2010-05-14

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Lucero Sevillano Garcia Mayeya
University of Miami, lucero_sevillano@bio.miami.edu

Recommended Citation
Sevillano Garcia Mayeya, Lucero, "The Effects of Biological Control Agents on Population Growth and Spread of Melaleuca quinquenervia" (2010). *Open Access Dissertations*. 406.
https://scholarlyrepository.miami.edu/oa_dissertations/406

UNIVERSITY OF MIAMI

THE EFFECTS OF BIOLOGICAL CONTROL AGENTS ON POPULATION GROWTH AND SPREAD OF *Melaleuca quinquenervia*

By

Lucero Sevillano García Mayeya

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

Coral Gables, Florida

May 2010

UNIVERSITY OF MIAMI

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THE EFFECTS OF BIOLOGICAL CONTROL AGENTS ON POPULATION GROWTH AND SPREAD OF *Melaleuca quinquenervia*

Lucero Sevillano García Mayeya

Approved:

_________________ Carol C. Horvitz, Ph.D. Professor of Biology	_________________ Terri A. Scandura, Ph.D. Dean of the Graduate School
_________________ Donald DeAngelis, Ph.D. Research Professor of Biology	_________________ Keith Waddington, Ph.D. Professor of Biology
_________________ Paul D. Pratt, Ph.D. Research Entomologist Invasive Plant Research Lab, USDA/ARS Ft. Lauderdale, Florida	_________________ Steven Franks, Ph.D. Assistant Professor of Biology Fordham University

SEVILLANO GARCIA MAYEYA, LUCERO (Ph.D., Biology)
The Effects of Biological Control Agents on Population Growth and Spread of *Melaleuca quinquenervia* (May 2010)

Abstract of a dissertation at the University of Miami.

Dissertation supervised by Professor Carol Horvitz.
No. of pages in text. (168)

Biological control programs against invasive plants traditionally evaluate the effects of agents on individual plant growth, reproduction and survival. However, the effects on individual plants do not necessarily translate into effects on plant populations. Invasive species are characterized by having populations that grow and spread at high rates. Since it is at the population level that invasions either fail or succeed, effective biological control programs should impact population-level characteristics of invasive species. The main goal of this study was to evaluate the effectiveness of two biological control agents in reducing population growth and spread of the invasive tree *Melaleuca quinquenervia* (Myrtaceae).

Melaleuca quinquenervia is a subtropical tree native to Australia, and invasive in south Florida, Puerto Rico, and the Bahamas among other areas of the Caribbean Islands. It is classified by the Florida Exotic Pest Plant Council as a Category I species. *M. quinquenervia* produces serotinous capsules that can remain attached to the tree for several years, forming a canopy seed bank. Massive dispersal of wind-dispersed seeds is episodic and favors the formation of dense monospecific even-aged stands. While in

Florida two insects (the weevil *Oxyops vitiosa*, and the psyllid *Boreioglycaspis melaleucae*) have been established as biological control agents for several years, in Puerto Rico only psyllids are present, and in the Bahamas a biological control program has not been implemented. This study combined demographic data, experiments and mathematical models to investigate the influence of the two biological control agents on *M. quinquenervia*'s spatial population dynamics.

In the field, permanent plots were established and demographic data was collected in populations in Australia (2003-2006), Florida (2003-2007), Puerto Rico (2005-2008), and the Bahamas (2006-2008). I characterized the size structure of *M. quinquenervia* populations in each region, and found that Australian populations are comprised mostly of large adult trees, while in the exotic ranges populations are comprised mostly of short plants (<1.3 m in height), and small adult trees.

In a shade-house, I performed an experiment to investigate the effects of insect type, density, and soil type on survival and growth of *M. quinquenervia* seedlings. I found that high density of insects, independently or in combination, reduce survival and growth of seedlings, thus having the potential to alter the seedling-short plant transition of the life cycle of *M. quinquenervia*.

Based on the demographic data, I developed integral projection models (IPMs) of the population dynamics of *M. quinquenervia*, to determine population growth rates in the native and exotic ranges, and to evaluate which stages of the life cycle contribute the most to population growth. I found that populations in Australia and the Bahamas are increasing, while populations in Florida and Puerto Rico are decreasing. Population growth is most sensitive to the seedling-short plant transition in all regions, except in

Florida, where population growth is most sensitive to survival of tall plants. Based on the IPMs, and on the experimental component of this study, I investigated the potential of biological control agents to reduce population growth rate in the exotic regions. By performing simulations I found that the effects of the insects on the seedling-short plant transition result in reductions in population growth rate in Puerto Rico and the Bahamas, particularly if plants are damaged by high density of psyllids. The impacts of insects on population growth are stronger in years with massive seed release events.

Finally, I combined seed dispersal and demographic data to develop an integrodifference structured model of population spread. I investigated the potential of the biological control agents to reduce the rate of spread of *M. quinquenervia* populations in the Bahamas, the only population in the exotic region that is increasing. Simulations indicated that seedlings contribute the most to population spread, and that by reducing growth and survival of seedlings, insects have the potential to reduce the rate of population spread in regular and massive seed rain scenarios.

Overall this study shows that the individual-level effects that biological control agents have on *M. quinquenervia* have translated into reductions in population growth rate and rate of spread of this invasive tree.

Dedication

To my family,

My mom, my dad, and my brother for their love and support every second of my life,
and particularly during this great adventure away from home.

To my husband,

For his encouragement, support and love during all this process,
for being present at all times in unique ways.

Acknowledgements

First, I would like to thank my advisor, Dr. Carol Horvitz, for her incredibly thoughtful guidance during every stage of the Ph.D. process. I feel very honored for the opportunity to work with a great scientist, a very caring teacher, and a wonderful human being. Carol has impacted my life in many different ways, and I will always be thankful for that.

My dissertation committee members, Dr. Donald DeAngelis, Dr. Keith Waddington, Dr. Paul Pratt, and Dr. Steven Franks gave me very insightful comments that improved my project and my writing. Dr. Guillermo Goldstein and Dr. Svata Louda were members of my committee up to the time of my defense, and provided very helpful comments during all the stages of my project.

This project was established as a collaboration between Paul Pratt and Steve Franks from the Invasive Plant Research Laboratory, USDA-ARS, and Carol Horvitz and I. My project was mostly supported by the Invasive Plant Research Laboratory, and I was fortunate to receive funding from the Society of Wetland Scientists, and the FLEPPC Julia Morton Invasive Plant Research award. My graduate studies were supported during six years by a National Council for Science and Technology (CONACyT) fellowship.

This project could not have been completed without all the field assistants who helped set up and collect data for several years in the demographic plots. In Florida, Steve Franks and Paul Pratt set up the plots, and many of their lab technicians and students helped with data collection: Marguerite Stetson, Sigfredo Gonzalez, Robyn Chiarelli, Deah Lieraunce, Karen Balentine, Cresida Silvers, Jorge Liedi and Reynaldo Moscat. Dr. Min Rayamajhi kindly shared with us demographic data from plots

established in Holiday Park. In Australia, Steve and Paul collaborated with Dr. Matthew Purcell and his group, from the Australian Biological Control Lab, to set up plots and collect data for several years. In Puerto Rico, Lourdes Bernier, Vicente Quevedo and Jose Sustache from the Departmento de Recursos Naturales y Ambientales helped us to locate and set up plots. Paul, Min, Deah, Jorge, and Lourdes helped in the data collection, and made the trips to Puerto Rico an incredibly productive and fun experience. In the Bahamas, Paul, Min, Cresida and Eduardo helped to set up and/or gather field data.

The development of my big experiment could not have been possible without the help of Dr. Waddington who shared his beeyard with me, and Paul, Deah, and Robyn for teaching me to rear insects. I was fortunate to have 23 enthusiastic undergraduate students participating in different stages of the experiment; without them I could not have built so many cages, rear so many insects, and take care of so many plants.

My labmates David Matlaga, Orou Gaoue, Carlos Garcia-Robledo, Robert McElderry, and John Cozza gave me helpful comments in all phases of my project, and provided an invaluable and intellectually exciting environment in the Zebra lab.

The love, support, and patience of my family and friends were fundamental during this exciting and challenging stage of my life. My parents Lucero and Francisco, and my brother Paco have always encouraged me to follow my dreams. My husband, Eduardo, not only assisted me in the field, the lab, and the writing phases, but he encouraged me to keep moving forward every day during my life as a graduate student. Catalina Aritstizabal, Anita Salazar, Tania Wyss and Floria Mora-Kepfer were a great personal support and made my life in Miami much more charming and fun.

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Chapter I

Interregional comparison of the size-structure of populations of *Melaleuca quinquenervia* in its native and exotic range, with and without biocontrol agents[1]

Background

Comparative demographic studies of invasive species in their exotic and native ranges may provide new insights into differential population dynamics (Hierro *et al.* 2005). We are investigating the impacts of two biocontrol agents on population growth of *Melaleuca quinquenervia* (Cav.) Blake. The first step, which we present here, is to describe the size structure and vital rates in native and exotic ranges, including areas with and without biological control agents. Specific objectives of this paper are to: 1) characterize the size structure and 2) estimate individual growth rates as well as population-level death and birth rates of *M. quinquenervia* populations in its native and exotic ranges.

Materials and Methods

Study system

Melaleuca quienquenervia Cav. Blake (Myrtaceae) is a tree native to sub-tropical Australia currently invading southern Florida, Puerto Rico, and the Bahamas (Serbesoff-King 2003). Melaleuca produces serotinous fruits (capsules) that may remain attached to

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[1] Coauthors: Paul D. Pratt, Steven Franks, and Carol C. Horvitz
Paper published in *Proceedings of the Sixteenth Australian Weeds Conference* 2008: 147-149.

the tree for several years. An adult tree can produce millions of seeds per year, with massive seed release episodically occurring after stress (Woodall 1982). For example, seed dispersal and seedling establishment is favored by frequent fires in both native and exotic ranges. Periodic massive seed release, after a disturbance event, into a previously unoccupied area favors the formation of even-aged stands (Turner *et al.* 1998). Two insects, both native to Australia, have been introduced to Florida as biological control agents: the leaf-eater weevil *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae), and the sap-sucker psyllid *Boreioglycaspis melaleucae* Moore (Homoptera: Psyllidae). Around 450 species of insect herbivores have been reported for Melaleuca in its native range (Balciunas *et al.* 1995). In Puerto Rico and the Bahamas, Melaleuca invasion is in early stages and no biocontrol program has been implemented. However, in 2006 psyllids were occasionally found in populations in Puerto Rico (Pratt *et al.* 2006).

Demographic plots

In 2003, we set up demographic plots in South Florida, and in the native range of *M. quinquenervia*, the east coast of Australia (Figure 1). In 2005 additional plots were established in northeast Puerto Rico and in the northern Bahamas. Plots were laid out to include patches with different size classes to capture demographic rates by size within each region. We subsequently lost three plots in Florida due to herbicide application and urban development. Initially, we tagged all *M. quinquenervia* plants in the plots, recording size and reproductive status of each. We recorded mortality, recruitment and size every year until 2007 (except in Australia where the last census was carried out in

2006). For plants < 1.3 m in height (hereafter denoted "seedlings"), diameter of the stem 5 cm above the ground was recorded and for plants > 1.3 m in height (hereafter denoted "larger plants"), the diameter at breast height (DBH) (1.3 m) was recorded. All new seedlings that appeared in each plot every year were tagged and followed.

Data analyses

Size distributions among geographic regions were compared using a chi-square test. Growth of individuals was calculated as the proportional change in diameter using the formula: [(final – initial)/initial]. Differences in growth rates among regions were compared using Kruskal-Wallis tests and P values were calculated based on Chi-square distributions (JMP 4.0).

Results

Size structure

In all regions, the shape of the size distribution (i.e. the proportion of individuals in each size class) was very similar across years, with the most variation in Florida (not shown). The shape of the size distribution differs between Australia and the exotic regions, and further differences exist among exotic regions ($\chi^2_{(111)} = 7591.4$; $P<0.001$) (Figure 1.1). The biggest contrast is in the large adults, which distinctly made up a larger proportion of the native populations, than the exotic populations. In Australia, 49% of the individuals were large adults; while in Florida, only 9% of the individuals. In Puerto Rico and the

Bahamas, the percentage of large adults was even lower (4% and 2%, respectively). The seedling portion of the population also varied. In the native region, on average 20% of the individuals were seedlings across years (min: 14% in 2006; max: 26% in 2003). In contrast, most of the individuals in the three exotic regions were seedlings. In Florida, seedlings comprised 43% of the individuals (min: 27% in 2006; max: 59% in 2005). In Puerto Rico seedlings were 37% of the individuals (min: 32% in 2005; max: 52% in 2007); and in the Bahamas, seedlings were 63% of the individuals (min: 59% in 2007; max: 67% in 2006).

Vital rates

Individual growth was significantly different among regions for both seedlings ($\chi^2_{(3)}$ = 764.19; P<0.0001) and larger plants ($\chi^2_{(3)}$ = 186.34; P<0.0001) (Figure 1.2). The Bahamas had the highest seedling growth (median = 0.27) while Florida and Puerto Rico Puerto Rico were nearly tied for the lowest growth rate, an order of magnitude lower. The Bahamas also had the highest growth of larger plants (median = 0.11), while Australia had the slowest growth rate, nearly two orders of magnitude lower. Mortality was highest in Florida and lowest in Australia (Table 1). Recruitment was highest in Puerto Rico lowest in Australia (Table 1.1).

Discussion

The greatest difference in size structure of *M. quinquenervia* is between Australia and the three exotic regions, but there are also differences between Florida and the other two regions. In Puerto Rico and the Bahamas populations are in earlier phases of invasion, while in Florida populations have had more time to mature so that small adults are also common. Australian populations are in a mature phase; there are many large adults (100-300mm dbh). It is surprising that per capita mortality in Australia is very low given the presence of the whole community of natural enemies. Mortality was highest in Florida, where populations are very dense. Biological controls have the potential to negatively impact survival (Franks *et al.* 2006), but so does intraspecific competition (Rayamajhi *et al.* 2006). For populations in Puerto Rico and the Bahamas, mortality was relatively lower and, although they are also very dense, insect herbivores are nearly absent. For all regions, mortality was higher than recruitment every year, which suggests that population numbers are decreasing over time. However, in the Bahamas the number of individuals that died and the number of newborns was very similar. In contrast, the number of individuals that died in Florida was much higher than the number of newborns, suggesting that populations are decreasing. Recruitment was also very low within our plots, but given that it is episodic and is known to be highest in newly colonized sites it has been difficult to capture. We observed a recruitment event of a newly colonized site in Florida in 2005. Size-structured demographic models are needed to explore the population dynamics of Melaleuca and determine 1) the rate at which populations are growing in each region, and 2) the potential influence of biocontrols in population growth[*].

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[*] We thank the USDA/ARS Agreement No. 58-6629-4-232 for financial support and USDA/ARS Invasive Plant Research Lab for field assistance.

Table 1.1. Number of individuals of *M. quinquenervia* marked at the beginning of the study in each geographic region, and per capita mortality and recruitment throughout the study (n/a: not available). Per capita mortality and recruitment were calculated as the

	No. individuals				**Per capita mortality**				**Per capita recruitment**			
	2003	2004	2005	2006	2003-04	2004-05	2005-06	2006-07	2003-04	2004-05	2006-07	2006-07
AUS	2037	1935	1850	1780	0.048	0.039	0.037	n/a	0.0005	0.0005	0.001	n/a
FL	7815	5045	4230	1948	0.266	0.104	0.549	0.428	0.0535	0.3665	0	0.3131
PR	n/a	n/a	2201	2068	n/a	n/a	0.048	0.375	n/a	n/a	0	0.5551
BAH	n/a	n/a	n/a	1298	n/a	n/a	n/a	0.080	n/a	n/a	n/a	0.0701

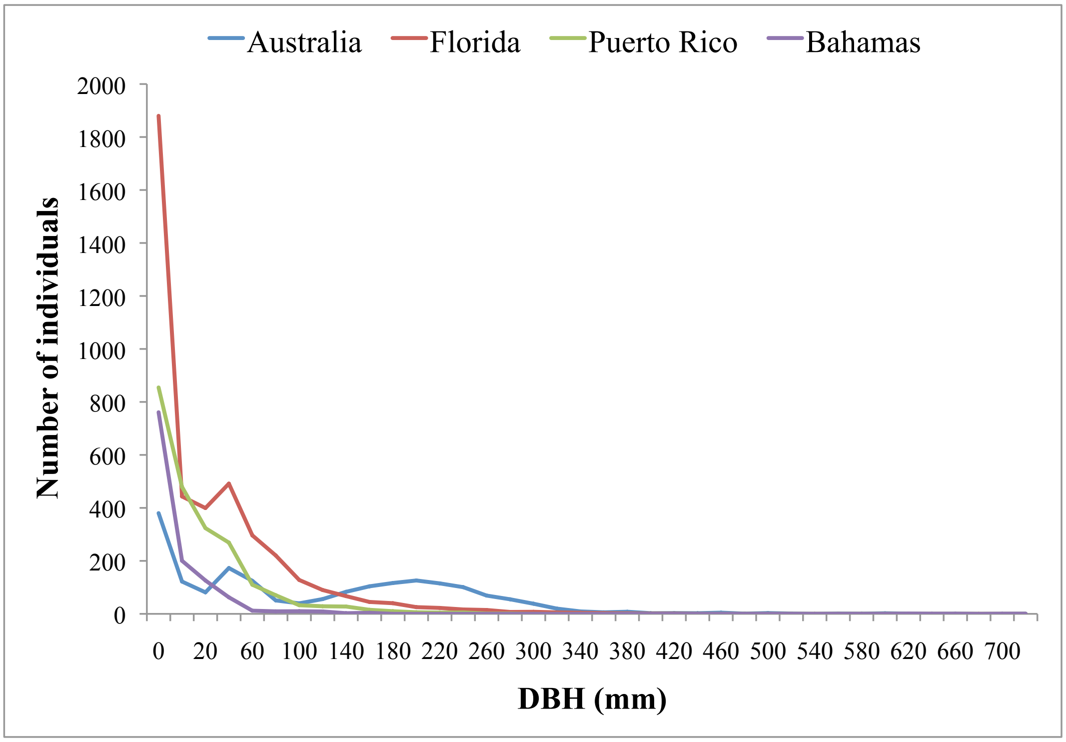

Figure 1. 1. Mean size distribution of *M. quinquenervia* populations across years in Australia (2003-2006), Florida (2003-2007), Puerto Rico (2005-2007), and the Bahamas (2006-2007). Size is reported as diameter at breast height (DBH) in categories of 20 mm (20-720); category 0 includes individuals <1.3m; category 10 includes individuals >1.3 m and <10 mm DBH; categories 20-720 include individuals >1.3m and its corresponding DBH cutoff. The initial sampling effort in Australia included: 2 sites, 7 plots, 533 individuals <1.3m, and 1510 individuals >1.3 m. In Florida included 7 sites, 39 plots, 3567 individuals <1.3m, and 4267 individuals >1.3 m. In Puerto Rico included 1 site, 6 plots, 1492 individuals <1.3m, and 707 individuals >1.3 m. In the Bahamas included 3 sites, 13 plots, 430 individuals <1.3m, and 352 individuals >1.3 m.

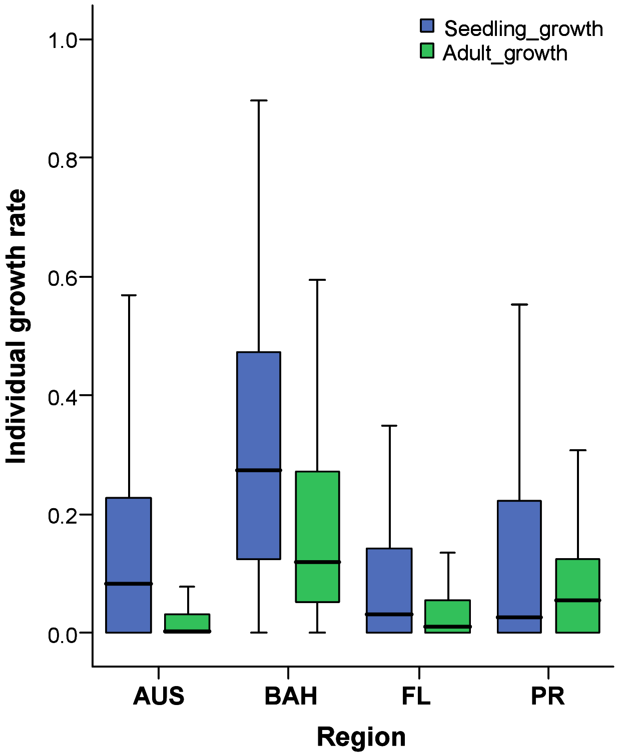

Figure 1.2. Box plot of the annual relative growth of *M. quinquenervia* individuals in Australia, Florida, Puerto Rico, and the Bahamas from 2005 to 2006.

Chapter II

Natural enemy density and soil type influence growth and survival of *Melaleuca quinquenervia* seedlings[2]

Background

Biological control is the use of natural enemies to reduce the density and spread of invasive species (McFadyen 1998), and it can be an effective method of suppressing invasive plants (Huffaker and Kennet 1959; Osmond and Monro 1981; Moran and Zimmermann 1984). Biological control programs generally employ multiple species of natural enemies to control a single target pest. Quantifying species-specific contributions to the control of an invasive plant can be difficult when multiple co-existing agents have been introduced (McEvoy and Coombs 1999a). A review of 26 biological control programs reported that control was attributable to only one agent in 81% of the case studies (Myers 1985). However, other studies have reported that the cumulative effects of several agents were needed to control weeds (Schroeder and Goeden 1986; Denoth *et al.* 2002, Milbrath and Nechols 2004). Considering that the introduction of natural enemies is costly, time-consuming (McEvoy and Coombs 1999a, b), and potentially risky (Simberloff and Stilling 1996; Louda *et al.* 1997; Louda *et al.* 2003), evaluating the relative contributions of already-established agents prior to introducing additional natural enemies is useful to managers. Of particular interest is to determine whether introduced natural enemies affect life stages or demographic processes (survival, growth or

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[2] Coauthors: Carol C. Horvitz, Paul. D. Pratt.
Paper published in *Biological Control* 53(2010): 168-177.

reproduction) that result in marked reductions in population growth (Shea and Kelly, 1998; Buckley *et al.* 2004; Davis *et al.* 2006; Ramula and Buckley, 2008).

Two insects, native to Australia, have been introduced as biological control agents of *Melaleuca quinquenervia* Cav. Blake (Myrtaceae), a tree that is native to Australia but invasive in subtropical southern Florida. These insects are: the leaf-eating weevil *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae), and the sap-sucker psyllid *Boreioglycaspis melaleucae* Moore (Homoptera: Psyllidae). The weevil *O. vitiosa,* was released in southern Florida in 1997 (Wineriter and Buckingham 1997; Center *et al.* 2000). Larvae and adults feed on newly developed foliage and expanding leaves at branch apices, producing paper-thin feeding trails (by larvae) and window-like feeding scars (by adults) (Pratt *et al.* 2004b). Weevils have four larval stages, and all of them are found on the plant. Since weevils pupate in the soil, their abundance is limited in permanently inundated areas (Center *et al.* 2000). Larval densities in Florida are highest during late fall and winter, and lower in spring and summer, unless fresh leaf tissue is available (Pratt *et al.* 2004b). Adults are present throughout the year.

The psyllid, *B. melaleucae,* was released in southern Florida in 2002. Both nymphs and adults feed on sap from leaves and stems by inserting their stylets into the phloem. Most damage, however, is attributed to nymphs, which feed on tender, expanding buds and leaves, as well as mature foliage (Purcell *et al.* 1997; Pratt *et al.* 2004a). Psyllids cause leaf desiccation, curling, discoloration, premature leaf senescence, and ultimately defoliation (Morath *et al.* 2006). Psyllids have five nymphal instars. First instars are mobile but later stages are sessile and congregate on leaves or stems (Pratt *et al.* 2004a). Psyllid nymphs produce a white waxy flocculence that covers them, making it difficult to quantify density in the field, particularly on large adult trees. Psyllids are common on *M. quinquenervia* throughout the year, although densities are highest from late fall through spring, before the start of the rainy season, which occurs in the summer in southern Florida.

Damage to *M. quinquenervia* by weevils and psyllids has been quantified in the field since their introduction. Herbivory on mature trees by weevils increased from 5% of leaves in 1999 to 45% of leaves in 2005 (Rayamajhi *et al.* 2006). Trees may compensate for weevil damage by replacing leaf-bearing branches that are attacked (Pratt *et al.* 2005; Silvers *et al.* 2008). However, Pratt *et al.* (2005) compared the incidence of inflorescence and capsule production between weevil-damaged and undamaged *M. quinquenervia* stands during spring 2000, and found that the probability of producing inflorescences/new capsules was 36 higher in undamaged versus damaged trees. The number of inflorescences and capsules were reduced by 80% and 54%, respectively, in damaged compared to undamaged trees (Pratt *et al.* 2005). Center *et al.* (2007) observed psyllid damage on 43% of surveyed coppices in 2003 with between 50% and 85% of the leaves being damaged on affected coppices. Sustained damage by psyllids in abundance (>15 per plant for >35 d) caused a reduction in the height of seedlings (Center *et al.* 2007). However, psyllid-damaged seedlings compensate for herbivory by increasing lateral leaf production (Center *et al.* 2007). *Melaleuca quinquenervia* stands (individuals 1-33 cm diameter at 1.3 m height) with high levels of damage by both insects experience significant reduction (12%) in aboveground biomass (Rayamajhi *et al.* 2008). Insecticidal exclusion experiments revealed that weevils and psyllids together reduced growth rates, biomass, number of capsules, and seed production (Tipping *et al.* 2008;

Franks *et al.* 2008a, b).

Although the effects of insect damage on survival and performance of *M. quinquenervia* have been studied in the field, the effects of different densities of each insect and the interaction between insects have not been investigated under controlled combinations. Both insects have become widely naturalized throughout southern Florida (Center *et al.* 2000; Pratt *et al.* 2003; Center *et al.* 2006), thus making it difficult to independently estimate the effects of either species under natural conditions (Rayamajhi *et al.* 2006; Tipping *et al.* 2008; Tipping *et al.* 2009). One previous experimental field study (Franks *et al.* 2006) examined the effects of combinations of psyllids and weevils by manipulating the density of psyllids but not of weevils. At the time the study was conducted, weevils had only been observed to occur at the low rate of one larva per seedling (Wheeler 2003; Franks *et al.* 2006). This study reported that: 1) high densities of psyllids ($\geq$ 15 nymphs per seedling) were required to reduce seedling survival, growth and biomass; 2) weevils did not reduce survival, growth and biomass of seedlings; and 3) the psyllids and weevils did not interact in their effects on seedlings. What remains unclear after this study is whether weevils might have a significant effect at higher densities than the density assayed. In recent years, up to three weevil larvae per seedling have been frequently observed in naturalized populations (L. Sevillano, personal observations).

Understanding the effects of multiple species and densities of herbivores on plant fitness is important both conceptually, in the framework of plant-insect interactions, and for management. The two insects introduced as biological control agents against *M. quinquenervia* have different feeding modes that may differentially affect plant survival and growth. Predicting which type of herbivore is most injurious is not easy. Damage inflicted by one herbivore may influence the vulnerability of plants being attacked by the other herbivore (Pilson 1992; Karban and Baldwin 1997). Multiple species of herbivores attacking a plant simultaneously can have additive or multiplicative effects on plant fitness (Strauss 1991), but interaction effects between herbivores in general have rarely been investigated (but see Meyer 1993). From a management perspective, multiplicative effects of biological control agents would be most effective in controlling invasive plants, providing the interaction is facilitative rather than interferential.

Plant response to herbivory may depend not only on the identity of the herbivore, but also on its density. Higher densities are expected to have a greater impact on plant fitness (Louda 1982), although Meyer (1993) showed that a few individuals of one type of herbivore (spittlebugs) had a greater impact on plant fitness of goldenrod (*Solidago altissima*), than did hundreds of aphids or several leaf-beetle larvae. Insect density might determine the strength and extent of the impacts of herbivory on plant fitness. From a management perspective, knowing whether insect density influences control is relevant considering the economic and possible ecological implications of introducing biocontrol agents (Louda *et al.* 1997).

The resilience of plants to herbivore-caused damage, might also depend on the resources available after damage (Coley *et al.* 1985; Meyer and Root 1993; Strauss and Agrawal 1999; Hawkes and Sullivan 2001). For example, according to the Resource Availability Hypothesis (Coley *et al.* 1985), plants in resource-abundant environments are expected to grow fast and easily replace lost tissues due to herbivory, while plants in resource-limited environments might be less able to replace lost tissue, and thus to allocate more resources to anti-herbivore defenses. Naturalized populations of *M. quinquenervia* in southern Florida inhabit sites with two different kinds of soil, nutrient-rich organic and nutrient-poor sandy soils. Plants growing in these two soil types would be expected to respond differently to herbivory. The predictions of the Resource Availability Hypothesis and other related hypothesis are still debatable (Hamilton *et al.* 2001; Wise and Abrahamson 2007), and this study can help to address the debate.

The current study sought to investigate the effects of density levels of both weevils and psyllids independently and interactively on survival and growth of *M. quinquenervia* seedlings. The study addressed the following questions: 1) How does the density of each of the herbivores affect survival and growth of *M. quinquenervia* seedlings? 2) Is the effect of psyllids on seedlings independent of the effects of weevils? and 3) Do the effects of the insects depend upon soil type? A three-way factorial experiment was conducted in a shade-house, manipulating weevil density (three levels), psyllid density (three levels), and soil type (sandy versus organic). We proposed the following hypotheses 1) as insect density increases survival and growth of seedlings will decrease; 2) the effects of psyllids on plants will be independent of the effects of weevils; and 3) plants will be more susceptible to damage in sandy soils, which have fewer nutrients than organic soils.

Materials and Methods

Study system

Melaleuca quinquenervia was introduced to southern Florida in 1886 (Dray *et al.* 2006), and is among the most invasive species in the region (Bodle *et al.* 1994; Rayamajhi *et al.*

2002). *Melaleuca quinquenervia* populations are found in dry and flooded habitats throughout southern Florida. The species produces flowers year-round (Vardaman 1994), which give rise to millions of wind-dispersed seeds that can be kept within serotinous capsules on the tree for several years. Massive seed releases and colonization events occur after vascular connections are disrupted by fire, mechanical damage, or herbicide applications, leading to the creation of dense monospecific carpets of *M. quinquenervia* seedlings (Meskimen,1962; Woodall, 1982; Rayachhetry *et al.* 1998). Seedling establishment and growth is expected to be particularly susceptible to biological control (Turner *et al.* 1998; Center *et al.* 2000).

Populations of *M. quinquenervia* in southern Florida are common in coastal areas as well as interior portions of the Florida Everglades (Turner *et al.* 1998). Soils on the east coast south of Lake Okeechobee are predominantly organic while on the west coast they are predominantly sandy. Although soil type has not limited the ability of *M. quinquenervia* to invade new areas in southern Florida (Bodle *et al.* 1994), the susceptibility of plants to biological control may differ with soil type.

Experimental design

This study was conducted in an ambient temperature (mean monthly temperature ranges from 26°C to 33°C over the entire year) outdoor growing facility at the University of Miami, Coral Gables, Florida. *M. quinquenervia* seeds were collected from five different populations on the east and west coasts of southern Florida. Seeds were germinated and six-month old seedlings, 12 ± 3.5 cm tall (mean ± SE), were transplanted to 1.1 liter pots randomly assigned to either organic or sandy soil (150 plants per soil type). Soils were collected from areas where there are naturalized forests of *M. quinquenervia*. Organic soil was collected in Holiday Park, Ft. Lauderdale, FL. Sandy soil was collected in the Picayu Strand State Forest, Naples, FL. General characteristics of the two soil types are presented in Appendix 2.1. At each site, soil was collected from several spots separated by 10-20 meters, and was mixed thoroughly before filling the pots.

