, edge biocontrol ($F_{int} = 6000$, $F_{edge} = 2000$) with $p_{so,e} = 1$ and $p_{so,i} = 1$; filled circles, edge biocontrol with $p_{so,e} = 0$ and $p_{so,i} = 1$. In the first two scenarios *M. pigra* can self-replace after senescence, in the third scenario *M. pigra* can self-replace in the interior of stands but not at the edge where biocontrol agents open up the canopy allowing grasses to invade and exclude *M. pigra* seedlings.

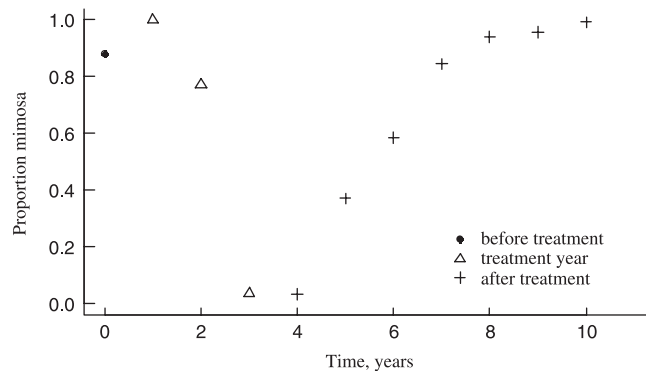


Fig. 4. The effect of IWM treatments over time; years are on the x -axis and proportion of *M. pigra* is on the y -axis. This figure is an example of a management simulation run at just one disturbance level and is presented in order to clarify understanding of the meaning of symbols in the following Figs 5–8, which are presented for a range of disturbance levels. The treatment is year 1, herbicide; year 2, mechanical control + fire; year 3, herbicide; $p_{distU} = 0.61$, $s = 0.05$, $A_{max} = 5$. The solid circle represents the proportion of *M. pigra* before chemical or physical control, the triangles represent the proportion of *M. pigra* in treatment years, and the crosses indicate the recovery of *M. pigra* over the following years (up to 10 years after the first treatment). These symbols are used in Figs 5–8.

control + fire/herbicide treatment) and subsequent recovery; the symbols used in Fig. 4 are subsequently used in all other IWM plots. The 2-year treatments tested (herbicide/fire; herbicide/mechanical control + fire) gave the same results and only reduced *M. pigra* site occupancy at low disturbance rates, $p_{distU} < 0.2$, low seedling survival probability, $s = 0.005$, and with edge biocontrol (see Fig. 5 for herbicide/mechanical control + fire; the abundance of + symbols in Fig. 5 indicates that sites recovered occupancy within 10 years of treatment). The 3-year treatments with edge biocontrol were the most effective, with elimination of *M. pigra*

achievable at all disturbance rates ($p_{distU} = 0-1$) for low seedling survival, and at low disturbance rates for higher values of seedling survival (Fig. 6; the absence of + symbols indicates effective control up to 10 years after treatment).

For the 3-year treatments, we investigated the effects of self-replacement of *M. pigra* on the proportion of sites occupied. Figure 7 shows the 3-year herbicide/mechanical control + fire/herbicide treatment without biocontrol, where *M. pigra* can recolonize senescent sites ($p_{so} = 1$). Compare this with Fig. 6, which has edge biocontrol and $p_{so,e} = 0$ and $p_{so,i} = 1$. Figure 7 has more

