

**Modeling the influence of resource availability on population densities of
Oxyops vitiosa (Coleoptera: Curculionidae), a Biological Control Agent of
the Invasive Tree *Melaleuca quinquenervia*.**

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Introduction

In its native range, *Melaleuca quinquenervia* (Cav.) S.T. Blake occurs along Australia's eastern coast from near Sydney in New South Wales to the northern tip of Queensland, in New Guinea, and in New Caledonia (Boland *et al.*, 1987). The tree was first introduced to south Florida by horticulturists in the late 1800's, where it remained innocuous for nearly half a century. More recently, however, *M. quinquenervia* (melaleuca) has aggressively invaded natural areas in south Florida, including forested and saw-grass (*Cladium jamaicense* Crantz.) dominated wetlands (Turner *et al.*, 1998). Melaleuca has reportedly spread at a rate of 2 850 ha/yr or approximately 7.8 ha/d over the last century (Center *et al.*, 2000) and recent assessments suggest that the weed now occurs on ca. 200,000 ha of Everglades wetland ecosystems (Turner *et al.*, 1998). Transitional stages of the invasion include savannahs with scattered, individual trees and mature dense melaleuca stands surrounded by relatively pristine marshes that contain moderate to low levels of melaleuca (O'Hare & Dalrymple, 1997).

In 1986 a classical biological control program was initiated and explorations for co-evolved natural enemies in eastern Australia resulted in the enumeration of over 450 herbivorous arthropods associated with this invasive tree and its congeners (Burrows & Balciunas, 1999). The melaleuca snout beetle, *Oxyops vitiosa* Pascoe, was the first candidate selected for host range testing and risk assessment (Purcell & Balciunas, 1994). Although adults feed superficially on both young and old leaves, larvae consume newly developing, expanding leaves that are generally produced in seasonal flushes at branch apices (Purcell & Balciunas, 1994). Quarantine-based host specificity testing predicted that this weevil would exploit only a very narrow range of related Australian plant species, none of which occur naturally in the Americas (Balciunas *et al.*, 1994), and was subsequently released at melaleuca-infested locations during the spring of 1997 (Center *et al.*, 2000). Nascent populations established at 9 of the original 13 release sites and closely monitored redistribution efforts were instigated thereafter.

Our laboratory is evaluating the ecological interactions among *O. vitiosa*, the target weed and the native plant communities. One component of our post-release evaluations includes quantifying the population dynamics of *O. vitiosa* when presented with the seemingly limitless melaleuca resource. The objectives of this study were to 1) estimate the amount of resource available for consumption by the biological control agent, 2) determine the relationship between insect densities and resource availability, and 3) model the maximum insect density for a given melaleuca stand. To achieve these objectives we quantified 1) the size distribution and density of melaleuca trees growing within four representative stands in south Florida, 2) the number of expanding foliar buds/tree/yr over a range of tree sizes and two habitat types, 3) the phenology and quantity of suitable foliage available for consumption by larvae/foliar bud, and 4) the potential larval densities from existing consumption levels. From these data we modeled *O. vitiosa* population densities at monthly intervals and ultimately calculated an annual estimate. Quantifying the

relationship between resource availability and *O. vitiosa* larval densities is an integral component of population dynamic models (Begon *et al.*, 1996) and may aid in decisions relevant to redistribution efforts (Pratt *et al.*, 2003a).

Materials & Methods

Estimating *Melaleuca quinquenervia* tree size distribution

Because tree size (~age) is positively correlated with the amount of suitable foliage for larvae, and subsequently with *O. vitiosa* densities, we quantified the tree size distribution of four representative melaleuca stands in south Florida. In general, these stands occurred in typical 'glades' ecosystems, characterized by high organic soils, and were equally distributed into two habitat categories: seasonally flooded and non-flooded (Table 1). It should be noted that melaleuca also invades permanently flooded habitats but, as *O. vitiosa* pupates in the soil and establishment has not been successful at constantly inundated sites (Center *et al.*, 2000; Purcell & Balciunas, 1994), this habitat type was not included in our assessment.

Tree size distribution was quantified at each site by delineating seven plots extending from the center of the stand (largest trees) to the stand edge (smallest trees) in a stratified random design. The seven sample regions consisted of four 10 X 10 m and three 5 X 5 m plots, from the center to the stand's edge, respectively. To quantify tree size distribution along the transect at each site, diameter at breast height (dbh, 1.3 m) was measured for all melaleuca trees in each plot (Van *et al.*, 2002). Trees <1.3 m in height and <1 cm dbh were excluded. Data from all sites were pooled and the dbh size distribution/ha was calculated to provide a generalized estimate of tree density for non-permanently flooded melaleuca habitats.

