Exploring interactions between cultural and biological control techniques: modelling bitou bush (*Chrysanthemoides monilifera* ssp. *rotundata*) and a seed fly (*Mesoclanis polana*)

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**Summary**

Weed seed-production and seedbank dynamics have been a focus of attention for many biological control campaigns. This interest has perhaps been promoted by the recognition of the important role of weed seed dynamics in annual cropping systems, and frequent observations that seed production is markedly increased in ranges into which a plant is introduced, compared with rates in its native range.

Seeds are the means by which most higher-order perennial plants disperse, and reestablish following disturbance. The role and importance of seeds in the population dynamics of weed populations depends upon factors such as successional state of the invaded vegetation association, the disturbance frequency, plant age at maturity, seed decay rate, and self-thinning patterns. The role of seeds and their predators in maintaining a plant population may be minimal, and decreasing the rate of seed production and the size of the seedbank may have only minor impacts on the population dynamics of perennial weeds.

The interactions between cultural management techniques for bitou bush and its seed fly were explored using a process-based population dynamics model. The role of the seed fly in reducing the invasive potential of bitou bush and modifying the population reestablishment rates following disturbance were studied. The seed fly has substantially reduced seed production, but the effect of the fly on canopy cover of bitou bush and on its invasion potential appears negligible. These findings highlight the importance of using models to explore beyond the immediate effects of an agent on its host to gauge its ultimate impact on the weed population, and to better understand the interactions between cultural and biological control processes.

**Keywords:** DYMEX, integrated weed management, population model, seedbanks, seed-feeder.

**Introduction**

Bitou bush, *Chrysanthemoides monilifera* ssp. *rotundata* (Asteraceae) is a noxious invasive weed within most temperate coastal areas of the eastern Australian mainland. The success of bitou bush as an invasive species has been attributed to its ability to outcompete and swamp other species in the community by its seed production and seedbank. Since 1989, bitou bush has been a target for biological control. *Mesoclanis polana* (Tephritidae), a native seed-fly predator of bitou bush in South Africa, has been established since 1996 within Australia. By feeding on the developing ovary of bitou bush fruits, *M. polana* larvae could reduce greatly the number of viable seed that enters the seed bank or is dispersed.

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Following releases in northern New South Wales (NSW), *M. polana* spread rapidly in Australia, extending into more southerly latitudes than in its native range in South Africa. However, despite the rapid nature of the invasion by *M. polana*, impact studies have indicated that bitou bush seed destruction rates have been generally low, ranging from 23% to 31% across the latitudinal range of bitou bush in Australia (Stuart et al. 2002). These rates are well below the 95% seed destruction levels thought necessary to achieve satisfactory control of bitou bush in the absence of other control techniques (Noble and Weiss 1989).

A population dynamics model (B2) was previously built using DYMEX™ (Maywald et al. 2004) to simulate the population dynamics and management of bitou bush at Moruya, on the south coast of NSW (D.J. Kriticos, unpublished data). The parameterization of B2 relied mostly on observations made by Weiss (1983) at Moruya, and included a mixture of growth index and chronologically based life processes. A review of this model (Kriticos & Groves 2000) argued that the model should be verified at sites apart from Moruya, and *M. polana* should be included. We could then explore the interaction between cultural control techniques and the best established biological control agent.

B2 was adapted so that it could simulate populations of bitou bush growing at different latitudes along the NSW coastline, and included modules describing the life cycle of *M. polana* and its interaction with bitou bush (Stuart et al. 2002). The adaptations required that the model life processes were reformulated from a weekly to a daily time scale to accommodate the faster rate of processes involved in the insect life cycle compared with that of bitou bush. The resulting model was named B2MP. To our knowledge B2MP is the first cohort-based process-driven population dynamics model built to simulate the dynamics of a weed species and its biological control agent (Barlow 1999).

In this study, B2MP is used to simulate the interactions between cultural techniques (fire and herbicide), and the introduced biological control agent *M. polana* with a view to understanding the ultimate impact of *M. polana* on bitou bush population dynamics, and identifying guidelines for integrated management of bitou bush.