A 3 × 3 × 2 fully-factorial experiment was conducted, with three levels of weevil density (zero, low and high), three levels of psyllid density (zero, low and high), and two levels of soil type (organic and sandy). Each of these 18 treatments was replicated five times. Each experimental unit (replicate) was comprised of three potted plants enclosed in a 25 × 50 × 75 cm PVC cage, covered with white mesh screen; a 25 × 50 cm tray was placed at the bottom of each experimental unit. The three plants within each experimental unit received the same treatment. To analyze survival, the experimental unit was every plant instead of the three plants within a tray (see below). To investigate if the cage with its white mesh covering had any effect on the response variables, five experimental units that had no-cages and no insects for each soil type were included. In total, there were 100 experimental units, 90 with cages (18 treatments × five replicates per treatment), plus 10 with no cages (five per soil type), for a total of 300 plants.

The dependent variables were plant survival, growth and biomass. Plant survival was recorded every two weeks. Plant size (height, diameter at 5 cm above the soil, and number of leaves) was measured at the beginning of the experiment and growth was estimated every two weeks as the change in the magnitude of each of these variables. Because many plants produced resprouting leaves on the main stem as a result of insect damage, new leaves emerging from the apical meristem (hereafter “primary leaves”) were distinguished from leaves produced through resprouting along the main stem, generally at the base of damaged leaves ("secondary leaves"). Secondary leaves were smaller than primary leaves, but this was only because they had not fully expanded and matured by the time the experiment was concluded. Biomass was quantified at the end of the experiment as the dry weights of shoots (stems + leaves) and roots of each plant.

Adult weevils and psyllids were collected in the field as well as from populations at the Invasive Plant Research Laboratory (USDA, Davie, Florida), and placed in a 2 × 2 × 2 m enclosure where weevil larvae and psyllid nymphs were reared for the experiment. For the weevils, the low density treatment consisted of a single first or second instar larva per plant, and the high density treatment consisted of three first or second instar larvae per plant. For psyllids, the low density treatment consisted of one to five first to third instar nymphs per plant, and the high density treatment consisted of 15-25 first to third instar nymphs per plant. Insect densities were chosen based on published literature and on recent field observations of natural insect densities in seedling stands (Franks *et al.* 2006; Center *et al.* 2007; L. Sevillano, personal observations). Insects were added twice during the experiment: once at the beginning (March 20-25, 2007), and once half way through (Apr 26-30, 2007). The second addition was done to maintain prescribed densities. One or two days after each insect addition, plants were surveyed to ensure that required insect densities were reached, and more insects were added if necessary. Seedlings were checked twice a week to monitor insect density levels and contamination by other herbivores. Psyllid adults were removed to prevent oviposition on the plants and alteration of the prescribed density. One yellow sticky card was placed inside each experimental unit to trap the other occasional unwanted other-types of insects that appeared. In addition, prior to the start of the experiment and before the second insect addition, control plants (i.e. with no weevils or psyllids) were sprayed with insecticide (Ortho® Systemic Insect Killer; 8.0% acephate, 0.5% fenbutatin oxide). The rest of the plants (i.e. those with different combinations of insect densities) were sprayed with equal amounts of water to simulate the effects of the insecticide application. Previous studies have shown that acephate does not alter survival, growth, or biomass of *M. quinquenervia* seedlings (Tipping and Center 2002).

Experimental units (three potted plants on a tray inside a cage) were placed on greenhouse tables and randomly arranged. Plants were protected from ambient rain by a clear plastic roofing material. Each plant within an experimental unit received 400 ml of water once a week, throughout the experiment. Plants were harvested on June 20, 2007 approximately three months after the experiment began. Stems and leaves were dried to constant weight (at 60°C), and weighed. Roots were stored in a refrigerator until carefully rinsed to remove all the soil, dried at 60°C, and weighed.

Statistical analyses

Caged and uncaged controls (zero density of weevils and psyllids) were pooled because no statistical differences were found between these treatments and measured response variables (survival; change in height, diameter, number of leaves; and biomass; t-tests, all $P>0.05$).

A generalized linear model (R Development Core Team, 2008) was ised to analyze the survival data as recommended by Crawley (2007) because the average value among the three plants within each tray is not a parameter with a continuous distribution and is not a very informative metric (there are four possible outcomes for each tray: 1, 0.67, 0.33, 0). In such cases the unit of analysis should be each individual plant with a binomial response variable (alive or dead) (Crawley 2007). The variation due to the tray is accounted for by incorporating the replicate number (tray number) as a random factor. The fixed factors are weevil density, psyllid density and soil type. Generalized mixed models are used in cases where errors are non-normal, or in cases where the response variable is binary with pseudoreplication (in this case, plants within each tray) (Pinheiro and Bates 2000; Crawley 2007); the error family is specified in the model (in this case, binomial).

Size and biomass measurements were made on the surviving plants and averaged in each experimental unit. The effects of the insects on the relative growth rates of seedlings were analyzed as follows. The dependent variable is a unit-less index of growth rate that controls for initial size ([final size – initial size]/initial size). For example, a relative growth rate of one means that a plant added an amount equivalent to its initial size during the study and a relative growth rate of two means that a plant added an amount equivalent to twice its initial size during the study. Similarly, a relative growth rate of 0.5 means that a plant added an amount equivalent to one-half its initial size during the study. Since these are unitless measures, the effects of insects on growth rates of different aspects of plant size can be compared. Differences among treatments on relative growth, measured as relative change in height, diameter or number of leaves were analyzed with a three-way analysis of variance (ANOVA) in which weevil density, psyllid density and soil type were fixed factors (JMP 7.0). Post-hoc Tukey tests were used to determine statistical differences among levels of each factor (e.g. insect density).

Final biomass of leaves, stems, and roots were natural log transformed, and analyzed with three-way ANOVA (JMP 7.0).

Results

Survival

Both weevil and psyllid density significantly affected survival (Table 2.1). In the controls (zero density of weevils and psyllids, caged and uncaged), all seedlings survived until the end of the experiment regardless of soil type. At high weevil density, only 77% of seedlings survived (Figure 2.1a). At high psyllid density only 43% of seedlings survived (Figure 2.1b). A significant interaction was observed between psyllid density and soil type (Table 2.1). At low psyllid density, seedling survival was higher in sandy as compared to organic soil (97% vs. 89% respectively), but this trend reversed at high densities. While 53% of the seedlings harboring high psyllid density survived to the end of the experiment in organic soil, only 38% survived in sandy soil. Survival was lowest, only 27%, when both weevils and psyllids were at high density (Figure 2.1c). Although the interaction weevils × psyllids was marginally significant ($P=0.07$, Table 2.1), at high psyllid densities there was a much greater effect of adding weevils than there was when psyllids were at either zero or low density (Figure 2.1c) which may be biologically significant.

Growth rates

Seedlings increased in height and diameter most rapidly in the controls (zero density of weevils and psyllids, caged and uncaged) and least rapidly when the insects were at high densities (Figure 2.2). In contrast, the number of leaves increased most rapidly at intermediate levels of insect density (Figure 2.3).

Weevils and psyllids significantly reduced the rate at which seedlings grew in height during the experiment (Table 2.2.). Seedlings in the controls (zero density of weevils and psyllids, caged and uncaged) increased in height by 201% with respect to initial size, compared to only a 115% increase in height of seedlings with psyllids but without weevils (zero weevil density) and a 167% increase in height of seedlings with weevils but without psyllids (zero psyllid density) (marginal means in Appendix 2.2A). When weevils were at low density, seedlings increased in height by 95%; and when weevils were at high density seedlings increased in height by only 53% (not shown). Similarly, when psyllids were at low density seedlings increased in height by 79%, and at high density they increased in height by only 17% (not shown). The influence of density levels of psyllids on growth in height was greater than density levels of weevils, at least according to the density levels defined in this study. Comparing the growth rates in the zero versus the high density category, there was a 10-fold difference in relative growth rates for psyllids, and only a two-fold difference for weevils. However this result does not compare the per-capita effects of the insects, since the “high” density treatment was only three individuals for weevils, but 15-25 individuals for psyllids. Soil type also had a significant effect on growth in height (Table 2.2); seedlings in organic soil grew 21% more quickly than seedlings in sandy soils (not shown).

Weevils and psyllids interacted significantly in their effects on diameter growth (Table 2.2). The level of psyllid density affected the variability in growth rate among weevil density levels. At zero psyllid density, there was a four-fold difference in growth rate among weevil levels and at high psyllid density, there was only a fractional difference in growth rates among weevil levels (Figure 2.2, Appendix 2.2B), indicating that the reduction in growth rate due to high density of psyllids was less in the presence than in the absence of weevils. The lowest growth rate in diameter was for seedlings where there was a high density of psyllids and a low density of weevils; in this category plants shrank slightly (by -2%). Seedlings with high densities of both insects did only slightly better, they grew by 1%. The effects of soil type, and weevil × soil type interaction on diameter were marginally significant (Table 2.2). Despite the significant weevil × psyllid interaction, the overall effects of the density of each insect on diameter growth were also significant (Table 2.2). Seedlings in the controls (zero density of weevils and psyllids, caged and uncaged) increased in diameter by 121% (Appendix 2.2B), compared to only a 73% increase in diameter of seedlings with psyllids but without weevils, and a 75% increase in diameter of seedlings with weevils but without psyllids (main effects not shown). Once again, the influence of density levels of psyllids on growth in diameter was greater than density of weevils, according to the density levels defined in this study. Comparing the growth rates in the zero versus the high density category, there was a 16-fold difference in relative growth rates for psyllids, and only a five-fold difference for weevils.

The three-way interaction among weevil density, psyllid density and soil type significantly influenced the rate at which the standing crop of leaves increased (no. of primary + no. of secondary leaves) (Table 2.2). The highest rate of increase in leaves was not for seedlings with no insects, but rather for seedlings with low densities of both weevils and psyllids; they increased in leaf number by 320% in both soil types (Figure

2.3, Appendix 2.2B). Seedling response to the weevil × psyllid interaction differed between soil types. Seedlings in the controls (zero density of weevils and psyllids, caged and uncaged) increased in leaf number by only 122%, with a slightly higher increase in the organic soils (Appendix 2.2B). The lowest rate of increase in standing crop of leaves was for seedlings with high density of both weevils and psyllids in sandy soil where increase in leaf number was about 100% (Figure 2.3). Seedlings with low density of weevils and high density of psyllids had a higher rate of increase in sandy than in organic soils, although in most other comparisons, seedlings added leaves more quickly in organic soil.

Number of leaves and biomass

The standing crop (total number) of leaves at the end of the experiment exemplified the plant's ability to compensate for mild attack by herbivores (similar to the results for the relative change in the number of leaves); it was higher when just a few insects were present, than it was when either zero or many insects were present (Figure 2.4). Seedlings in the controls (zero density of weevils and psyllids, caged and uncaged) had produced on average 44 primary leaves and one secondary leaf, by the end of the experiment. In comparison, seedlings with no weevils produced on average 31 primary and 32 secondary leaves, and seedlings with no psyllids produced on average 36 primary and 17 secondary leaves (Appendix 2.2C). The number of primary leaves decreased as insect density increased; but the number of secondary leaves increased in the presence of insects (Figure 2.4). Although total number of leaves was highest in plants with few insects (weevils or psyllids), leaf biomass of primary plus secondary leaves decreased as insect density increased (Figure 2.5), indicating that the photosynthetic tissue in plants with insects decreased as insect density increased. Leaf biomass of seedlings without insects was on average 0.73 grams, compared to 0.54 g for plants with no weevils and 0.5 g for plants with no psyllids.

Weevil density, psyllid density, and soil type all significantly affected the total plant biomass (final weight) (Figure 2.5). While all three factors also affected shoot biomass, only the insects and not soil type affected root biomass (Table 2.3). Overall, seedlings in the controls (zero density of weevils and psyllids, caged and uncaged) reached greater biomass than those with insects. Total seedling biomass in the absence of herbivory was on average 1.57g while seedlings with psyllids but zero weevils weighed on average 1.13g and seedlings with weevils but zero psyllids weighed 1.06g (Appendix 2.2C). Seedlings with low and high densities of weevils weighed 29% and 57% less, respectively, than plants without weevils (Figure 2.5a). Similarly, seedlings with low and high densities of psyllids weighed 21% and 59% less, respectively, than plants without psyllids (Figure 2.5b). Seedlings in organic soil weighed 20% more than plants grown in sandy soil (Figure 2.5c). Also, soil type significantly interacted with weevil presence in their effects on plant biomass (Table 2.3): the influence of soil type disappeared when weevils were introduced into the system (not shown).

Discussion

Herbivory by weevils and psyllids reduced survival, growth, and biomass of *M. quinquenervia* seedlings. While previous studies have shown that herbivory can impact *M. quinquenervia's* seedling survival and growth, this study shows that the magnitude of these negative effects is density dependent. High density levels of either weevils or psyllids consistently reduced seedling performance (survival, growth and biomass), while low density levels did not. These results are consistent with previously reported field studies in that psyllids attacking *M. quinquenervia* seedlings or coppicing stumps at high densities (≥ 15 nymphs per plant) markedly reduce survival by ≥ 50% (Franks *et al.* 2006; Center *et al.* 2007). For some of the plant performance parameters, the effects of one insect depended not only on the density of that insect, but also on the density of the other insect. The marginally significant weevil × psyllid interaction suggests that survival is particularly affected when both insects are present. These results indicate that although psyllids are effective at high densities, both insects in concert will most effectively reduce seedling survival. In this sense, it would be relevant to investigate the population dynamics of both species of biological control agents to understand how insect densities fluctuate over time in the field, and predict the consequences of such fluctuations for the plant.

Soil type affected growth (measured as height), and biomass of *M. quinquenervia* (organic>sandy), and in some cases, the effects of insect herbivory depended on soil type. Sandy soils where *M. quinquenervia* lives in southern Florida are poor in terms of nutrient content and organic matter, and have low water holding capacity compared to organic soils (Appendix 2.1). Plants in organic soil would be more likely to overcome herbivory by replacing lost tissue, than those in sandy soil (Resource Availability Hypothesis, Coley *et al.* 1985). Although final biomass was higher in plants growing in organic soil, the results of this study indicate that plant responses to herbivory under different resource conditions also depend on insect density/damage intensity. For example, only seedlings with high psyllid density had higher survival in organic than in sandy soil. Although the significant psyllid × soil interaction suggests that plants growing in sandy soils can also overcome insect damage and keep growing; after a certain threshold (high density of psyllids) plants can no longer compensate for losses due to herbivory, and survival is lower. Overall *M. quinquenervia* seedlings growing in sandy soils would be expected to allocate more resources to plant defense than seedlings in organic soil. It would be relevant to study whether these two biocontrol agents can naturally achive higher densities in sandy than organic sites. Regardless of soil type, high density of insects impact *M. quinquenervia* seedling performance more efficiently.

Franks *et al.* (2006) did not find a significant interaction between weevil and psyllid damage in the field, although only the effects of low density of weevils across different levels of psyllids were tested. They suggested that the effects of the insects were additive but our experiment found a significant interaction effect of weevils and psyllids on relative growth (i.e. diameter). The negative impacts of psyllids observed on plants with zero or low density of weevils was diminished when weevils were present in high densities. This is what would be expected if the insects were competing with each other. Competition for resources between weevils and psyllids was not assessed in this study, but it is likely that some level of competition exists (Strauss, 1991; Denno *et al.* 1995; Paynter and Hennecke 2001), particularly on seedlings or saplings in which the amount of leaf tissue is limited compared to larger plants. For adult *M. quinquenervia* trees, it has been suggested that defoliation produced by psyllids promotes the production of new foliage that, in turn, attracts weevil larvae (Center *et al.* 2006), further increasing the vulnerability of plants to damage (Pilson, 1992; Karban and Baldwin 1997). Despite the strong effects of the weevils and psyllids on seedling growth and survival, a previous study (Franks *et al.* 2008b) showed that there was no selection for increased resistance to herbivory in the presence of the insects. Fortunately for biological control efforts, this indicates that the strong effects of herbivory shown in the present study are not likely to lead to *M. quinquenervia* evolving increased defense, at least over the relatively short term.

The interaction effects between weevils and psyllids have different consequences for survival than they do for growth of *M. quinquenervia* seedlings. For survival, the effects of psyllids at high density levels are enhanced when weevils are also present at high density levels. However, for growth, the effects are not enhanced when both insects are present but, on the contrary, having both insects is not as effective in reducing growth, as is having only one type of insect at high density levels.

Melaleuca quinquenervia seedlings that experienced herbivory produced secondary leaves, revealing that one of the mechanisms that these plants use as defense against herbivory is to compensate for defoliation by replacing damaged leaves (Rosenthal and Kotanen, 1994; Mauricio *et al.* 1997; Agrawal, 1998). Compensation is a commonly observed mechanism that plants use to tolerate insect herbivore damage (Trumble *et al.* 1993; Rosenthal and Kotanen 1994; Dhileepan *et al.* 2000) and has been demonstrated for *M. quinquenervia* previously (Pratt *et al.* 2005). The magnitude of the compensatory response to herbivory can vary depending on intensity of herbivory (Marquis, 1984; Gadd *et al.* 2001; Wirf, 2006). Herein for instance, compensation was higher in seedlings receiving moderate levels of herbivory (low density of either weevils or psyllids) than high levels (Figure 2.4). Understanding the mechanisms of defense against herbivory is particularly important for systems in which insects are used as biological controls of invasive plants. Small to moderate looses of plant tissue do not always have measurable impacts on plant performance, suggesting that below a threshold, compensatory responses might mitigate the effectiveness of biological control agents (Karaban 1993). Research should concentrate on testing if invasive plants have the ability to compensate or overcompensate for the effects of herbivory by growing or reproducing more than undamaged plants (Belski 1986; Strauss and Agrawal 1999). The results of this study indicate that *M. quinquenervia* seedlings can compensate for insect damage by producing new leaves (secondary leaves) but these leaves are much smaller initially and have less photosynthetic capacity. Some of those secondary leaves developed into new shoots, which in turn altered plant architecture. This mechanism has been observed in other plants as a response to leaf beetle herbivory (Nozawa and Ohgushi 2002; Schat and Bloosey 2005). Although the production of new leaves as a consequence of herbivory could be beneficial for *M. quinquenervia* seedlings in the short term, it can also induce new events of herbivory (Center *et al.* 2007), because both weevils and psyllids are particularly attracted to young tissue. Newly developed leaves were commonly damaged by both biological control agents, particularly on plants in which most primary leaves had already been damaged. This observation suggests that damage by weevils or psyllids increases the vulnerability of plants being further attacked by either (or both) insect, and thus having both insects in the same area will increase, at least at the seedling stage, the effectiveness of the biological control program.

The compensatory mechanism observed in growth did not result in an increase in seedling biomass. Both insects significantly reduced above and belowground biomass.

Although seedlings that received relatively low herbivory had more leaves than those with no or high herbivory by the end of the experiment, they did not have higher leaf biomass. Indeed, leaf biomass followed the same trend as that observed for survival and growth (relative change in height and diameter): as insect density increased, leaf biomass decreased. This trend was also observed for root and stem biomass, and thus for total biomass (Figure 2.5). Psyllid impacts on *M. quinquenervia* seedling biomass have also been reported in the field (Franks *et al.* 2006; Center *et al.* 2007), and this study shows that weevils and soil type can also influence biomass.

The results of this study showed that independently or in concert, both insects introduced as biological control agents against the invasive tree *M. quinquenervia* in southern Florida can reduce survival, growth, and biomass of seedlings. Psyllids are generally more effective than weevils, and the effects of the insects are consistently stronger when they are in high densities (except for the change in number of leaves). Interaction effects between biological control agents are in some instances positive in that the impacts on *M. quinquenervia* seedling survival are greater when both weevils and psyllids are in high densities than when only psyllids are in high densities. In other instances, the presence of only one agent in high densities (i.e. psyllids) is enough to reduce growth. Biological control agents were introduced with the expectation that their primary contribution to the reduction of the growth and spread of *M. quinquenervia* populations would be through the reduction of seedling and sapling survival, and seed production (Turner *et al.* 1998; Center *et al.* 2000). This study shows that both insects affect the seedling-sapling transition of the life cycle of this plant by reducing seedling survival and performance, and thus the number of plants that reach the next life cycle stage, or the rate at which they reach such stage (saplings). Other studies have shown that seedlings, and other stages of the Melaleuca life cycle, can be negatively affected by weevils and psyllids (Pratt *et al.* 2005; Franks *et al.* 2006; Center *et al.* 2007; Franks *et al.* 2008a; b; Rayamajhi *et al.* 2008; Tipping *et al.* 2008). The next step in understanding the effectiveness of Melaleuca's biological control program is to study if the negative impacts of the biocontrol agents at the individual level translate into a reduction of the population growth rates and rates of spread of *M. quinquenervia.* We are developing mathematical models of spatial population dynamics for this tree to address this question.

Studies of the impacts of biological control agents should concentrate now on understanding the role that the agents play on the population dynamics of invasive plants, which is fundamental to improving weed biocontrol. Successful suppression of invasive plants requires that biological control agents, or any other control strategy, alter stage transitions that are important for plant population growth[*].

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[*] **Acknowledgements**

We thank Steven J. Franks, Svata Louda, and two anonymous reviewers for comments on earlier versions of the manuscript. We also thank Deah Lieurance, Robyn Chiarelli, and Sigfredo Gonzalez for assistance with insect rearing and experiment set up. Undegraduate biology students from the University of Miami were actively involved during the experiment set-up, insect rearing, and data collection. This research was supported by Cooperative Agreement No. 58-6629-4-232 between the Invasive Plant Research Laboratory, USDA, ARS, and C.H. at the University of Miami and by a Consejo Nacional de Ciencia y Tecnologia (CONACyT-Mexico) fellowship to L.S.

Table 2.1. Generalized mixed model of the effects of weevil density, psyllid density, and soil type on survival of *M. quinquenervia* seedlings. Bold indicates p<0.05; italics indicates p<0.10.

		Survival	
	df	*F*	*P*
Weevil density	**2**	**6.5771**	**0.0022**
Psyllid density	**2**	**77.7330**	**<0.0001**
Soil type	1	0.1281	0.7213
Weevil x Psyllid	*4*	*2.2403*	*0.0717*
Weevil x Soil	2	0.7901	0.4572
Psyllid x Soil	**2**	**3.6035**	**0.0316**
Weevil x Psyllid x Soil	4	0.6540	0.6257

Table 2.2. Fully-crossed ANOVA of the effects of weevil density, psyllid density, soil type, and all interactions on growth of *M. quinquenervia* seedlings measured as relative change in height, diameter, and number of leaves.

		Height		Diameter		Total No. leaves	
	df	*F*	*P*	*F*	*P*	*F*	*P*
Weevil density	**2**	**11.26**	**<0.0001**	**21.62**	**<0.0001**	**4.17**	**0.02**
Psyllid density	**2**	**70.16**	**<0.0001**	**29.26**	**<0.0001**	**15.54**	**<0.0001**
Soil type	**1**	**4.02**	**0.024**	3.62	0.06	0.01	0.89
Weevil x Psyllid	4	1.85	0.12	**3.32**	**0.01**	1.75	0.15
Weevil x Soil	2	2.62	0.07	2.69	0.07	0.06	0.94
Psyllid x Soil	2	0.50	0.60	0.76	0.47	0.28	0.75
Weevil x Psyllid x Soil	4	1.39	0.24	0.69	0.60	**2.60**	**0.04**

Table 2.3. Fully-crossed ANOVA of the effects of weevil density, psyllid density, soil type, and all interactions on total final biomass, shoot and root biomass of *M. quinquenervia* seedlings.

		Total biomass		Shoots		Roots	
	df	*F*	*P*	*F*	*P*	*F*	*P*
Weevil density	**2**	**27.61**	**<0.0001**	**27.42**	**<0.0001**	**20.68**	**<0.0001**
Psyllid density	**2**	**26.27**	**<0.0001**	**28.11**	**<0.0001**	**12.11**	**<0.0001**
Soil type	**1**	**6.62**	**0.01**	**10.89**	**0.001**	0.65	0.42
Weevil x Psyllid	4	1.62	0.18	1.18	0.32	**3.28**	**0.02**
Weevil x Soil	**2**	**5.11**	**0.008**	**4.99**	**0.009**	**4.39**	**0.02**
Psyllid x Soil	2	1.60	0.21	1.30	0.28	2.11	0.13
Weevil x Psyllid x Soil	4	2.13	0.09	1.96	0.11	1.45	0.23

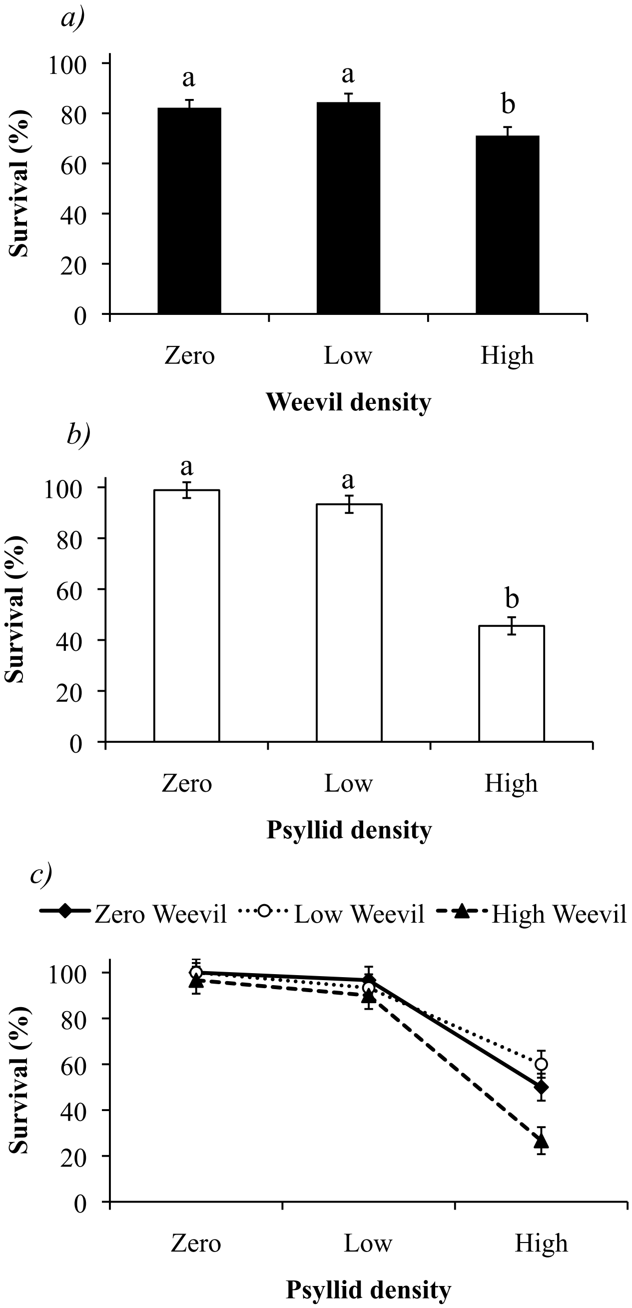

Figure 2.1. Survival of *M. quinquenervia* seedlings exposed to different densities of weevils (*a*) and psyllids (*b*). Bars correspond to the least square means ± one standard error. Different letters indicate significantly different means acoording to the Tukey post hoc test. (*c*) Interaction effects of weevil and psyllid density on seedling survival. Points correspond to the least square means ± one standard error in each one of the nine weevil × psyllid treatment categories. Lines connect the means of each weevil density level, and psyllid density levels are shown on the x-axis.

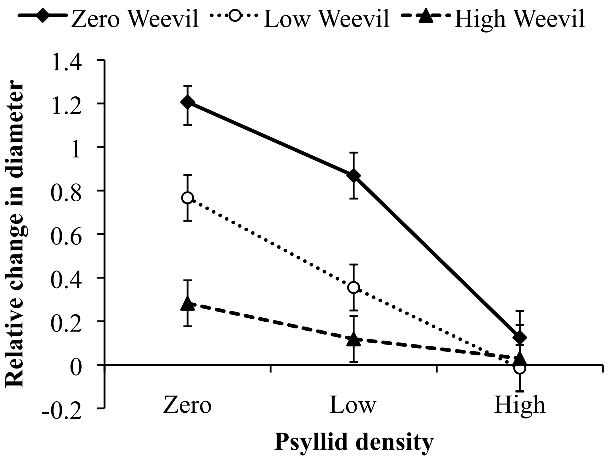

Figure 2.2. Effects of weevil density across psyllid densities on growth, measured as the relative change in diameter, of *M. quinquenervia* seedlings. Points correspond to the least square means ± one standard error in each one of the nine weevil × psyllid treatment categories. Lines connect the means of each weevil density level, and psyllid density levels are shown on the x-axis.

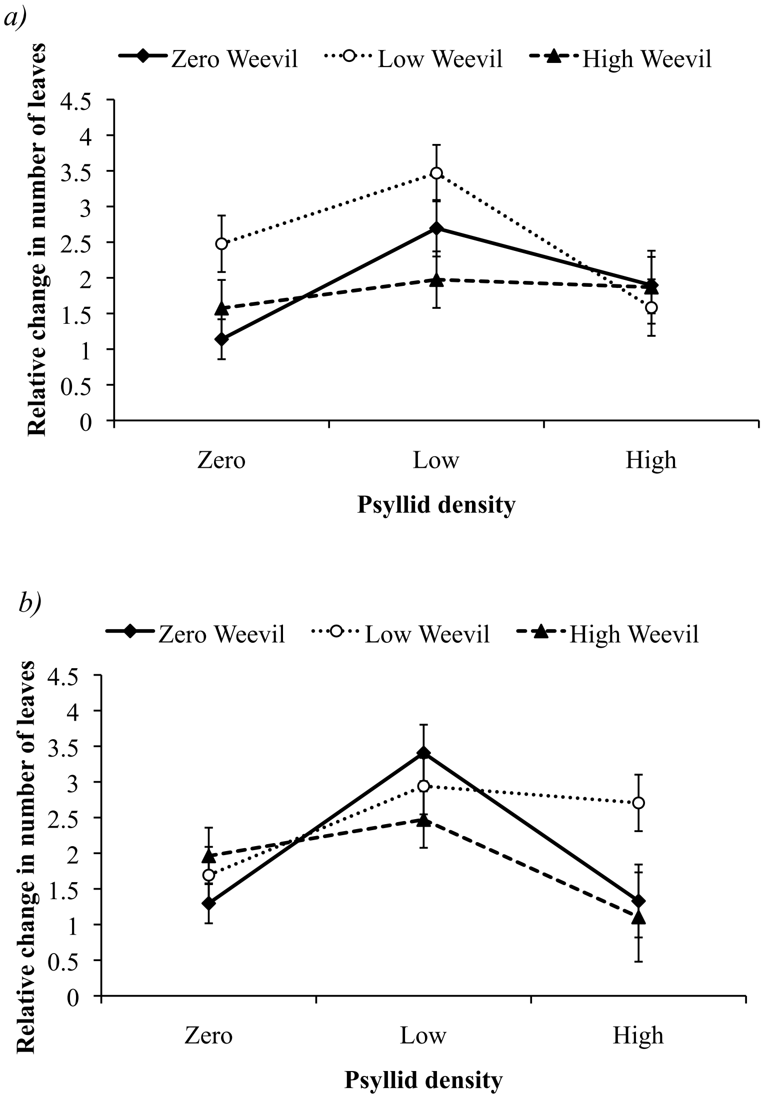

Figure 2.3. Interaction effects of weevil and psyllid density on growth estimated as the relative change in total number of leaves of *M. quinquenervia* seedlings growing in (*a*) organic and (*b*) sandy soil. Points in each figure correspond to the least square means ± one standard error in each one of the nine weevil × psyllid treatment categories. Lines connect the means of each weevil density level, and psyllid density levels are shown on the x-axis.

