Modelling the biological control of bitou bush (*Chrysanthemoides monilifera*: Asteraceae) by *Mesoclanis polana* (Tephritidae)

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Summary Bitou bush has been the subject of a biocontrol campaign in Australia since 1987. Several agents have been successfully established, including the bitou bush seed fly, *Mesoclanis polana*.

Recently, there has been increasing interest in assessing the impact of weed biocontrol programs including bitou bush, so that the success of importations could be gauged in more meaningful terms than simply whether the agent became established, or whether it reduced seed production by a measured amount (Kriticos and Groves 1999). In the case of bitou bush, the perceived 'weediness' is not related to either its fauna, or its seedbank, but rather, to its dominance of coastal vegetation communities and suppression of native vegetation. These factors are directly related to the canopy cover proportion of bitou bush in any land catena. Depending upon the life history traits of the agent and target, the disturbance regime, plant community composition, and other environmental factors, there may be very little relationship between the average bitou bush canopy cover and its seed production rate.

A modelling methodology was adopted to explore the likely impact of *M. polana* upon bitou bush across the range of the fly in Australia. A process-based population dynamics model of bitou bush was modified to incorporate the effects of *M. polana*. This involved changing the timestep from weekly to daily, including a detailed lifecycle module for *M. polana*, and creating the linkages between the lifecycles of the weed and the seed fly. The model was used to assess the impact of the seed fly on the population dynamics of bitou bush under a variety of environmental conditions, and in association with the typical cultural management techniques employed against bitou bush.

Keywords Biological control, bitou bush, DYMEX, ecological modelling, *Mesoclanis polana*.

INTRODUCTION

Bitou bush (*Chrysanthemoides monilifera* ssp. *rotundata* (DC.) T.Norl. (Asteraceae: Calenduleae)) is a noxious invasive weed within coastal areas of eastern Australia. Within NSW, it inhabits more than 60% of the coastline, and is the dominant plant species in more than 20% of the coastline vegetation (Love 1984).

Bitou bush populations are able to produce up to 5000 seeds m^{-2} during the year, with about 80% produced during the main flowering period in autumn. Thus, with very few natural seed predators and seed dispersal via birds, bitou bush has a formidable seedbank within Australia. Consequently, the success of bitou bush as an invasive species in Australia has been partly attributed to seed dispersal, and its ability to numerically swamp other species in the community via the seed bank, and partly to a higher relative growth rate of seedlings (Weiss 1983, Noble and Weiss 1989). Bitou bush displaces native dune species, such as *Lomandra longifolia* and *Acacia longifolia*, suppresses the regrowth of native *Banksia* spp., and thus, limits native biodiversity within dune areas (Weiss 1983).

Since 1987, bitou bush has been the subject of a biological control program. In 1996, a seed-feeding fly (*Mesoclanis polana* Munro. (Diptera: Tephritidae)), native to bitou bush in South Africa, was released in northern NSW. What followed was a rapid population expansion, with the seed fly managing to establish in virtually all bitou bush populations along more than 1200 km of the eastern Australian coastline within two years of release (Edwards *et al.* 1999). The widespread distribution in all populations suggests that the fly has both very high dispersal ability and is capable of very rapid population growth rates.

Satisfactory control of bitou bush with a predispersal seed predator has been predicted to be achieved only if there is a greater than 95% reduction in seed-fall to the seedbank over the entire year (Noble and Weiss 1989), and especially during the peak flowering period (i.e., when seed-fall is abundant). The seedbank size influences the initial number of recruits following a disturbance. In combination with seedling and juvenile growth rates, and time to maturity, the seedbank size influences the rate of invasion of a site, and the rate of population recovery following disturbance. Based upon ring counts, bitou bush appears to live for upwards of 35 years, and any effects of massive seedbank reduction will take a long time to become apparent unless coupled with cultural control (i.e., fire or herbicide) to accelerate the rate of disturbance.

It is highly unlikely that a seed predator such as *M. polana* alone would be able to achieve the massive

seedbank reductions necessary to significantly affect the weediness of bitou bush. However, if other biological control agents such as *Comostolopsis* or *Tortrix* spp. were able to indirectly reduce the reproductive effort of bitou bush, especially during the main flowering period, then the combined effects may be enough to substantially limit seed production. Attack on the vegetation of bitou bush, especially the shoot tips, may result in fewer flowers produced throughout the year. However, with a reduced flower production throughout the year, there are concerns for the persistence of *M. polana* populations.

This paper describes aspects of the population dynamics of bitou bush and the seed fly in terms of biological control and integrated weed management. The annual pattern of attack of the seed fly on bitou bush fruit is described via (1) field survey analysis of bitou bush fruits, and (2) a population dynamics model. This is the first time a cohort-based population dynamics model has been constructed to simulate the complex, interacting dynamics of a weed species and its biological control agent. The model is used to explore the depth of current biological understanding of this system, and to investigate the effectiveness of integrated weed management techniques for the control of bitou bush.

