Biological control of *Melaleuca quinquinervia*: goal-based assessment of success

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Summary

Success means different things to different people. Unfortunately, the success or failure of weed biological control projects is often evaluated by nonparticipants lacking knowledge of the original goals set by project architects. Criteria for success should match objectives and goals clearly articulated so that success can be properly archived for future synthesis. The Australian tree *Melaleuca quinquinervia* (Cav.) S.T. Blake, an aggressive invader of the Florida Everglades, may be the largest plant ever targeted for biological control. We realized early on that biological control agents would not remove the many tons of woody biomass that comprised these infestations and so would be unlikely to reduce the infested acreage. Control of this plant by other means, however, was complicated by the billions of canopy-held seeds that are released following injury to the tree. A plan was developed in coordination with land management agencies wherein the goal of biological control was to curtail *melaleuca* expansion and suppress regeneration while using other means to remove mature trees. Three insect species have been released and others are under consideration. These agents, supplemented by the impacts of an adventive rust fungus and a scale insect, have met established goals and this project shows signs of an emerging success based on the established goals.

Keywords: Everglades, invasive plants, habitat restoration.

Introduction

‘Success has many fathers while failure dies an orphan’. This oft-quoted aphorism illustrates the political necessity of highlighting successes when they occur so that one’s endeavors continue to be supported in the future. Unfortunately, weed biological control projects are rarely undertaken based on the likelihood of a successful outcome (Peschken and McClay, 1995). Instead, biological control is often the method of last resort after other methods against recalcitrant weeds have failed. This is not conducive to improving the overall statistical success rate but is often the most responsible or economic option. Biological control of many serious weed problems would likely never be attempted if target choice was based primarily on maximizing the probability of success as advocated by Peschken and McClay (1995).

Many investigators have focused on the performance of individual agents to gauge success, primarily with an aim toward predicting which taxonomic groups make the best biological control agents. Such post-hoc analyses suggest a low success rate for weed biological control, with only a small proportion of successfully established agents producing effective control (Crawley, 1989a,b). Critics have used these statistics to advise against the use of biological control as a weed management tool (Louda and Stiling, 2004). McFa-dyen (1998, 2000), however, strongly disagreed with this advice and emphasized the need for project-based assessments.
Most authors use the term ‘success’ to refer only to ‘complete success’, wherein no other measures are needed to reduce the weed populations to acceptable levels. However, this neglects the importance of partially successful projects that have value when less effort is subsequently required to control the weed, because the density or extent of weed populations is reduced, or the weed is less able to reinvoke cleared areas or is slower to disperse (Hoffmann, 1995). Success and failure are at the extreme ends of a continuum of many possible outcomes and even moderate amounts of stress can reduce the competitive ability of a weed and render it less invasive (Center et al., 2005; Coetzee et al., 2005).

Successful biological control agents often act by preventing continued expansion of a weed population, rather than by reducing population densities (Hoffmann, these proceedings). Hoffmann also noted that it may be necessary to model weed outbreaks that never happen to perceive biological control effects. Documentation of such effects is difficult, at best, which explains why so many projects are incompletely evaluated and even successful projects may be undervalued or forgotten. Thus, statistical success rates should be viewed with circumspection, inasmuch as only obvious successes are reported. Furthermore, weed declines may occur incrementally over many years or even decades and may not be easily observed, especially when observational baselines shift over time, project funding terminates, or personnel changes interrupt collection of critical data.

Success of projects should be assessed in terms of the project’s original goals and objectives. Hence, a project can and should be deemed successful whether or not the density of the weed is reduced so long as the goals set out by the project architects are met. In this sense, it is possible to have complete success without complete control so long as the project goals are clearly stated, understood and documented. A recent project aimed at the control of *Melaleuca quinquenervia* (Cav.) S.T. Blake (melaleuca) in South Florida as part of a broader Everglades restoration effort is used herein to illustrate this concept.

**The target**

Melaleuca is a large tree (up to 30 m tall) of Australian origin that was introduced into southern Florida during the latter part of the 19th century (Dray et al., 2006). It has invaded wetland habitats, especially fire-maintained Everglades ecosystems, where the burning regime now favours melaleuca over less fire-tolerant native species. As a result, vast areas of these heterogeneous marshes have been transformed into swamp forests consisting of melaleuca monocultures. Melaleuca rapidly dominates infested areas after its initial colonization (Laroche and Ferriter, 1992) and at its peak was estimated to occupy at least 607,000 ha of conservation lands in the southern part of Florida (Bodle et al., 1994).