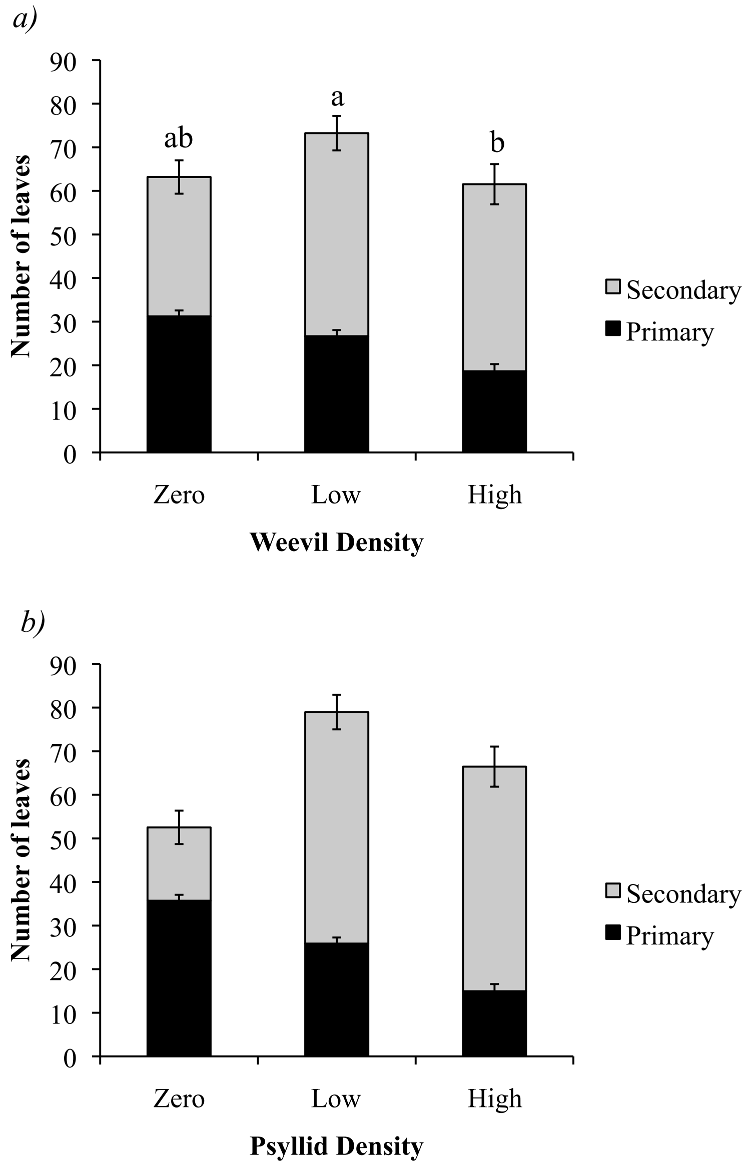

Figure 2.4. Total number of leaves (primary + seconday) produced by *M. quinquenervia* seedlings exposed to different densities of (*a*) weevils, and (*b*) psyllids. Total number of leaves is the result of adding primary leaves (produced at the apical meristem of the plants), and secondary leaves (produced through resprouting along the main stem). Different letters indicate significantly different means acoording to the Tukey post hoc test.

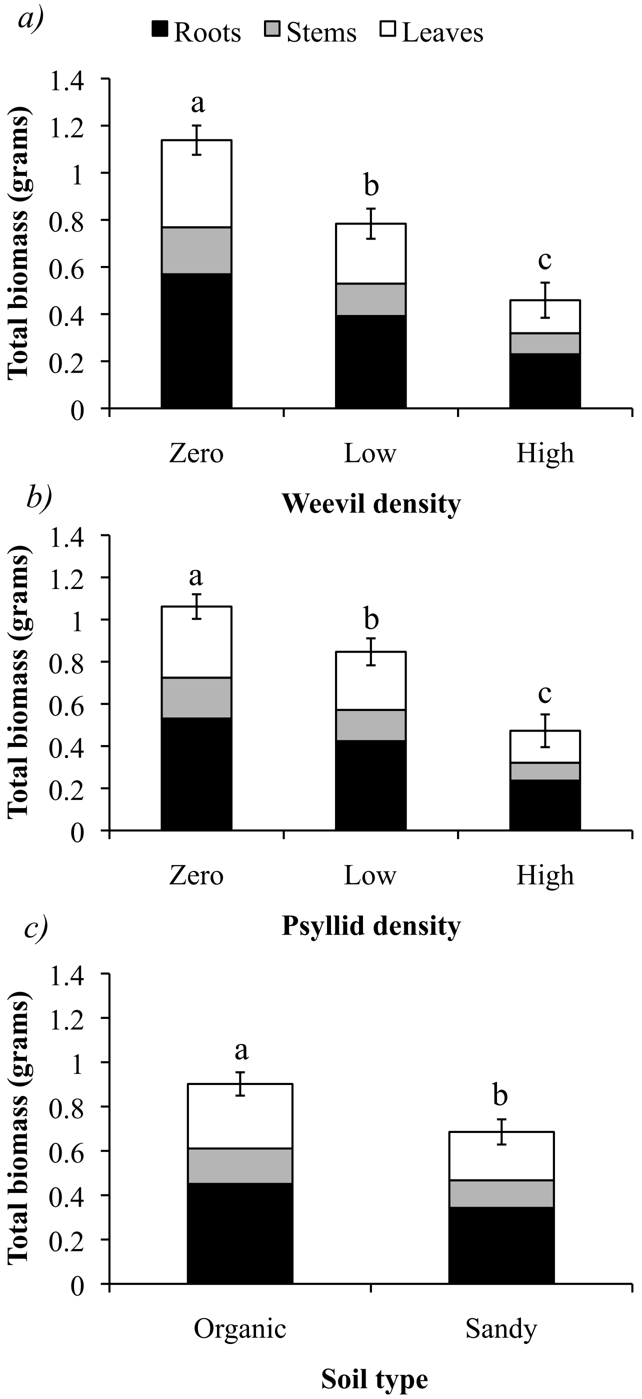

Figure 2.5. Effects of weevil (*a*) and psyllid density (*b*), and (*c*) soil type on total biomass (grams) of *M. quinquenervia* seedlings. Biomass is partitioned into root, stem, and leaf biomass. Least square means ± one standard errors of the total biomass are shown.

Chapter III

Population dynamics of the invasive tree *Melaleuca quinquenervia* in its native and exotic ranges[3]

Background

Comparative studies of population dynamics of invasive species in their native and exotic ranges can provide useful insights into the factors and mechanisms that have influenced success in the exotic range. In particular, quantitative studies of invasive plant species in the native and exotic ranges provide the basis to understand differences in individual and population performance, and guide strategies for effective control (Hinz and Schwarzlaender 2004, Hyatt and Araki 2006, Ramula *et al.* 2008). One of the fundamental characteristics of species that become invasive is that commonly, in the exotic range, their abundance and observed population growth is higher compared to the native range, suggesting differences in population dynamics between environments (Grigulis *et al.* 2001). Thus, comparative studies on the demography and population dynamics of invasive species in their native and exotic ranges can provide a comprehensive understanding of the factors that regulate their density, abundance, distribution, and population growth.

Fundamental questions to answer in comparative studies are whether or not invasive species are more abundant in the exotic region, whether they grow faster and reproduce more at the individual-level, and whether populations increase at a faster rate.

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[3] Coauthors: Carol C. Horvitz, Steven Franks, Paul D. Pratt

In recent years, several studies have compared individual and population-level characteristics of invasive species in their native and exotic ranges (see reviews in Hinz and Schwarzlaender 2004, Hierro *et al.* 2005, and Ramula *et al.* 2008). A common observation has been that introduced plants grow larger and are more vigorous than plants of the same species in the native range as is the case for *Solidago gigantea* (Jakobs *et al.* 2004) and several other species (Crawley 1987, Blossey and Nötzold 1995; Bastlová-Hanzélyová 2001). Reasons for the apparent increased vigor are not yet fully understood (Noble 1989; Crawley *et al.* 1996; Rees & Paynter 1997). Indeed, some studies have found no differences in performance, such as in *Cytisus scoparius* (Paynter *et al.* 2003) and *Melaleuca quinquenervia* (Franks *et al.* 2007, Franks *et al.* 2008). Fecundity is also often higher in the exotic range, as in *Cytisus scoparius* (Noble 1989, Rees and Paynter 1997), but this has not been the case for some species such as *Echium plantagineum* (Grigulis *et al.* 2001). Other individual-level traits such as seed size (Buckley *et al.* 2003), and population-level processes such as seedling establishment and seed bank incorporation rates (Grigulis *et al.* 2001) often differ between native and exotic regions.

In structured populations, differences in population dynamics between native and exotic ranges must be understood by quantifying mortality, fertility and growth rates across all ages or sizes when considered explicitly from a demographic perspective (Grigulis *et al.* 2001). Demographic data used to parameterize models on population dynamics can provide insights into how changes of particular demographic rates or size-specific transitions impact population growth. The use of such models has increased in the last few years (Lonsdale 1995, Rees and Paynter 1997, Shea and Kelly 1998, McEvoy and Coombs 1999b, Parker 2000, Buckley *et al.* 2003, 2004, Davis *et al.* 2006). One application is identification of key demographic processes or life stage transitions to target for effective control of invasive species, where the goal is to reduce population growth (Byers *et al.* 2002, Ramula *et al.* 2008). Ramula and collaborators quantitatively compared the population dynamics of 21 invasive and 179 native plant species (Ramula *et al.* 2008). They found that as expected, population growth rates (λ) were overall higher for invasive than for native species. Using sensitivity and elasticity analyses, they also found that population growth rates of invasive species are more sensitive to growth and reproduction, while population growth rates of native species are more sensitive to survival (Ramula *et al.* 2008). The acquisition of long-term demographic data in the native and exotic ranges of invasive species is time-consuming and costly, but this type of study represents a good approach to quantify the effectiveness of management strategies such as the introduction of biological control agents (Rees and Paynter 1997, Paynter *et al.* 2003).

Survival, growth, and reproduction of species in the native environment may be limited by both abiotic and biotic factors. Many invasive species become problematic in regions where the abiotic conditions are similar or even more favorable than their native regions for population growth. Biotic factors that might regulate survival, growth and reproduction, and consequently population growth include pollination, competition with other species, predation, diseases, parasitism, and herbivory (Crawley 1986). Some of these factors are diminished or even absent in exotic regions (Crawley 1987). One of the most cited hypotheses to explain why some plants become successful invaders is the Enemy Release Hypothesis (Elton 1958, Keane and Crawley 2002, Colautti *et al.* 2004).

The hypothesis proposes that invasive species are released from the negative impacts of their natural enemies in their exotic range, and are able to divert resources that would be lost to defense to other functions. Therefore, they may gain competitive advantage over other species that are naturally suppressed by native enemies and have to invest in defense (Keane and Crawley 2002). Comparisons of the effects of natural enemies in the native and introduced ranges are crucial to evaluate the enemy release hypothesis (Wolfe 2002).

The enemy release hypothesis assumes that natural enemies (i.e. herbivores and pathogens) have the capacity to limit population growth of their hosts. This concept underlies classical biological control programs, the intentional introduction of natural enemies to suppress invasive species (DeBach and Rosen 1991). The implementation of biological control is controversial (Simberloff and Stiling 1996, Louda *et al.* 1997, Louda *et al.* 2003), and the criteria to evaluate its effectiveness have varied greatly. For many years, the criterion of interest was demonstration that agents had naturalized in the target populations. Another criterion was demonstration that agents reduced individual-level growth, survival or reproduction. Evaluations of whether biocontrol agents actually limit the population size of their target species were not common until recently. Herbaceous plants have been studied more frequently that woody plants in this respect. For example, population growth of *Carduus nutans* and *Senecio jacobea* has been reduced by biocontrol agents introduced from their native ranges (McEvoy and Coombs 1999, Shea and Kelly 1998).

The success of biological control agents in reducing population growth might vary across the invaded range (Woodburn 1993, 1997). Local ecological conditions might influence the relative success of biological control programs across different parts of the invaded range (Harris 1984; Kelly & McCallum 1992; Shea & Kelly 1998; Shea *et al.*2005, Garren and Strauss 2009). Demographic models of population dynamics, and their sensitivity and elasticity analyses are key to address these issues.

Melaleuca quienquenervia Cav. Blake (Myrtaceae) is a tree native to sub-tropical Australia and currently invading southern Florida, Puerto Rico, and the Bahamas (Serbesoff-King 2003). While around 450 insect herbivores have been reported to feed on *M. quinquenervia* (Balucinas *et al.* 1994, 1995) in its native range, only two insect herbivores have been introduced as biological control agents in Florida: the leaf-eater weevil *Oxyops vitiosa* (Coleoptera: Curculionidae), and the sap-sucker psyllid *Boreioglycaspis melaleucae* (Homoptera: Psyllidae). In Florida, the biological control program was initiated in 1997, and at the present time, both insects have dispersed throughout *M. quinquenervia* populations (Pratt *et al.* 2003). In Puerto Rico and the Bahamas, no biocontrol program has been implemented. However, in 2006, low densities of psyllids were unexpectedly observed in *M. quinquenervia* populations in Puerto Rico (Pratt *et al.* 2006). The differential presence of insects in the native and exotic ranges allows interregional comparisons of *M. quinquenervia* population dynamics, and the role of these insects in regulating the dynamics. Particularly, studies in Australia, Florida, Puerto Rico and the Bahamas provide an opportunity to compare populations where regulation by insects is most likely (Australia), where impacts of biological control agents have been confirmed at the individual-level (Florida), and where the impact of biological control has been very limited (Puerto Rico), or null (Bahamas). In this study, we developed integral projection models to compare the population dynamics of *M. quinquenervia* in its native and exotic ranges, which differ in the presence of insect herbivores. In particular, we answer the following questions:

1) Are populations of *M. quinquenervia* increasing in numbers more rapidly in their exotic than in their native range?
2) Is population growth rate higher in exotic regions where biocontrol has not been implemented (the Bahamas) than in exotic regions where biocontrol agents are present (Florida, Puerto Rico)?
3) Which demographic transitions contribute the most to population growth in native *versus* exotic populations, as measured by proportional sensitivity analysis of the population growth rate?

We expected population growth rate to be higher in the exotic regions than in the native region. And we expected population growth rates to be lower in regions where insect herbivores are present, than where they are absent. We also expected population growth rate to be more sensitive to growth and reproduction in the exotic range than in the native range, because it has been shown that in their exotic ranges, invasive species grow taller, are more vigorous, and produce more seeds than in the native ranges (Crawley 1987, Balciunas 1990, Blossey and Nötzold 1995, Bastlová-Hanzélyová 2001).

Materials and Methods

Study system

Melaleuca quinquenervia was first introduced in Florida in 1886 (Dray *et al.* 2006) and it is considered one of the worst invasive species in south Florida (Laroche 1999). It produces flowers throughout the year with a flowering peak in the fall and winter. Adult individuals may flower up to 5 times a year (Meskimen 1962). *M. quinquenervia* produces serotinous fruits (capsules) arranged in clusters that may remain attached to the tree for several years (Meskimen 1962, Rayachhetry *et al.* 1998). Capsules (30 to 70) are formed on the twig and each contains on average 264 seeds in Florida (Woodall 1982, Vardaman 1994), and 271 seeds in Australia (Rayamajhi *et al.*2002). Adult trees can produce millions of small wind-dispersed seeds per year.

Although seeds are released in small amounts throughout the year producing what we call a *low seed rain*, massive seed release is episodic occurring after stresses that break vascular connections of branches holding capsules (e.g. fires, frosts, mechanical damage, herbicide applications) (Woodall 1982, Hofstetter 1991). Such massive seed release produces what we call a *high seed rain*. Periodic massive seed release into a previously unoccupied area favors the formation of stands comprised entirely of a single age class in which individuals are very similar in size (Turner *et al.*1998, Sebersoff-King 2003). Dense monoculture Melaleuca forests prevent survival of seedlings. Such local population size structure is common in South Florida, Puerto Rico, and the Bahamas. Population dynamics under this circumstance is studied on a regional basis by combining data from different stands, each of which represents a different part of the life cycle. In Australia, young stands have a very similar structure but they do not maintain such a high, monospecific density over time and older Melaleuca forests include several ages and size classes within the same area and are mixed with other species.

Mechanical eradication, herbicides, physical techniques and biological control have all been employed to control *M. quinquenervia* in Florida. Throughout the years, since the insects were introduced in Florida (1997 and 2002), several studies have shown that both insects impact survival, growth, and reproduction of *M. quinquenervia* at the individual level (see Chapter 2).

Demographic plots

To study the population dynamics of *M. quinquenervia*, we recorded survival, growth and reproduction of marked individuals of different sizes in its native and exotic ranges. In 2003, we set up demographic plots in seven different sites on the west and east coasts of southern Florida, and, with collaborators, we established plots in two different sites on the east coast of Australia (Table 3.1). In addition, in 2005 we established plots at one site in northeast Puerto Rico and on three different islands in the northern Bahamas (Table 3.1).

Plots were chosen to ensure we had data across the full range of plant sizes in each geographic region, given that only a few stages (sizes) are present in each plot. The number and size of plots in each geographic region differed, according to the plant and stand sizes. Another criterion to choose the plots was the feasibility of maintaining them for several years without any human intervention (any type of land management, such as herbicide or mechanical control in the exotic regions).

In Australia we set up plots in two sites: Bribie Island, in the south east coast of Queensland; and Port Macquarie, in the north east coast of New South Wales. Both plots were in seasonally flooded habitats with sandy soils. In Florida, plots were established in permanently flooded, dry or seasonally flooded habitats that differ in the types of soils (organic or sandy soils). An additional set of plots were established in Florida in 2005 at

Prairie Pines, Ft. Myers, FL, and included recently emerged seedlings which were not represented in the previously established plots. In Puerto Rico, plots were established in one of the largest naturalized populations on the island, in the north central region (Pratt *et al.*2005a). Plots were established in permanently or seasonally flooded habitats characterized by organic soils. In the Bahamas, plots were established in three different northern islands. Both in Andros Island and Nassau plots are dry and have sandy soils. Plots in Grand Bahama are seasonally flooded and sandy with outcrops of weathered oolitic limestone.

Within each plot, we tagged all the plants at the beginning of the study and recorded their size and reproductive status (presence/absence of capsules). In addition, we recorded mortality and recruitment at each site every year until 2006 in Australia, 2007 in Florida, and 2008 in Puerto Rico and the Bahamas. Each plant within a plot was individually marked using an aluminum tag (short trees) or coin tag (tall trees) attached to the plant. Size was estimated by measuring the diameter of the stem at 5 cm from the ground in plants less than 1.3 m in height (hereafter *short trees*); and the diameter at breast height (DBH) of the trunk at 1.3 m from the ground in plants 1.3 m in height and taller (hereafter *tall trees*). Reproductive status of the plants was recorded as the presence or absence of capsules and/or flowers. After the first census at each site, all new seedlings that appeared in each plot every year were tagged and followed.

Melaleuca's life cycle

M. quinquenervia has a complex life cycle that includes two different seed banks (canopy and soil). Seeds in the canopy can remain in the canopy, become part of the soil seed bank, or become seedlings within one year (Figure 3.1). Similarly, seeds on the soil can remain on the soil or become seedlings in one year. Surviving seedlings (plants <12cm height) can become short trees within a year. In this study, the metric used in the field to estimate size of short trees was different than that used to measure the size of tall trees. Thus the dynamics of these two groups of plants required separate model components. Short trees include all those plants that were at least 12 cm in height, but were shorter than 1.3 m in height. At this stage, plants that survive may increase or decrease in diameter but still remain shorter than 1.3m. Short plants may cross the minimum height threshold, moving to the tall tree domain (i.e. plants that one year are shorter than 1.3 m, and the next year have attained 1.3 m in height). We refer to this phenomenon as *transition from short to tall trees* ($trans_{S-T}$). The tall tree category includes all those plants that are at least 1.3 m in height. Plants that survive may stay in the tall tree stage, even though they change diameter, or they may also decrease in height, returning to the short tree domain (Figure 3.1). This transition occurs when, for diverse reasons, the upper section of the plant dries out and, from one year to the next, plants become too short. We refer to this phenomenon as *transition from tall to short trees* ($trans_{T-S}$). Only tall trees are reproductive, and within one year they may produce seeds that stay in the canopy or that fall to the soil and remain as seeds or become seedlings (Figure 3.1). The number of seeds or seedlings produced by tall trees depends on size (DBH) (Rayachhetry *et al.*2001). Seeds have no diameter and seedlings are too tiny to have meaningful size measurements. Therefore, seeds in the canopy or soil and seedlings are considered discrete stages, and they do not belong to either the short tree or the tall tree domains. Short and tall trees are characterized by continuous state variables, diameter at 5 cm from the ground and diameter at breast height (1.3 m), respectively.

M. quinquenervia capsules that remain attached to the tree for several years form the canopy seed bank. Although most seeds are held on the tree, there is also a constant non-synchronous seed rain (low seed rain), which contributes to the soil seed bank (Woodall 1982). The episodic, synchronous massive seed release (high seed rain), also contributes to the soil seed bank. At present, no data are available on the amount of time that capsules can remain on the tree. Although previous researchers asserted that capsules can remain in the canopy for over seven years (Meskimen 1962), our reconsideration of the data behind this idea found that it was based on the number of adjacent clusters that can be accumulated in a single branch (Rayachhetry *et al.* 1998). Since *M. quinquenervia* can produce flowers several times in a year (Meskimen 1962, Sevillano, pers. obs.), the presence of seven or more adjacent clusters in a branch does not necessarily indicate that clusters can be held in the tree for seven years. Data on the proportion of newly produced seeds that stay in the canopy, and the proportion of newly produced seeds over one year that fall on the soil have not been collected in the field. When modeling population dynamics of *M. quinquenervia*, these pieces of information become very relevant. Below, we explain how we made use of existing data from several other studies to estimate these parameters of the life cycle.

Model

An integral projection model (IPM) was developed to compare *M. quinquenervia* population dynamics in the native and exotic ranges, and to evaluate whether the effects of the two biological control agents have reduced population growth rate. IPMs model population dynamics over a discrete time interval, by integrating demographic contributions across a range of plant sizes (Easterling *et al.* 2000, Ellner and Rees 2006).

The more traditional matrix projection models (Caswell 2001) divide individuals into discrete stages (i.e. seeds, seedlings, adults of various size categories). The matrix, A, with entries a_{ij}, represents the probabilities that an individual in stage j contributes to, or moves to stage i by time $t+1$; n(t) is a vector representing the number of individuals in each stage at time t. The population size at $t+1$ is $n(t+1)=A \cdot n(t)$. Matrix models have limitations that may decrease the precision and accuracy of estimated population parameters. Classification of individuals into categories is often based on a continuously varying trait (e.g. total leaf area, LeCorff and Horvitz 2005), and matrix models assume that all plants in a given category have the same demographic rates (Caswell 2001). The number of categories has been shown to influence the population growth rate estimation (Ramula and Lehtilä 2005), and an accurate estimation of the demographic transition from one class to another requires having a large number of individuals in each class. Additionally, sensitivities and elasticities are very sensitive to stage duration (Enright *et al.* 1995, Ramula and Lehtilä 2005).

In contrast to matrix models, IPMs project population dynamics based on continuous state variables, like size. Statistical relationships between size and survival, growth, and fecundity are at the heart of the model. A projection kernel replaces the projection matrix, A. The dynamics of a population using an IPM is usually defined as

$$n(y,t+1) = \int_{L}^{U} K(y,x)n(x,t)dx$$

where [L,U] is the range of possible sizes. The projection kernel is $K(y,x)=P(y,x) + F(y,x)$. The function $P(x,y)$ incorporates both survival and growth from size x to size y,

$P(x,y) = s(x)g(x,y)$. The fertility function $F(y,x)$ represents the production of size y offspring by size x parents. The functions that make up the kernel are estimated by size-dependent regressions. The appropriate model complexity for the available data is identified through well established statistical criteria, rather than the ad hoc process of choosing the number of size classes and their boundaries used in matrix models (Ellner and Rees 2006). The population vector in matrix models is replaced in an IPM by a distribution function $n(x,t)$, which is the number of individuals with size in the range $[x,x + dx]$ (Easterling *et al.* 2000, Ellner and Rees 2006). IPMs can be implemented for species with complex life cycles, where some stages are continuous, and other stages are discrete (Ellner and Rees 2006). In such cases, there are four possible kernel components: discrete-to-discrete, discrete-to-continuous, continuous-to-discrete, and continuous-to-continuous.

M. quinquenervia's life cycle includes both discrete and continuous stages. To model *M. quinquenervia*'s population dynamics, we defined five categories: seed bank in the canopy, seed bank on the soil, seedlings, short trees, and tall trees (Figure 3.1). Transitions from one category to another and among sizes within continuous domains happen over annual time steps (Δt=1 year). Short and tall trees are two different continuous domains (as in Ellner and Rees 2006). Within each of these domains there is a range of plant sizes. Size in our model is diameter at 5 cm above the ground for short trees, or diameter at 1.3 m (~ breast height), (DBH) for tall trees. Since the classification of individuals is based on two different size ranges (diameter at 5 cm or at 1.3 m), the dynamics within each of the continuous domains of the *M. quinquenervia*'s life cycle were modeled independently (Table 3.2, Figure 3.2). Thus, there are two continuous domains and two different kernel components of the continuous-to-continuous type. The number of seeds and seedlings are discrete components (discrete points, Ellner and Rees 2006). Seeds and seedlings produced by tall trees of size *x* are added to the model as continuous-to-discrete fecundity kernels. Seed dormancy (canopy and soil) and emergence into seedlings form discrete-to-discrete components of the kernel (a number), and seedling transition to different sizes in the short trees domain is a discrete-to continuous component of the kernel.

After obtaining the functions that define the IPM kernels, a high dimensional matrix is created by subdividing the continuous size variable into small categories. The high dimensional matrix is created because integral kernels cannot be solved directly but can be numerically estimated; the dynamics of the matrix is then analyzed. Implementing an IPM on the computer as a matrix iteration is only a technique for computing integrals and not a discretization of the life cycle. For *M. quinquenervia*, different sections of the high dimensional matrix were constructed independently (Figure 3.2). We defined 5 stages, but instead of having a 5 × 5 matrix, those categories that are continuous (size-dependent), were subdivided in such a way that for example, instead of having a single entry corresponding to tall plant stasis, we had an $N \times N$ matrix defining the dynamics within each continuous domain.

The high dimensional matrix was assembled by first creating an $N \times N$ matrix for tall trees, and an $n \times n$ matrix for short trees. The dimensions differed since the tall trees domains spans a much wider range of sizes than the short trees domain. Plants that crossed the minimum height threshold from short to tall were incorporated in the row just below the short trees matrix (Figure 3.2), since short trees that cross from short to tall enter the smallest sizes of the tall tree category. Similarly, tall plants that become reduced in height and crossed back into the short plant domain were incorporated in the row just above the tall plant matrix. The fertility entries (number of seeds in the canopy, on the soil, and seedlings) were "bolted on" as the three top rows above the tall plant matrix, with the same number of columns as the tall plant matrix since fertilities are a function of tall plant size. The fate of seeds in the canopy, seeds on the soil, and seedlings were "bolted on" as three columns to the left of the short trees matrix (Figure 3.2).

As in matrix projection models, the goal of developing an integral projection model is to estimate the asymptotic population growth rate (λ) of *M. quinquenervia*, and its associated stable stage and reproductive value distributions. These are given by the dominant eigenvalue of the matrix and its associated right and left eigenvectors. Well-developed theory exists to perform sensitivity and elasticity analysis from IPM's (Easterling 1998, Easterling *et al.* 2000). Those analyses are particularly relevant in this study since they reveal the stage transitions that contribute the most to population growth rate (λ), and will help to focus management efforts on those stages.

Model parameterization

Data from all plots within each region were pooled to model population dynamics of *M. quinquenervia* by geographic region (Australia, Florida, Puerto Rico, Bahamas) because we were interested in modeling the dynamics of all plant sizes in each region. Similarly, data were pooled across years. For example, for Florida demographic data were collected from 2003 to 2007; size at time *t* included censuses from 2003-2006, and size at time *t*+1 included censuses from 2004-2007. For each region, we performed two sets of regressions, one for short trees and one for tall trees. The parameter estimation below for survival and growth was based on the ln of diameter at 5 cm for short trees, and the ln of diameter and 1.3 m (DBH) for tall trees.

The survival function was estimated by logistic regression of ln (size) at time *t*, versus survival at time *t*+1. The model was fit using a logistic regression with the linear link $\ln(s(x)/(1-s(x)) = a + bx$. The growth function $g(x,y)$ was estimated by a linear regression of ln (size) at time *t*+1, as a function of ln (size) at time *t*. The model was $y = a + bx$. Variance in size at *t*+1 was obtained from the regression analysis and was modeled as being independent of size at *t*. The growth and survival function $P(\mathrm{x,y})$ was estimated as

$$P(x,y) = s(x)g(x,y).$$

The statistical models just described were parameterized for tall trees and for short trees, separately.

The development of the reproduction functions, estimated only for tall trees, involved several steps. For details on the development of these functions, see Appendix 1. The only information that can be obtained readily in the field on *M. quinquenervia*'s reproduction is whether or not plants have capsules. The probability of producing capsules by a tree of DBH *x* was obtained through a logistic regression model of ln (DBH) at *t*, versus presence/absence of capsules at *t*+1. It is important to note that this is only part of the protocol used to develop the fecundity kernel, because the presence of capsules in a given year is not equivalent to capsule production in that year since capsules may be held in the canopy for several years. Seed production in a given year is indicated by a positive net change in the number of capsules between two years. Thus we also had to have estimates of how many seeds are found on plants of each size and how size changes between years (see Appendix 1 for details).

The *probability* of producing new seeds within a year ($f_s(x)$) was estimated using a logistic regression of ln (DBH) at time t, versus positive seed production during the interval t to t+1. The model was fit using a logistic regression with the linear link $\ln(s(x)/(1-s(x)) = a + bx$. The *number* of new seeds that a tree of size x produces within a year ($f_n(x)$) was estimated by a four parameter logistic regression of ln (DBH) at time t, as a function of ln number of seeds at time t. The four parameter logistic model was

$$y = a + \left(\frac{b-a}{1+e^{\frac{c-x}{d}}} \right)$$

Since both size and number of seeds were ln transformed, the model estimated the natural logarithm of the number of seeds, so we obtained the antilog ($e^{\text{number of seeds}}$) to obtain the actual number of seeds. The number of new seeds produced by a tree of size x was estimated by multiplying the probability of producing seeds, $f_s(x)$, by a tree of size x, times the number of seeds produced by a tree of size x, $f_n(x)$.

We apportioned the new seeds produced in one year ($f_s(x)f_n(x)$) to either the canopy or the soil (Table 3.2). The proportion of new seeds that was held in the canopy was (1-SR), where seed rain (SR) was estimated as 0.074 (based on Woodall 1982, see Appendix 3.1). Seed survival (SS) was set to be 9% based on the study by Rayachhetry *et al.* 1998 where they estimated viability of *M. quinquenervia* seeds in the canopy. The proportion of surviving seeds that remain alive as part of the seed bank on the soil (p_G)

over one year was guesstimated to be 5%, and we assumed that the rest, 95%, become seedlings over one year (p_S).

The fate of seeds and seedlings, which correspond to the discrete parameters in the first three columns of the high dimensional matrix, was calculated as follows. The proportion of the seeds in the canopy that remain in the canopy after one year was 0.083 (SS × (1-SR)). The proportion of seeds in the canopy that rain and survive on the ground after one year was 0.0003 (SS × SR × p_G). The proportion of seeds in the canopy that become seedlings after one year was 0.006 (SS × SR × p_S). Seed stasis on the ground (seeds that remained dormant) was 0.0045 (SS × p_G), and seeds on the ground that became seedlings in one year was 0.0855 (SS × p_S). The proportion of seedlings that became short trees in one year was 0.3, which was directly estimated in the field by counting and marking seedlings within 0.5 × 0.5 m plots, and censusing them twice a year for over 2 years. These data showed that surviving seedlings after one year do not stay as seedlings (as defined in this study, <12 cm tall), but become short trees.

When developing IPMs, once all the functions are evaluated and the high dimensional matrix is constructed, it is recommended to try different numbers of categories in the high dimensional matrix, until the asymptote of the parameter of interest is found (Esterling *et al.* 2000, Rees and Ellner 2009). For *M. quinquenervia*, the criterion was to find a combination of matrix sizes (short and tall trees) that would not change the fourth decimal place of the parameter of principal interest, the dominant eigenvalue λ. We set the short trees matrix to be 100 × 100, and the tall trees matrix to be 200 × 200, so the high dimensional matrix was 303 × 303, including both continuous domains as well as three discrete stages. This was the case for all geographic regions.

Once all the different kernels were constructed and the high dimensional matrix was obtained, we estimated population growth rates, stable stage distributions, reproductive values, sensitivities and elasticities using standard matrix methods (Caswell 2001, Easterling *et al.* 2000).