Number of seasonal growth units per tree

Melaleuca trees produce a single (primary) flush of new growth from foliar buds at branch apices, individually described hereafter as a seasonal growth unit (Briggs & Johnson, 1979). To quantify the number of seasonal growth units (SGUs) per tree, in March 2001 we felled 15 melaleuca trees ranging from 1.0 to 40.0 cm dbh at four stands each (Table 1). The total number of newly developed SGUs were noted for each tree with a dbh <10 cm. For trees >10 cm dbh, the leaf-bearing branches were removed from the trunk, weighed (fresh) and a randomly selected subsample of ca. 2 kg was removed. The number of SGUs within the subsample was then assessed and the gravimetric ratio of total leaf-bearing branches to the subsample was multiplied by the number of SGUs in the subsample to estimate total SGUs per tree. The number of SGUs/tree were pooled among all sites and both response as well as explanatory variables were log transformed (double-sided natural logarithm) to account for non-constant variance, thereby converting the exponential model to a linear relationship (Baskerville, 1972; Sprugel, 1983; SPSS, 1999). Other researchers have noted (Sprugel, 1983; Jokela *et al.*, 1986; Yamakura *et al.*, 1986; Bartelink, 1996, 1997; Clough *et al.* 1997; Rayachhetry *et al.* 2001) that an inherent bias occurs when a linear regression is applied to the ln-transformed data and the predicted values are converted to arithmetic units. Sprugel (1983) suggested the integration of a correction factor to the biomass equation as a means of removing the systematic bias introduced through transformation. Therefore, the back-transformed (anti-ln(y)) data were

multiplied by the correction factor $\text{anti-ln}(\text{standard error})^2/2$ to adjust for inherent biases of the SGU transformation as shown in Sprugel (1983).

Phenology and quantity of suitable foliage

As stated earlier, *O. vitiosa* larvae are specialized feeders of newly developed melaleuca shoots (SGUs), which are ephemerally available during the year. To quantify the seasonality and amount of suitable foliage per expanding bud, plant samples were collected by grabbing branches within arm's reach while walking through each site (Table 1) in as random a manner as possible (Center *et al.*, 2000). At first, this was done by grasping branches that were contacted by one's outstretched arms while looking away. However, these samples were collected to quantify plant phenology and suitable foliage so it was desirable to sample branches that were undamaged by the weevil. This became increasingly difficult as weevil populations increased, which necessitated a biased search for undamaged branches. Only the apical 25-cm of each branch was collected. Once leaves begin to expand, the seasonal growth units become unsuitable for consumption by larvae after ca. 60 d (Pratt, unpub. data). Therefore, to ensure samples were independent, branches were collected every 60 d beginning in September 1998 to July 2000. The branch samples were taken to our laboratory where the leaves were stripped from the stems, classified as young (suitable for consumption by *O. vitiosa* larvae) or old foliage (unsuitable), and counted. The young leaves for each SGU were then weighed while fresh.

When the point of demarcation between young and old leaves on a branch was not obvious, leaf hardness was assessed using a gram-gauge modified to a penetrometer as described by Wheeler & Center (1996). Young leaves were then defined as those producing a penetration measurement of less than 65 g on the gauge, which calibrated to 53 g by depression of the pan on a digital balance (Ohaus Galaxy 4000D, Ohaus Corporation, Florham Park, NJ 07932).

Fresh weight (FW) of suitable foliage/SGU was quantified at all sites and an experiment-wise mean FW/SGU/sample interval (60 d) was calculated. Ultimately, FW/SGU/yr was calculated by averaging FW over the SGU developmental interval (60 d) and then summing the value for each interval over the period of a year.

TABLE 1. Size distribution and within-stand densities for the invasive tree *Melaleuca quinquenervia* at four sites in south Florida.

Site	GPS ^a coordinates	Hydroperiod ^b	Size (dbh) distribution/ha ^c							Total
			1-5	6-10	11-15	16-20	21-25	25-30	>31	
1	N25.93521 W-80.44711	SF	28632	5642	1979	989	526	84	63	37916
2	N26.05633 W-80.44016	NF	16716	3705	1158	358	211	0	0	22147
3	N26.05374 W-80.4409	NF	20063	3937	1116	400	168	0	21	25705
4	N26.894066 W-80.1216	SF	12758	2000	1263	505	358	211	379	17474
		\bar{X}	19542	3821	1379	563	316	74	116	25811

^a: Global positioning system in decimal degrees

^b: NF= non-flooded; SF= seasonally flooded (<6 months of the year)

^c: dbh= diameter at breast height (1.3 m), measured in cm

Consumption and density calculations

The amount of melaleuca foliage required to complete development by *O. vitiosa* (C) was quantified gravimetrically by Wheeler (2003). In general, consumption was estimated by placing newly hatched 1st instar larvae into individual petri dishes containing excess melaleuca leaves under environmentally controlled conditions as described in Wheeler & Halpern (1999). Foliar consumption was monitored daily until pupation. The amount of foliage consumed was calculated by subtracting the final dry mass of the uneaten portion of leaves from an initial estimated dry mass (Wheeler & Halpern 1999). These data were then converted to FW by dividing the dry mass consumed by the proportion of dry mass of the leaves.