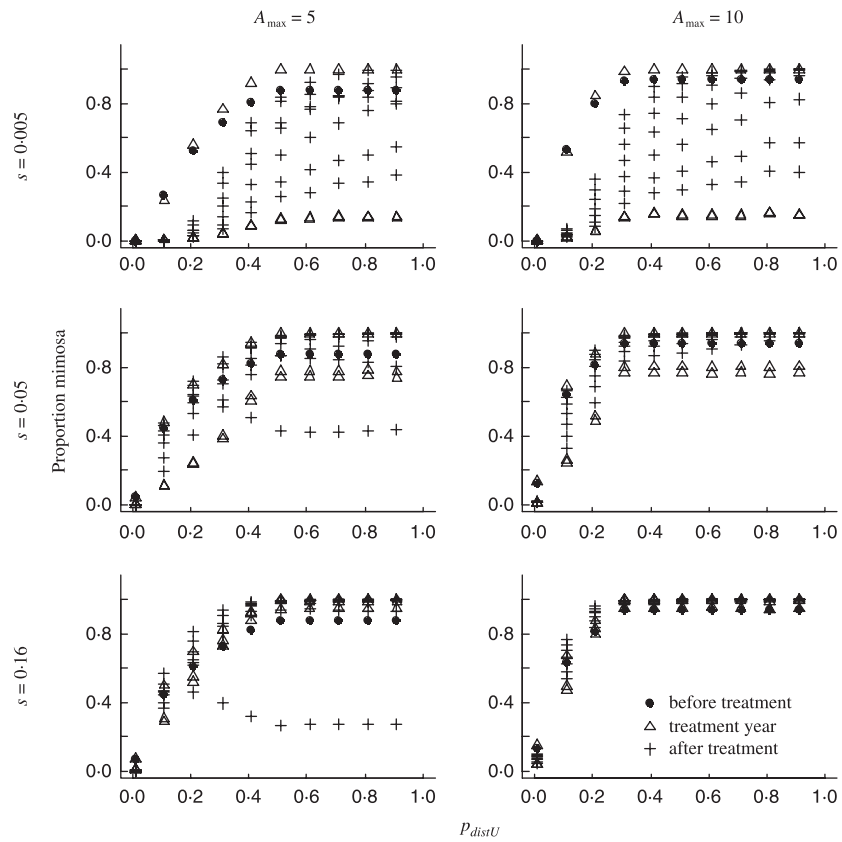


Fig. 5. Impact of a 2-year treatment with edge biocontrol on proportion of sites occupied by *M. pigra*. Year 1, herbicide; year 2, herbicide, mechanical control and fire; $p_{so,e} = 0$ and $p_{so,i} = 1$. See Fig. 4 for an example of the use of symbols in a chronology.

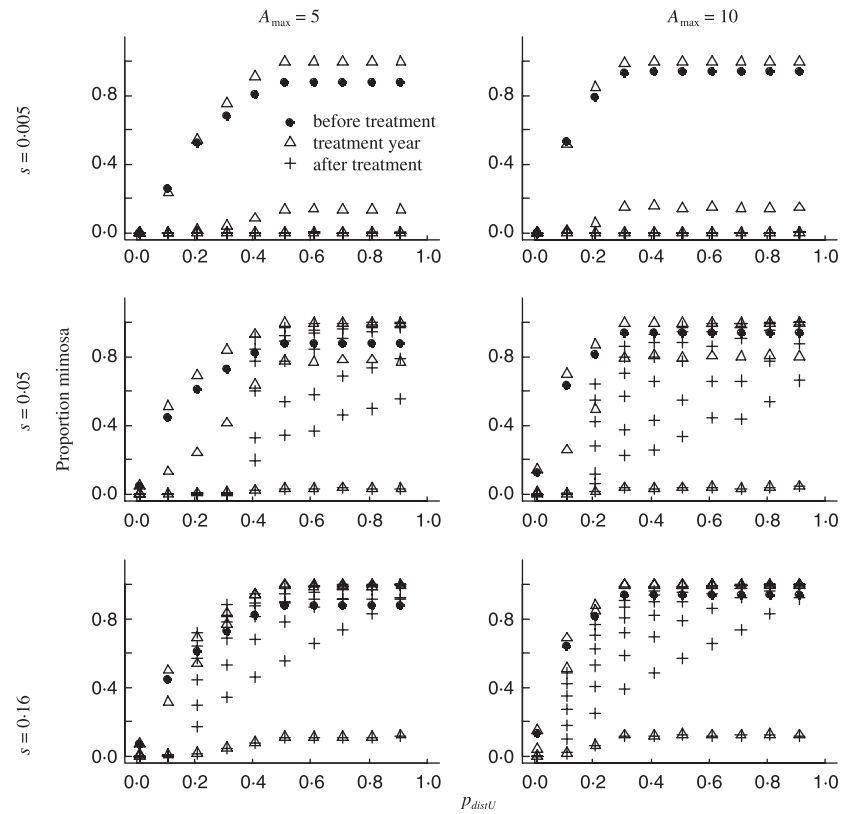


Fig. 6. Effects of a 3-year treatment on proportion of sites occupied by *M. pigra*. Year 1, herbicide; year 2, mechanical control and fire; year 3, herbicide. Edge biocontrol with $p_{so,e} = 0$ and $p_{so,i} = 1$. See Fig. 4 for an example of the use of symbols in a chronology.