Results

Kernels

The statistical models used in this study to describe the demography of *M. quinquenervia* in each region are presented in Table 3.3. Diameter of short trees at *t* significantly predicted survival, diameter at 5 cm, and the probability of short plants crossing the height threshold and becoming tall plants, >1.3m in height) at *t*+1, in the native and exotic regions (Figs. 3.3a-c, 3.4a-c, 3.5a-c, 3.6a-c). Similarly, DBH of tall trees at *t* significantly predicted survival, DBH, the probability of tall plants loosing enough height to cross back into the short plant domain (i.e. becoming shorter than 1.3m), capsule production, and number of seeds at *t*+1, in the native and exotic regions (Figs. 3.3d-f, 3.4d-f, 3.5d-f, 3.6d-f, and 3.7-3.10). There was a positive relationship between size at *t* (diameter at 5 cm or DBH) and survival, growth and transition from short to tall trees at *t*+1 in all regions. The probability of surviving in short trees increased with size fastest in Australia, followed by the Bahamas, Florida and Puerto Rico (see slopes in Table 3.4). An asymptote was not reached even in the largest sizes (ln(diameter at 5 cm) ≈ 2) in

Australia. For tall trees, the probability of surviving increased with size fastest in the Bahamas, followed by Puerto Rico, Florida and Australia (Tables 3.4). In the Bahamas, the asymptote was reached at ln(DBH) ≈ -0.7, and in Australia it was reached at ln(DBH) ≈ 1.

Growth in short trees was fastest in the Bahamas, followed by similar growth in Florida, Puerto Rico, and Australia. Growth in tall trees was similar in all regions, although slightly faster in Florida, followed by Puerto Rico, Australia, and the Bahamas (Table 3.4). It is common that both short and tall trees lose bark throughout the year, which can result in the diameter at 5 cm or at breast height (DBH) decreasing over one year (see for example Fig. 3.4b). The probability of becoming a tall tree ($trans_{S\text{-}T}$) increased with size fastest in Florida, followed by Australia and Puerto Rico (Figs. 3.3c, 3.4c,and 3.5c), and it was slower in the Bahamas (Fig. 3.6c). In all regions, short trees can become tall trees (>1.3m in height) at (ln(diameter at 5 cm) ≈ -0.5). Although in the Bahamas the slope of the diameter at 5 cm *vs.* $trans_{S\text{-}T}$ in the logistic model was the smallest (Table 3.4), short trees (ln(diameter at 5 cm) ≈ -1.5) have a slightly higher probability of becoming tall trees, than plants of the same size in other regions. Plants of similar diameter increase faster in height in the Bahamas than in other regions. The probability of loosing enough height to re-enter the short plant domain (i.e. $trans_{T\text{-}S}$) decreased with size (DBH), indicating that it is the thinnest of the tall trees that will transition to short trees within one year (Figs. 3.3f, 3.4f, 3.5f, and 3.6f). The highest probability of tall trees becoming short trees was found in Florida, where the smallest plants of the tall trees (ln(DBH)< -2) have a 20-50% probability of becoming short within one year . Plants can make the transition from the tall to the short plant domain only when the upper section of a tree dries out. In Florida, it is common to observe plants drying out in the upper section, where fresh leaf tissue is relatively more abundant and insect damage is higher.

There was a positive relationship between DBH at *t* and the probability of producing capsules at *t*+1 in all regions (Figs. 3.7a, 3.8a, 3.9a, 3.10a). The slope was steeper in Puerto Rico, followed by Florida, Australia, and the Bahamas (Table 3.4). Although in Puerto Rico, the probability of producing capsules between sizes $0 < \ln(\text{DBH}) < 1$, is much slower than in the other regions, the slope becomes steeper more quickly when $\ln(\text{DBH}) > 1$. In the Bahamas, the smaller plants in the DBH size range do not produce capsules, but the production of capsules in trees where $-1.5 < \ln(\text{DBH}) < 1.5$ varies greatly. Around 9% of the short trees (<1.3 m) that were part of this study in the Bahamas did produce capsules. These short trees producing capsules might be underground sprouts of bigger trees that used to live in the same area where we established our plots, and were greatly damaged by fire (M. Rayamajhi, personal comm.). We did not include those plants in our fecundity analyses because the estimation of the number of seeds that a tree would produce are based on DBH, and not on diameter at 5 cm (see Appendix 3.1).

The probability of producing seeds at *t*+1 was positively related to DBH at *t* only in Australia and Florida (Figs. 3.7b, 3.8b; Tables 3-6). This probability comes from estimating the number of seeds that a tree of a certain size would produce in one year, given that it increases in size (see details in Appendix 3.1). The probability was obtained to control for those plants that reduced size due to bark lost from one year to another, which would produce a *negative* number of seeds, since the estimation of the number of seeds produced by a tree of DBH *x*, is based on size (Rayachhetry *et al.* 2001, see Methods and Appendix 3.1 for details). The number of seeds produced in one year increased with size but not linearly. Thus, we used a S-shaped model (four-parameter logistic) to determine the relationship between size (DBH) at *t* and number of seeds produced at *t*+1 (Figs. 3.7c, 3.8c, 3.9c, and 3.10c). In all regions, the number of seeds produced starts increasing once plants have reached 1 cm in DBH (ln(DBH) = 0). However, seed production in Florida and Puerto Rico increases with size faster (steeper slope), compared to the Bahamas. In Australia, the slope is not as steep as in Florida or Puerto Rico. An asymptote was reached at a smaller size in Puerto Rico (ln(DBH) = 3), than in Florida. In Australia and the Bahamas, the asymptote was indeed not yet attained at the largest observed sizes in each region (Figures 3.7c and 3.10c). The *predicted* number of seeds produced in a year per tall plant of a given size, which are the specific values entered in the fecundity section of the high-dimensional matrix (Figure 3.1), were estimated by multiplying the probability of producing seeds (Figures 7b-10b), by the number of seeds that a tree of DBH *x* would produce (Figures 7c-10c). The predicted number of seeds at *t*+1 is significantly related to size at *t* (Figs. 7d-10d). In Australia, the number of seeds produced at *t*+1 increases exponentially once plants reach 7.4 cm DBH (ln(DBH) = 2). That is also the case in the other regions, although the size structure is quite different between regions (Sevillano *et al.* 2008, Chapter 1), and that influences the predicted number of seeds for tall trees in each region.

Kernel components

The kernel components were overall similar among regions. The different components are presented in 3D plots for matrices, where the height (*z*) of the plot represents the value of a parameter that is indexed by the row (*i*) and column (*j*) of the high dimensional matrix. The (0,0) corner of the 3D plots is found the upper left, where i=0 and j=0. In each plot (except Figs. 11c-14c) the axis on the right represents the size category at time *t* (the column of the matrix), and the axis on the left represents size category at time t+1 (the row of the matrix). Since we created high dimensional matrices of the same dimensions (303 × 303) in all regions, and the range of plant sizes differs among regions (Sevillano *et al.* 2008), the size categories are not strictly comparable among regions. In each range, the full size range (on a log scale) for short trees is divided into 100 intervals, and for tall trees 200 intervals, but the unscaled width of the range varies among regions. Also the absolute widths of the size intervals for short vs. tall trees are not comparable even within a region. The values of *z,* however, are comparable among regions in the Figures 11a-14a. Transitions among discrete stages (seeds in the canopy, seeds on the ground, and seedlings) are represented in the upper left corner of the surfaces.

Putting together the survival-growth functions of short ($P_S(x,y)$) and tall trees ($P_T(x,y)$), and the $trans_{S\text{-}T}(x)$ and $trans_{T\text{-}S}(x)$ functions produces surfaces portrayed in Figures 11b-14b. The main feature of the growth-survival function for short trees ($P_S(x,y)$) is a ridge running below the diagonal, which represents individuals that survive the time interval and increase in size (Figs. 11-14b). The variance in size t+1 for a given size *t* forms the sloping surfaces around the ridge. This pattern was followed in all regions. In Puerto Rico (and to a lesser extent in Florida), the ridge top increases in height towards the largest sizes at time *t*. This is because survival of short trees in Puerto Rico is more sensitive to size than in the other regions. The growth-survival function for tall trees ($P_L(x,y)$) is similar in that there is a ridge running below the diagonal, representing the individuals that survive and increase in size in one year (Figures 11b-14b). The sloping surfaces around the ridge represent the variance in the tall plant growth function. Although the ridge is present in all regions, in the exotic regions the ridge top increases in height towards the largest sizes at time *t*, because survival of tall trees in the exotic region is more sensitive to size, than in Australia. The $trans_{S\text{-}T}(x)$ function is represented in only one row of the surface (horizontal ridge along size at *t*) just below the short trees kernels. The probability of a short tree becoming tall at time *t*+1 consistently increased with size at time *t* in all regions. Similarly, the $trans_{T\text{-}S}(x)$ function is represented in the row just above the tall plant category. The probability of a tall tree to become part of the short tree category at time *t*+1 consistently decreased with size at time *t* in all regions.

The fecundity functions (per capita seeds produced that remain in the canopy, per capita seeds produced that fall to the ground and remain as seeds, and per capita seedlings that are produced by tall trees of size *x*), are represented by isolated peaks along the upper edge of the surfaces (Figures 11a-14a). Reproduction is restricted to tall trees, and all three functions are proportional to the predicted number of seeds produced by trees of size *x* at *t*. The peaks observed in the surfaces (Figures 11a-14a) represent the number of seeds produced and held in the canopy. The number of seeds in the *soil* seed bank, and the number of seedlings produced cannot be distinguished in the surface as portrayed because they are both proportionally much lower (0.03 and 0.6 %, respectively) than the estimated number of seeds that are produced and held in the canopy in one year. However, they would have essentially the same shape, with a peak at the far corner of the surface, which indicates that the bigger the plants, the higher number of seeds produced. We used the same *z* scale in these surfaces (Figures 11a-14a) for comparison among regions, to show that since the predicted number of seeds depends on size, and the size structure of *M. quinquenervia* individuals among regions is different, the number of seeds produced in each region is also very different. Australia, having the largest trees, produced the highest number of seeds. Although the predicted numbers of seeds are lower in the exotic regions, these are still millions of seeds being produced in the exotic regions (scale of z is $\times 10^6$).

The visual presentation of the surfaces do not change much if the growth-survival kernels, the transition from short to tall and tall to short tree kernels, and the fecundity kernels are put together, given the large numerical values of the fecundity kernels (>1), compared to the numerical values of the rest of the kernels in all regions.

Sensitivity and elasticity analyses

Sensitivity analyses, which provide insights into how perturbation by a small fixed amount of particular size-specific transitions in the kernels impact the population growth rate (λ), showed a single peak in the first column of the kernel surface, in all regions (Figsures 11c-14c). We note that in order to properly visualize the results, we altered the view orientation of the sensitivity surfaces so that it is different than the other surfaces. The 0,0 is in the upper *right* corner, rather than the upper *left* corner. The first column of the matrix is represented at the back of the plot; this column represents the fate of seeds in the canopy. According to these analyses, if the seeds in the canopy were to germinate and grow extremely rapidly and become large reproductive plants in one year, that type of transition would have a very large impact on λ. Such extreme rapid transition to adulthood does not occur in nature in *M. quinquenervia*. In Australia, although seeds becoming extremely tall trees is the most sensitive transition, seeds becoming short trees is also a highly sensitive transition. This can be observed at the base of the seed fate peak, which is wider than in the exotic regions (Figure 11c). In Puerto Rico and the Bahamas the peak is not as wide, and in Florida, the peak is relatively narrow (Figures 12c-14c).

Elasticities provide insights into how proportional perturbations of particular transitions would result in a proportional change in population growth rate (de Kroon *et al.* 2000). The elasticity surface was different among regions (Figures 11d-14d). In Australia and the Bahamas, the seedling-short trees transition had the highest elasticity (Figures 11d and 14d). Another important peak in these regions was the short to tall plant transition. A little hump in the upper section of the short trees stasis, and a ridge running below the diagonal in short and tall trees was also distinguished in the elasticity surfaces. In Florida and Puerto Rico the elasticity was very different. In these regions tall plant stasis had the highest elasticity (Figures 12 and 13d). In Puerto Rico, the seedling-short trees transition, and the canopy seed-seedling transition were notable in the surface, as well as a ridge running below the diagonal (Figure 13d).

Population growth

Based on the data collected in the plots chosen in each geographic region, population growth rate of *M. quinquenervia* was highest in the Bahamas, and lowest in Florida (Figure 3.15). Indeed, the estimated λs indicate that, based on the stands included in each region, *M. quinquenervia* populations are increasing in the Bahamas and Australia, but decreasing in Florida and Puerto Rico. Taking the native range as a reference (λ=1.02), population growth rate was 12% slower in Florida, 5% slower in Puerto Rico, and 1.7% faster in the Bahamas.

Discussion

In this study we compared the population dynamics of the invasive tree *M. quinquenervia* in its native and exotic ranges, and found that, based on the stands included in our study in each region, populations are increasing in the native range (Australia) and one of the exotic ranges (Bahamas), while they are decreasing in the other exotic ranges (Florida and Puerto Rico). These results reveal the importance of including in comparative studies, populations of different parts of the exotic range, particularly when management strategies differ among regions. We expected that, as characterized by invasive populations, *M. quinquenervia* populations would be increasing in the three exotic regions, but in Florida and Puerto Rico they are not.

Surprisingly, we found that populations in Australia are increasing (1.022). This conclusion is based on data collected in two plots in Bribie Island, and five plots in Port Macquire, in which a wide range of tree sizes (short and tall) are found. Ideally, using a stratified random design along the east coast of Australia where *M. quinquenervia* is distributed would probably be a more appropriate sampling strategy particularly when doing geographic comparisons. This is also true for the other regions included in this study. However, finding sites where long-term plots can be established is very challenging in all the regions. For instance, in Australia many of the sites where *M. quinquenervia* populations are found are private land, and therefore not available for long term studies. In Florida, three of the eight established sites were lost a few years after the data collection started, because the areas were managed (i.e. herbicide applications). The unbalanced number of sites and plots established in our study in each region is related to such limitation. Further demographic studies of *M. quinquenervia* should be carried out in a wider range of habitats, to understand how demographic processes vary in different habitats.

Besides the logistic limitations, studies involving geographical comparisons of population dynamics are challenging because an ideal design to establish long-term plots comparable across geographic regions does not exist. In our study, plots were set up to capture the variation in plant sizes across each geographic region. In general, *M. quinquenervia* plants form even-aged stands that include only a few different plant sizes. Stand dynamic models are interesting to understand how plant size affects regeneration, growth and mortality on individual trees. However, the central question is this study was to understand the dynamics of *M. quinquenervia* at the population level. Since different stages of the life cycle of *M. quinquenervia* exist in different stands that are commonly in different sites, stand dynamics models would not help us to understand dynamic processes at the population level.

According to our IPMs, *M. quinquenervia* populations are growing only in one of the exotic ranges, the Bahamas. It has been suggested that population growth rates of invasive species are generally higher, partially because demographic rates of invasive species are commonly quantified during the phase of rapid expansion, while the demographic rates of native species are quantified when populations are stable or declining (Meiners 2007, Ramula *et al.* 2008). *M. quinquenervia* was first introduced in the Bahamas in the late seventies and early eighties (Campbell 1978, Correll and Correll

1982), and the size structure of the populations in this region indicates that populations are relatively young compared to the other exotic regions (Sevillano *et al.* 2008, Chapter 1). It is not surprising that these young populations in the Bahamas are increasing, particularly considering that no biocontrol program or any other management strategy has been implemented in that region. The differences in the population growth rate between the Bahamas and Australia however are small, only 1.7% higher in the Bahamas. Parker (2000) has suggested that plant density is likely to start limiting population growth of invaders after the initial phase of the invasion process, equalizing differences in population growth rate between native and exotic populations. If this is true, populations in the Bahamas might actually not be in a rapid expansion phase, and population growth rate could have been much higher in the past when *M. quinquenervia* was first introduced.

Florida populations showed the lowest population growth rate (12% lower than Australia). These populations have been exposed to weevils (*Oxyops vitiosa*), since 1997, and to psyllids (*Boreioglycaspis melaleucae*) since 2002, and several studies have demonstrated that survival, individual growth, and reproduction have been negatively impacted by the insects (Morath *et al.*, 2006, Rayamajhi *et al.*, 2006, Pratt *et al.*, 2005a; Silvers *et al.*, 2008, Rayamajhi *et al.*, 2008, Tipping *et al.*, 2008; Franks *et al.*, 2006, Sevillano *et al.* 2010). Although population growth rate was not compared between populations with and without biocontrol agents in Florida, it is likely that the individual-level effects of the biocontrol agents have impacted the population dynamics of *M. quinquenervia*, and have translated into reductions in population growth rate. We explore the effects of the insects on population growth through simulations in Chapter 4.

Populations in Puerto Rico on the other hand, have been exposed to low densities of psyllids only since 2006. Psyllid damage in our Puerto Rican plots is not very evident, and other factors, such as intraspecific competition, might be influencing the decrease in population numbers.

One of the main differences among the studied populations in the exotic regions is the type of insects, and the amount of time that populations have been exposed to biocontrol agents. Although such differences might be influencing the observed differences in population growth, other factors independently or in conjunction, might be regulating the population dynamics of the species in the different exotic regions. Plant density might have an important role in regulating the dynamics of the populations in the different regions (Buckley and Metcalf 2005). Naturally, tree densities tend to decrease in a density-dependent manner due to competition for resources such as space, nutrients, and light, which leads to self-thinning (Davies 2001). Despite decreases in stand density caused by the mortality of suppressed trees, there is often an increase in stand characteristics such as stand basal area and biomass (Binkley *et al.* 2004). In general, these trends in the stand attributes are negatively affected if and when natural enemies colonize the system (Straw *et al.* 2005). Rayamajhi and collaborators suggested that absolute density of *M. quinquenervia* prior to the introduction of natural enemies in Florida declined primarily due to self-thinning. However, they showed that after the introduction of natural enemies in Florida, absolute density declined at a significantly greater rate (Rayamajhi *et al.* 2006). In all exotic regions, some of our plots were very dense. In our plots in Australia, density was lower than in the exotic regions, but very dense stands of young *M. quinquenervia* individuals also exist (L. Sevillano, pers. obs.).

Although density was not quantified and incorporated in our population models, Rayamajhi and collaborators (2006) have shown that competition and the presence of biocontrol agents in conjunction decrease absolute density, which in turn might be regulating *M. quinquenervia*'s population numbers.

The results of the sensitivity analyses were similar for all regions, indicating that population growth in most sensitive to seeds in the canopy becoming tall trees. If the seeds in the canopy would become seedlings and grow extremely rapidly to become tall reproductive plants in one year, they would have the largest impact on λ. This extremely rapid transition does not occur in nature in *M. quinquenervia*. Earlier descriptions of *M. quinquenervia* in Florida commonly mentioned this rapid growth as a characteristic of the invading tree, stating that they may become reproductive within a year of germination (Meskimen 1962). In recent years however, such rapid transition is not common (L.Sevillano, pers. obs.) but no quantitative data is available on this observation. Indeed, the introduction of the biocontrol agents might have reduced the frequency of this phenomenon.

Elasticities inform how proportional changes in particular transitions would result in a proportional change in population growth rate, and it is generally not known whether invasive plant species show similar elasticity patterns to those of native plant species (Hinz and Schwarzlaender 2004). Our analyses indicated that elasticities for populations in Australia and the Bahamas are similar. Population growth in Australia and the Bahamas is most sensitive to the seedling-short trees transition. Population growth in both places is also sensitive to short trees becoming tall trees (which indicates rapid growth of short trees particularly in height). In Australia, population growth is also sensitive to tall plant stasis, although to a lesser extent. The similarity in the elasticity analyses between Australia and the Bahamas is surprising considering the differences in size structure and the presence of insect herbivores between the regions. Populations in the Bahamas are comprised of mostly short trees, and a limited range of sizes in the tall plant category. In contrast, Australia includes a wide range of sizes in the tall plant category, and most individuals in this category are very large trees compared to trees in the Bahamas and the other exotic regions (Sevillano *et al.* 2008).

These elasticity analyses suggest that controlling the seedling-short trees transition in populations in the Bahamas would result in a reduction in population growth rate (see simulations in Chapter 4). In Australia, it is relatively rare for seedlings to survive and grow to become short trees. The seedling stage is particularly susceptible to herbivore damage (Franks *et al.* 2006, Sevillano *et al.*, 2010), and considering all the insects that have been reported to interact with *M. quinquenervia* in Australia (Balucinas *et al.* 1994, 1995), it is not surprising that the negative effects of several natural enemies and other biotic and abiotic factors affecting seedling growth and survival would reduce population growth rate, specially when annual recruitment in *M. quinquenervia* is very low. As a reminder, the seedling-short trees transition probability, which is a discrete stage in our model, was based on data from Florida populations since this piece of information is not available for Australia. Likewise, the dynamics of the seedbanks (canopy and ground), as well as the seed rain might be very different in Australia, but we used the same transition probabilities in all regions, assuming they are similar. Some studies have shown different patterns of seedling survival or germination in the exotic compared to the native range (Noble 1989, Grigulis *et al.* 2001, Sheppard *et al.* 2002). It would be relevant to study the dynamics of these life cycle transitions in the native range, to see if our projections of population dynamics in the native range would change.

Population growth in Florida and Puerto Rico is most sensitive to tall plant stasis. The elasticity surfaces for these two regions are similar, although in Puerto Rico population growth is also sensitive to the seedling-short trees transition. These results are surprising particularly because control efforts in Florida have concentrated in targeting smaller stages of *M. quinquenervia*'s life cycle, and according to the elasticity analysis, effects on younger stages of the life cycle would not have an impact on population growth (see Chapter 4). As mentioned before, several studies have shown that biocontrol agents have reduced survival, growth and reproduction of different stages of the life cycle. It is also known that although biocontrol agents reduce growth and reproduction, they rarely impact survival of the largest trees in the tall plant category. Simulations of the effects of insects on the seedling-short trees transition and the effects on population growth rate in Florida are explored in Chapter 4.

Management actions that focus on demographic transitions with the greatest elasticity value generally have the greatest influence on population growth, which shows that elasticity analyses can be used to identify those transitions and increase control success. However, simulations are important and required to assess the exact quantitative impacts of reductions in particular life cycle transitions on population growth rate (Ramula *et al.* 2008).

To our knowledge, this is one of the few studies that have investigated how population growth rates of an invasive tree change between the native and several exotic regions. Our results indicate that the population dynamics is different in the different exotic regions, and in some cases similar to the population dynamics in the native region. For those regions where management programs have not been implemented, this study helps to identify the stage transitions that are most important for population growth, with the objective of reducing *M. quinquenervia*'s population growth rates. And for those regions where management efforts have been implemented already, this study aids in directing future management efforts.

Table 3.1. Sites and number of plots within each site established for demographic studies of *Melaleuca quinquenervia* in its native and exotic ranges. Short trees were < 1.3 m height; tall trees were ≥ 1.3 m height.

Geographic region	Site	Number of plots	Number of short individuals originally marked	Number of tall individuals originally marked
Australia	Bribie Island	2	474	595
	Port Macquarie	5	59	915
Florida	FGCU	1	21	331
	Holiday Park	14	82	1649
	Krome	7	30	890
	Miami	1	41	647
	Prairie Pines	16	1849	0
	Strazula	3	5	446
	Treetops Park	3	2	165
	West Palm	4	3386	139
Puerto Rico	San Juan Bay Estuary	6	1492	707
Bahamas	Andros Island	4	31	52
	Grand Bahama	6	264	151
	New Providence	3	136	149

Table 3.2. Kernel components describing each section of the high dimensional matrix constructed for *M. quinquenervia*.

	Matrix section	Kernel
1	Tall trees	$P_L(x,y) = \mathrm{s}_L(x)\mathrm{g}_L(x,y)$
2	Short trees	$P_S(x,y) = \mathrm{s}_S(x)\mathrm{g}_S(x,y)$
3	Transition trees (short to tall)	$transition_{S\text{-}T}(x)=s_S(x)\ trans_{S\text{-}T}\ (x)$
4	Transition trees (tall to short)	$transition_{T\text{-}S}\ (x)=s_L(x)\ trans_{T\text{-}S}\ (x)$
5	Canopy seed bank	$canopy.seeds(x)=f_s(x)f_n(x)(1\text{-}\mathrm{SR})$
6	Soil seed bank	$ground.seeds(x)=f_s(x)f_n(x)\mathrm{SR}\ \mathrm{SS}\ p_{\mathrm{G}}$
7	Seedlings	$seedlings(x)=f_s(x)f_n(x)\mathrm{SR}\ \mathrm{SS}\ p_{\mathrm{S}}$

s_L(x) Survival function of tall trees

g_L(x) Growth function of tall trees

s_S(x) Survival function of short trees

g_S(x) Growth function of short trees

grad(x) Probability of plants of diameter x to become ≥1.3 m tall

shnk(x) Probability of plants of DBH x to become <1.3 m tall

$f_s(x)$ Probability of producing seeds

$f_n(x)$ Number of seed produced by plants of size x

SR Seed rain; (1-SR) is the proportion of new seeds that are held up in the canopy

SS Seed survival in one year

p_{G} Proportion of surviving seeds that remain on the ground after one year

p_{S} Proportion of seeds that become seedlings after one year

Table 3.3. Statistical models of size-dependent survival, growth, and fecundity used to construct the kernel components developed for *M. quinquenervia* in the native and exotic regions. All model predictions are over one year. Size refers to either diameter at 5 cm from the ground (for short trees), or to DBH (for tall trees).

Demographic process	Model
Survival	
Short trees	Logit(surv$_S$)= $surv_{S}.intercept + surv_{S}.slope\ ln$(diameter at 5 cm t)
Tall trees	Logit(surv$_T$)= $surv_{T}.intercept + surv_{T}.slope\ ln$(DBH t)
Growth	
Short trees	ln(diameter at 5 cm t+1) = $grw_{S}.intercept + grw_{S}.slope\ ln$(diameter at 5 cm t)
Tall trees	ln(DBH t+1) = $grw_{T}.intercep + grw_{T}.slope\ ln$(DBH t)
Transition short-tall	Logit($trans_{S\text{-}T}$)= $trans_{S\text{-}T}.intercept + trans_{S\text{-}T}.slope\ ln$(diameter-at-5 cm t)
Transition tall-short	Logit($trans_{T\text{-}S}$)= $trans_{T\text{-}S}.intercept + trans_{T\text{-}S}.slope\ ln$(DBH t)
Capsule presence	Logit(capsules presence)= $caps.intercept + caps.slope\ ln$(DBH t)
New seeds presence	Logit(seeds presence)= $seeds.intercept + seeds.slope\ ln$(DBH t)
Number of seeds	$seeds = a + [(b - a)/(1+e((c - ln(\text{DBH } t))/d))]$

Table 3.4. Parameter estimates describing the demography of *Melaleuca quinquenervia* over one year in the native and exotic regions. Data across sampling years in each region were pooled for analyses. All parameters were significant (α=0.05) except when $^{+}$, which indicates that parameter was not significant.

Parameter	Australia	Florida	Puerto Rico	Bahamas
Survival				
$surv_{S}.intercept$	2.16	0.83	0.54	2.41
$surv_{S}.slope$	0.98	0.80	0.20	0.92
$surv_{T}.intercept$	4.0	0.73	2.15	5.59
$surv_{T}.slope$	0.36	0.62	0.84	1.48
Growth				
$grw_{S}.intercept$	0.062	0.03	0.004^{+}	0.19
$grw_{S}.slope$	0.83	0.87	0.84	0.96
$grw_{S}\ \sigma$	0.23	0.33	0.32	0.24
$grw_{T}.intercep$	0.13	0.06	0.12	0.17
$grw_{T}.slope$	0.95	0.98	0.95	0.92
$grw_{T}\ \sigma$	0.10	0.14	0.19	0.24
Transition $_{S\text{-}T}$				
$trans_{S\text{-}T}.intercept$	-2.27	-1.47	-3.36	2.09
$trans_{S\text{-}T}.slope$	1.89	2.41	1.80	1.37
Transition $_{T\text{-}S}$				
$trans_{T\text{-}S}.intercept$	-4.46	-5.45	-4.98	-4.08
$trans_{T\text{-}S}.slope$	-1.03	-1.93	-1.26	-1.56
Capsule presence				
caps.intercept	-1.37	-1.66	-5.98	0.14
caps.slope	0.96	1.31	3.09	0.54
Seeds presence				
seeds.intercept	1.75	0.67	2.96	3.62
seeds.slope	0.59	0.72	-0.07^{+}	0.38
Number of seeds				
a	5.21	6.27	4.96	6.54
b	16.4	14.1	13.2	14.3
c	1.71	1.41	1.09	0.94
d	1.58	0.83	0.50	1.26

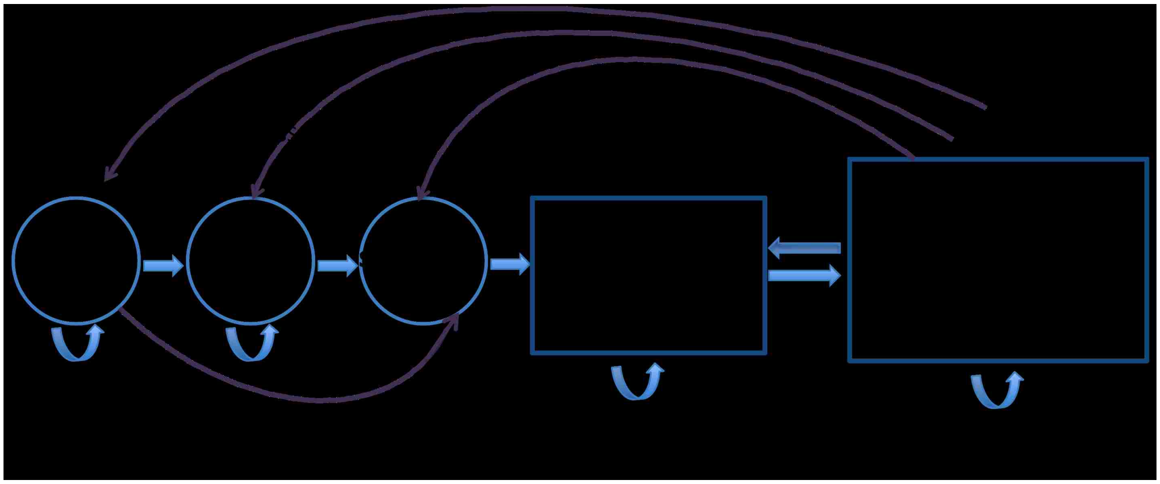


Figure 3.1. Life cycle of *M. quinquenervia*. Five stages were used to develop an integral projection model: two different seed banks (canopy and ground), seedlings, short and tall trees. The stages in circles were modeled as discrete points, and the stages in squares were modeled as continuous domains. Transitions between stages are indicated by arrows, and occur over the time scale of one year. Transition labels indicate the probability of individuals at one stage moving or contributing to the next. Within each continuous domain there is a range of sizes, where size is measured as diameter at 5cm above the ground for the short plant domain, and diameter at breast height (DBH) for the tall plant domain. Survival and growth of short and tall trees were modeled as a function of size (x). Transitions from short to tall trees or from tall to short trees were also modeled as a function of size (x). Tall trees can produce seeds that may stay in the canopy seed bank, become part of the soil seed bank, or become seedlings within one year. Fecundity was also modeled as a function of size (x). The probabilities s_3 and s_4 refer to dormancy in the canopy or the ground. The probabilities g_3-g_5 refer to growth between stages. See Table 3.2 for explanation on the functions.