Expected weevil density for a given melaleuca stand was calculated as:

$$D = \frac{\left[\sum f(sgu) \right] F}{C},$$

990) Searching behavior patterns in insects. *Annual Review of Entomology* **35**, 447-467. where $f(sgu)$ represents the regression between the number of SGUs and melaleuca dbh (see above). The summation of all SGUs/ha is multiplied by the 60 d or annual mean FW/SGU, designated as F , and finally divided by the *O. vitiosa* consumption value C . It should be noted that this calculation assumes that F is entirely consumed by *O. vitiosa* larvae. Although this assumption may be unrealistic at low population densities, complete removal of all suitable foliage is regularly observed in nature, thus full exploitation of available resources seems to occur (Pratt, personal observation).

The distribution of melaleuca trees in early or late stages of invasion is not adequately represented by the generalized melaleuca size distribution/ha due to the preponderance of small or large trees, respectively. Therefore, we also calculate weevil density/ha for *O. vitiosa* in small (1.3-10.0 dbh), medium (10.1-20.0) and large (>20.1) stands independently. To do this we determined the tree density and dbh range for each sampled plot located near the center (large trees), middle (medium) or edge of the stand (small), respectively and calculated expected population densities for individual size classes as described earlier.

Model validation

Mature melaleuca trees may exceed 30 m in height, thereby complicating visual observations and data collection of larval densities over time. Therefore, validation data for comparison with model output were limited to weevil population densities observed on smaller, more accessible trees occurring in an 8.1 ha field near Estero, Lee County, Florida (N 26.035483 and W -80.43495; Center *et al.*, 2000). Land managers cut melaleuca trees in the summer of 1998, resulting in multiple branches coppicing from individual stumps. Within this field, transects were arranged in a grid pattern with 20 transects oriented east to west at 20 m intervals and 9-10 points on each transect spaced 20 m apart. In the fall of 1997 through the spring of 1998 ca. 4 000 larvae were liberated near the center of the field. Melaleuca plants were sampled at 50 randomly selected transect points every six wks (approximate generation time; Purcell & Balciunas, 1994) beginning in November 2000 and continuing through September 2001. Plants were selected at each sampling point using the quarter method of vegetation sampling (Smith, 1966). The area was divided into four quadrants at each sampling point based on the four cardinal directions. The nearest plant to the sample point in each quadrant was examined to determine the number of *O. vitiosa* larvae. We also quantified the number of SGUs per coppicing stump and input these values into the equation $f(sgu)$ to predict the typical tree dbh

these stumps represent. The resulting dbh data were then entered into the density model to calculate larvae/ha/yr and the output was compared to the observed data.

Caution should be used when drawing inferences from comparisons between coppicing stumps and undamaged melaleuca canopies because data were not adjusted for differences in plant size, plant architecture, mechanical injury or other parameters that may influence larval performance. In addition, acquiring validation data in this manner assesses the accuracy of predicting F and C but not $f(sgu)$, as this equation was used to obtain the dbh represented by the regrowth from cut stumps.

Results and Discussion

The number of melaleuca trees/ha was 25 811 (SD=8 746) (Table 1) when data from all sites were pooled. This density is comparable with previous estimates for stands of the invasive weed in south Florida that also contain a range of tree sizes. Van *et al.* (2002), for instance, reported melaleuca density estimates ranging from 11 450 to 36 275/ha. While higher densities of melaleuca have been observed (Rayachhetry *et al.*, 2001), such stands consist primarily of seedlings or saplings and are not typical. The within-stand size distribution along the sampled transect for each site is presented in Table 1. The skewed distribution reflects the presence of numerous juvenile trees (dbh ≤ 5 cm) occurring on the invasion front of mature stands, representing >75% of the total number of trees in the stand (Table 1). The abundance of juvenile trees characterizes the high regenerative capacity and successful recruitment of melaleuca in its adventive range.

Not surprisingly, the number of SGUs available for consumption by *O. vitiosa* increased in relation to tree diameter (dbh, Fig. 1). The relationship between SGU and tree dbh is best described by the equation:

$$\log_e(y) = 1.7836 * \log_e(x) + 1.6467,$$

where y is the number of SGUs and x is tree dbh. This single parameter, dbh, accounts for >88% of the variation in the number of SGUs/tree (Fig. 1). The relationship observed between SGU quantity and dbh is consistent with previous reports that demonstrated a significant relationship between melaleuca diameter and total standing biomass, as well as various other plant characteristics (Rayachhetry *et al.*, 2001; Van *et al.*, 2002). However, our estimates, and those reported earlier, are based on data collected from trees growing within stands under crowded conditions and may not accurately describe open growing, non-crowded pioneer trees with more fully developed canopies. Because the majority of melaleuca trees occur within stands and not in isolation, we have not incorporated these open-growth trees in our analysis.