Control of melaleuca is complicated by the fact that it grows in areas that are hazardous and strenuous to work in and where access is difficult. These difficulties are exacerbated by the tree’s reproductive biology. Melaleuca flowers numerous times each year, often several times on the same stem axis due to indeterminate growth, forming spike-like clusters composed of multiple, dichasial groups of three flowers each (Tomlinson, 1980). Each cluster contains up to 75 individual flowers. Fruits arising from these flowers are persistent serotinous capsules that each contains 200–350 minute seeds (Meskimen, 1962). These generally remain in the fruits until disruption of the vascular connection causes the capsules to desiccate and open, often en masse, after a fire, freeze, drought, or herbicide treatment (Meskimen, 1962). A few (about 12% per year) open continuously, as radial growth of the stem separates the vascular connection, producing a light, perpetual seed rain of about 3 billion seeds/ha/year (M. Rayamajhi et al., unpublished data). Seeds that fall to the ground form a rather short-lived soil seed bank with a half-life of less than 1 year (Van et al., 2005). A single large tree located within a dense stand retains about 50 million seeds in its canopy with stands holding as many as 25 billion seeds/ha (M. Rayamajhi, unpublished data). An isolated tree may hold twice as many seeds as one of similar size in a dense stand. Surprisingly, a large proportion (85–90%) of these are actually hollow seed coats (Rayachhetry et al., 1998; Rayamajhi et al., 2002). Nonetheless, the remaining 10–15% of embryonic seeds create an enormous regenerative capacity capable of producing seedling densities of up to 2256 seedlings/m² (Franks et al., 2006) following a massive simultaneous seed shed induced by fire, drought, or herbicide application. These may grow into thickets of up to 130,000 small trees/ha (Van et al., 2000). As the stand matures, it thins to about 8000–15,000 trees/ha comprised mostly of mature trees with an understory of suppressed saplings (Rayachhetry et al., 2001). The standing biomass in these forests has been estimated at 129–263 metric tonnes (t)/ha (Van et al., 2000).

Isolated individual trees constitute a seed source for further encroachment. The seeds, when released, generally fall within 15 m of the parent tree (Meskimen, 1962). They often grow into dome-shaped clumps or ‘heads’ with the parent trees in the centre and progressively younger trees toward the periphery. These eventually coalesce with others blanketing vast acreages of wetlands with dense swamp forests. The isolated ‘outliers’ therefore are regarded as potential new infestations and, as part of a quarantine strategy, are first priority for control operations (Woodall, 1981). The trees within these stands produce multiple adventitious roots that form an intertwined skirt at the waterline or on saturated soil (Meskimen, 1962). These contribute biomass to the forest floor and trap large amounts of litterfall as well as organic debris causing soil accretion (White, 1994), thus increasing the local
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elevation (T. Center, personal observation). Altering the elevation of the Everglades even by a few centimeters dramatically shifts plant community composition (Ogden, 2005), thus these newly created melaleuca islands forever change the physiography and ecology of the area. There is also evidence that essential oils in melaleuca litter may be allelopathic (Di Stefano and Fisher, 1983). These changes render infested habitats unsuitable for many native species making restoration difficult if not impossible.

**The melaleuca management plan**

The South Florida Water Management District in conjunction with the Exotic Pest Plant Council convened a meeting of the major agencies that were managing the melaleuca problem. They developed a ‘Melaleuca Management Plan for Florida’, published during 1990 and revised in 1994 and 1999.

Two points were evident during the development of this plan. First, biological control could not eliminate the huge amounts of woody biomass present; herbicidal and mechanical control would therefore be needed to reduce the infestations to a maintenance level. Second, public agencies could not expend public funds to control melaleuca infestations on private lands that often abutted cleared tracts of public lands. These unassailables stands provided an invasion front and a potential seed reservoir to support reinvasion of cleared areas. The role of biological control in this plan was to neutralize the reproductive potential of these remaining stands by reducing seed production, seedling recruitment and regeneration; thereby inhibiting spread, reducing reinvasion of cleared areas and facilitating traditional control measures. However, implementation of biological control would take time, whereas chemical and mechanical control could be employed rapidly. So the plan relied on an early deployment of traditional control measures that would gradually be supplanted by biological control as agents became available (Figure 1).