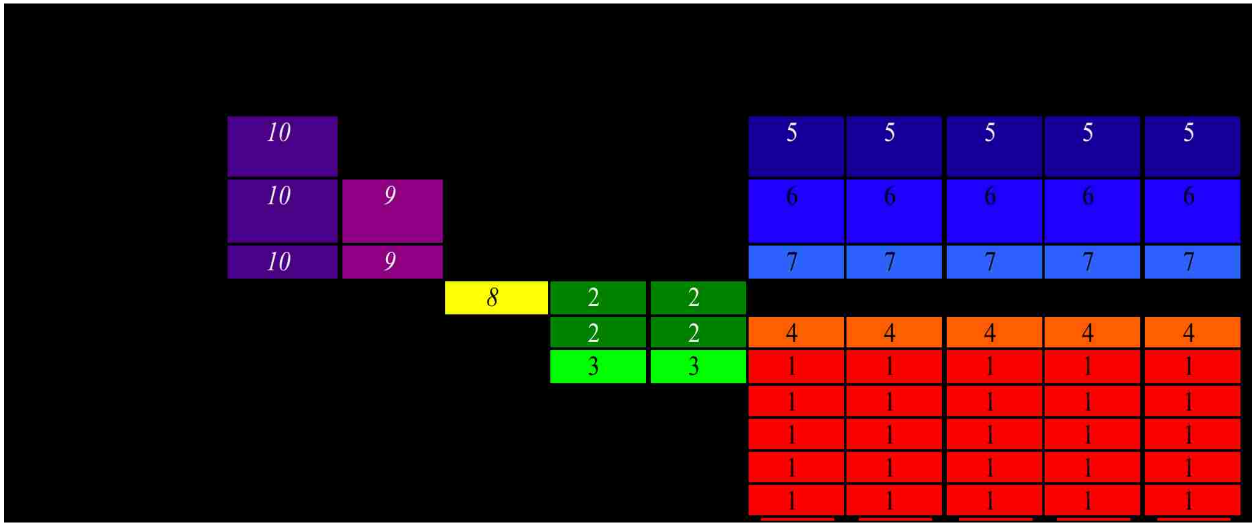


Figure 3.2. Schematic diagram for the construction of the high dimensional matrix used to develop an integral projection model of population dynamics for *Melaleuca quinquenervia*. The high dimensional matrix includes discrete and continuous components all representing transitions among states or contributions to states over one time step. 1: transitions among tall trees; 2: transitions among short trees; 3: transition from short to tall trees; 4: transition from tall to short trees; 5: per capita production by tall trees of seeds that remain in the canopy; 6: per capita production by tall trees of seeds that fall to the ground and remain as seeds; 7: per capita production of seedlings by tall trees; 8: fates of seedlings; 9: fates of seed on the ground; 10: fates of seeds in the canopy.

Figure 3.3. *Next page.* Fitted regression relationships of survival and growth for *M. quinquenervia* in <u>Australia</u>. All regressions are a function of size and *t*. (a) Probability of surviving at *t*+1 of short trees; (b) Size at *t*+1 of short trees; (c) Probability of becoming tall at *t*+1 of short trees; (d) Probability of surviving at *t*+1 of tall trees; (e) Size at t+1 of tall trees; (f) Probability of becoming short at *t*+1 of tall trees. Estimated parameters for fitted relationships shown in Table 3.4.

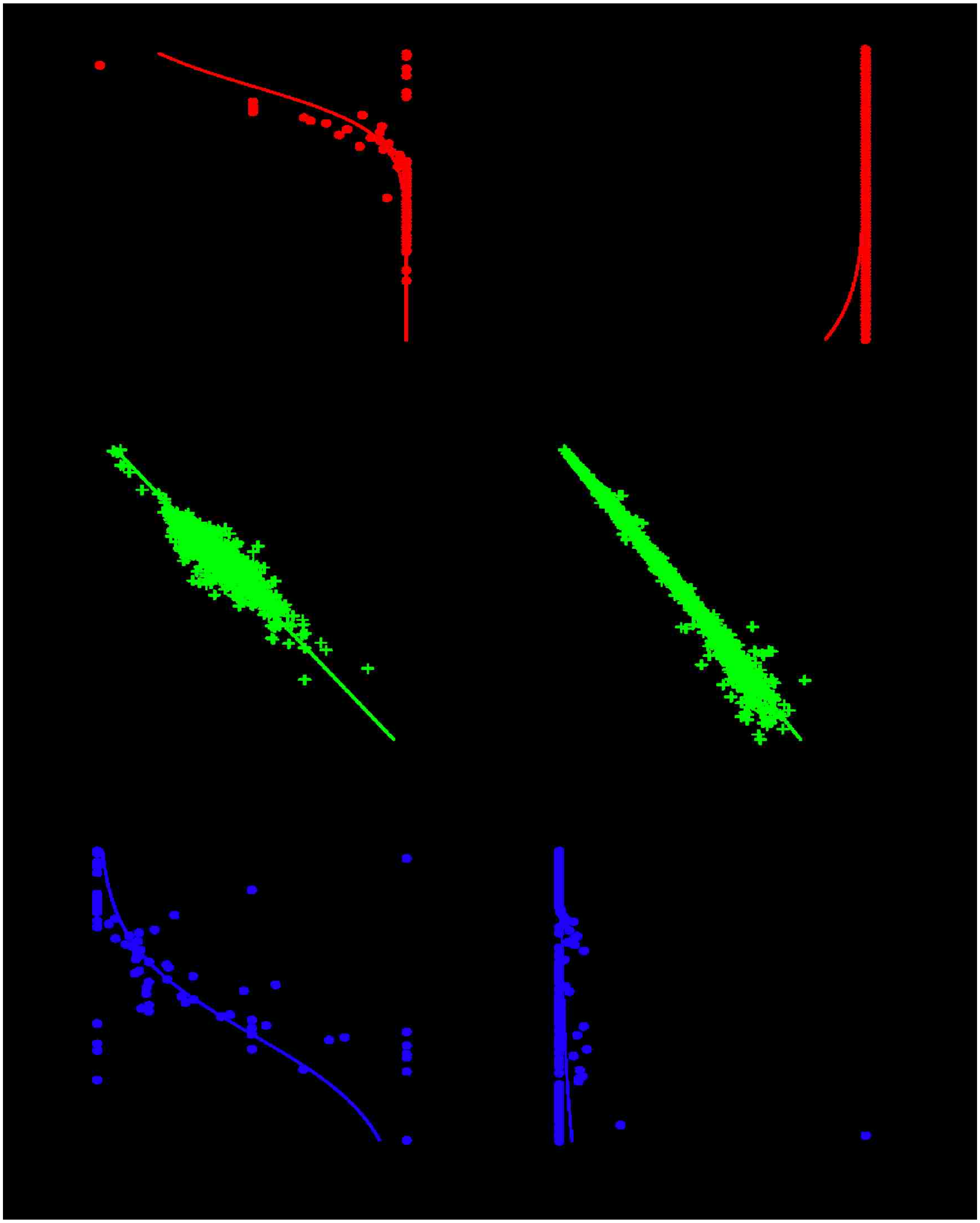


Figure 3.4. *Next page.* Fitted regression relationships of survival and growth for *M. quinquenervia* in Florida. All regressions are a function of size and *t*. (a) Probability of surviving at *t*+1 of short trees; (b) Size at *t*+1 of short trees; (c) Probability of becoming tall at *t*+1 of short trees; (d) Probability of surviving at *t*+1 of tall trees; (e) Size at t+1 of tall trees; (f) Probability of becoming short at *t*+1 of tall trees. Estimated parameters for fitted relationships shown in Table 3.4.

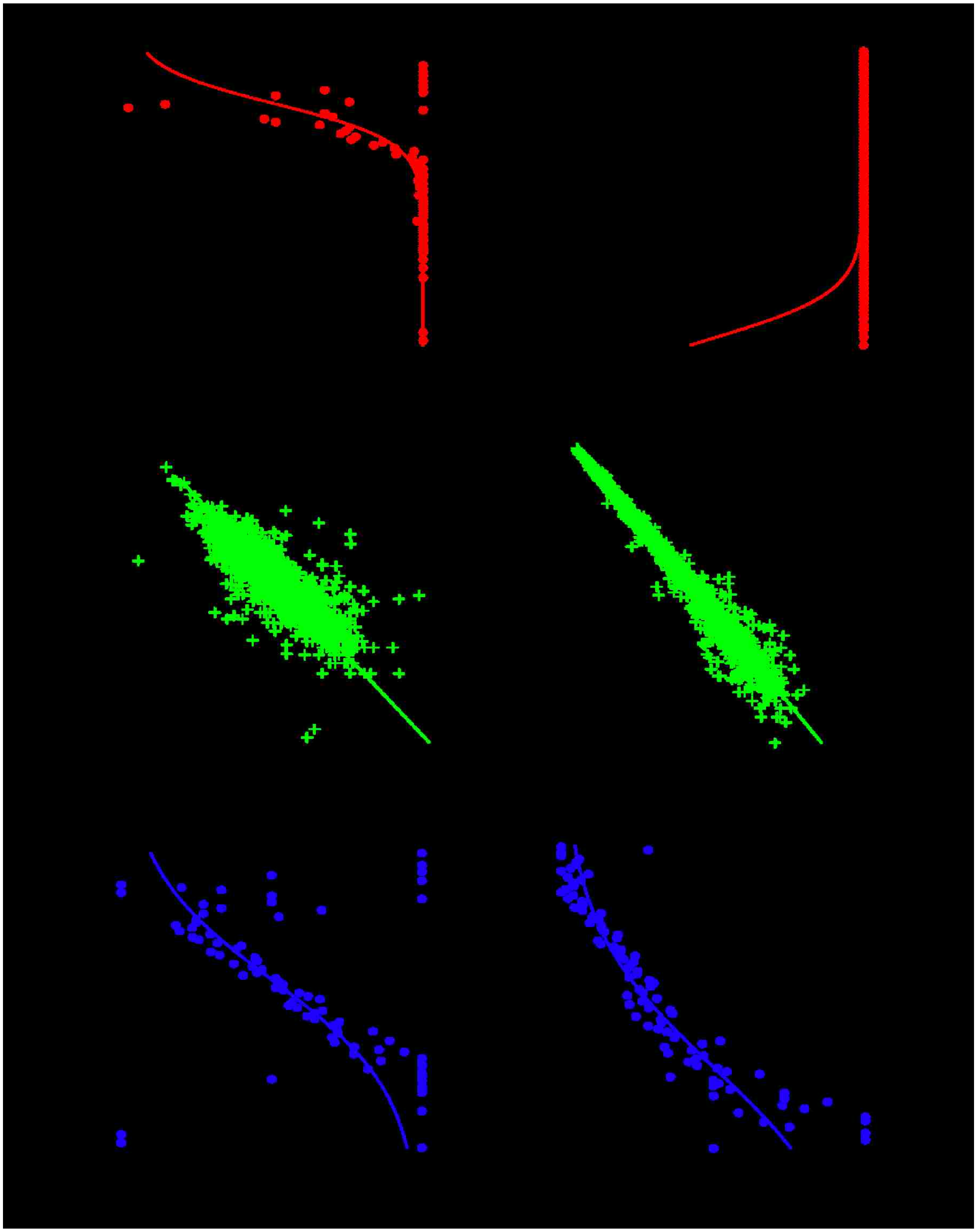


Figure 3.5. *Next page.* Fitted regression relationships of survival and growth for *M. quinquenervia* in Puerto Rico. All regressions are a function of size and *t*. (a) Probability of surviving at *t*+1 of short trees; (b) Size at *t*+1 of short trees; (c) Probability of becoming tall at *t*+1 of short trees; (d) Probability of surviving at *t*+1 of tall trees; (e) Size at t+1 of tall trees; (f) Probability of becoming short at *t*+1 of tall trees. Estimated parameters for fitted relationships shown in Table 3.4.

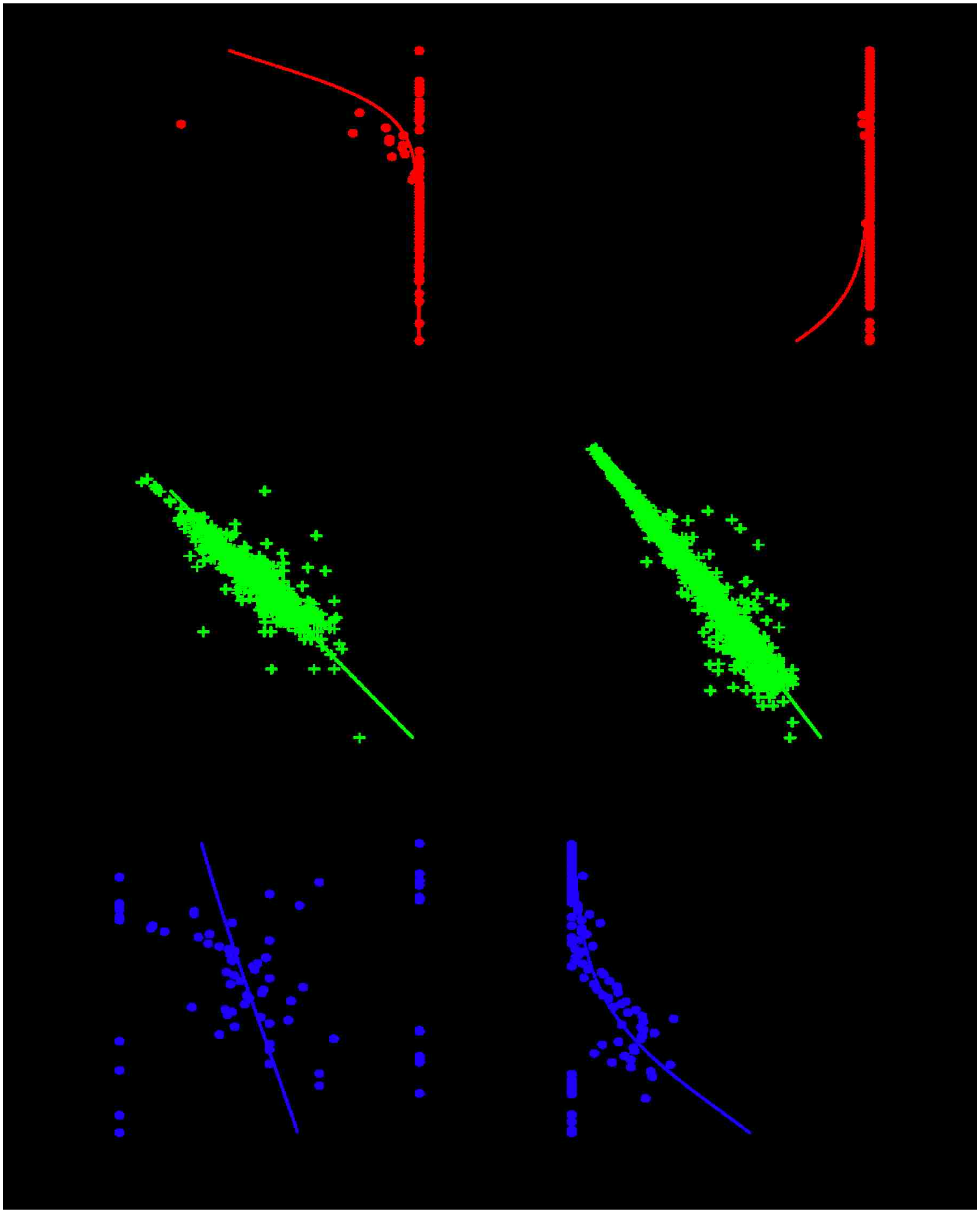


Figure 3.6. *Next page.* Fitted regression relationships of survival and growth for *M. quinquenervia* in the <u>Bahamas</u>. All regressions are a function of size and *t*. (a) Probability of surviving at *t*+1 of short trees; (b) Size at *t*+1 of short trees; (c) Probability of becoming tall at *t*+1 of short trees; (d) Probability of surviving at *t*+1 of tall trees; (e) Size at t+1 of tall trees; (f) Probability of becoming short at *t*+1 of tall trees. Estimated parameters for fitted relationships shown in Table 3.4.

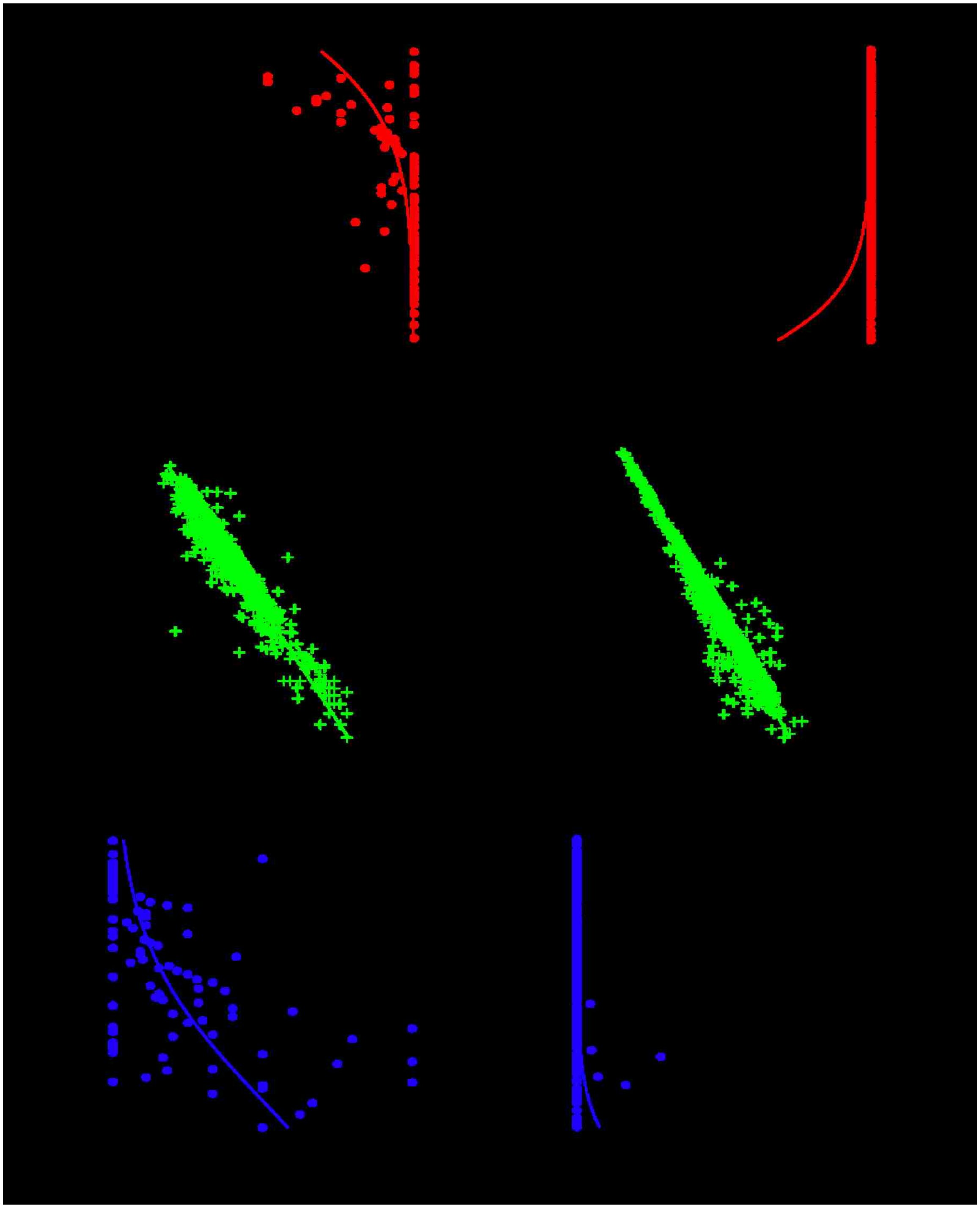


Figure 3.7. *Next page.* Fitted regression relationships of reproductive components for *M.quinquenervia* in Australia. All regressions are a function of size (DBH) and *t*. (a) Probability of producing capsules at *t*+1; (b) Probability of producing seeds at *t*+1; (c) Number of seeds produced at *t*+1; (d) Predicted number of seeds produced at *t*+1. Estimated parameters for fitted relationships shown in Table 3.4

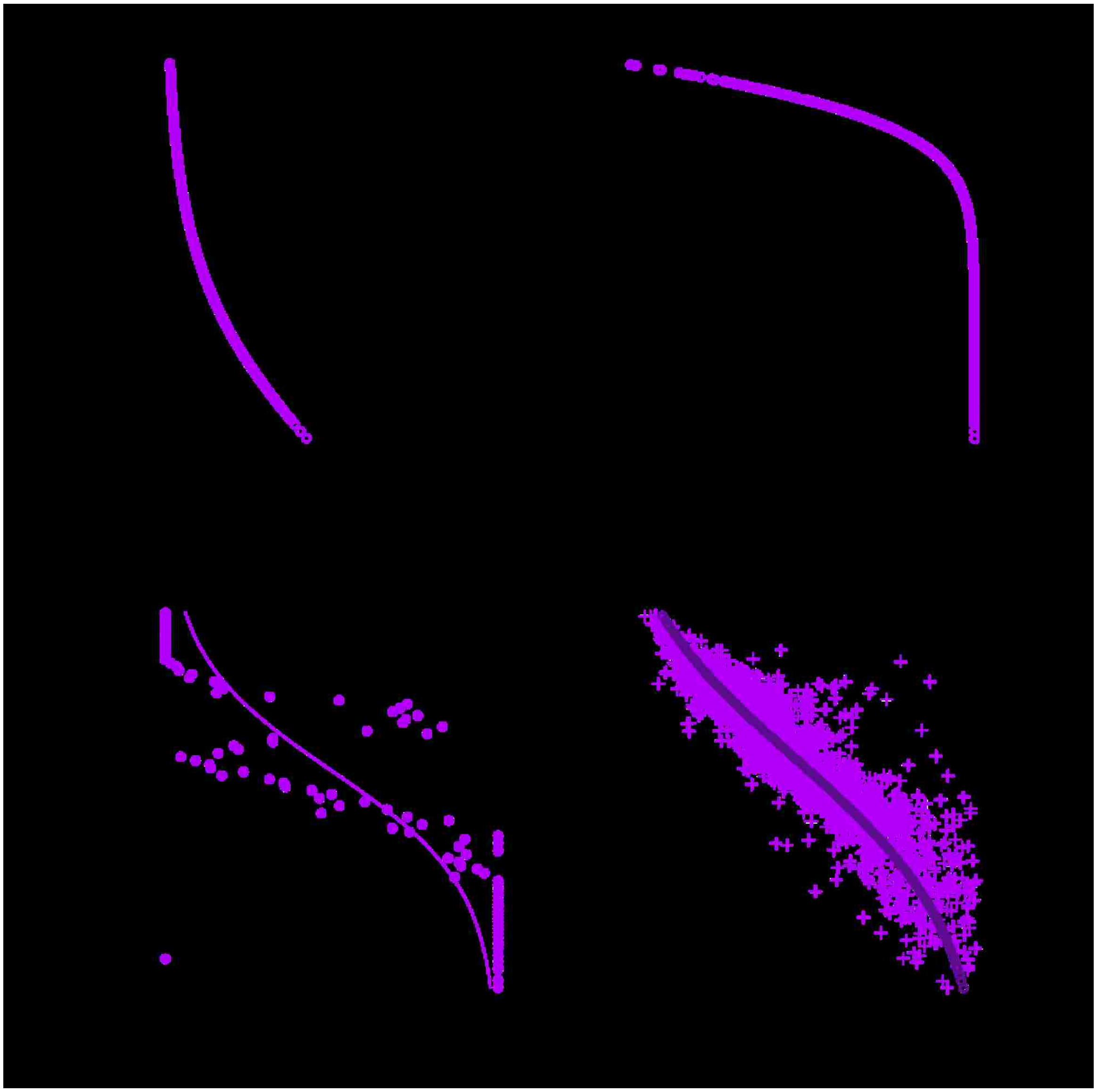


Figure 3.8. *Next page.* Fitted regression relationships of reproductive components for *M. quinquenervia* in Florida. All regressions are a function of size (DBH) and *t*. (a) Probability of producing capsules at *t*+1; (b) Probability of producing seeds at *t*+1; (c) Number of seeds produced at *t*+1; (d) Predicted number of seeds produced at *t*+1. Estimated parameters for fitted relationships shown in Table 3.4.

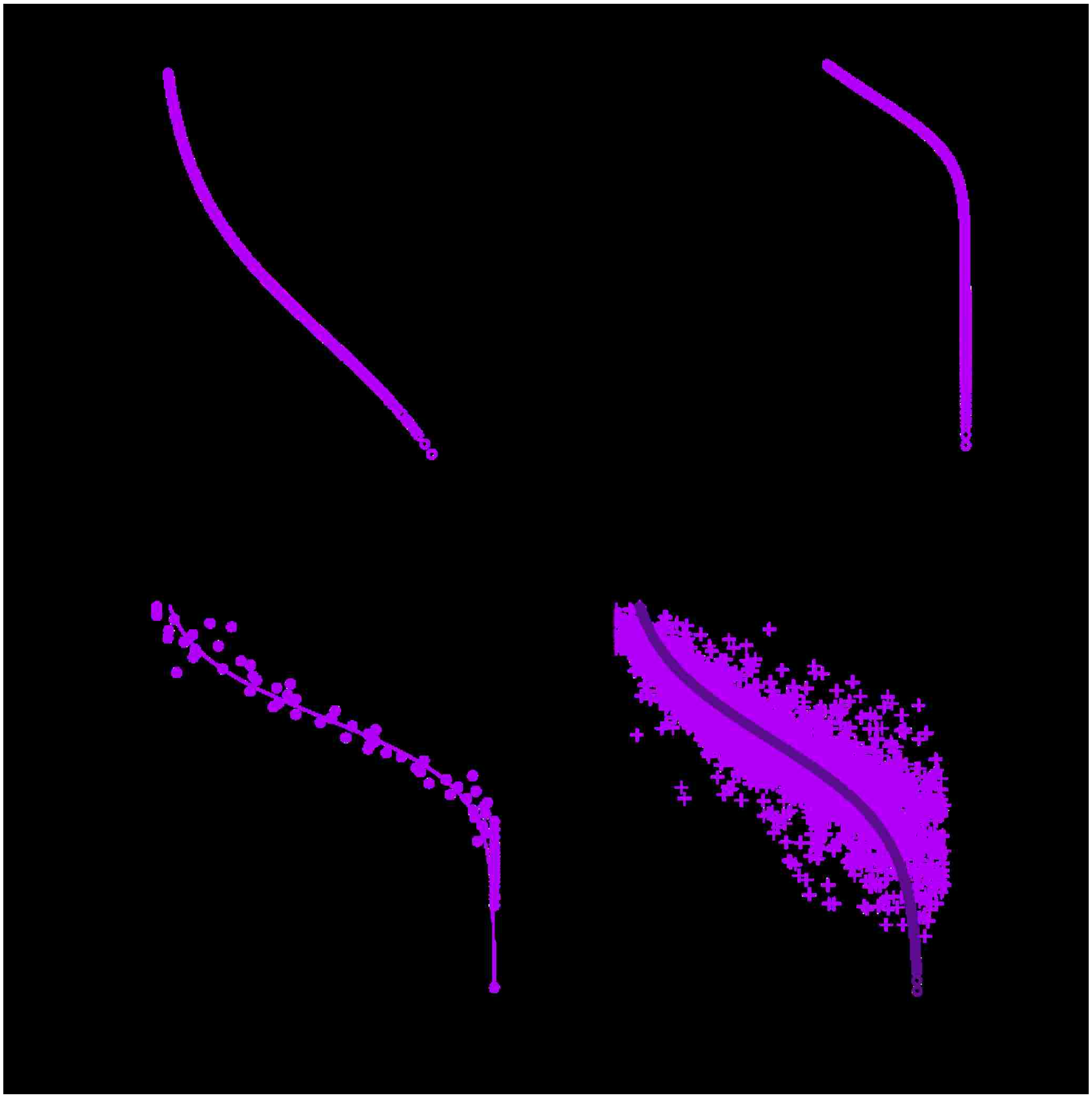


Figure 3.9. *Next page.* Fitted regression relationships of reproductive components for *M. quinquenervia* in Puerto Rico. All regressions are a function of size (DBH) and *t*. (a) Probability of producing capsules at *t*+1; (b) Probability of producing seeds at *t*+1; (c) Number of seeds produced at *t*+1; (d) Predicted number of seeds produced at *t*+1. Estimated parameters for fitted relationships shown in Table 3.4.

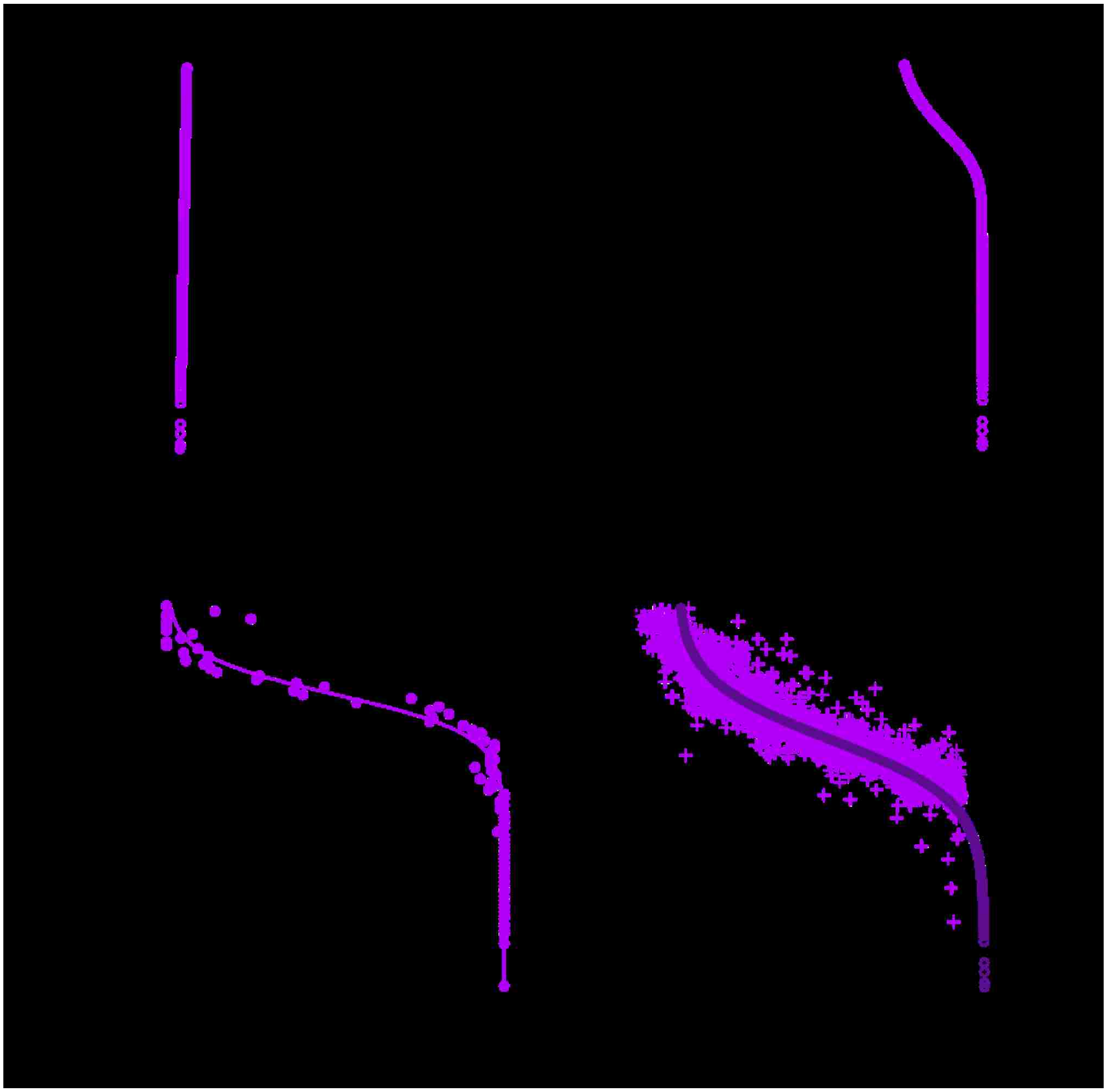


Figure 3.10. *Next page.* Fitted regression relationships of reproductive components for *M. quinquenervia* in the Bahamas. All regressions are a function of size (DBH) and *t*. (a) Probability of producing capsules at *t*+1; (b) Probability of producing seeds at *t*+1; (c) Number of seeds produced at *t*+1; (d) Predicted number of seeds produced at *t*+1. Estimated parameters for fitted relationships shown in Table 3.4.