**Materials and methods**

**The model**

B2MP (Stuart et al. 2002) is a process-based population dynamics model built using DYMEX™ (Maywald et al. 2004). The model includes life cycles for bitou bush and *M. polana* (Fig. 1), ignoring the presence of other vegetation. The modelled interactions between bitou bush and *M. polana* include density-dependent feedback on oviposition and larval survival rates (Fig. 2). The development and survival of *M. polana* larvae are related to the growing conditions of bitou bush through the growth index, which is based on temperature and modelled soil moisture.

**Figure 1.** Life cycle diagrams of (A) bitou bush and (B) *Mesoclanis polana* included in the B2MP model. Unshaded boxes indicate life stages that are endostages – stages that are “within” (and therefore dependent upon) another stage – in this case, the adult bitou bush plant. Endostages are removed from the simulation whenever the cohorts containing those stages are removed through stage transfer or death.
B2MP includes an immigration function for *M. polana*. When enabled, the immigration process introduces two teneral females on each day that the following conditions are met: there are no other female flies, the temperature is suitable for flight (>11°C), and there is at least one bitou bush ray floret. This function was introduced to deal with a scaling problem where there are insufficient flowers and seeds available in a 1 ha patch at certain times of the year in order to support a population of *M. polana*. Similarly, without such an immigration process, post-fire populations of *M. polana* would not reestablish.

Herbicide application and fires of various intensities are the two cultural control techniques included in B2MP. Herbicide kills seedlings and immediately removes them from the simulation. Juvenile and adult plants are moved into the standing dead plant category which maintains their contribution to canopy cover and therefore suppression of seedling development and survival until they decay. Herbicide is assumed to have no direct effect upon fly populations. The death of adult plants removes the reproductive endostages (Fig. 1), which in turn kills *M. polana* larvae and pupae.

The effects of each fire depends upon its intensity (class 1 fires have a negligible effect on plants or the seedbank, whilst class 3 fires clear all standing plant material and reduce the seedbank). Moderate or high intensity fires are assumed to kill eggs, larvae and pupae of *M. polana*. Adult flies are also removed from the simulation following moderate to high intensity fires on the assumption that fires prompt them to migrate out of the simulation zone. Fly populations can then reestablish from small numbers of immigrant females. Following fires, a nutrient pulse is added to a soil fertility module. This is used to increase the growth rate of bitou plants for up to two years. For simplicity, the amount of the fertility pulse is always set to top up the nutrient store to capacity following each fire. It is likely that the nutrients added to the soil are the non-volatile components of plants, and so the mechanism is thought to be adequate, even under repeated fires. In B2MP, the intensity of fires is a user-defined parameter. Simulations that include high frequency, high intensity fires should therefore be avoided as it is unreasonable to expect that the plant community could support repeated high intensity fires without time for the standing biomass to accumulate sufficient fuel.

**Model validation**

Comprehensive validation of a complex process-based simulation model such as B2MP, involving a long-lived perennial plant, is impossible. Instead, it is necessary to undertake a diffuse validation process, gradually building up confidence in the model by comparing model results with field and experimental evidence (Starfield & Bleloch 1991). Stuart (2002) compared model predictions of flower production with field observations for five sites across the range of bitou bush in Australia; the level of agreement in terms of seasonality and intensity of flowering was quite acceptable. The close linkage between plant growth and flowering in bitou bush makes this a good state variable with which to assess the overall behaviour of the model. Otherwise, the model appears to behave in accord with field observations in terms of plant growth rates, maturation rates, seedling recruitment patterns, seedbank dynamics etc. Whilst the annual attack rate of seeds at all sites compared favourably with field observations, during the winter months (August to October), predicted attack rates were much higher than field observations. The reasons for the discrepancy are unknown, but sugges-

![Figure 2. A schematic diagram of the interactions between the bitou bush and Mesoclanis polana life cycles used in B2MP.](image-url)
tions include reduced oviposition rates under cool or clouded conditions, or the use of an index of oviposition site finding efficiency that is inappropriate at low flower densities. Fortunately, the net effect of this discrepancy on the overall model behaviour is minimal because the seed-production rates during this period are minimal.