**The biological control agents**

Insects associated with melaleuca were enumerated in Australia during the late 1980s and early 1990s (Balciunas, 1990). These inventories revealed an entomofauna of over 400 species (Balciunas, 1990; Balciunas et al., 1993a,b, 1994, 1995a,b,c; Burrows et al., 1994, 1996). The most promising species were studied further and three have now been released.

The first insect evaluated was the weevil *Oxyops vitiosa* Pascoe (Purcell and Balciunas, 1994). This insect, being a flush feeder on growing stem tips, was desirable because of its ability to disrupt flower production, which depends on continual growth of the stem axis. It proved to be host-specific (Balciunas et al., 1994; G. Buckingham, unpublished report) and was released during 1997 (Center et al., 2000). Its need to pupate in dry soil (Purcell and Balciunas, 1994; Center et al., 2000), however, limited it to habitats that were not permanently under water. Field and laboratory assessments of a mirid, *Eucerocoris suspectus* Distant, in Australia (Burrows and Balciunas, 1997; Buckingham, 2001) suggested that its host range was sufficiently narrow (Burrows and Balciunas, 1997; Buckingham, 2001), but after discovering that larvae synthesize toxic octapeptides...
(Oelrichs et al., 1999), we elected not to release it out of concern over potential negative effects to insectivorous wildlife.

The melaleuca psyllid *Boreiglycaspis melaleucae* Moore was found to be host-specific (Purcell et al., 1997; Wineriter et al., 2003), and was released during 2002 (Center et al., 2006, 2007). It feeds mainly on the new growth but will also utilize older leaves and the green stems. Furthermore, it completes its life cycle entirely on the plant so it is less restricted by habitat. The tube-dwelling pyralid *Poliopaschia lithochlora* (Lower) was highly rated because of its ability to damage melaleuca and its preference for low-lying, humid habitats (Galway and Purcell, 2005), but its use of an ornamental species, *Melaleuca viminalis* (Sol. ex Gaertner) Byrnes, during testing diminished its prospects (M. Purcell, unpublished data). A fergusoninid gall fly, *Fergusonina turneri* Taylor, and its mutualistic nematode *Fergusobia melaleucae* Davies and Giblin-Davis, also proved to be highly specific (Giblin-Davis et al., 2001) and were first released during 2005 (Blackwood et al., 2006). It has proven difficult to establish but efforts are continuing.

Most recently a stem-galling cecidomyiid, *Lophodiplosis trifida* Gagné, has proven to be host-specific (S. Wineriter et al., unpublished data) and should gain approval for release. A bud-feeding weevil *Haplonyx multicolor* Lea and a leaf-galling cecidomyiid *Lophodiplosis indentata* Gagné are currently under consideration.

Two adventive organisms have also recently infested melaleuca trees in Florida. A pestiferous, undescribed scale insect (Pemberton, personal communication) was detected in Florida during 1999. It attacks melaleuca trees as well as some 300 other plant species (Pemberton, 2003; R. Pemberton, unpublished data). The guava rust *Puccinia psidii* G. Winter (Basidiomycetes: Uredinales), which infects mainly young foliage, appeared during 1997 (Rayachhetry et al., 1997) and is now widespread.

### The effects of the biological control agents

Numerous studies aimed at determining the impacts of *O. vitiosa* and *B. melaleucae* have been conducted or are ongoing. However, determinations of the individual effects of one have been confounded by the presence of the other, as well as by the presence of the adventive rust fungus and scale insect. These studies have included comparisons of melaleuca stands with and without the agents, caging studies, defoliation experiments, insecticide and fungicide exclusion experiments, and before and after comparisons of stand dynamics.