MATERIALS AND METHODS
Field surveys Monthly field surveys were conducted at five bitou bush populations (Table 1) along the NSW coastline between May 2001 and April 2002. In this paper we only present results from Moruya, through the model was built incorporating results from all sites. Within each site, where possible, bitou bush plants were sampled at a fore-, mid- and hind-dune zone. Ten to fifteen plants were selected haphazardly at each site, and tagged plants were at least 2 m apart. On each plant, five capitula (i.e. flowers or flowerheads) of immature fruits were collected for analysis.

Each fruit was removed from its capitula and analysed for scars that indicate the presence of *M. polana* larvae or pupae. The degree of attack on the fruit was categorised as:
1. Full attack, with the larvae or pupae feeding within the ovary wall of a developing fruit.
2. Full attack, with an early attack by a larva resulting in the fruit aborting.
3. Minimal attack, with an early, but not sustained, attack by a larva having no negative effects on the seed as it is developing into a mature fruit.
4. No attack on the fruit.

Modelling A climate-driven, process-based population dynamics model, B2 (Kriticos, unpublished

Table 1. The location of field survey sites along the east coast of NSW, and the proportion of bitou bush fruits attacked by *M. polana* at each site between May 2001 and March 2002.

Site	Latitude	Fruits attacked	se	n
Iluka	29°59'S	0.26	0.008	2732
Coffs Harbour	30°24'S	0.28	0.008	3029
Port Macquarie	31°45'S	0.23	0.008	2493
La Perouse	34°0'S	0.23	0.01	1633
Moruya	35°91'S	0.31	0.007	3356

data) was built using DYMEX™, a cohort-based population modelling tool (Maywald *et al.* 1999). Within the bitou bush lifecycle, life processes and life-history properties of the average individual in each cohort are simulated on a weekly time-step. Inputs to the bitou bush lifecycle are temperature rainfall, and evaporation records. The rainfall and evaporation data are used to drive two single-bucket soil moisture modules (a shallow germination module, and a deeper plant growth module). Plant growth is driven by a growth index (a combination of a temperature index and soil moisture index which were fitted to field and laboratory observations, not presented).

B2 treats seedbank dynamics in detail, with processes describing dormancy, rotting, dispersal, and germination of seeds, mostly derived from Weiss (1983).

B2 simulates herbicide and fire management effects, creating standing dead plants following herbicide applications, and a nutrient pulse following fires. The nutrient pulse increases plant growth rates for two years following a fire. Total plant canopy cover, including that of standing dead plants, reduces germination.

In order to explore the population dynamics of bitou bush and its seed fly, B2 was modified to include the lifecycle of *M. polana*. A weekly time-step is appropriate for modelling a moderately long-lived perennial plant (~35 years). The more rapid life processes of the seed fly required the model to be redeveloped on a daily timestep. The extended model was named B2MP.

Flowering in B2MP is driven by the annual accumulation of the growth index from the winter solstice.

The lifecycle module of *M. polana* interacts with the flower and fruit stages of the bitou bush lifecycle. Egg-laying was restricted to a maximum of three oviposition bouts, each with two eggs, on a flower. This was based on field attack rate data, and suggests that

only about half of the female florets on each capitula are likely to be attacked. Egg and larval development are driven by temperature and bitou bush growth rate, respectively. Egg and larval mortality rates were based on field data. Female adults become gravid five days from emergence from a fruit, and can potentially lay 56 ± 48 (SD) eggs (n = 21) (Adair and Bruzzese 2000). The effectiveness with which oviposition sites are identified by *M. polana* was assumed to increase from 25% at 2 flowers m^{-2} to 100% at 77 flowers m^{-2}.

Simulations We used B2MP to explore three aspects of the interactions between bitou bush and *M. polana* at Moruya. Firstly, we simulated the mid-term (10 year) effect of *M. polana* on the production of viable seeds, as this is the most proximal effect of the fly on bitou bush. Secondly, in order to get an indication of more ultimate effects we simulated the effect of *M. polana* on the rate of seedling recruitment following a herbicide treatment. Thirdly, the effect of reduced flower production due to the presence of vegetative biological control agents on *M. polana* larval and pupal abundance and attack rate on fruits was examined by running a simulation with heavily reduced flower production (one flower produced per day within an established bitou bush stand).

<div align="center">RESULTS</div>

Field fruit attack rate The proportion of fruits attacked by *M. polana* at each site during the field survey period is shown in Table 1. The average fruit attack rates over all sites ranged from 23% to 31%, with no indication of any latitudinal trends.