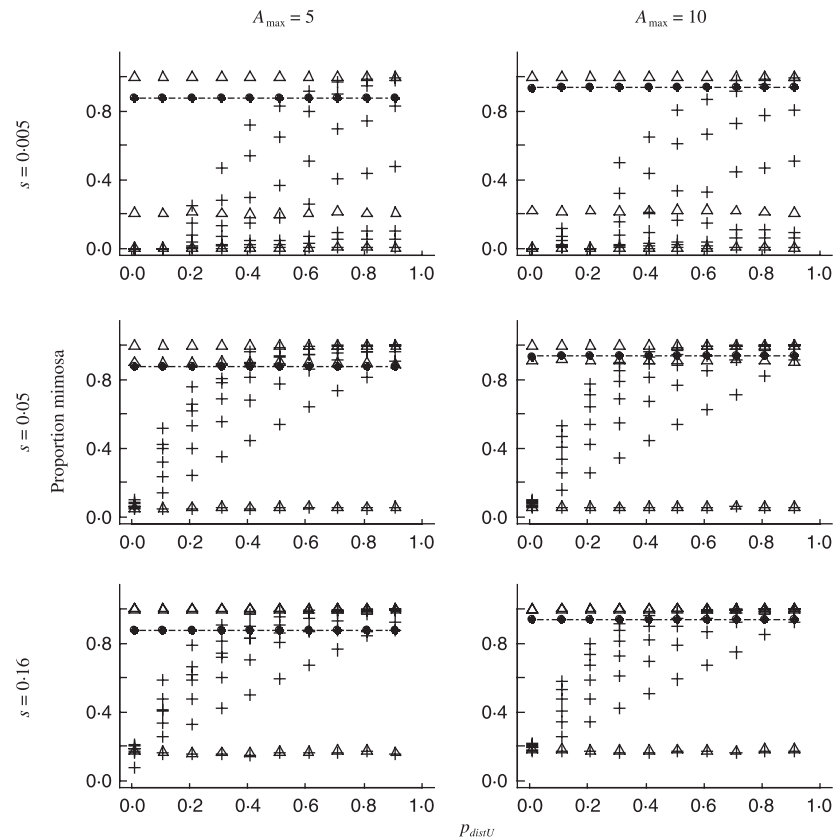


Fig. 7. Effects of a 3-year treatment on proportion of sites occupied by *M. pigra*. Year 1, herbicide; year 2, mechanical control and fire; year 3, herbicide. No biocontrol with self-replacement, $p_{so} = 1$. The broken line gives the saturation approximation for M^* at $p_{so} = 1$ (equation 5). See Fig. 4 for an example of the use of symbols in a chronology.

+ symbols at lower disturbance levels than Fig. 6, indicating faster recovery at low disturbance. Biocontrol greatly increases the range of parameter values over which complete control can be achieved. Without biocontrol, complete control is only achieved at low seedling survival ($s = 0.005$) and low disturbance rates ($p_{distU} < 0.2$) (Fig. 7). With edge biocontrol, elimination of *M. pigra* is achieved at low seedling survival ($s = 0.005$) at all disturbance rates, and at low disturbance rates ($p_{distU} < 0.4$) for $s = 0.05$ and $A_{max} = 5$ or $p_{distU} < 0.2$ for $A_{max} = 10$, (Fig. 6). The additional value of biocontrol is not just due to reduced fecundity. Prevention of *M. pigra* self-replacement at the edges is important. At a higher seedling survival probability, one can see how edge effects of biocontrol help by comparing the biocontrol scenario in Fig. 8, where $p_{so,e} = 1$ and $p_{so,i} = 1$, with the biocontrol scenario in Fig. 6, where $p_{so,e} = 0$ and $p_{so,i} = 1$. The fecundities are the same in Figs 6 and 8, $F_{edge} = 2000$ and $F_{int} = 6000$; they only differ in the probability of recolonization at the edges.

Discussion

We have demonstrated that a 3-year herbicide/mechanical control + fire/herbicide management system should be effective at controlling *M. pigra* at low disturbance rates and low seedling survival probabilities. Control over a wider range of disturbance rates and seedling

survival probabilities is achievable only if edge biocontrol is added. The 2-year herbicide/mechanical control + fire treatment is only effective at the lowest seedling survival and disturbance rates, with populations of *M. pigra* quickly recovering once control is removed.

