Population dynamics and selection of an invasive tree species in response to herbivory

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Introduction

Invasions by exotic species pose one of the largest threats to global biodiversity and the functioning of natural ecosystems (Cox 1999, Mooney and Hobbs 2000, Rossman 2001). One important tool for managing invasive species is biological control, which is the use of natural enemies, such as predators, herbivores, or pathogens, to reduce or eliminate pest populations (Debach and Rosen 1991). In many cases, biological control may be a less costly, less ecologically damaging, and more sustainable means of managing invasive species than mechanical or chemical means (Bellows and Fisher 1999). However, biological control may be ineffective or even damaging if a thorough understanding of the relevant ecological and evolutionary dynamics of the system in question is lacking.

Biological control agents are generally selected based on the damage they can do to target species at the individual level. The goal of biological control projects, however, is usually to cause a population level reduction in the rate of increase of the target species. Even a substantial amount of individual damage at a particular life stage may not have any significant effect on population growth rate if the overall rate of population increase is relatively insensitive to effects at that life stage (Caswell 2001, Hoffmann 1999, Doak 1992). Despite this fact, few biological control programs use a matrix modeling approach to determine the effects of a biological control agent on the population dynamics of the target species (but see Shea and Kelly 1998). Through matrix models and life table response experiments (Caswell 2001), it is possible to project, given a set of assumptions, how a biological control agent would be expected to affect the overall rate of growth of the target population.

Even if a biological control agent is able to cause damage to target individuals and cause a decline in the growth rate of the target population, the biological control program may not be effective over the long term. This situation may occur if the target species is able to evolve resistance or tolerance to the effects of the control agent. Evolutionary theory predicts that natural enemies may act as strong selective agents and result in phenotypic changes in target populations. While few empirical studies have directly tested this prediction, there is evidence to support the hypothesis that defensive traits are under selection by natural enemies (Stinchcomb and Rausher 2001, Mauricio and Rausher 1997). If traits conferring resistance or tolerance to a biological control agents are under selection and spread through a population, the biological control agent may become ineffective over time. Such evolutionary considerations are thus critical for designing effective invasive species management plans.

By combining the demographic information and selection studies, it is possible to address a key idea in evolutionary theory that thus far has received little empirical attention. Theory predicts that traits involved in the most critical life stage transitions are likely to be under the most intense selection (Caswell 2001, Grant 1997, Horvitz and Schemske 1995, Fisher 1958). This idea forms the basis for much current thinking on life history evolution and relates fundamental ecological and evolutionary processes. However, few studies have measured both the demographic and selection parameters needed to test this hypothesis.

My research involves studying population dynamics and selection in the invasive exotic tree *Melaleuca quinquenervia* (Cav.) Blake (Myrtaceae). This tree is native to Australia and was introduced to south Florida in the early 1900's (Turner et al. 1998). The proposed research will include two components: a demographic study and a quantitative genetics study. The demographic study will consist of tagging individuals in many different sites differing in the presence and abundance of psyllids, hydrology, soil type, and stand age structure. Periodic censuses will assess growth and reproduction of all individuals for two years. The effects of psyllids on the growth and reproduction of plants of different life stages will be determined from the demographic data as well as from separate controlled field experiments. Matrix models and life table response experiments (Caswell 2001) will be used to project the effects of psyllids on the growth rate of melaleuca populations. In the quantitative genetics study, we will collected seeds from individuals throughout the range of melaleuca in Florida and Australia. The seeds were germinated in a greenhouse, and seedlings were transplanted to the field and subjected to an herbivory treatment or a no-herbivory treatment (insects excluded with pesticide). Plants are periodically censused for growth, and traits relating to defense, including leaf toughness, hairiness, and the concentrations of terpenoids, phenolics, and nitrogen will be measured after one year. Total biomass, reproduction, and plant survival will also be measured at the end of the experiment. We will use phenotypic selection analysis (Rausher 1992) to determine the pattern of selection acting on the putative defensive traits.

Objectives- Demographic Study:

1) Assess the overall population growth rates of *Melaleuca*
2) Determine the sensitivities and elasticities, as well as transient dynamics, of stage-specific demographic events to overall *Melaleuca* population growth rate
3) Evaluate the effects of insects, hydrology, and soil type on *Melaleuca* population growth rate

Objectives- Selection Study:

1) Determine which traits in *Melaleuca* relate to tolerance and resistance to psyllid herbivory
2) Evaluate the strength and direction of selection on these defensive traits and the relationship between the traits and overall plant fitness
3) Test whether the expression of traits at the most demographically sensitive life stages is under the strongest selection

Methods:

Study species

Melaleuca quinquenervia (Cav.) Blake (Myrtaceae) is a native Australian tree that was introduced into south Florida in the early 1900's (Meskimen 1962). Populations in Florida are generally found south of Lake Okeechobee, and major infestations occur in Lee, Collier, Hendry, Palm Beach, Broward, and Dade counties (Turner et al. 1998). Individuals can be found in permanently and seasonally flooded areas of the Everglades, as well as dry upland areas. The tree can grow in height at rates of up to two m/yr (Alexander and Hofsteter 1975), can reach sexual maturity in less than two years (Meskimen 1962), and can flower several times per year. Flowers are perfect and arranged along spikes (Tomlinson 1980). The flowers are usually pollinated by insects, especially honey bees, and although self-compatible and autogamous, are generally outcrossing (Vardman 1994). Each flower spike can contain 30-70 capsules, each containing 200-350 seeds (Meskimen 1962). A single tree can produce upwards of 100 million seeds in one flowering period (Rayamajhi et al. 2002). One study showed that only 15% of all seeds were embryonic, 50% of embryonic seeds were viable, and 73 % of viable seeds were germinable after 10 days (Rayachhetry et al. 1998). Trees can resprout from cut or toppled stumps or branches, but extensive clonal growth is not known in this species.

Demographic study

For the demographic study, we will establish plots at each of 30 sites that vary in psyllid densities, hydrology, soil type, and stand age structure. Over 6,000 individuals at all life stages at 7 sites have already been tagged and measured. Additional plots will be established at two sites in Australia. At each site, we randomly place one-five plots within the study area. All *Melaleuca* individuals within each plot are marked for the study. Seedlings and saplings are marked with wire tags, and larger trees are marked with aluminum tags nailed into the trunk. Individuals will be divided into size classes based on the algorithm developed by Moloney (1986). The size of all individuals will be measured as diameter at 1.3 m height (DBH) for individuals > 1.3 m tall and as stem diameter at soil level (DAS) and height for individuals < 1.3 m tall. DBH has been shown to correlate well with total biomass for *Melaleuca* trees ($r^2 > 0.95$; Van et al. 2000). Size and survival will be measured for all individuals annually for at least two years. Fertility will be estimated for saplings by counting the number of flower spikes and for large trees by counting spikes on three haphazardly selected branches and multiplying the average by the total branch number. Fertility measurements will be taken every 6 months for at least two years.

Population dynamic parameters (population growth rate, sensitivities, elasticities) will be calculated for each plot using the methods described in Caswell (2001). The effects of insects, hydrology, soil type, and stand age structure will be estimated using regression and analysis of variance (ANOVA) techniques as well as life table response experiments (Caswell 2001). The demographic data described above as well as separate experiments on the effects of psyllids at different life stages will be used to parameterize the models.

Quantitative genetics study

To investigate which *Melaleuca* traits may be involved in tolerance or resistance to psyllid herbivory, we collected leaf tissue from infested and uninfested plants in the field. There are two field sites: Estero (Lee County) and Holliday Park (Broward County). At each site, we collected fresh new leaf tissue from 30 pairs of trees: 15 trees infested with psyllids (at least one colony observed) and 15 uninfested trees. Each uninfested tree was near the infested paired tree but not less than 0.5 m away, and was otherwise as similar as possible in height, presence of new growth, and other characteristics. Sampling consisted of collecting 1 - 2 branch ends with new leaf growth. Each sample was placed in a plastic bag, with bags placed in a cooler until returning to the lab. Leaves were brought back to the lab and stored at - 4 C until measurements were taken. We measured terpenoids using FID (GC/MS referenced) and nitrogen using a Perkin Elmer CHN analyzer. The results showed no relationship between infestation and any of the chemical traits measured ($p > 0.05$ for all chi-square tests). However, it is possible that these chemical traits may still be important for determining herbivory response and that manipulative experiments are necessary to detect the effects of the traits.

After this preliminary study, I began work on the quantitative genetics study. Seed capsules were collected from 60 trees in Florida and 60 trees in Australia (120 maternal source trees). Capsules were air dried, and seeds were germinated on flats of potting soil in a USDA greenhouse. From each maternal family, 24 seedlings were planted in a common garden in the field outside of the USDA Invasive Species Research Lab in Ft. Lauderdale, FL. The total number of seedlings used in the experiment is 2,880 (N = 120 maternal families x 2 treatments x 12 replicates = 2,880). Half of the seedlings are protected from psyllids using Orthene (containing Acephate) and half are unprotected. The treatments are arranged in a split-plot design. We have measured plant height and leaf number at the beginning of the experiment, and plant height, leaf number, leaf toughness, leaf hair density, phenolics, terpenoids, nitrogen, plant biomass, and the number of psyllid colonies per plant will be measured at the end of the experiment. The effects of site, family, block, and treatment and their interactions will be determined with a multivariate analysis of variance (MANOVA). The strength of directional and stabilizing selection on each trait will be analyzed by regressing family means of each trait on estimated fitness (total biomass) following Rausher (1992). Preliminary results show a significant effect of family on germination date ($F_{119,2519} = 7.24$, $p < 0.0001$), with seedlings from Florida germinating 1.27 days earlier on average than Australian seedlings.

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