### Flower and seed production

The effects of herbivory by *O. vitiosa* on melaleuca performance were possible early during the release program when none of the other organisms were present. Pratt et al. (2005) compared flowering frequency in melaleuca stands where the weevil had been released to stands without them. They found that the likelihood of flowering increased with tree size but that undamaged trees were 36 times more likely to reproduce than damaged trees in similar habitats (Figure 2). Overall, about 45% of the weevil-free trees were flowering compared to about 2% of infested trees.***

In another study, Pratt et al. (2005) enclosed the canopies of small (2.9 cm diameter at breast height or

![Figure 2](image-url). Release of the weevil *Oxyops vitiosa* profoundly affected flowering of melaleuca trees. The proportion of the trees that produced flowers was much lower after being damaged by the weevils regardless of size.
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dbh) trees with sleeve cages and introduced weevil larvae into the enclosures, either once or twice, to produce one or two defoliations of the young foliage. The second defoliation was done about 10 weeks after the first. These treatments were compared to controls with no defoliation or to trees artificially defoliated by manually removing all foliage. Flower production on all trees was monitored monthly for 1 year. The control trees flowered normally during this period, whereas trees artificially defoliated failed to produce any flowers. Trees defoliated once or twice by the weevil larvae produced a few flowers but numbers were not statistically different from each other or from the artificial defoliation treatment (Figure 3).

Interestingly, in a comparison of ten herbivore-impacted trees with ten non-impacted trees at similar, nearby sites at Estero, Florida, Rayamajhi *et al.* (unpublished data) found that herbivory by *O. vitiosa* resulted in higher rates of capsule abortion when compared to sites without natural enemies. Mean number of capsules in herbivore-impacted infructescences was reduced by nearly 50% compared to the herbivore-absent site. This decreased density of capsules was apparent as gaps in the capsule clusters caused by abortion of the undeveloped fruits. The herbivore-impacted trees were very similar to those near Brisbane, Australia where the average infructescence was 5.7 cm long but contained only 18 capsules (Rayamajhi *et al.*, 2002). The average numbers of seeds per capsule were similar in both the Florida and Australian sites.

Rayamajhi *et al.* (unpublished data) have also found that when the trees were subjected to attack by *O. vitiosa*, the percentage of embryonic seeds decreased, as did seed viability and germination ability. Seed viability and germination tests (Van *et al.*, 2005) also revealed reductions in both measures of seeds from herbivore-attacked trees compared to controls.

**Seedling survival**

Franks *et al.* (2006) described the effects of the weevil larvae and the psyllids, alone and in combination, on growth and survival of melaleuca seedlings by caging the insects on 26 cm-tall seedlings in field plots. They compared these results to a natural infestation of the insects on nearby seedlings. *O. vitiosa* larvae had no effect on seedling height, leaf number, or survival, whereas psyllids caused all of these measures to decrease by about 55–60% over the 5-month term of the study. About 95% of seedlings survived when protected from psyllids as compared to only 40% when exposed to herbivory (Center *et al.*, 2007).

In another study, Tipping *et al.* (unpublished data) found that after becoming infested by both the psyllid and the weevil, melaleuca trees recruited a much lower density of seedlings than trees without either herbivore. They also compared densities of saplings in plots 9 m$^2$ that were periodically treated with insecticide to exclude herbivory to saplings in untreated plots. The plots were located in an area that had burned during June 1998, resulting in a massive seed rain and thickets of about 1000 seedlings/m$^2$. By the time the study was initiated during 2002, these had become saplings and had grown to about 70 cm in height. Densities in

![Figure 3](chart.png)

**Figure 3.** Small trees were caged then subjected to herbivory by *Oxyops vitiosa* either once (Herbivory 1) or twice (Herbivory 2) or to mechanical defoliation and compared to undefoliated controls. Defoliated trees, regardless of the manner of defoliation, produced very few flowers relative to the controls.
the protected plots were virtually unchanged during the 5-year period of the study as compared to those in the unprotected plots which declined by almost half.

**Sapling growth**

Tipping et al. (unpublished data) conducted two insecticide exclusion studies on the growth of melaleuca saplings in common garden experiments over about a 3-year period. The first experiment investigated the effect of the melaleuca weevil, O. vitiosa, and supplemental irrigation on the growth of small trees. The second examined the effects of herbivorous insects (both the psyllids and the weevils) and plant chemotype (nerolidol or viridifloral). In both cases, plants treated with insecticide more than doubled in stature, whereas those not treated grew very little. In the first study, plants attacked by O. vitiosa grew at a much slower rate compared to the protected plants (Figure 4). The unprotected plants produced more stem tips per unit of height, creating a shorter, bushier habit, which provided more resource for the tip-feeding insects. Supplemental irrigation improved the growth of insecticide-treated trees but had no effect on trees that were not treated with insecticide. Chemotype had no apparent effect on the impact of the insects. Seed capsule production was much lower among unprotected plants in both studies.