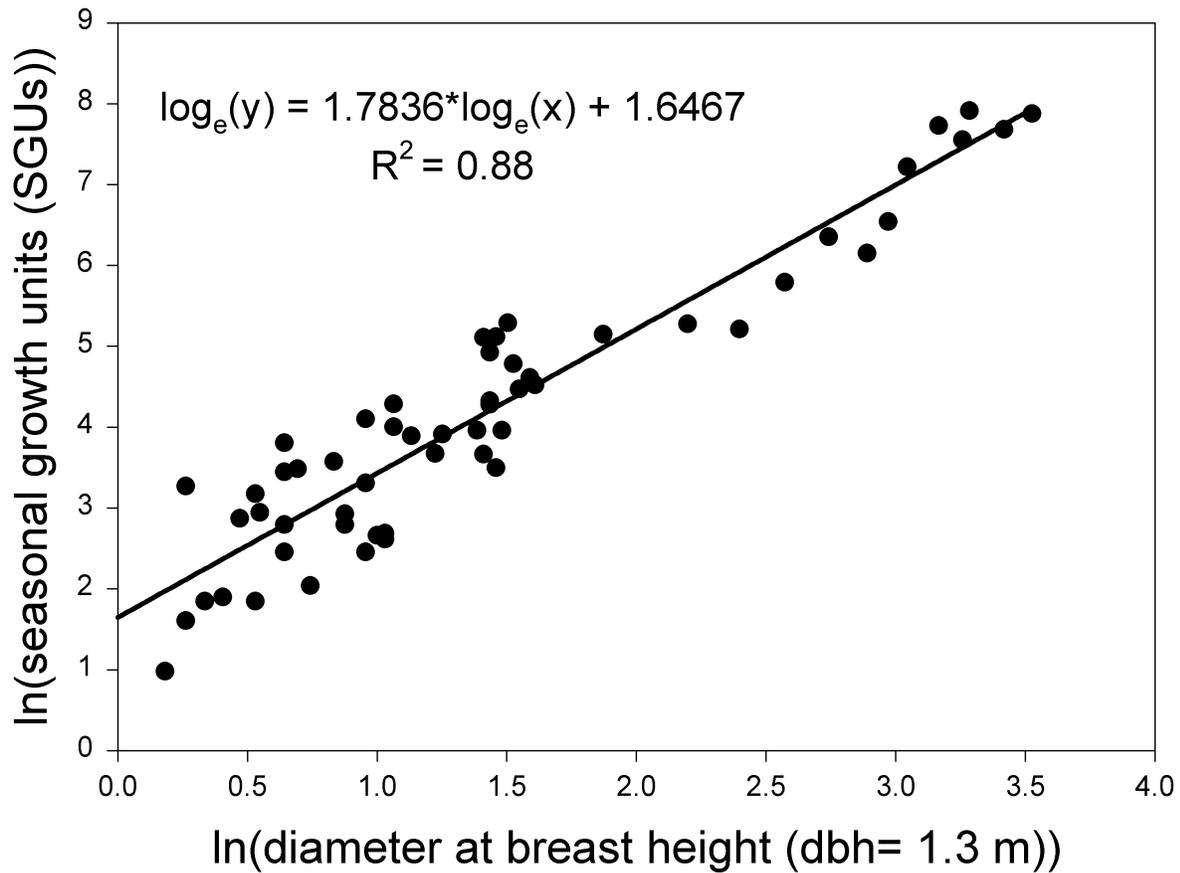


FIGURE 1. Relationship between the number of seasonal growth units (foliar buds) produced/melaleuca tree/year and tree diameter at breast height (d.f. 1,57; $F= 427$; $P=<0.0001$).