The transient nature of the bitou bush seedbank is well illustrated in B2MP with large numbers of seedlings germinating and then, in the presence of competition from larger established plants, the seedlings succumb to competition.

Model simulations

For comparative purposes, all simulations were initialized in the same manner, starting on the 1st January 1995 with 1200 juvenile plants and 2000 adult plants. This choice gave some age structure to the population and was based upon previous experience that indicated that site occupancy by bitou bush is rapid, and once the canopy has closed, a dynamic equilibrium seedbank was rapidly established. Two thousand adult flies (one per 5 m$^2$) were introduced in April 1995. Treatments were then imposed in 1998, leaving time for significant initialization artefacts to wash out of the system prior to imposing management treatments.

High intensity fires were applied in late Summer (March), when temperatures had started to wane. Similarly, herbicide was applied in Autumn (late April) when bitou bush growth is generally strong, to facilitate translocation of the herbicide.

Weather data for the simulations were obtained from the Queensland Department of Natural Resources and Mines silo datdrill website <http://www.nrm.qld.gov.au/silo/>.

The simulations included firstly a partial factorial combination of *M. polana* presence, fire event and herbicide application. After considering the results of these simulations, the effects of herbicide followed by a fire, and the combination of *M. polana* and a generic vegetative control agent were simulated.

All simulations that included fly populations also included fly immigration processes; on any day that flower buds were present and flies were absent from the simulation, two teneral flies are introduced into the study population.

Results

No control

In the absence of any management disturbance or biological control effects, bitou bush rapidly attains canopy closure (100% canopy cover) and a dynamic equilibrium seedbank size that accords with the field observations (Fig. 3). The adult plants subsequently undergo self-thinning as remaining plants increase in size. Seedlings emerge and die due to competition with adult plants before they reach juvenile size (not shown).

Biological control – *M. polana*

The inclusion of *M. polana* in the simulation (Fig. 4) has a negligible effect on the population dynamics of bitou bush due to the limited seed damage rate and high seedling mortality due to asymmetric competition between seedlings and adults.

Fire

In the absence of *M. polana*, a high intensity fire applied in March 1997 removed the adult bitou bush plants and a proportion of the seedbank (Fig. 5). Within a month of the fire, the remaining seedbank produced a carpet of seedlings that closed the canopy. The growth rate of the seedlings in the high nutrient post-fire conditions was sufficient for them to mature within one and a half years of germinating. *Mesoclanis polana* had a negligible effect on the post-fire population dynamics of
bitou bush (Fig. 6). Density-dependent self-thinning processes act to buffer the effect of a reduction in the size of the post-fire seedling flush.

**Herbicide**

Herbicide applied in late April 1997 killed the standing adult bitou bush plants, creating standing dead plant material that reduced the vigour of the seedlings and juveniles that developed subsequently (Fig. 7). In the four years it took for the first post-herbicide adult plants to develop, the seedbank was depleted due to the suspension of inputs and the continuation of the germination and seed decay processes. The presence of flies had a negligible effect on these processes (Fig. 8).

Figure 4. Simulated population dynamics of bitou bush and *Mesoclanis polana* at Moruya without cultural management disturbance.

Figure 5. Simulated population dynamics of bitou bush at Moruya in the absence of *Mesoclanis polana* with a fire in March 1997.

Figure 6. Simulated population dynamics of bitou bush and *Mesoclanis polana* at Moruya with a fire in March 1997.
Except for continued presence of adults immediately following the herbicide application, flies are absent when there are no flowers present (i.e. no adult plants present).

**Herbicide and fire**

Applying a herbicide to the population in April 1997, and then applying a fire in March 2000 after the seedbank had been depleted, resulted in the elimination of bitou bush from the simulation (Fig. 9).

*Figure 7.* Simulated population dynamics of bitou bush at Moruya in the absence of *Mesoclanis polana* with herbicide applied in April 1997.

*Figure 8.* Simulated population dynamics of bitou bush and *Mesoclanis polana* at Moruya with herbicide applied in April 1997.