Both plant attributes and attributes of the ecosystem, such as disturbance regimes and succession trajectories, are responsible for regulating weed occupancy in these models. *Mimosa pigra* occupancy is determined by disturbance, longevity and probability of recolonization of senescent sites. The positive effect of disturbance on *M. pigra* site occupancy provides further evidence that the culling of large populations of feral water buffalo, which heavily overgrazed floodplain vegetation, was responsible for a decline in the rate of expansion of *M. pigra* (Lonsdale 1993). It is not always possible to reduce disturbance if feral mammals such as water buffalo and pigs cannot be controlled, or if fuel loads build up and increase fire frequency. Management techniques in addition to biocontrol will have to be employed where disturbance cannot be reduced. Disturbance has been implicated as a causal or aggravating factor in many studies of invasive plants (D'Antonio, Dudley & Mack 1999). Seabloom *et al.* (2003) showed experimentally that exotic annual grasses in California are not superior competitors to the native perennials but are better at exploiting disturbances caused by overgrazing and drought.

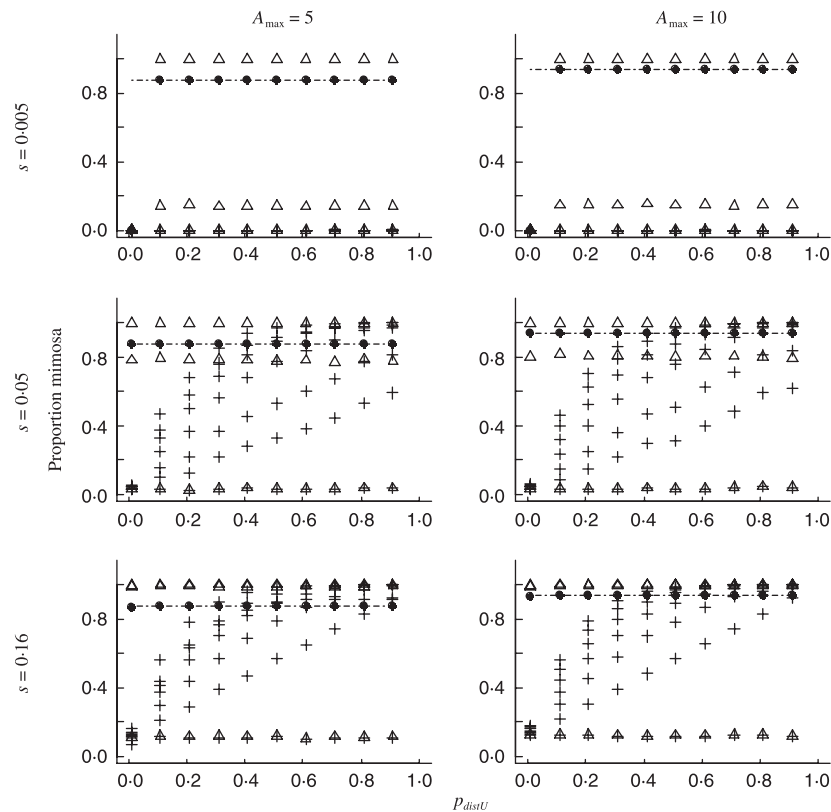


Fig. 8. Effects of a 3-year treatment on proportion of sites occupied by *M. pigra*. Year 1, herbicide; year 2, mechanical control and fire; year 3, herbicide. Edge biocontrol with self-replacement at edge and interior sites, $p_{so,e} = 1$ and $p_{so,i} = 1$. The broken lines gives the saturation approximation for M^* at $p_{so} = 1$ (equation 5). See Fig. 4 for an example of the use of symbols in a chronology.

As is the case for other woody legume shrubs (Rees & Paynter 1997; Rees & Hill 2001), it is clear that biocontrol alone may not always reduce *M. pigra* populations, especially when seedling survival and disturbance levels are high and continuous cover of an alternative plant community is not always maintained. Insects that reduce plant fecundity alone will have to be extremely efficient in order to reduce *M. pigra* occupancy. We have shown that, even under optimistic parameter values where biocontrol can reduce *M. pigra* populations to < 5% cover, this can take decades to occur, making other control strategies necessary in the short to medium term. It is the effects of the biocontrol agents on self-replacement that most affect *M. pigra* occupancy, and not the reduction in fecundity. Even in the IWM scenario this effect can be detected. This indirect manipulation of succession by biocontrol agents is a novel addition to models of this kind. Our results are supported by Paynter, Downey & Sheppard (2003), who argued that, in the native range, stands of the woody legume shrub *Cytisus scoparius* L. (Link) were less likely to be recolonized after senescence compared with exotic populations, due to insect herbivory enabling competing vegetation to establish beneath attacked stands and reducing seedling survival, as well as the effects of the insects on plant fecundity.