One explanation for the failure of introduced herbivores to establish in adventive habitats is asynchrony with host plant phenology (Beirne, 1975). Herein we quantify the seasonal variation of newly developed, expanding foliage for melaleuca in Florida (Fig. 2). Seasonal growth units were present during all sample intervals although >74% of the bud's FW was concentrated during November through April, the coolest and driest months in south Florida (Fig. 2). These findings suggest that *O. vitiosa* larvae, and other similarly adapted specialist herbivores, have the greatest resource available for consumption during winter but a small population of larvae may continue to thrive year round. Consistent with our findings, Center *et al.* (2000) reported highest *O. vitiosa* larval densities from October - February but larvae were rare, or nonexistent, in undisturbed habitats during the remainder of the year. One possible explanation for the incongruity between the presence of SGUs and the rarity of *O. vitiosa* larvae during summer months (June-September) may be related to dispersion of the limited resource. Larvae may not persist if multiple SGUs are required to complete development and these limited SGUs are dispersed beyond the larval search radius. Increased searching may also result in higher mortality rates due to increased exposure to natural enemies (Bell, 1990; Costello *et al.*, 2002). Additionally, multiple eggs are often laid on a single SGU, thereby increasing both interspecific competition and the probability of multiple search bouts to complete development. An alternative explanation for the paucity of larvae may be that adult females enter a reproductive diapause during summer months. In its native range, *O. vitiosa* is reported to cease ovipositing during summer in southeastern Queensland, Australia. In contrast, weevils in more northerly (tropical) regions of eastern Queensland did not enter a reproductive diapause whenever suitable foliage was present (Purcell & Balciunas, 1994). The effect of food quality, abiotic conditions and age on the reproductive biology of *O. vitiosa* remains unclear.

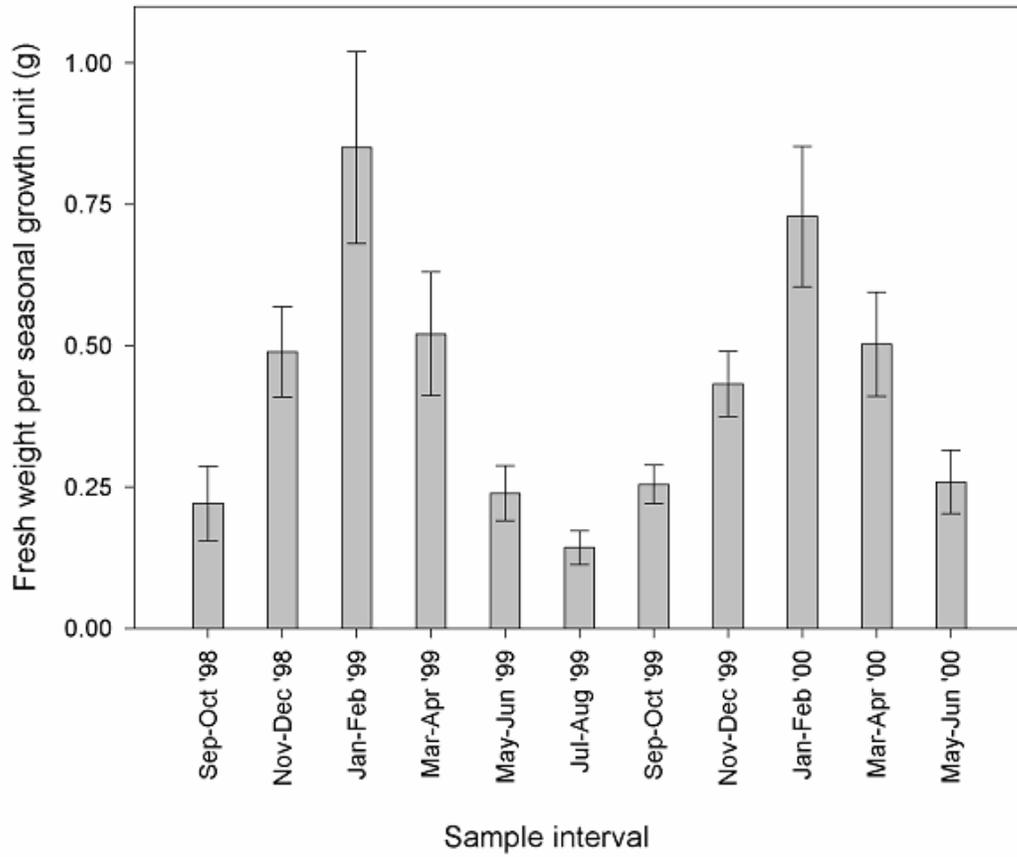


FIGURE 2. Seasonal variation in the quantity of suitable tissue for consumption by *O. vitiosa* larvae/seasonal growth unit (foliar bud) over time.

Commonly cited characteristics of successful arthropod invaders include a high intrinsic rate of increase and high carrying capacity (MacArthur & Wilson, 1967; Crawley, 1986). Biological invasion theory suggests that, upon introduction, those exotic species encountering habitats with high levels of resource availability have a lower probability of extinction from environmental and demographic stochasticity (Lawton & Brown, 1986; Leigh, 1981), as well as generalist predators (Crawley, 1986). When calculated at 60 d intervals, larval densities for *O. vitiosa* varied greatly in response to plant phenology (Fig. 3). When calculated for the generalized (mixed) melaleuca distribution for instance, larval densities ranged from 4 589 877 larvae/ha in February-March to 830 946 larvae/ha in July-August. These data suggest that initial introductions or redistribution efforts may suffer greater risk of establishment failure if releases are made during summer months, when weevils have reduced potential for population increase.