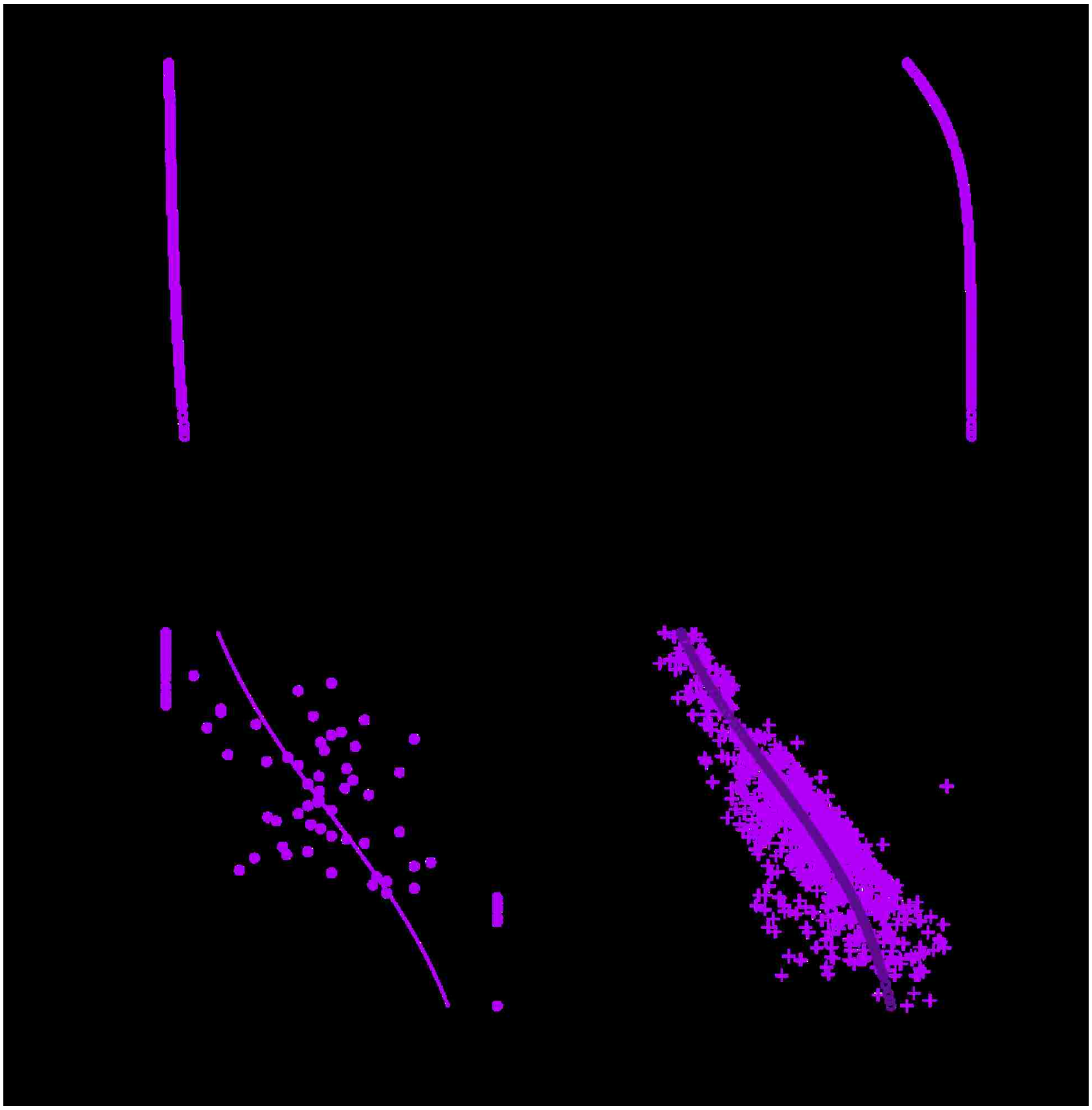


Figure 3.11. *Next page.* Components of the kernels and sensitivity and elasticity surfaces for the integral projection model fitted to *M. quinquenervia* in Australia. (a) the fecundity functions (*canopy.seeds*(x), *ground.seeds*(x), *seedlings*(x)); (b) the growth-survival functions ($P_L(x,y)$ and $P_S(x,y)$) and the transitions $trans_{S\text{-}T}(x)$ and $\mathrm{trans}_{\mathrm{T\text{-}S}}(x)$ functions; (c) sensitivity; (d) elasticity. Size categories include the three discrete stages and the two continuous domains. For the later, the categories are based on dividing the observed range of sizes (on a log scale) into 100 equal intervals for the short trees and 200 equal intervals for the tall trees. In this region the short trees ranged in size from 0.01 to 7.07 cm (-4.6 to 1.95 on a natural log scale), while the tall trees ranged in size from 0.085 to 70.92 cm (-2.46 to 4.26 on a natural log scale).

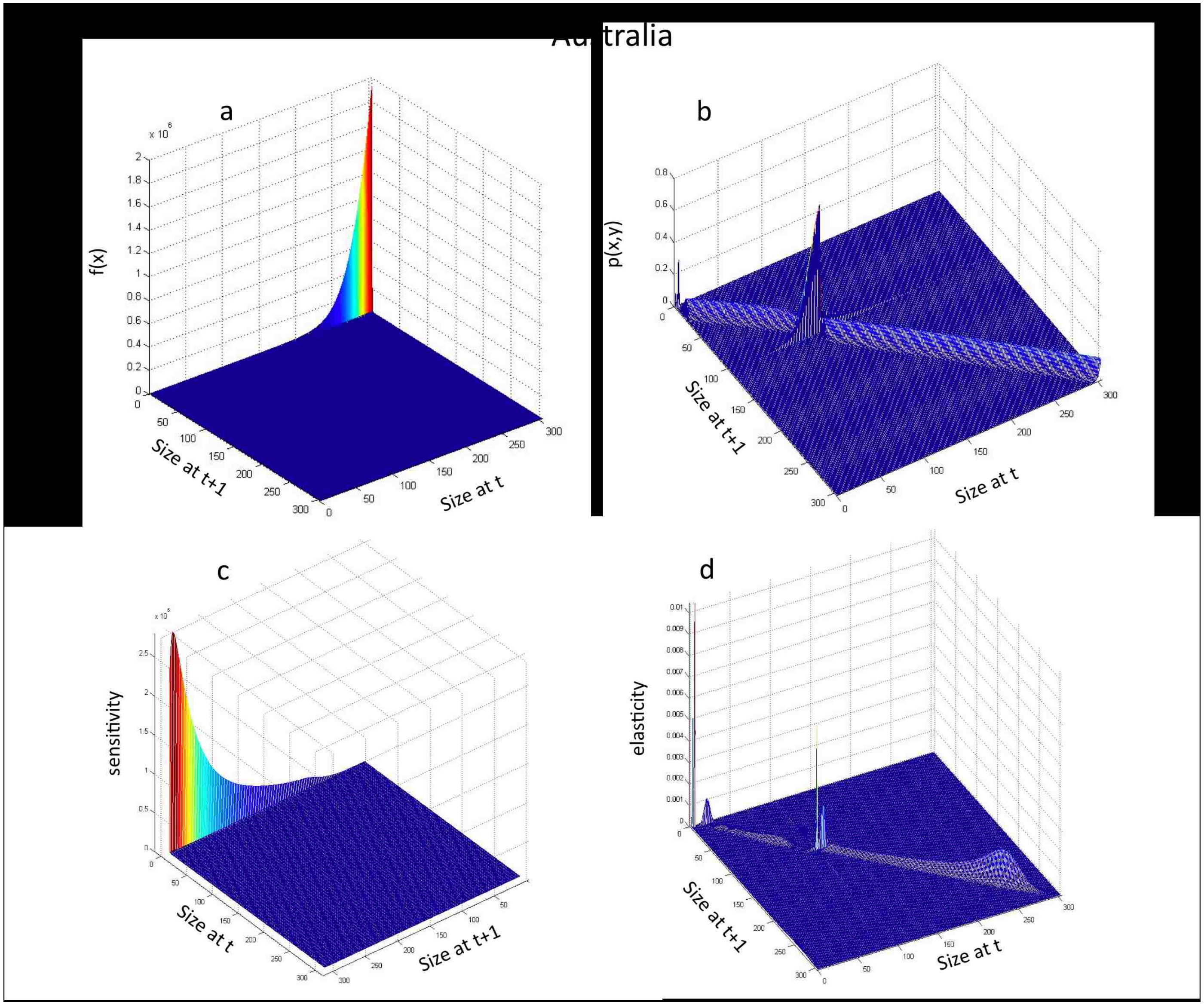

Au tralia
a
x 10^6
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
f(x)
Size at t+1
Size at t
0
50
100
150
200
250
300
b
p(x,y)
0.8
0.6
0.4
0.2
0
Size at t+1
Size at t
c
x 10^5
2.5
2
1.5
1
0.5
0
sensitivity
Size at t
Size at t+1
d
0.01
0.009
0.008
0.007
0.006
0.005
0.004
0.003
0.002
0.001
0
elasticity
Size at t+1
Size at t

Figure 3.12. *Next page.* Components of the kernels and sensitivity and elasticity surfaces for the integral projection model fitted to *M. quinquenervia* in Florida. (a) the fecundity functions (*canopy.seeds*(*x*), *ground.seeds*(*x*), *seedlings*(*x*)); (b) the growth-survival functions ($P_L(x,y)$ and $P_S(x,y)$) and the transitions $trans_{S\text{-}T}(x)$ and $\mathrm{trans}_{\mathrm{T\text{-}S}}(x)$ functions; (c) sensitivity; (d) elasticity. Size categories include the three discrete stages and the two continuous domains. For the later, the categories are based on dividing the observed range of sizes (on a log scale) into 100 equal intervals for the short trees and 200 equal intervals for the tall trees. In this region the short trees ranged in size from 0.01 to 7.07 cm (-4.6 to 1.95 on a natural log scale), while the tall trees ranged in size from 0.085 to 70.92 cm (-2.46 to 4.26 on a natural log scale).

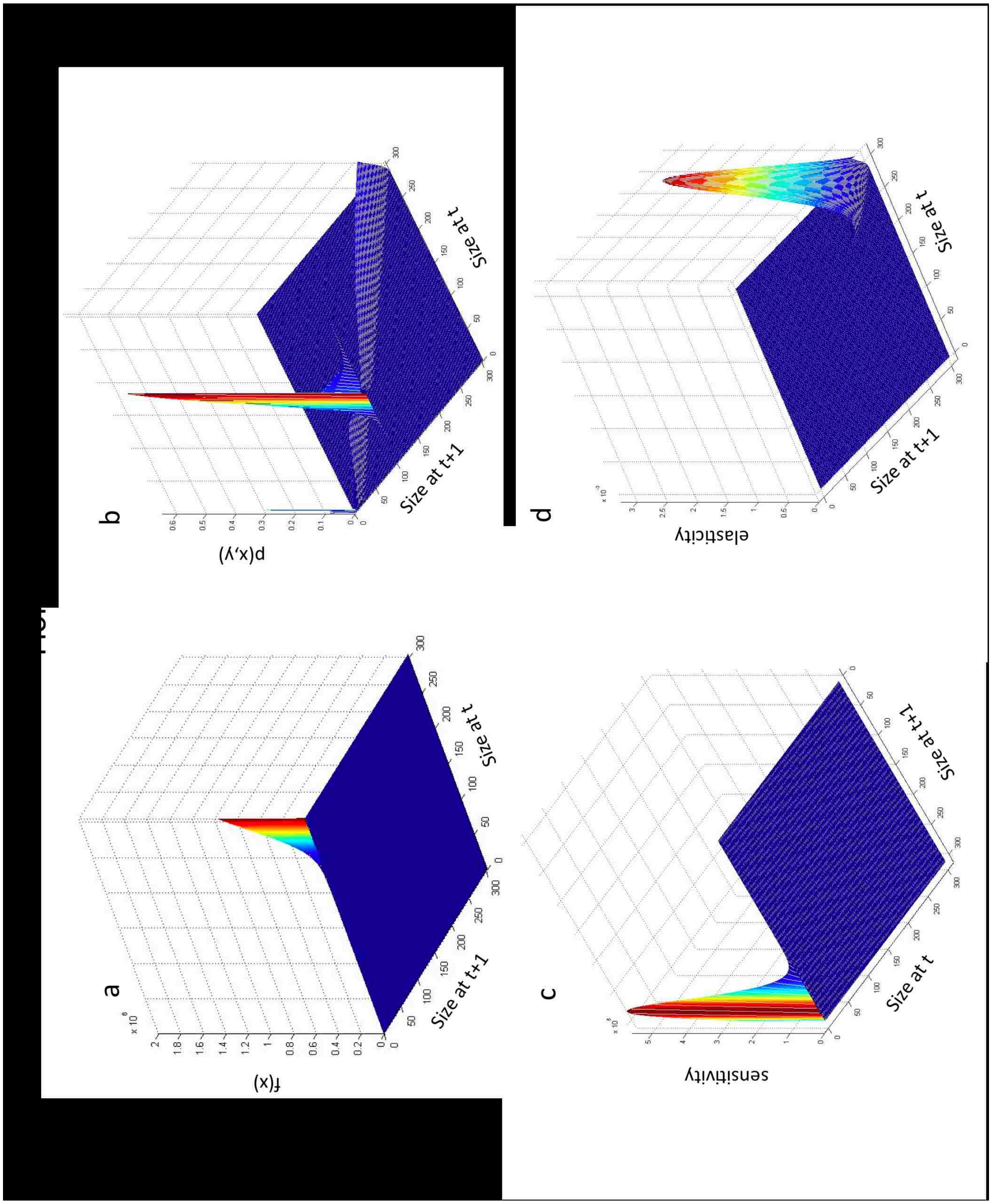

a
f(x)
x 10^-6
Size at t+1
Size at t
b
p(x,y)
Size at t+1
Size at t
c
sensitivity
x 10^-6
Size at t
Size at t+1
d
elasticity
x 10^-3
Size at t+1
Size at t

Figure 3.13. *Next page.* Components of the kernels and sensitivity and elasticity surfaces for the integral projection model fitted to *M. quinquenervia* in Puerto Rico. (a) the fecundity functions (*canopy.seeds*(*x*), *ground.seeds*(*x*), *seedlings*(*x*)); (b) the growth-survival functions ($P_L(x,y)$ and $P_S(x,y)$) and the transitions $trans_{S\text{-}T}(x)$ and $\mathrm{trans}_{\mathrm{T\text{-}S}}(x)$ functions; (c) sensitivity; (d) elasticity. Size categories include the three discrete stages and the two continuous domains. For the later, the categories are based on dividing the observed range of sizes (on a log scale) into 100 equal intervals for the short trees and 200 equal intervals for the tall trees. In this region the short trees ranged in size from 0.01 to 7.07 cm (-4.6 to 1.95 on a natural log scale), while the tall trees ranged in size from 0.085 to 70.92 cm (-2.46 to 4.26 on a natural log scale).

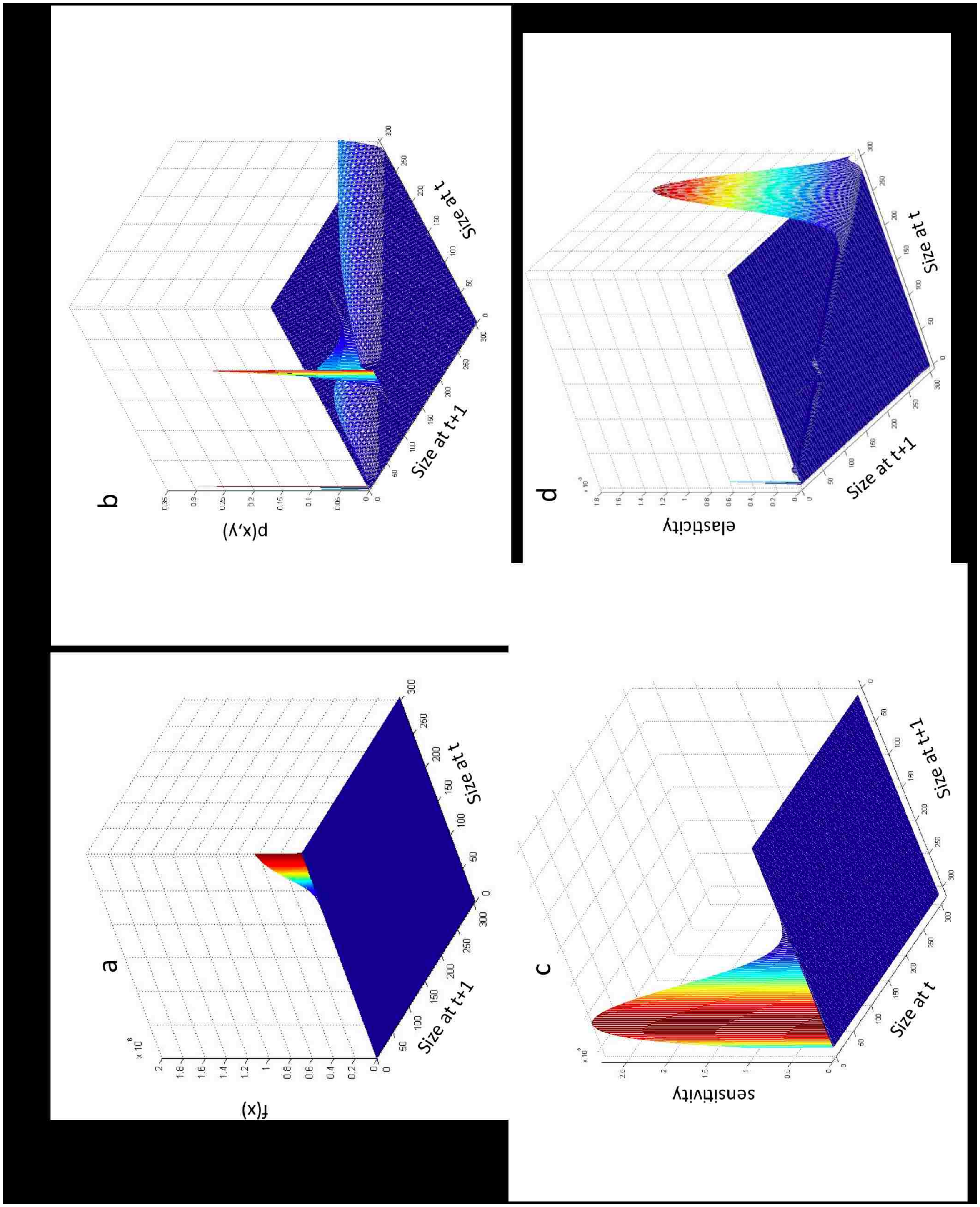
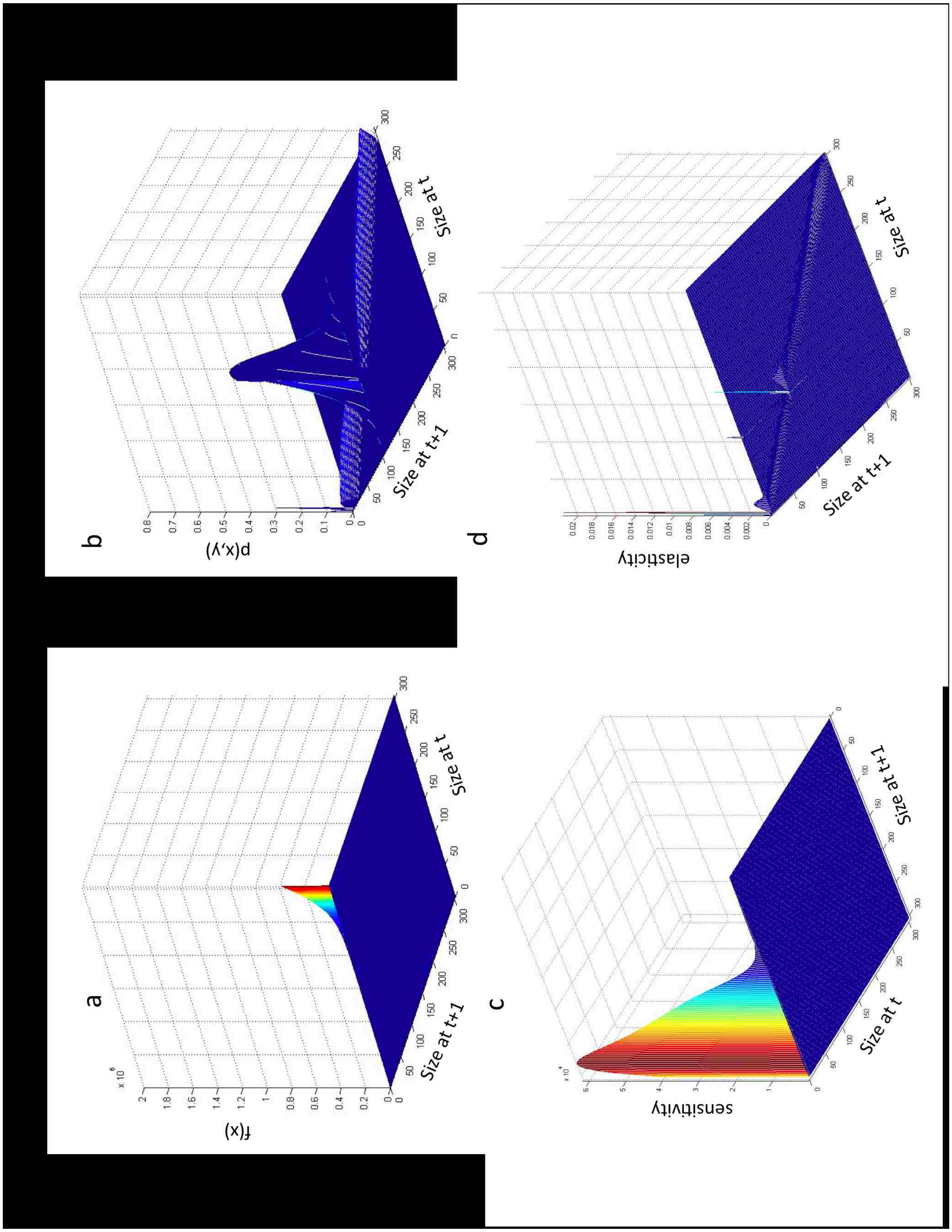

a
f(x)
x 10^6
Size at t+1
Size at t
b
p(x,y)
Size at t+1
Size at t
c
sensitivity
Size at t
Size at t+1
d
elasticity
Size at t+1
Size at t

Figure 3.14. *Next page.* Components of the kernels and sensitivity and elasticity surfaces for the integral projection model fitted to *M. quinquenervia* in the Bahamas. (a) the fecundity functions (*canopy.seeds*(*x*), *ground.seeds*(*x*), *seedlings*(*x*)); (b) the growth-survival functions ($P_L(x,y)$ and $P_S(x,y)$) and the transitions $trans_{S\text{-}T}(x)$ and $\mathrm{trans}_{\mathrm{T\text{-}S}}(x)$ functions; (c) sensitivity; (d) elasticity. Size categories include the three discrete stages and the two continuous domains. For the later, the categories are based on dividing the observed range of sizes (on a log scale) into 100 equal intervals for the short trees and 200 equal intervals for the tall trees. In this region the short trees ranged in size from 0.01 to 7.07 cm (-4.6 to 1.95 on a natural log scale), while the tall trees ranged in size from 0.085 to 70.92 cm (-2.46 to 4.26 on a natural log scale).


a
f(x)
x 10^6
Size at t+1
Size at t
b
p(x,y)
Size at t+1
Size at t
c
sensitivity
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d
elasticity
Size at t+1
Size at t

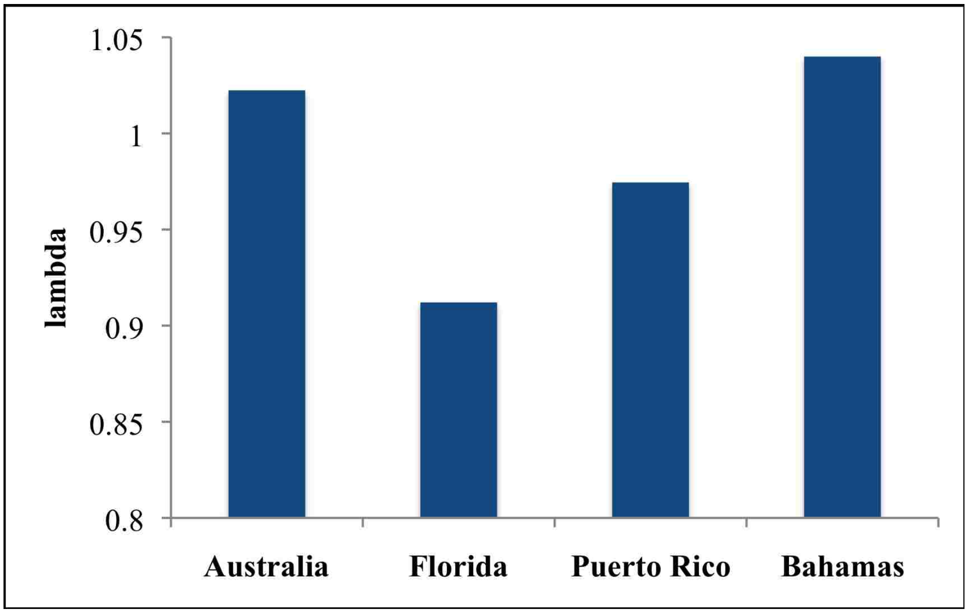

Figure 3.15. Estimated population growth rates of *M. quinquenervia* in its native and exotic regions over one year. Data include more that one year, but was combined across years to obtain the population growth rate over one time step (one year).

Chapter IV

Consequences of insect damage on the population growth of the invasive tree *Melaleuca quinquenervia*[4]

Background

One of the ultimate goals of biological control programs against invasive plants is to limit population growth and spread. Traditionally, however, biological control assessments have been focused on evaluating the consequences of insect herbivore damage on short-term individual level performance parameters such as stage-specific growth, reproduction, and survival (reviewed in Morin *et al.* 2009). However, biological control of invasive plants should be assessed at the population level, since it is at such level that invasion of exotic species fails or succeeds (Parker 2000, Morin *et al.*2009).

It is commonly assumed that the introduction of specialist herbivores or pathogens as biological control agents will result in the suppression of introduced plant populations. The assumption relies on extensive evidence from natural communities, that insect herbivores can impact plant population dynamics (Harper 1977, Crawley 1989, Maron and Crone 2006 (and references therein), Miller *et al.* 2009). Although a few biological control programs have succeed in suppressing invasive plants (e.g. Osmond and Monroe 1981, McFadyen 2000, Keane and Crawley 2002), many others have failed, suggesting that the introduction of insects may not always result in successful control (Lawton 1985, 1990, Crawley 1989, McEvoy and Coombs 1999, McFadyen 2000, Denoth *et al.* 2002, Davis *et al.* 2006, Schutzenhofer and Knight 2007). Biocontrol agents that have their strongest effect on life history transitions to which population

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[4] Coauthors: Carol C. Horvitz, Paul D. Pratt, Steven Franks

growth of the pest is relatively insensitive, will not be effective.

A small but growing number of studies have concentrated on predicting and/or quantifying the consequences of biocontrol damage at the population level (Shea and Kelly 1998, McEvoy and Coombs 1999, Parker 2000, Buckley *et al.* 2003a, Paynter *et al.* 2003, Buckley *et al.* 2004, Davis *et al.* 2006, Shea *et al.* 2006). Most of these studies are based on modeling population dynamics as a function of stage-specific demographic rates. Matrix projection models, and more recently integral projection models (IPMs) provide insights into how factors that influence plants at the individual level may contribute to overall population dynamics (Caswell 2001, Easterling *et al.* 2000). They also help to understand several aspects of the invasive nature of exotic species (Grigulis *et al.* 2001; Paynter *et al.* 2003) and can be used to implement and quantify the effectiveness of different management strategies (Shea and Kelly 1998, McEvoy and Coombs 1999).

By incorporating the effects of biocontrol agents on life history transition transition rates of the invasive into structured population models, one can investigate how much insect damage at particular stages results in the reduction of plant population growth rate (Shea and Kelly 1998, Horvitz and Schemske 2002, Buckley *et al.* 2003). Moreover, models can help determining the best combination of biological control agents, or other control techniques, to reduce population growth rate. The combination of experiments and structured population models can provide good insights into the effects of herbivores on plant populations (Halpern and Underwood 2006).

One of the first studies that developed structured population models for an invasive species, *Carduus nutans*, found that the percentage seed losses (30-40%)

observed in the field as a consequences of weevil damage were not enough to decrease population growth rate (Shea and Kelly 1998). In contrast, in the tree *Sesbania punicea*, reductions of 98% in the seed set of the tree by weevils resulted in important reductions in the density of immature plants, although the density of mature plants was not affected (Hoffmann and Moran 1991). Years later in this same system, it was shown that long-term effects of three biocontrol agents affecting several parts of the plant did result in a decrease in mature plant density (Hoffmann and Moran 1998). For some species, like the invasive shrub *Clidemia hirta*, matrix models revealed that a reduction in fecundity by biocontrol insects would not be the most cost-effective control. Rather, a reduction in survival of all vegetative stages would be more effective as a means to decrease population growth rate (DeWalt 2006).

The Australian tree *Melaleuca quinquenervia* is an invasive species in south Florida, Puerto Rico, and the Bahamas, and other areas of the Caribbean (Pratt *et al.* 2005b, Dray *et al.* 2006, Pratt *et al.* 2007). In Florida, a biological control program against *M. quinquenervia* was initiated in 1997 with the release of the leaf-eating weevil *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae). A few years later (2002), the psyllid *Boreioglycaspis melaleucae* Moore (Homoptera: Psyllidae) was introduced, and both insects have spread and naturalized throughout South Florida (Pratt *et al.* 2003, Center *et al.* 2007). In Puerto Rico and the Bahamas, no biocontrol program has been implemented. However, in 2006, low densities of psyllids were unexpectedly observed in *M. quinquenervia* populations in Puerto Rico (Pratt *et al.* 2006).

Biological control agents were mainly expected to reduce seed production in adult plants, and to reduce survival and individual growth rates of seedlings and saplings, which in turn would reduce the rate of spread of *M. quinquenervia* in south Florida (Turner *et al.* 1998). This expectation was based on the results of an experiment carried out in Queensland, Australia, were the exclusion of naturally occurring insects from *M. quinquenervia* saplings using insecticide, resulted in a significant increase in individual growth compared to plants with insects (Balciunas and Burrows 1993). The seedling stage in the life cycle of plants is expected to experience stronger negative effects of herbivory because they have fewer carbon stored reserves (Hendrix 1988, Crawley 1989); this is particularly true for trees. Several studies now have confirmed that both biocontrol agents of *M. quinquenervia* in Florida have negative impacts on seedlings (Franks *et al.* 2006, 2008a, Center *et al.* 2007, Sevillano *et al.* 2010). What is still not clear is whether the negative impacts of the insects on the seedling-sapling transition (saplings are referred to as short plants in this study) of the life cycle of *M. quinquenervia* result in significant reduction of its long term population growth rate.

In this study we developed simulations on the basis of integral projection models of population dynamics developed previously for *M. quinuenervia* (Chapter 3), and on experimental results that quantify the effects of insects on seedling growth and survival (Chapter 2, Sevillano *et al.*2010), to investigate the consequences of insect damage to population dynamics in Florida, Puerto Rico, and the Bahamas. In particular, we investigated how different density combinations of weevils and psyllids affecting the seedling-short plant transition would result in significant reductions of *M. quinquenervia*'s asymptotic population growth rate (λ).

Methods

Effects of biocontrol agents on population growth

To determine the effects of insects on population dynamics, we used the quantitative results of experiments (Sevillano *et al.*, 2010) to simulate changes in life history rates that would be brought about by insects, altering (1) the proportion of seedlings that survive one year (*s*) and (2) the parameters of a statistical model of growth for plants larger than seedlings but shorter than 1.3 m in height. The seedling survival parameter also measures the probability that seedlings will grow into the group of plants which are larger than seedlings but shorter than 1.3 m in height; in other words the only the seedlings that survive are those that grow and transition into this next life stage. The statistical model focuses on the relationship between size now and size later, which is estimated as a linear model with the log(stem diameter 5 cm from the base) acting as the state variable to predict future size,

$$\log X_{t+1} = m \log X_t + b \quad (1).$$

We assumed that annual survival of plants larger than seedlings but shorter than 1.3 m in height was size dependent and that insects did not directly affect their survival, except as they acted indirectly through their effects on plant growth. Alterations in parameters *s*, *m* or *b* will result in changes to elements of the high dimensional matrices used to numerically estimate the integral projection models which were developed for *M. quinquenervia* populations from its native and exotic range, and thus to new estimates of asymptotic population growth rate (λ) and its sensitivity structure under different regimes of insect herbivory. We performed simulations of insect effects for each region by combining data from shade house experiments (Chapter 2) with demographic data from natural populations in Florida, Puerto Rico, and the Bahamas, respectively (Chapter 3).