Seed production Running B2MP for 10 years at Moruya with and without *M.polana* resulted in an average annual fruit attack rate of 31% and a 20% reduction in the number of viable seeds produced during the peak flowering period (10 million fewer viable seeds ha^{-1}) (Figure 1).

Seedling emergence A herbicide treatment after a 10-year run at Moruya with *M. polana* attack projected the emergence of only slightly fewer seedlings compared to 10 years without *M. polana* attack (Figure 2). Sixteen days following the herbicide treatment there were 141 seedlings m^{-2} emerged in the absence of *M. polana* attack, and 117 seedlings m^{-2} with *M. polana* attack.

***Mesoclanis polana* persistence** Under artificially low flower production rates, larval and pupal abundance was predicted to be low, reaching a maximum of 11 larvae or pupae m^{-2} at any one time (Figure 3). The
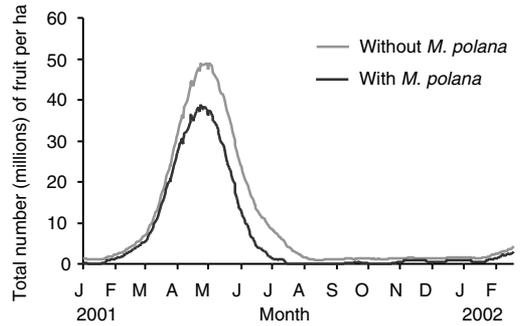

Figure 1. Effect of *Mesoclanis polana* on Bitou bush seed production.
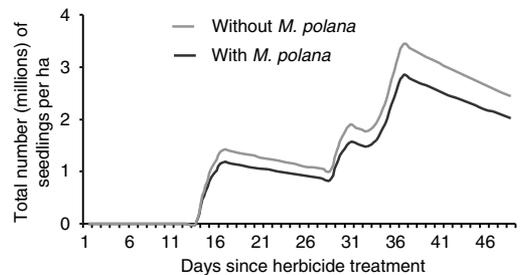

Figure 2. Effect of *Mesoclanis polana* on Bitou bush seedling recruitment following herbicide application.

proportion of fruits attacked by *M. polana* is also low, ranging from 10–40% of fruits attacked throughout most of the year (Figure 4).

<div align="center">DISCUSSION</div>

A sustained 23–31% reduction in viable seed production due to the presence of *M. polana* is likely to have little effect on the persistence and recolonisation ability of an established bitou bush stand. The number of seedlings that emerged following the herbicide treatment with *M. polana* present was more than enough to rapidly recolonise the area.

The B2MP simulations suggest that *M. polana* is able to persist at low flower production levels, but may have a more limited proportional effect on the production of viable bitou bush seeds when flowering is reduced.

The results of this analysis emphasise that effective biological control of perennial weeds is likely to require multiple agents, each influencing different aspects of the target plant's lifecycle.
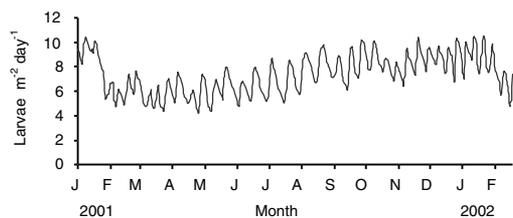
Figure 3. *Mesoclanis polana* larval and pupal numbers when bitou bush flower production is restricted.
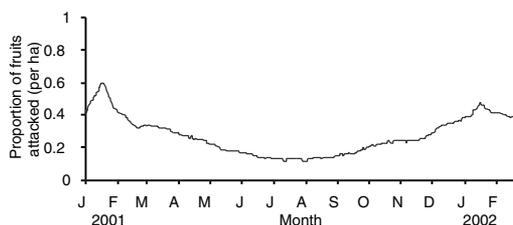

Figure 4. Attack rate of *Mesoclanis polana on* bitou bush fruits when bitou bush flower production is restricted.

The role of seed-destroying agents in reducing the weedy traits of perennial plants involves reducing the rate of weed invasion, and reducing the rate of recolonisation of a site following a disturbance. In the case of *M. polana*, the reduction in seed production has minimal effect on either of these rates.

The disappointingly small impact of *M. polana* on seedling recruitment following disturbance contrasts with its rapid invasion of the Australian range of bitou bush; underlining that agent *establishment* does not equate to agent *impact*. As performance indicators, agent establishment and proximal effects such as seed attack rate, in the case of a seed-feeder, are necessary components in a chain of evidence. Ultimately, however, weed managers are concerned to see that factors such as canopy cover are reduced through time, or that recolonisation rates are markedly reduced. Such factors therefore need to be considered in studies of agent impacts.

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