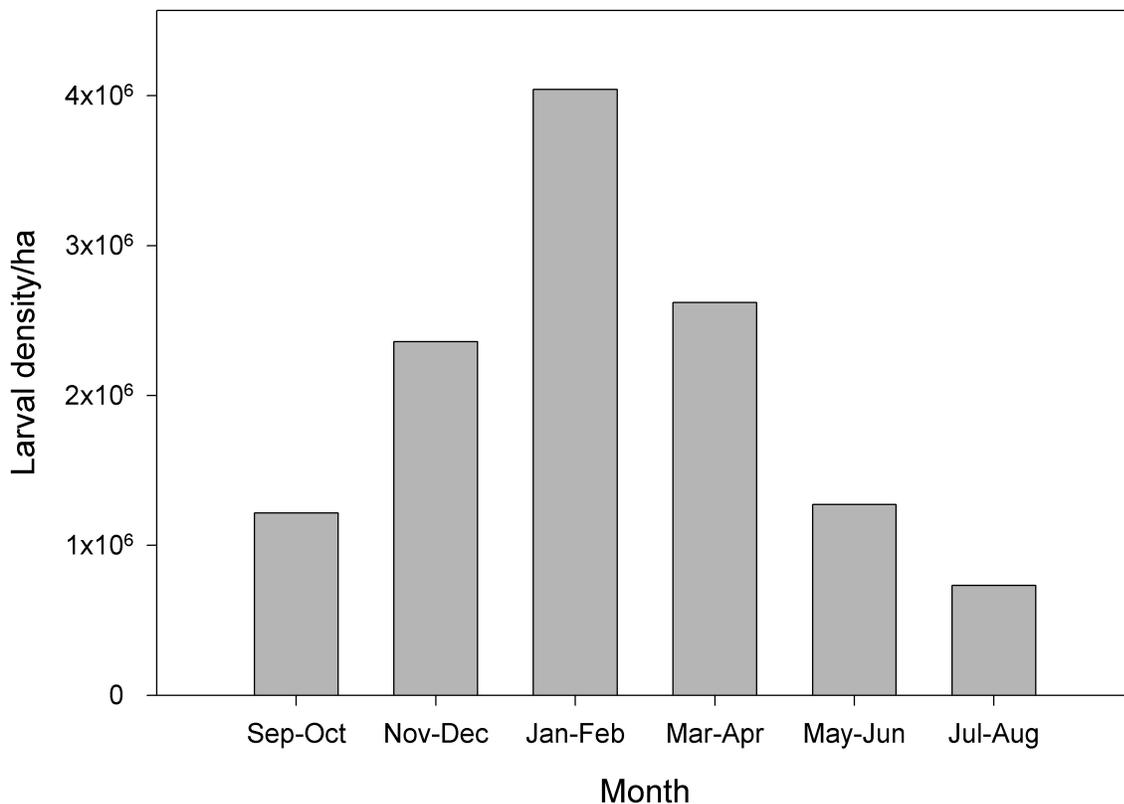


FIGURE 3. Monthly larval densities for the generalized (mixed size class) melaleuca ha.

The experiment-wise estimate of available foliage/SGU/yr is 2.31g (SD=0.24). The use of a single estimate to describe annual foliage availability assumes, therefore, that a constant (2.31g) and a fluctuating value (Fig. 2) of available resource during a year has no influence on successful larval development. As described earlier, this seasonal fluctuation does appear to either 1) modify larval competition and mortality, 2) alter reproductivity of females or 3) produce a combinatory effect over time. Therefore, to provide a more realistic estimate of grams/SGU/yr we excluded grams FW from the model for those months when larvae are rare or nonexistent in undisturbed melaleuca stands (Center *et al.*, 2000). These months were typically

May through October and all had FW <0.25g/SGU. Therefore, the adjusted available FW/SGU/yr used for calculating predicted densities was 2.04g. The amount of foliage consumed by *O. vitiosa* larvae during the developmental period was 0.5g (Wheeler, 2003). These findings suggest that a single SGU can support development of 4 larvae.

Annual estimates of larval densities for the range of tree sizes occurring in the generalized melaleuca stand are presented in Figure 4. The mathematical relationship describing the influence of dbh on expected larval density is:

$$D = 5.3746 * x^{1.7836},$$

where D is the predicted density and x is dbh. From this equation, expected density/ha/yr can be calculated for each tree within a melaleuca stand, assuming the sizes and habitats are within the range tested herein. Predicted weevil densities for the generalized tree distribution (Table 1), for instance, is estimated to be 13.9 million larvae/ha/yr (Fig. 5). Weevil densities increase to 18.8 million larvae/ha/yr when large trees (>20 cm dbh) represent the dominant size class, whereas invaded areas dominated by medium (10-19 cm) and small (1.3-9 cm) trees are predicted to have larval densities of 11.3 and 6.3 million, respectively (Fig. 5).