**Stand dynamics**

Rayamajhi et al. (2007) studied the dynamics of melaleuca stands before and after the widespread impacts of the biological control agents. They found that the average density of the trees in mature stands declined by 72% overall from 15,800 trees/ha during 1996 to 4400 trees/ha during 2003. Interestingly, the standing biomass based on harvesting studies increased somewhat from an initial average of 263 t/ha to 274 t/ha during the latter harvest. This was because most of the mortality was among the smaller suppressed trees in the understory that represented a small proportion of the biomass. The density of small trees, those with a dbh of less than 10 cm, decreased 83% from 12,600 to 2200 trees/ha; density of intermediate-sized trees with a dbh of 10–20 cm decreased 46% from 2600 to 1400 trees/ha; density of large trees >20 cm increased from 600 to 800 trees/ha.

Another study (Rayamajhi et al., 2007) showed that densities decreased between 1997 and 2006, in part due to self-thinning. The decline accelerated after the effects of biological control became apparent and the rate of decline was inversely related to the position of the trees within the stands. Densities of trees at the periphery, which consisted mostly of small individuals, decreased by about 6076 individuals/ha/year before 2001.
as compared to 16,725 individuals/ha/year after 2001. Densities in the inner portions of the stands, which contained higher proportions of larger trees, decreased at relatively constant rates. This further demonstrated the greater effect of herbivory on smaller trees. The average diameter of the trees increased, not because they grew but because of selective mortality of smaller individuals. This was corroborated by a decrease in or leveling off of total basal area coverage during the post-release period in contrast to a prior increasing trend.

Despite the finding that the surviving larger dominant trees accounted for most of the biomass, biomass allocation changed due to extensive defoliation of all of the trees. The foliage of large trees growing in dense stands was limited to the upper branches at the treetops and this accounted for only 5.1% of the total biomass during 1996, before insect-induced defoliation. This decreased from 17 to 8 t/ha to represent only 1.5% of the total biomass during 2003 (Figure 5). The biomass allocated to seed capsules decreased by 85% from 6.7 t/ha, or 0.46% of the total biomass to 1.0 t/ha, or 0.29% of the total biomass.

Litter-traps were placed under mature melaleuca stands to collect leaf litter in an attempt to measure the activity of the biological control agents in the canopy of taller trees. The proportion of fallen leaves that exhibited weevil damage symptoms was analysed. Though the weevil releases began in 1997, the first weevil-damaged leaves did not appear in the traps until 1999 (represented by 5% of the trapped leaves) and by 2005, the proportion of damaged leaves reached approximately 45% (Rayamajhi et al., 2007). This increased percentage of damaged leaves reflected the decreasing proportion of leaf biomass (stem to leaf biomass), increasing tree mortality, and decreasing tree densities.

**Discussion**

Clearly, many melaleuca stands have undergone significant declines and remaining trees are now in poor condition. However, vast stands of melaleuca still exist that overtly appear unchanged. Yet after closer scrutiny, we have revealed that the dynamics of these stands have changed in very significant ways. Fewer trees now produce flowers, those that do flower produce
fewer inflorescences and the inflorescences produced contain fewer individual blossoms. Many of the fruits abort and those that do manage to set seed produce a smaller proportion of viable seeds. The constant defoliation of the stem tips causes the capsules to desiccate and release seeds during drier periods when conditions are unfavourable for germination. Those that do fall, lodge in a favourable site and manage to germinate are infested by psyllids that kill a large proportion before they attain a significant size. If they survive, they grow slowly due to constant defoliation and produce few flowers. Meanwhile, existing stands have nearly been removed from publicly held lands and those on private lands are less invasive. Hence, the goals of the project, as stated above, have been met so the project should be considered a success. It is not yet a ‘complete’ success in that biological control is more effective in some habitats and during some periods than others but additional agents that are currently under development may fill these gaps.

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