Our factorial experiment, carried out in a shade house, tested the independent and combined effects of different weevil and psyllid densities (zero, low and high), on growth and survival of *M. quinquenervia* seedlings over a twelve week period in a controlled environment with abundant light, water, nutrients and space. There were nine treatment categories (Table 4.1). These data, analyzed in detail elsewhere, provided estimates of monthly survival and weekly growth rates under different conditions of herbivore pressure. Plant size was estimated by stem diameter at 5 cm from the base of the plant. Survivorship was calculated as the proportion alive of an initial cohort after a fixed amount of time. Here we make use of the means from the different treatment groups after a set amount of time to focus on the effects of the insects on rates of change of survivorship and size.

Annual rates are required for the population dynamics models and the translation of short term experimental results to annual rates was straightforward, assuming multiplicative effects of constant rate over time. Specifically, “instantaneous” (=monthly for survivorship or weekly for stem diameter) exponential rates of change in survivorship and in stem diameter were calculated by obtaining the linear regression of the log of survivorship and of the log of diameter, respectively, against time (in corresponding units). Then, assuming multiplicative models, these weekly or monthly rates were scaled up to a full year. If we follow individuals over time and we consider X_t to be the size or the survivorship at time t, either can be expressed as,

$$X_t = X_o e^{rt}$$

or, on a log scale as,

$$\log X_t = \log X_o + rt \quad (2),$$

where $X_0 = 1$ for survivorship and $X_0 =$ initial stem size for diameter and r is the "instantaneous" exponential rate of change obtained as the slope of the regression of the log of survivorship, or of the log of size, against time. Then, to scale up to any amount of time, we can calculate rt as the increment of change on a log scale or e^{rt} as the multiplicative change on a linear scale. Specifically for survivorship, which was calculated in terms of a monthly rate, we multiplied its corresponding r by 12 to scale up to annual survival and for stem diameter, which was calculated in terms of a weekly rate, we multiplied its corresponding r by 52 to scale up to annual (Table 4.1). The value of r is, of course, specific to a particular analysis; we obtained one r for the rate of change in survivorship and a distinct r for rate of change in stem diameter for each of the nine experimental categories. For survivorship r is always negative and for growth it was either negative or positive, since plants can either increase or decrease in diameter over time.

The annual increment on a log scale represents proportional change, so we can also express the different insect treatments as proportional to one another by choosing one reference treatment. This is useful to be able to translate the results of the experiments in relative terms to the field populations. We choose the treatment with the highest growth rate, the one without weevils and without psyllids as the reference. Then, for each of the other treatments relative to this one, we calculated the difference between the annual increment on the log scale for that treatment and the annual increment on the log scale for the reference treatment. This constituted, for each herbivore treatment, the “intercept adjustment parameter for statistical growth models” (Table 4.1) and was subtracted from the value for *b* (equation 1) obtained from analysis of demographic data in natural populations, as a way to simulate the effects of insects (for each of the nine different treatment categories) on the statistical growth model for each region. The *b*’s varied among the regions, but in each case the insect effects were simulated by the same adjustment parameters, under an assumption that the observed *b* in each region corresponded to a “no insects” treatment and that the proportional effects of adding herbivores would be consistent across regions.

Finally, for each herbivore pressure treatment level, a new integral projection model was constructed incorporating the altered annual seedling survival parameter (*s*) and the altered intercept (*b*) of the model for annual change in plant size. Each IPM was numerically integrated by use of a high dimensional matrix, and the resulting population growth rate was calculated as the dominant eigenvalue of this matrix (λ) (Easterling *et al.* 2000). In this way we obtained a distinct estimate of population growth rate for each region and insect treatment level.

Melaleuca’s seed rain

Although *M. quinquenervia* seeds are released in small amounts throughout the year producing a “regular” seed rain, “high” seed rain occurs episodically after stresses that break vascular connections of branches holding capsules (e.g. fires, frosts, mechanical damage, herbicide applications) (Woodall 1982, Hofstetter 1991). In these high seed rain episodes, all seeds in the canopy seed bank are released and the surviving plants either become part of the soil seedbank, or become seedlings.

The IPMs developed in Chapter 3 assumed regular seed rain. However, the dynamics and particularly the population growth rate of *M. quinquenervia* might increase in years when high seed rain occurs. Thus, we simulated high seed rain and investigated the consequences of insect damage on population growth rate of *M. quinquenervia* under such conditions. High seed rain simulations were developed by first estimating the number of seeds accumulated by a tree of size *x* in the canopy seedbank (i.e. seed crop), based on the ln-ln relationship of size (DBH) and dry seed weight in Rayachhetry *et al.* 2001 (see Appendix 1, Chapter 3). Second, to estimate the number of seeds in the canopy produced in *previous years*, we subtracted the number of new seeds produced in one year from the number of seeds accumulated in the canopy. This correction was needed because Rayachhetry's equation estimates the standing seed crop which already includes the number of new seeds produced by a tree of size *x* within that year. Finally, we added the number of new seeds produced in that year (see Appendix 1, Chapter 3), to the number of seeds accumulated in the canopy in previous years, to obtain the total number of seeds that would be dispersed that year by a tree of size *x*.

We assumed that no seeds would remain in the canopy, and so all the surviving seeds would either become part of the soil seed bank, or become seedlings (5% and 95% respectively, as assumed for a regular seed rain year).

We simulated the effects of insect damage (all insect density combinations, Table 4.1) in a regular and a high seed rain year, and obtained the population growth rates on each of these scenarios (18) for *M. quinquenervia* populations in Florida, Puerto Rico, and the Bahamas.

Results

Although insect damage significantly affects seedling survival and the growth of short plants of *M. quinquenervia* (see Chapter 2), the simulations that we ran for populations in Florida indicated that adding further insects to the current populations would not result in further decreases in population growth rate. Effects were minimal; comparisons across all combinations of insect densities, including years with either regular or high seed rain (Figures 1a and 2a, respectively), affected λ only in the 10th decimal point. The population growth rate in all cases was close to 0.91208, indicating that in Florida, populations would decrease over time under any regime, which was also the case in our analysis of the IPM for the natural populations in this region.

The simulations for Puerto Rico indicated herbivore pressure on seedlings and plants larger than seedlings (but shorter than 1.3 m) could reduce population growth rate a bit more than in Florida, particularly in high seed rain years (Figures 1b and 2b). The highest population growth rate was for plants without any insects (λ's were 0.9754 and 0.9965 in low and high seed rain years, respectively). Although the IPMs estimated for natural populations in Puerto Rico are indicate that they are currently in decline ($\lambda<1$) (Chapter 3), our simulations indicate a further decrease in population growth rate could be brought about by adding insects to the system. In general, in low rain years adding insects to the system in any density reduced population growth rate by about 0.14%, where the percent change was calculated as,

$$(\lambda_{\text{with insects}} - \lambda_{\text{without insects}}) / \lambda_{\text{without insects}}$$

with respect to the *no insect* scenario (Figure 4.1b). In high seed rain years, adding insects in low densities reduced population growth rate by about 2.15%, while adding them in high densities reduced population growth rate by about 2.25% with respect to the *no insect* scenario (Figure 4.2b). High densities of psyllids with any combination of weevil densities had the highest impact (Figure 4.2b).

Our simulations for the Bahamas indicated herbivore pressure on seedlings and plants larger than seedlings (but shorter than 1.3 m) could reduce population growth rate quite a bit more than in the other two regions, especially in high seed rain years (Figures 1c and 2c). The highest population growth rates were for plants without any insects (λ's of 1.0699 and 1.1818 in low and high seed rain years, respectively). According to our IPMs for the natural populations (Chapter 3), populations in the Bahamas are currently increasing ($\lambda>1$). The simulations show that adding insects could change that and result in declining populations. In low seed rain years, adding low densities of either insect to the system reduced population growth rate by about 5.6%, while adding high densities of both insects reduced population growth by 8.25%, relative to the *no insect* scenario (Figure 4.1c). In high seed rain years, adding insects in low densities reduced population growth rate by about 6.6-6.7%, while adding them both in high densities reduced population growth rate by about 16.24%, with respect to the *no insect* scenario (Figure 4.2c).

Discussion

The aim of the simulations presented here was to assess the impacts that the weevil *O. vitiosa*, and the psyllid *B. melaleucae* have had in reducing *M. quinquenervia*'s population growth rate in Florida, by affecting the survival of seedlings and the growth of plants larger than seedlings but shorter than 1.3 m. We also wanted to explore the potential consequences of biocontrol damage on this stage, to *M. quinquenervia*'s population growth in other exotic regions.

The projected growth rate in Florida based on field observations is low (λ=0.91) and does not correspond to the status of the species as an invasive tree. Although several studies have demonstrated the impacts that biocontrol agents have, particularly in young stages of the life cycle of *M. quinquenervia* (Franks *et al.* 2006, 2008a, Center *et al.*2007, Sevillano *et al.* 2010), our simulations indicate that adding more insects that impact these stages, in addition to those already established in the field populations, would not result in a meaningful reduction of population growth rate. Even in the extreme cases when we simulated 100% seedling survival (which is unrealistic in the field) impacts on λ were minimal. Moreover, the simulations indicate that even a high seed rain event would not result in an important increase in population growth rate under any of our simulated scenarios.

Our simulations did not incorporate the effects of insect damage on reproduction. It has been shown that weevil damage reduces the proportion of trees (1-6 cm DBH) that produce flowers, and the number of inflorescences and capsules produced per tree (Pratt *et al.* 2005a). It is expected that the effects of weevils on *M. quinquenervia*'s reproduction would result in a reduction of population growth rate and this will be investigated in future modeling efforts. The elasticity analysis of the high dimensional matrix obtained by integral projection modeling (Chapter 3) revealed that population growth rate of *M. quinquenervia* in Florida is mostly sensitive to tall plant stasis. This means that changes in survival of tall trees would greatly affect *M. quinquenervia*'s population growth rate. According to Turner and collaborators (1998), no insect species in Australia seems capable of routinely causing the death of tall trees, even though they are capable of killing seedlings and short plants. However, perhaps a search for bark beetles, moths that feed on canopy foliage or others that tend to attack mature trees could yield additional useful biocontrol agents.

The results of our simulations for populations in Florida are surprising for a couple of reasons. First, populations of an invasive species are expected to be increasing. Second, reductions of survival and growth of the seedling-sapling stage consistently reported in this and other studies were expected to impact population growth rate (Turner *et al.* 1998, Center *et al.* 2007). One interpretation is that the demographic data which were collected from 2003 to 2007 and form the basis of our models already exhibit the dynamics of populations that have been impacted by well-established naturalized biocontrol agents. A different experimental study in which the biocontrol agents were excluded from *M. quinquenervia* plots by applying insecticide from 2003 to 2007, showed that these insects can significantly reduce density, survival, growth, and seed production of *M. quinquenervia* (Tipping *et al.* 2009). Variation in population growth rate among years has not been accounted for in our population models so far, since data was pooled across years (see Chapter 3). We predict that the population growth rate of *M. quinquenervia* from 2003 to 2004 is at least slightly higher than the population growth rate from 2006 to 2007, as the incidence of insect damage has increased (Rayamajhi *et al.* 2006). Our demographic and experimental studies, and the results of these simulations suggest that additional biocontrol agents in Florida affecting mainly young stages of the life cycle of *M. quinquenervia* (i.e. seedlings and short plants) are not expected to contribute to further reductions in population growth rate.

For populations in Puerto Rico and the Bahamas, the simulations revealed that biocontrol damage to seedlings and short plants can impact population growth rate. In both regions, the impacts of both insects, at either low or high densities, are predicted to reduce λ, although high densities of psyllids are predicted to have the greatest impact. The observed population growth rate in Puerto Rico is 0.97 indicating that populations are decreasing, but the impacts of the biocontrol agents would decrease λ a little bit more. According to the elasticity analysis for Puerto Rico, tall plant stasis contributes the most to population growth (Chapter 3). To a lesser extent, seedlings surviving and becoming short plants also contribute to population growth and thus we observed that impacts on that stage would slightly reduce λ. In contrast, the elasticity analysis for the Bahamas revealed that the seedling-short plant transition has the highest impact on population growth rate. The simulations predicted that the magnitude of the impacts on λ as a consequence of insect damage would be stronger in the Bahamas than in Puerto Rico. Indeed, impacts at that stage of the life cycle would cause a shift from an increasing to a declining population.

The predicted impacts of the biocontrol agents in Puerto Rico and the Bahamas are similar for regular and high seed rain years in that as insect density increases, the reductions on λ are higher. However, for both regions population growth rates are predicted to be overall higher in high seed rain years. For instance, population growth rate in Puerto Rico with no insect impacts would increase from 0.975 to 0.996 in a high seed rain year, and in the Bahamas λ would increase from 1.07 to 1.18 in high seed rain year. What is interesting is that the relative decrease in population growth rate in the high psyllid density treatments with respect to the no insect scenario would be higher in a high than in a regular seed rain year. Indeed, population growth rates predicted as a result of high densities of psyllids would be very similar in regular or high seed rain years. This prediction suggests that the impacts of the biocontrol agents might be stronger in high than in regular seed rain years. Large seedling carpets are formed after massive recruitment events in a high seed rain year (Turner *et al.* 1998, Sebersoff-King 2003). The increase in the available amount of young leaf tissue in these seedling stands would be expected to attract more insects, which in turn could result in higher densities of insects per plant, and finally in stronger impacts on growth and survival of the seedlings-short plant stage.

The simulations presented here for *M. quinquenervia* populations in Puerto Rico and the Bahamas should only be used as a guide to learn the possible consequences of altering the seedling-short plant transition on population growth rates, as it has been done for other invasive plants (e.g. Shea and Kelly 1998, McEvoy and Coombs 1999, Buckley *et al.* 2003). Considering the costs, time, and potential risks involved in introducing biocontrol agents (McEvoy and Coombs 1999a,b, Simberloff and Stiling, 1996; Louda *et al.* 1997, 2003), these simulations are not intended to suggest that a biocontrol program should be implemented, particularly in the Bahamas. The goal is to demonstrate that any strategy that would reduce seedling survival by ~40% (corresponding to the effects of high densities of insects on survival, Sevillano *et al.* 2010) might reduce the population growth rate of this invasive tree in those regions.

Our model simulations indicate that damage of biocontrol agents at the seedling-short plant transition of the life cycle of *M. quinquenervia* can reduce population growth rates in Puerto Rico and the Bahamas. In Florida, however, despite the substantial impacts of insects on that stage, they do not translate into reductions in population growth rates. In this study, we have simulated the effects of different intensities of insect damage on population growth rates without considering how these damage intensities may vary over time. Moreover, we simulated the effects of insect damage in regular and high seed rain years again without considering for example how often a high seed rain year would occur, and the consequences of the frequency of such rare events on population dynamics. Stochastic demographic models might help understanding the effects of temporal variability in insect damage, on the dynamics of plant populations (Tuljapurkar 1990, Caswell 2001, Tuljapurkar *et al.* 2003). Temporal variability in the environment, due for example to fires and hurricanes, may also impact plant population dynamics (Pascarella and Horvitz 1998). Considering that *M. quinquenervia* inhabits regions where fires and hurricanes are natural components of the ecosystem, and that the intensity of herbivory may vary randomly over time, stochastic models could help understanding the role of random temporal variation of these phenomena, on the demography and the population dynamics of this invasive tree (Mengues 2000, Tuljapurkar *et al.* 2003, Fieberg and Ellner 2006).

Table 4.1. Parameter values used in the integral projection models of *M. quinquenervia* populations to simulate insect damage (insect type and density) on seedling survival and short plant growth.

Insect treatment	**Seedling survival (proportion)**	**"Instantaneous" exponential rate of change (one week)**	**Yearly exponential rate of change (52 weeks)**	**Seedling growth model intercept adjustment parameter**
No insects	1	0.08846	4.59992	0
Psyllids (Low density)	0.8853	0.07280	3.7856	-0.8143
Psyllids (High density)	0.0625	0.03123	1.62396	-2.9760
Weevils (Low density)	1	0.06370	3.3124	-1.2875
Weevils + Psyllids (Low density)	0.7481	0.02951	1.53452	-3.0654
Weevils (Low density) + Psyllids (High density)	0.1296	-0.001968	-0.102336	-4.7023
Weevils (High density)	0.8853	0.02853	1.48356	-3.1164
Weevils (High density) + Psyllids (Low density)	0.6555	0.005976	0.310752	-4.2892
Weevils + Psyllids (High density)	0.0053	-0.002758	-0.143416	-4.7433

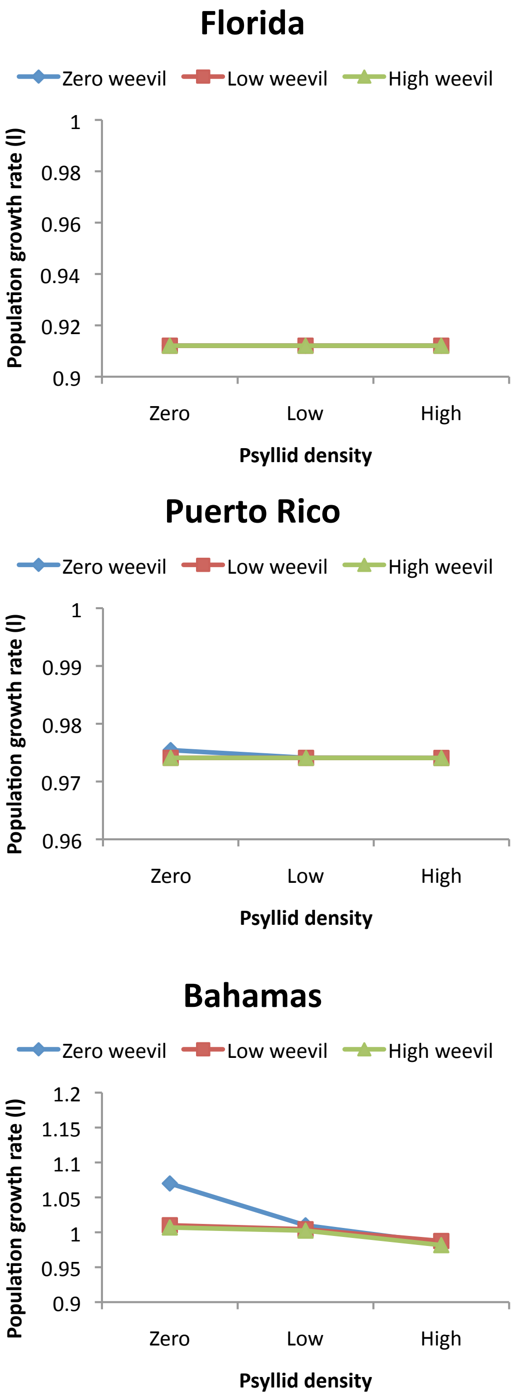

Figure 4.1. Effects of insect damage on the population growth rates (λ) of *Melaleuca quinquenervia* in Florida (a), Puerto Rico (b), and the Bahamas (c), in a *regular* seed rain year . Simulations of damage of different combinations of weevil and psyllid densities were performed by altering the seedling-short plant transition.

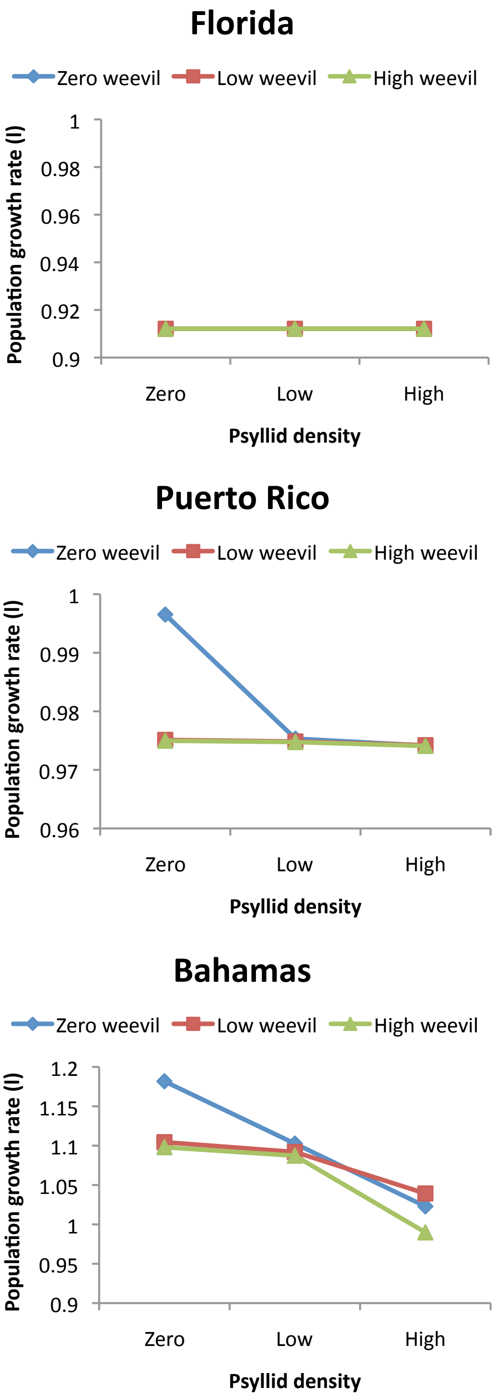

Figure 4.2. Effects of insect damage on the population growth rates (λ) of *Melaleuca quinquenervia* in Florida (a), Puerto Rico (b), and the Bahamas (c), in a *high* seed rain year . Simulations of damage of different combinations of weevil and psyllid densities were performed by altering the seedling-short plant transition.

Chapter V

Spatial population dynamics of *Melaleuca quinquenervia*: Can biocontrol agents reduce its spread?[5]

Background

Invasive species are characterized by having populations that rapidly increase in size and expand their range. Two processes determine the speed of plant invasions: local demographic processes that determine how many new individuals are produced; and dispersal processes that determine how far the new individuals move (Shigesada *et al.* 1995, Neubert and Caswell 2000). The rate at which invasion takes place, the rate of spread (c^*), is the basic descriptive statistic for spatial population dynamics. Understanding the spread dynamics of invasive species is fundamental to management planning and implementation (Skarpass and Shea 2007). Control strategies that affect population growth and/or dispersal are expected to reduce population spread. Indeed, targeting dispersal processes might be more important than targeting local population dynamics to control invasions (Caswell *et al.* 2003). Quantifying population spread of invasive species for which management strategies have been implemented allows us to assess the effectiveness of the control methods.

Spread has been studied in different contexts such as gene flow (Fisher 1937), species migrations (Clark 1998), habitat colonization (Fagan and Bishop 2002), and invasions (Shigesada and Kawasaki 1997). Several models have been developed to quantify spread (reviewed in Higgins *et al.* 1996, Shigesada and Kawasaki 1997, Neubert and Parker 2004, Shea 2004, Fagan *et al.* 2005, Bullock *et al.* 2006, Jongejans *et*

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[5] Coauthors: Carol C. Horvitz, Paul D. Pratt, Steven Franks

al. 2008a). Integrodifference equation models, originally formulated in the 1970s to describe the spatial spread of advantageous alleles, have been used by population biologists to describe the spread of populations (Neubert and Caswell 2000).

Neubert and Caswell (2000) developed an integrodifference model for structured populations, considering that for many species, individuals differ not only in demographic rates, but also in their dispersal characteristics depending on stage or size. The model combines population growth and dispersal, and as in structured population growth models, it is possible to identify life-history stages or transitions that are most important to target when attempting to reduce the rate of spread of invasive species. This dispersal model strictly speaking, addresses one-dimensional movement of a population comprised of several stages from an occupied area to a previously unoccupied area over time. A critical determinant of spread rates is the probability distribution of dispersal distances, which is called the dispersal kernel (Kot *et al.* 1996, Neubert and Caswell 2000, Bullock and Clarke 2000, Nathan *et al.* 2003, Neubert and Parker 2004, Katul *et al.* 2005, LeCorff and Horvitz 2005). The Neubert-Caswell model requires estimating the shape of the dispersal kernel. In addition to non-spatial models, spread models have been increasingly used in the last few years to understand factors that have contributed to the spread of invasive species, and to find optimal control strategies (Neubert and Parker 2004, Shea 2004, Taylor and Hastings 2004, Buckley *et al.* 2005, Fagan *et al.* 2005, Jogenjans *et al.* 2007, Skarpass and Shea 2007, Bullock *et al.* 2008, LeMaitre *et al.* 2008, Jogenjans *et al.* 2008a, b).

The invasive tree *M. quinquenervia* (Myrtaceae) was first introduced to south Florida at the end of the 19th century (1886) (Dray *et al.* 2006). It has also become invasive in Puerto Rico, the Bahamas, and other parts of the Caribbean Islands (Sebersoff-King 2003). In 1912, *M. quinquenervia* was introduced to the west coast of Florida at Estero in Lee County, and this is considered the most severe infestation on the lower gulf coast of Florida (Dray 2003, Serbesoff-King 2003). Another important introduction took place in 1936, when *M. quinquenervia* seeds were spread by airplane in the east Everglades, invading wet prairies and marshes (Serbesoff-King 2003). In 1993, *M. quinquenervia* occupied approximately 197,500 hectares (Ferriter 1999). However, by 1999 the area of occupation was reduced to 158,000 hectares (Ferriter 1999), presumably as a consequence of several management methods, including mechanical, physical and herbicidal controls (Laroche 1999). In 1990 *M. quinquenervia* expansion was defined as uncontrolled, representing one of the most serious threats to the existing biodiversity of many ecosystems in south Florida (Thayer and Bodle 1990).

M. quinquenervia produces serotinous capsules containing wind-dispersed seeds. Capsules might remain attached to the tree for several years forming a large canopy seed bank (Meskimen 1962, Hofstetter 1991, Rayachhetry *et al.* 1998). A small proportion of seeds in the canopy, 7.4%, are released every year ("regular" seed rain year) (see Appendix 1, Chapter 3). Massive seed release is related to stress events such as the cutting or breaking off the stems, herbicide treatment, fire or frost damage, and natural death (Woodall 1982, Hofstetter 1991). In such cases, all seeds in the canopy are released in one year ("high" seed rain year). These two scenarios (regular/high seed rain) are likely to influence not only population growth but also population spread of *M. quinquenervia* because the probability that some of those seeds will travel long distances and establish in new areas increases. In fact, new *M. quinquenervia* seedling stands/carpets are commonly the result of a massive seed release event in which millions of seeds were transported long distances with respect to the seed source stand, arriving at new areas suitable for establishment. The small *M. quinquenervia* seeds (30,000 per gram) are the main means by which the tree spreads. The majority of seeds simply fall from the tree within a short distance from the trunk, no farther than 8.5 times the height of the seed source (Woodall 1982). Browder and Schroeder (1981) modeled *M. quinquenervia*'s seed dispersal and suggested that 99% of the seeds released from one tree during an ordinary year (i.e. regular seed rain year) would disperse no farther than 170 m. Note, however, that this means that if a *M. quinquenervia* tree produces one million seeds at a time, as is typical (Rayachhetry et al. 1998), this means that 10,000 seeds would be dispersed further than 170 m.

The rate of expansion of *M. quinquenervia* was assessed from 1965 to 1990 in Miami-Dade County, Florida, by obtaining aerial photographs of approximately every 5 years within this period (Laroche and Ferriter 1992). The percentage of *M. quinquenervia* infestation was estimated within eight one squared mile plots (2.58 km^2) each period. This study revealed that *M. quinquenervia* expansion was characterized by a sigmoid growth curve, with three differential rates of expansion over the 25-year period analyzed. An increase in radius is more typically reported in the invasion literature than an increase in area (Shigesada and Kawaski 1997). Thus the increase in occupied area reported by Laroche and Ferriter (1992) was converted to an increase in the radius of the occupied area. During the first seven years (1965-1971), the rate of expansion occurred in a few isolated locales increasing the radius of the area it occupied at a rate of 338 meters/year. Between the 7th and the 19th year (1972-1984), the rate of expansion was 531 meters/year.

Finally, the last phase (1985-1990) was characterized by a lower rate of expansion, 80 meters/year, reaching a steady state due to space limitation. The authors concluded that once *M. quinquenervia* infestation reached a level of approximately two to five percent, it took about 25 years for 95 percent infestation to occur within the sampled areas (Laroche and Ferriter 1992). When this study took place, potential biological control agents were under investigation in Australia (Balciunas 1990). Since the introduction of the *M. quinquenervia* biological control agents in 1997 and 2002 (weevils and psyllids, respectively) in Florida, no studies have assessed if the biological control agents have contributed to reduce spread.

The objective of this study was to investigate the potential of biological control agents to reduce the population spread of *M. quinquenervia*. We performed simulations using a Neubert-Caswell stage-structured integrodifference model. Since populations of *M. quinquenervia* in Florida appear to be currently decreasing according to our population growth models (see Chapters 3 and 4), we used demographic data of populations from the Bahamas, which are increasing (see Methods) to meet the assumptions of the Neubert-Caswell model. A hypothetical dispersal kernel was generated based on a previous study of *M. quinquenervia* seed dispersal (Browder and Schroeder 1981). The effects of insects were simulated by altering survival and growth of the seedling-short plant transition of *M. quinquenervia*'s life cycle, based on the results of Sevillano *et al.* 2010 (Chapter 2). The specific objectives of the study were to 1) compare in regular and high seed rain years the rate of spread of populations with and without biological control agents; 2) compare the relative importance of different life-cycle stages to population growth and population spread in populations with and without biological control agents; and 3) compare the relative importance of different life-cycle stages to population spread in populations with and without biological control agents. We hypothesized that the effects of biological control agents on survival and growth of the seedling-short plant transition would result in a reduction of *M. quinquenervia*'s rate of spread.

Methods

Population spread was modeled for *M. quinquenervia* populations in the Bahamas, because an assumption of the Neubert-Caswell model (2000) is that population growth rate is larger than one. According to our integral projection models for population growth, the Bahamas is the only region where populations are increasing ($\lambda > 1$) (Chapters 3 and 4). Although a biocontrol program has not been implemented in this region, we simulated population spread with and without insects affecting the seedling-short plant transition. For the "insect" treatment, we used the high weevil-low psyllid density combination (see Chapter 2), since high densities of both insects result in a decrease in population growth ($\lambda < 1$) (Chapter 4). The simulations of the effects of insects on population spread were performed for regular and high seed rain years.

Demography

In 2005, we established plots on three different islands (Andros, Grand Bahama, and New Providence) in the northern Bahamas. To study the population dynamics of *M. quinquenervia*, we recorded survival, growth (diameter/DBH), and reproductive status (presence/absence of capsules) of each plant within each plot, yearly until 2008 (see details in Chapter 3). All new seedlings that appeared in each plot every year were tagged and followed. Population dynamics was modeled using an integral projection model (IPM) from which we generated a 303 × 303 matrix (Chapter 3).

Dispersal

We generated a hypothetical dispersal kernel, the probability distribution of the location of individuals travelling from a starting location, based on a previous study of *M. quinquenervia* seed dispersal (Browder and Schroeder 1981). In that study, *M. quinquenervia* seed travelling-distance was modeled using the Rombakis equation, which describes the most probable distance traveled by a seed as a function of seed terminal velocity, seed release height, horizontal wind speed, and turbulence (Browder and Schroeder 1981). Their model was validated using seed terminal velocities and seed-trap data collected for *M. quinquenervia* in south Florida in 1978 (Woodall 1982), before the insects were introduced as biological controls. Seed terminal velocity in Woodall's study (1982) was estimated using a 3m tall free-fall chamber. The maximum most-probable distance traveled by seeds of average terminal velocity (1.16 m/second) released at 3 meters height is 94m, according to Browder and Schroeder's model. As in some examples in Clark *et al.* 1999 and Koop 2003, seed dispersal was assumed to follow a Gaussian distribution for polar coordinates,

$$f(r_{ij}) = \frac{1}{\pi\alpha^2}\exp\left[-\left(\frac{r_{ij}}{\alpha}\right)^2\right],$$

assuming that the mean radial dispersal distance traveled by *M. quinquenervia* seeds is 100 m (Figure 5.1). It should be considered that the higher the release height, the higher the distance that seeds could travel (Browder and Schroeder 1981, Woodall 1982). However, according to their model only 1% of the seeds would travel beyond 170m, and of those, only 5% would be viable seeds (Browder and Schroeder 1981).