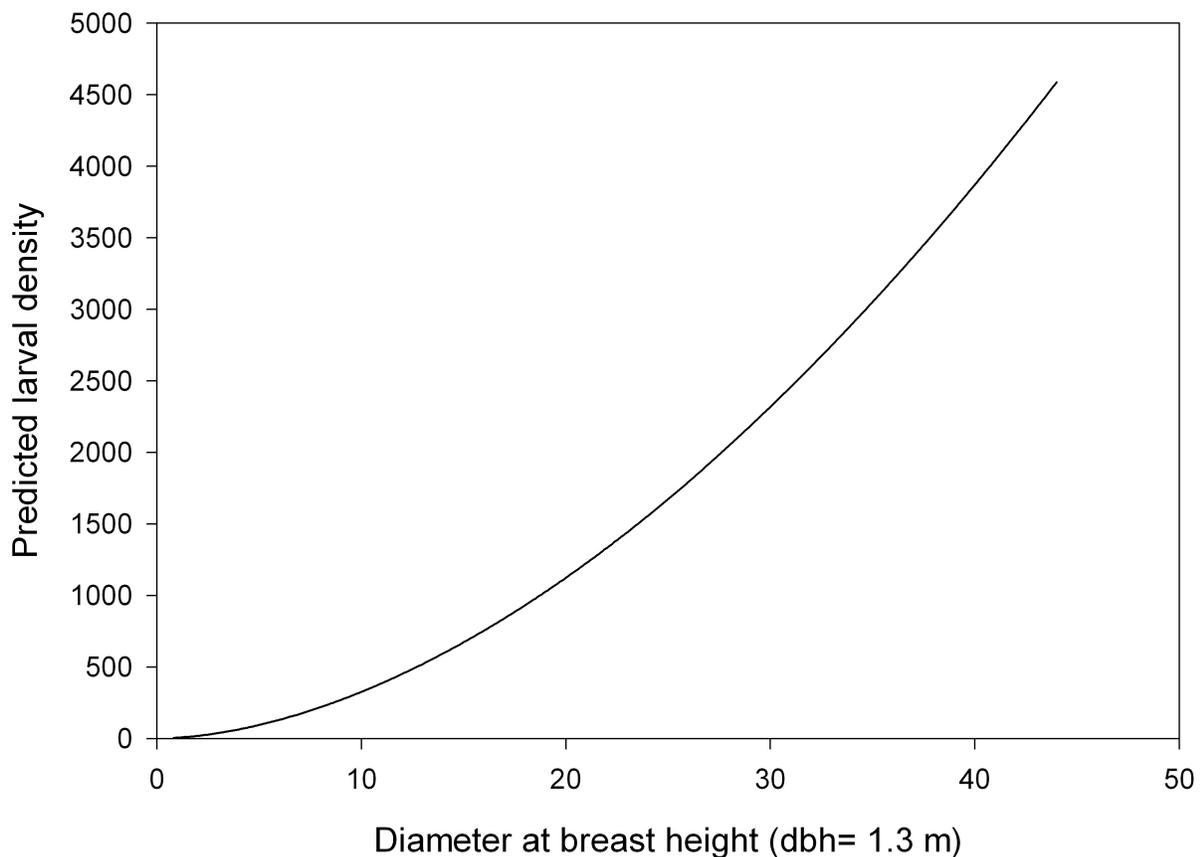


FIGURE 4. Predicted larval density/tree for *O. vitiosa* as a function of melaleuca tree diameter.

How do these modeling results relate to observations of *O. vitiosa* larval densities in the field? Direct observations of larvae in canopies of tall (>5 cm dbh) melaleuca trees are difficult to

obtain, expensive and therefore rare. For this reason, data describing actual population densities of larvae are limited to saplings or regrowth from cut trees (Center *et al.*, 2000; Pratt *et al.*, 2002). When comparing model predictions for this subset of tree sizes with actual observations, the model slightly overestimated cumulative larval densities by 9%, or 15 416 larvae/ha/yr. The most intuitive explanation for the discrepancy among modeled and realized densities may be related to the inability of weevils to approach the theoretical maximum density (instantaneous carrying capacity) due to suppressive biotic and abiotic factors. One of these factors may include the acquisition of higher trophic levels (parasites, predators, and pathogens) in the agent's adventive range (Goeden & Louda, 1976; Pratt *et al.*, 2003b). The predatory bug *Podisus mucronatus* Uhler, for instance, was recently observed preying on *O. vitiosa* larvae in south Florida, although the impact of this new association on weevil densities has not been quantified (Costello *et al.*, 2002). Unsuitable environmental conditions may also limit population densities below optimal levels. As stated earlier, *O. vitiosa* pupates in the soil and, even in well drained soils, weevils may suffer high mortality rates when substrates become temporarily saturated during periods of high rainfall. The influence of these factors on population dynamics is poorly understood and will be the focus of future studies.