*Figure 9.* Simulated population dynamics of bitou bush and *Mesoclanis polana* with a herbicide applied in April 1997 and a fire in March 2000.
Biological control – generic foliage feeder

The inclusion of a generic vegetative biological control agent as a complement to *M. polana* in the simulation had a marked effect on the seasonal pattern of bitou bush canopy cover, though no effect on the number of adult plants (Fig. 10). The generic agent reduced the number of *M. polana* present due to reduced flowering and seeding.

**Discussion**

Integrated weed management (IWM) has become something of a catchcry amongst weed scientists and managers. As with the term weed, the definition of IWM is problematical because it is subjective; varying widely depending upon the weed management context and the perspective of the user. However, the basic notion of IWM includes recognition that single weed management techniques are unlikely to be sufficient to achieve satisfactory control, and that different techniques may have interactive effects.

Bitou bush has a *transient* seedbank *sensu* Begon et al. (1996) and a short to moderate maturation period depending upon nutrient conditions. Following fires, the maturation period is 1–2 years at Moruya, and in the order of 5–6 years in the absence of a fire-induced nutrient pulse. From Figure 9, it appears that there may be an opportunity to usefully combine a herbicide treatment with a fire or a second herbicide application several years later when the seedbank has been depleted, but juvenile plants have not yet matured. As a follow-up to a herbicide application, fire has the advantage that a portion of any remaining seed may be killed by the fire. If fire is used, the nutrient-enhanced seedbed could also support restoration plantings and sowings. At northern sites, the window of few or no seeds of bitou bush combined with juvenile plants may be narrower, or may not exist due to higher growth rates of bitou bush plants. A set of experiments to test this hypothesis across several sites would be instructive.

As a seed fly, *M. polana* can only act upon mature bitou bush plants. Its role in the biological control program is therefore confined to suppressing seed dispersal from existing mature stands of bitou bush, and reducing the size of the seedbank beneath such stands. The effect of *M. polana* may be to widen any gap between the depletion of the seedbank and the recommencement of flowering in a patch following herbicide application (Figs 7 and 8). If such an effect is real, then it appears to be a small benefit. B2MP ignores any increase in soil fertility due to litter fall following herbicide application and, consequently, any potential increase in seedling growth rates, and hence rate of attainment of maturity. This may act to diminish any potential management window between the depletion of seedbank and attainment of maturity in the bitou bush population.

A 23–31% reduction in seed production is unlikely to lead to similar reductions in the rate of invasion from occupied patches. Reduced seed production may lead seed dispersers to forage more extensively, and there is a large degree of density-dependent reduction in site invasion rates due to clumped dispersal of seed under perch trees employed by currawongs and fox dung sites (Weiss 1983).

From Figure 10, it appears that biological control agents that open up the bitou bush canopy periodically offer hope that other (native) species may invade and occupy that space. Such modelling indications support ongoing efforts to get *Comostolopsis germana* and *Tortrix* spp. established in the field.

This study raises the question: what level of fitness reduction by biological control agents is necessary for bitou bush’s competitors, such as *Acacia longifolia* to gain an advantage? Is there a competitive crossover

![Figure 10. Simulated population dynamics of bitou bush with *Mesoclanis polana* and generic biological control agent that attacks the leaves of bitou bush, removing 0.5% of the canopy per day for the three month active period during autumn.](image-url)
point where whole plant fitness would lead to a rank
reversal in plant community composition between bitou
bush and A. longifolia. The fact that A. longifolia
outcompetes bitou bush in South Africa (Henderson
2001) suggests that such a point does exist. The corol-
mary of this question is whether this crossover point can
be achieved with herbivores and pathogens of bitou
bush which have so far been identified as potential
biological control candidates. The lack of consideration
of the presence of other vegetation means that it is
impossible using B2MP in its current form to consider
whether control techniques could affect the competitive
relationship described by Weiss (1983) between A.
longifolia and bitou bush in such a manner that A. longi-
ofolia could either resist invasion by bitou bush, or rein-
vade sites dominated by bitou bush.

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