Biocontrol will obviously only be effective in an IWM programme if the biocontrol agents can be

maintained in the system. *Neurostrota gunniella* populations can be maintained in herbicide-treated populations of *M. pigra* (Paynter 2003), but biocontrol agent populations are likely to be wiped out locally after fire. In order to maintain biocontrol in an IWM programme, the agents should be able to disperse quickly or be re-released into the treated areas. *Neurostrota gunniella* is known to disperse extremely rapidly over many kilometres (Wilson & Forno 1995). However, *C. mimosa* is less mobile, spreading at a rate of $c. 2 \text{ km year}^{-1}$ (Ostermeyer 2000), so redistribution of this agent may be required when very large or isolated *M. pigra* stands are treated.

The modelling approach taken in this study is particularly informative as the analytical solutions highlight parameters of interest. These are then explored in detail in simulation models that incorporate more realistic management regimes and the complex spatial effects of the biocontrol agents. The predictions and recommended management strategies from this work should now be tested more extensively in the field so that robust recommendations for land managers can be developed. These recommendations are justifiable in terms of the biology of the system and are therefore more likely to be acted upon by risk-averse farmers and land managers, rather than 'black box' prescriptions that have to be taken on trust.

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Appendix 1

Notation	Description
A_{\max}	Maximum age of <i>M. pigra</i> plant
d	Probability of loss from the seed bank (subsumes decay and germination losses)
F	Average plant fecundity
F_{edge}	Average plant fecundity in edge sites
F_{int}	Average plant fecundity in interior sites
f_r	Fraction of sites of reproductive age
g	Germination probability
M_t	Proportion of sites occupied by <i>M. pigra</i> at time t
M^*	Equilibrium fraction of sites occupied by <i>M. pigra</i>
O_t	Proportion of sites previously occupied by <i>M. pigra</i> that have reached A_{\max} and senesced, becoming suitable for recolonization with probability $p_{so} > 0$
p_c	Probability of colonization, a function of S_i
$p_{\text{dist}M}$	Probability of disturbance for <i>M. pigra</i> site
$p_{\text{dist}U}$	Probability of disturbance of unsuitable site (U_i)
p_{so}	Probability of recolonization by <i>M. pigra</i> of a senescent M_t site
$p_{so,e}$	As for p_{so} but referring to edge sites
$p_{so,i}$	As for p_{so} but referring to interior sites
S_t	Average density of seeds in a site
S^*	Equilibrium average seed density in a site
s	Seedling survival probability
U_t	Proportion of sites occupied by other vegetation and therefore unsuitable for <i>M. pigra</i> recruitment at time t
z_i	proportion of <i>M. pigra</i> sites aged i
z_{\max}	proportion of <i>M. pigra</i> sites aged A_{\max}
θ	the critical proportion of seeds that must be destroyed to eliminate <i>M. pigra</i>

Appendix 2

Here we derive the condition for invasion of *M. pigra* into a virgin habitat. To do this we linearize the equations for M_{t+1} , S_{t+1} and O_{t+1} (equation 3), using the substitution $U_t = 1 - M_t - O_t$, about the point $M_t = S_t = O_t = 1$, and form the Jacobean matrix given by:

$$\mathbf{A} = \begin{pmatrix} \partial M_{t+1} / \partial M_t & \partial M_{t+1} / \partial S_t & \partial M_{t+1} / \partial O_t \\ \partial S_{t+1} / \partial M_t & \partial S_{t+1} / \partial S_t & \partial S_{t+1} / \partial O_t \\ \partial O_{t+1} / \partial M_t & \partial O_{t+1} / \partial S_t & \partial O_{t+1} / \partial O_t \end{pmatrix}. \quad \text{eqn 11}$$

The eigenvalues, λ , of \mathbf{A} , which determine the success of an invasion, are solutions of the characteristic equation:

$$\lambda[\lambda^2 - [(1 - p_{\text{dist}M})(1 - z_{\max}) + (1 - d)]\lambda + (1 - d)(1 - p_{\text{dist}M}) + z_{\max}(1 - d)(1 - p_{\text{dist}M}) - Ff_r g s p_{\text{dist}U}] = 0 \quad \text{eqn 12}$$

Clearly $\lambda = 0$ is one root and given this there is a single root greater than one (indicating successful invasion) providing:

$$(1 - p_{\text{dist}M})(1 - z_{\max}) + \frac{p_{\text{dist}U} g s F f_r}{d} > 1. \quad \text{eqn 13}$$

This is the invasion condition given in the main text.