Impacts of biological control agents depend, in part, on sufficient population densities to stress target weeds (Marohasy, 1997; Parker *et al.*, 1999). Our data describe those larval densities that will fully exploit the melaleuca foliar resource and may be used as target levels for land managers when redistributing the agent. With field or lab-based mass production (Wheeler & Zahniser, 2001; Wheeler, 2002) of weed biological control agents, damaging densities may be produced and liberated at early stages of a program to expedite impact. While those densities calculated herein are predicted to fully exploit melaleuca trees, the insect densities required to realize sublethal impacts (i.e., reduced regenerative potential) remains unclear and will be the subject of ongoing investigations.

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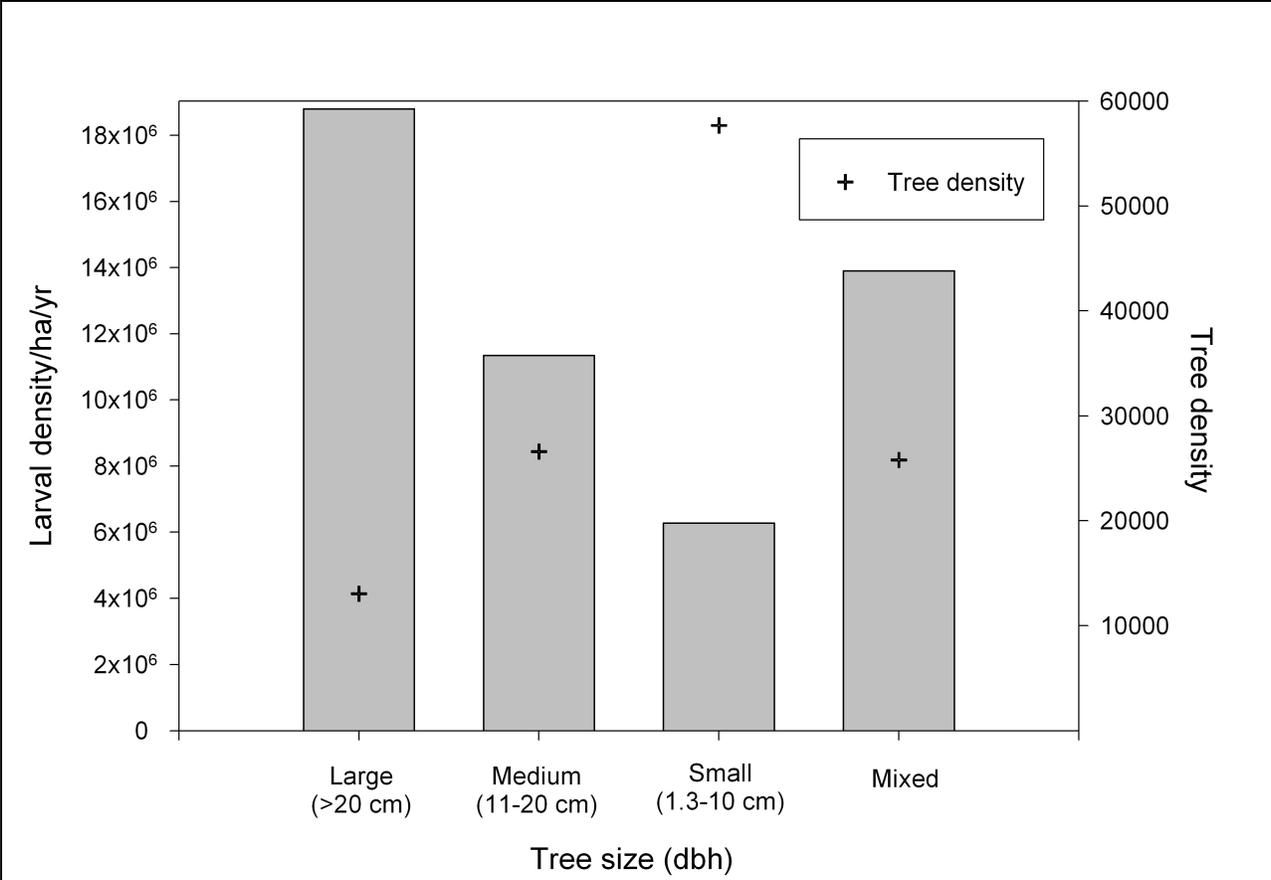


FIGURE 5. Larval density predictions for hectares of melaleuca dominated by large, medium, small or mixed tree size classes.

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