Spread modeling

To determine the potential effects of the two biological control agents to reduce population spread of *M. quinquenervia*, we developed a population spread model using the kind of integrodifference equation model of spatial population dynamics for structured populations described by Neubert and Caswell (2000). The model is:

$$n(x,t+1) = \int \left[K(x-y) \circ B_n \right] n(y,t)\,dy$$

The $\mathbf{n}(x, t+1)$ term is the population vector at location x at time t+1. This model couples on the one hand a model for stage-structured dispersal, $\mathbf{K}(x - y)$ (a matrix of dispersal kernels) with a model for stage-structured population growth, $\mathbf{B}_n$ (the density-dependent population projection matrix at location y) to obtain an estimate of the rate of population spread across space.

The dispersal kernel matrix is structured and describes how each stage moves in space when undergoing life history transitions. In the model the population vectors at all locations y at time t determine the population vector at a given location x at time $t+1$.

A matrix of moment generating functions is used corresponding to the matrix of dispersal kernels of the integrodifference equation. The moment generating function has an associated wave shape parameter M(s). This matrix is multiplied elementwise by the population projection matrix to obtain a new matrix H(s) that combines dynamics of demography and dispersal. The dominant eigenvalue of the new matrix is represented by $\rho(s)$. Neubert and Caswell (2000) showed that the asymptotic rate of spread (wave speed) of a structured population into a previously unoccupied area is given by c^*,

$$c^* = \left[\min\left(\frac{1}{s}\right)\ln\left(\rho(s)\right)\right],$$

where s is a vector of possible values for the waveshape parameter and c^* corresponds to the value of s that minimizes $\ln(\rho)/s$. When a given value of s is chosen, $M(s)$, $H(s)$, and $\rho(s)$ are evaluated repeatedly.

The Neubert-Caswell model is formulated using matrices and therefore, all analyses traditionally associated with models of population dynamics can be performed (i.e. sensitivity and elasticity analyses) on both c^* and λ (Caswell 2001). Since to model population growth of *M. quinquenervia* in the Bahamas we used a 303 × 303 matrix (see Chapter 3), our dispersal kernel matrix was of the same dimensions. Determining the sensitivity of invasion/spread rate to changes in dispersal in any life-history stage is a fundamental aspect of the applicability of the model in the context of our study. Seed dispersal ability in *M. quinquenervia* could be affected by the biological control agents not only directly through reducing seed production, but also indirectly through the potential effects of the insects on the stage (or size) transitions. We performed elasticity analyses on λ and c^* and particularly compared the elasticity of c^* to the most sensitive stage transitions in populations with insects versus populations without insects.

Results

Growth rate of *M. quinquenervia* populations in the Bahamas without insects is λ=1.07, and with insects is λ=1.0024 per year (not shown, see Chapter 4), in a year with regular seed rain. In a year with high seed rain, population growth rate without insects is λ=1.18, and with insects is λ=1.09 (not shown, see Chapter 4).

Our simulations using the Neubert-Caswell model for spread indicated that insects can reduce the asymptotic rate of population spread of *M. quinquenervia*, both in years with regular and with high seed rain (Figure 5.2). In a regular seed rain year, the estimated *c** in populations without insects was 9.4 times higher than in populations with insects (Figure 5.2). In years where there is a massive seed dispersal event, not only population growth but also population spread is higher. In that scenario, the estimated *c** in populations without insects was 1.6 times higher than in populations with insects (Figure 5.2).

We calculated the elasticity of *c** and the elasticity of λ to determine whether the rate of population spread is more sensitive than population growth to changes in particular demographic parameters. The seedling-short plant transition is the most sensitive to population spread in all four scenarios simulated in our study (with/without insects, regular/high seed rain). We found that population spread is more sensitive to the seedling-short plant transition (Figure 5.3) than it is to population growth (Figure 5.4).

The stable stage distribution at the wave front was compared for populations with and without insects in regular, and high seed rain. In a regular seed rain year, seeds in the canopy dominated the stable stage structure in populations with and without insects

(Figure 5.5). However, the distributions differed in that seeds in the canopy in populations with insects contributed a slightly greater proportion to stage structure at the invasion front, than populations without insects (95% *vs.* 90%). In a high seed rain year, the structure changes a lot because all seeds in the canopy are released (Figure 5.6). Seedlings and the smallest plants in the short plant domain dominated the stable stage structure in populations with and without insects. Here again, the distributions differed in that seedlings in populations with insects contributed a greater proportion to stage structure at the invasion front, than in populations without insects (58% *vs.* 46%). Interestingly, the opposite trend was true for short plants. They contributed 36% to structure in populations without insects, compared to 28% in populations with insects.

Discussion

One of the goals of biological control programs is to reduce growth and spread of invasive populations. This study shows that the two biological control agents introduced in Florida have the potential to reduce the rate of spread of *M. quinquenervia* populations that are increasing in size. Given the rate of estimated population growth in the Bahamas and the parameter estimates in our model, we estimated that biological control insects would reduce the rate of population expansion in a regular seed rain year from 4.6 to 0.49 m per year, a decrease of 89.4%. In a high seed rain year, insects would reduce the rate of population expansion from 9.8 to 6.3 m per year, a decrease of 36%. However, it should be noted that this analysis is only intended to examine possible effects of insects on rates of spread, that actual effects may be greatly different, and that many other factors need to go into decisions regarding the implementation and management of biological control programs.

Biological control agents introduced in Florida were mainly expected to reduce seed production in adult plants, and reduce individual growth rates and survival of seedlings and saplings (Turner *et al.* 1998). Our simulations have not incorporated the effects of insects on seed production; in Florida the number of capsules can be significantly reduced by weevil damage (Pratt *et al.* 2005a). Likely, incorporating those effects in the model would result in a further reduction in population spread. Le Maitre and collaborators (2008) developed an individual-based model of the invasive shrub *Hakea sericea* in South Africa, to investigate the impacts of biological control agents on the rate of spread. By simulating the effects of seed predators, they found that reductions in seed production lead to reduction of *H. sericea*'s rate of spread.

Changes in the seedling-short plant transition of *M. quinquenervia* populations in the Bahamas have the highest impact on both population growth (Chapter 3) and population spread, compared to changes in any other stage/size transitions. Considering that this transition is particularly susceptible to insect damage (Franks *et al.* 2006, Sevillano *et al.* 2010), it is not surprising that biological control agents alter both population growth and spread. Most interesting however, is the analysis that revealed that insect damage on the seedling-short plant transition has higher impacts on population spread than on population growth, for regular and high seed rain years (Figures 5.3 and 5.4). Thus, the negative impacts of insects on seedling survival and growth are more effective to control population spread, that to control the increase in number of individuals of *M. quinquenervia* over time. In the absence of insects, survival and growth of seedlings and short plants is higher (see Chapter 2), and therefore the contribution of these plant stages to population spread is relatively higher particularly in cases where seedlings establish in open areas relatively far from the seed source population (i.e. high seed rain years). This idea is partially supported when we compare the relative contribution of short plants to the stable stage structure at the invasion front, which is higher without than with insects. However, the contribution of seedlings to the stable stage structure at the invasion front is slightly higher in populations with insects. The progress of colonization can be significantly slowed, if insects damage recently established seedlings. Browder and Schroeder (1981) hypothesized, based on their seed dispersal study, that eliminating outliers could be an effective control mechanism for *M. quinquenervia*. Our analysis concurs with this recommendation.

The successful establishment of a population in a new area depends on factors associated with the plants and factors associated with the environment (Shea and Chesson 2002). These factors include the production and dispersal of seeds, the availability of suitable microsites at the time of recruitment, and competition (Eriksson and Ehrlen 1992, Jongejans *et al.* 2006). One of the factors that influences *M. quinquenervia* colonization is disturbance in the form of an altered hydroperiod. Once established in such disturbed areas, invasive species like *M. quinquenervia* tend to expand into neighboring areas easily (Ewel 1986). However, Laroche and Ferriter (1992) pointed out that it is not clear whether *M. quinquenervia* requires an initial disturbance to create an environment for its establishment. The invasion potential of *M. quinquenervia* appears to vary among plant communities and by locality, wetter areas being more susceptible than drier areas (Sebersoff-King 2003).

The estimated spread rates in our study (0.49 and 4.62 m/year) are orders of magnitude lower than the expansion rates observed for Florida by Laroche and Ferriter (1992), between 80 and 531 m/year. Although our estimations are for populations in the Bahamas, such drastic differences are not expected. Some studies have compared estimated and observed rates of spread and commonly, the estimated rates using spread models are lower (Lonsdale 1993, Neubert and Caswell 2000). Such discrepancy is due mainly to an inadequate parameterization of the dispersal components rather than an inadequacy of the spatial model. Given the complexity involved in collecting seed dispersal data, the dispersal kernel used in the spread model is based on dispersal data collected in Florida during the 1980s. It is known that invasion rates are extremely sensitive to the shape of the dispersal kernel, particularly to the tail, which depicts the rare long-distance dispersal events (Kot *et al.* 1996; Neubert and Caswell 2000; Neubert and Parker 2004). Such events are the most difficult to quantify empirically (Skarpass and Shea 2007). However, the interest in modeling long-distance seed dispersal has recently increased, particularly to investigate how does it affect patterns and rates of spread (i.e. Clark 1998, Clark *et al.* 1998, Nathan *et al.* 2001, 2002, 2003). Katul and collaborators (2005) developed an analytical model, the Wald analytical long-distance dispersal (WALD) model, for estimating dispersal kernels of wind-dispersed seeds, which is based on key factors affecting wind dispersal such as wind statistics, seed release height, and seed terminal velocity. The development of such a model to obtain dispersal distances does not require field data collection and has been shown to be fairly accurate in predicting the shape of dispersal kernels obtained directly in the field (Skarpass and Shea 2007).

Spread models such as the Neubert-Caswell model (2000) lack the complexity and stochasticity that are likely to influence the rate of spread of introduced plants. The frequency, intensity and type of disturbance have been shown to influence the population dynamics of some species (Horvitz *et al.* 2005). For instance, the type of disturbance experienced by *M. quinquenervia* populations is likely to influence recruitment and spread (Rayamajhi *et al.* 2002). Our results show that in massive seed release events, population growth and spread are higher; it is likely that the frequency of these events and other disturbance events (i.e. hurricanes) influence the magnitude of those rates (Horvitz and Schemske 1986, Tuljapurkar *et al.* 2003, Horvitz *et al.* 2005, Tuljapurkar and Horvitz 2006).

The Neubert-Caswell model developed in this study is useful to understand how individuals of different sizes/stages in *M. quinquenervia* populations may contribute to population spread. Particularly, our model allowed us to identify that population spread of *M. quinquenervia* in the Bahamas is most sensitive to the seedling-short plant transition, which is particularly susceptible to insect damage. However, other type of spread models should be coupled with the model developed here to understand the long-term consequences of biological control program of *M. quinquenervia*. For instance, niche-based models that take into account features and attributes of the species and landscape to more accurately predict rates of spread of invasive species. Such models are helpful to managers particularly in patchy systems such as *M. quinquenervia,* because species habitat relationships and the arrangement of habitats in space and time are considered. Spatially explicit models have been developed for *H. sericea* to estimate the potential of biological control agents to reduce population spread (Le Maitre *et al.* 2008), and have shown that biological control agents have the potential to reduce spread of this invasive shrub.

The spread of invasive species threatens the structure and functioning of many ecosystems (Drake *et al.* 1989). Understanding the dynamics of spatial spread has proved important in many areas of applied ecology (Fagan *et al.* 2005). Models on spatial population dynamics that incorporate space explicitly, as well as environmental stochasticity would provide managers with more realistic information to implement effective control strategies, in order to reduce growth and spread of invasive plant species.

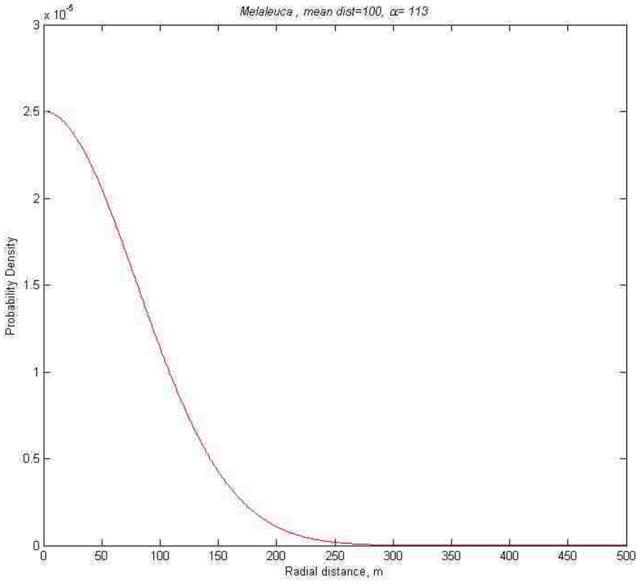

Figure 5.1. Simulated dispersal kernel of *M. quinquenervia* based on a Gaussian distribution; radial distance is reported.

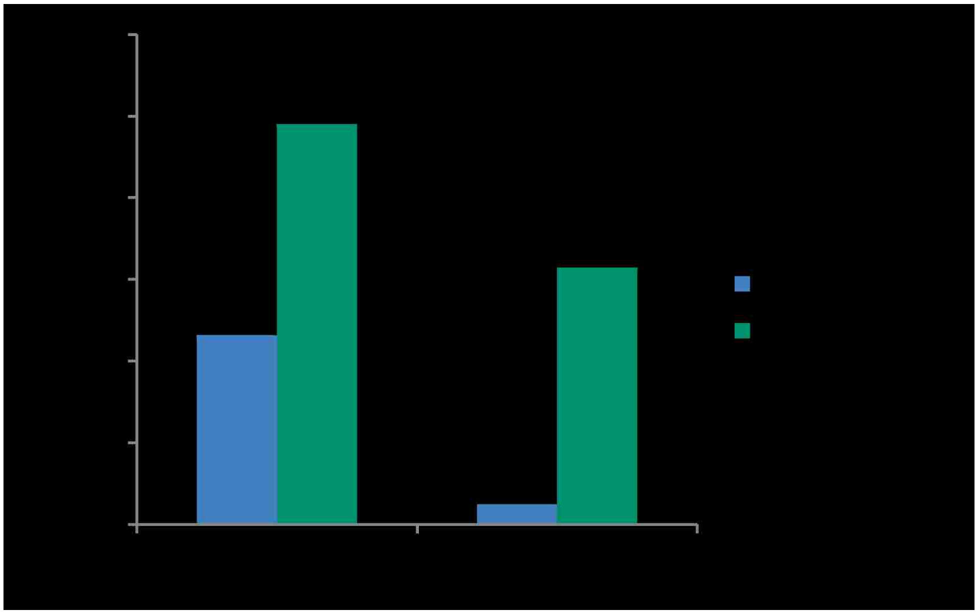

Figure 5.2. Predicted rate of spread of *M. quinquenervia* populations in regular and high seed rain years, with and without biological control agents.

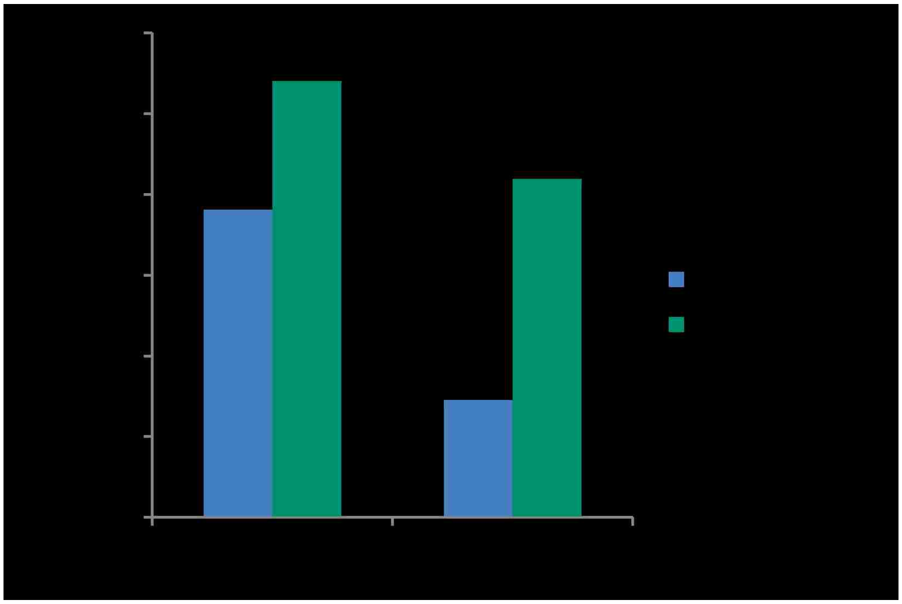

Figure 5.3. Elasticity of rate of spread (c^*) to changes in the seedling-short plant transition of *M. quinquenervia* populations in regular and high seed rain years, with and without biological control agents.

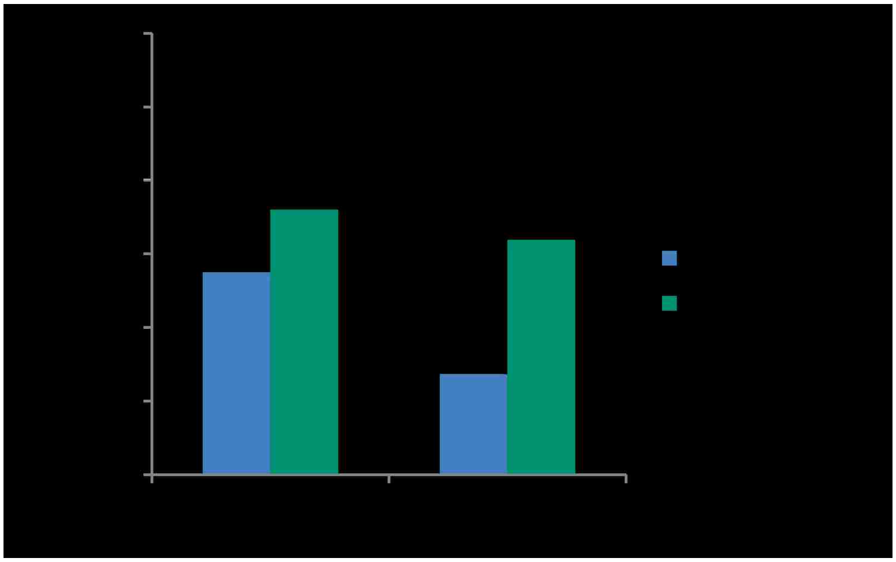

Figure 5.4. Elasticity of population growth rate (λ) to changes in the seedling-short plant transition of *M. quinquenervia* populations in regular and high seed rain years, with and without biological control agents.

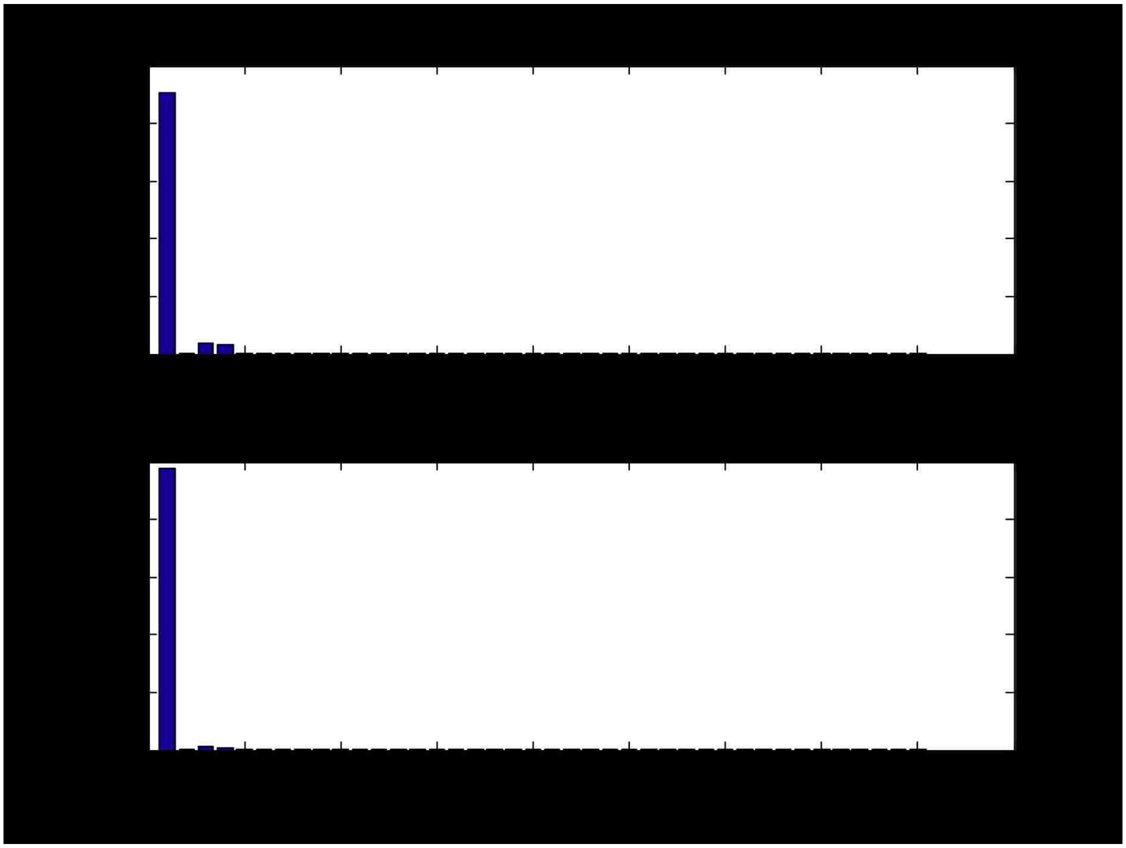

Figure 5.5. Stable stage distribution of *M. quinquenervia* at the wave front in populations without insects (a) and with insects (b), in a regular seed rain year. The first 40 stages are shown, including seeds in the canopy (first), seeds on the ground (second), seedlings (third), and the first 37 sizes within the short plant domain.

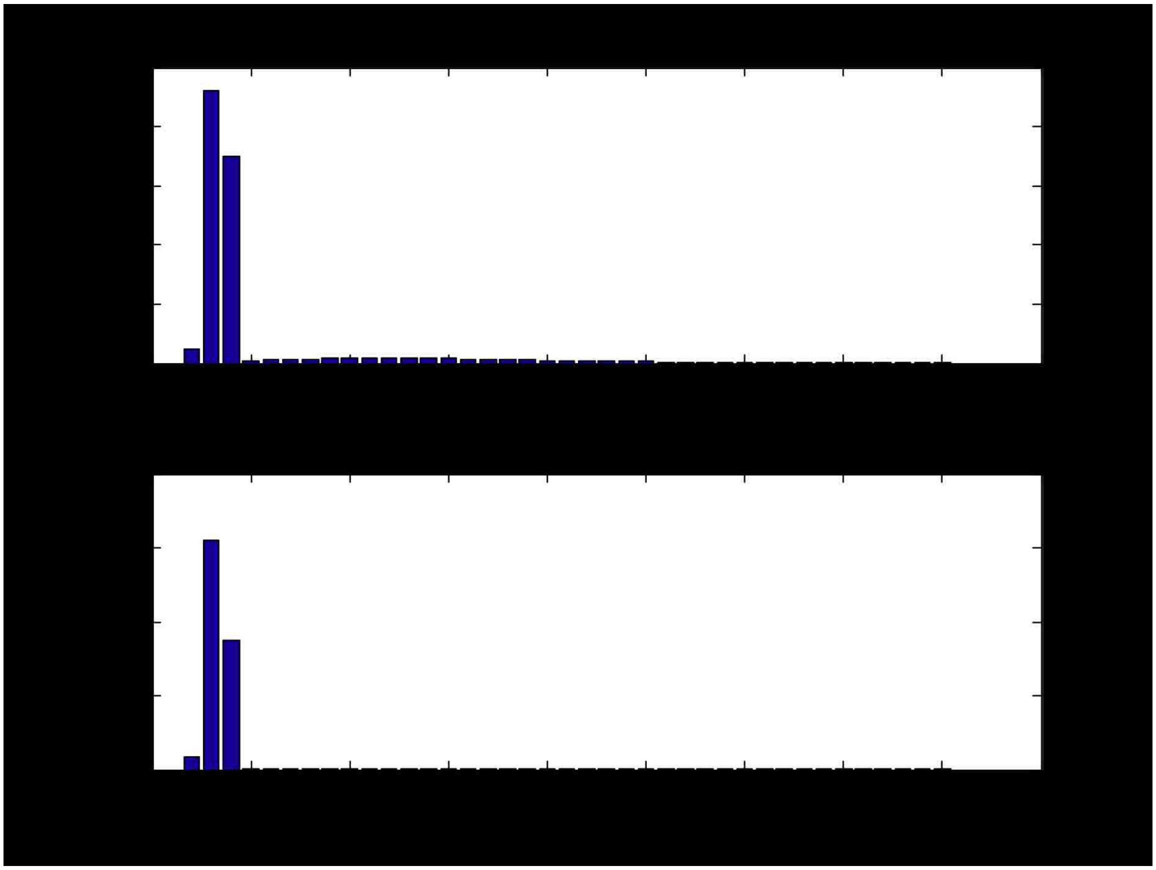

Figure 5.6. Stable stage distribution of *M. quinquenervia* at the wave front in populations without insects (a) and with insects (b), in a high seed rain year. The first 40 stages are shown, including seeds in the canopy (first), seeds on the ground (second), seedlings (third), and the first 37 sizes within the short plant domain. The column in stage four represents the smallest size category of the short plant domain.

Appendices

Appendix 2.1. General characteristics of the two types of South Florida soils used in the experiment.

	Organic	**Sandy**
Organic matter (%)	5.93 ± 0.14	0.73 ± 0.09
Estimated Nitrogen release (lbs./A)	162.50 ± 2.87	60.75 ± 2.56
Available phosphorus – weak (ppm)	3.75 ± 0.85	3.50 ± 0.29
Available phosphorus – strong (ppm)	12.00 ± 3.44	5.00± 0.41
Exchangeable Potassium (ppm)	14.25 ± 1.93	6.75 ± 1.89
Exchangeable Magnessium (ppm)	93.50 ± 2.99	17.00 ± 1.87
Exchangeable Calcium (ppm)	3187.50 ± 245.54	67.50 ± 22.5
Soil pH	7.85 ± 0.16	9.05 ± 0.51
Cation exchange capacity (meq/100g)	16.75 ± 1.25	0.50 ± 0.12
% K	0.20 ± 0	3.45 ± 0.28
% Mg	4.73 ± 0.27	32.93 ± 5.92
% Ca	95.08 ± 0.27	63.65 ± 5.82
NH_4 (ppm)	113.00 ± 29.04	26.75 ± 24.43
Loss on ignition (Weight)	83.65 ± 1.84	2.45 ± 1.08
Loss on ignition (Volume)	77.00 ± 1.29	18.50 ± 2.22

Appendix 2.2. Marginal means ± standard errors (SE) for survival (*A*), growth (*B*), total numbers of leaves (primary and seconday) (*C*), and final biomass (*D*) for all the combinations of weevil and psyllid densities used in the experiment, across the two levels of soil type (organic and sandy).

A)

Weevil density	**Psyllid density**	**N**	**SURVIVAL (%)**
Zero	**Zero**	20	100 ± 0
	Low	10	96.67 ± 3.33
	High	10	50 ± 10.24
Low	**Zero**	10	100 ± 0
	Low	10	93.33 ± 4.44
	High	10	60 ± 8.31
High	**Zero**	10	96.67 ± 3.33
	Low	10	90 ± 7.11
	High	10	26.67 ± 9.69

B)

			GROWTH (RELATIVE CHANGE)		
			Height	**Diameter**	**No. Leaves**
Weevil density	**Psyllid density**	**N**	**Mean ± SE**	**Mean ± SE**	**Mean ± SE**
Zero	**Zero**	20	2.02 ± 0.13	1.21 ± 0.09	1.22 ± 0.05
	Low	10	1.12 ± 0.27	0.87 ± 0.16	3.05 ± 0.36
	High	8	0.37 ± 0.11	0.14 ± 0.09	1.68 ± 0.48
Low	**Zero**	10	1.95 ± 0.19	0.77 ± 0.10	2.09 ± 0.25
	Low	10	0.74 ± 0.10	0.35 ± 0.15	3.20 ± 0.22
	High	10	0.16 ± 0.07	-0.02 ± 0.09	2.14 ± 0.45
High	**Zero**	10	1.06 ± 0.12	0.28 ± 0.07	1.77 ± 0.21
	Low	10	0.51 ± 0.12	0.12 ± 0.05	2.22 ± 0.31
	High	5	0.04 ± 0.08	0.01 ± 0.07	1.56 ± 0.21

C)

			TOTAL NUMBER OF LEAVES	
			Primary leaves	**Secondary leaves**
Weevil density	**Psyllid density**	**N**	**Mean ± SE**	**Mean ± SE**
Zero	**Zero**	20	44.33 ± 1.16	0.95 ± 0.29
	Low	10	33.5 ± 3.02	50.62 ± 8.47
	High	8	16.6 ± 3.83	44.3 ± 10.31
Low	**Zero**	10	38.13 ± 1.7	19.23 ± 3.59
	Low	10	27.55 ± 2.51	57.93 ± 5.31
	High	10	14.32 ± 1.38	62.57 ± 14.07
High	**Zero**	10	24.63 ± 3.29	30.3 ± 6.05
	Low	10	16.58 ± 2.69	50.75 ± 6.45
	High	5	15.1 ± 2.61	49.3 ± 6.35

D)

			BIOMASS (FINAL WEIGHT, GRAMS)			
			Total Biomass	**Leaves**	**Stems**	**Roots**
Weevil Density	**Psyllid density**	**N**	**Mean ± SE**	**Mean ± SE**	**Mean ± SE**	**Mean ± SE**
Zero	**Zero**	20	1.57 ± 0.11	0.73 ± 0.05	0.41 ± 0.03	0.43 ± 0.03
	Low	10	1.24 ± 0.18	0.61 ± 0.09	0.31 ± 0.06	0.32 ± 0.04
	High	8	0.67 ± 0.19	0.34 ± 0.11	0.17 ± 0.04	0.16 ± 0.04
Low	**Zero**	10	1 ± 0.1	0.49 ± 0.05	0.27 ± 0.03	0.24 ± 0.03
	Low	10	0.83 ± 0.07	0.40 ± 0.03	0.21 ± 0.02	0.21 ± 0.02
	High	10	0.52 ± 0.14	0.24 ± 0.08	0.12 ± 0.03	0.16 ± 0.05
High	**Zero**	10	0.61 ± 0.06	0.29 ± 0.03	0.18 ± 0.02	0.14 ± 0.01
	Low	10	0.47 ± 0.05	0.22 ± 0.02	0.13 ± 0.01	0.12 ± 0.01
	High	5	0.29 ± 0.06	0.12 ± 0.02	0.09 ± 0.01	0.09 ± 0.03

Appendix 3.1. Estimation of the number of seeds produced by *M. quinquenervia* trees based on size (DBH).

The only information that can be obtained directly in the field on *M. quinquenervia*'s reproduction is whether or not plants have capsules. The first step then, was to obtain the probability that a tree of DBH *x* would produce capsules. This probability was obtained through a logistic regression model of ln (DBH) at *t*, versus presence/absence of capsules at *t*+1. The second step was to estimate the number of seeds produced by a tree of DBH *x*. We used the parameters published by Rayachhetry *et al.* (2001) on the ln-ln relationship between DBH and seed weight of *M. quinquenervia*, where ln of DBH at *t* is the independent variable. In their study, several adult trees in Florida were cut down, and weight of all above ground components was obtained, including capsule and seed weight. DBH of each tree (range 0.36-55 cm) was measured, and they obtained a linear relationship between ln of DBH and ln of seed weight. To obtain this relationship, only trees with capsules were considered. Total seed weight was estimated as:

$$\ln \mathit{seed\ weight} = -6.4857 + 1.5408 \ln (\mathit{DBH})$$

We estimated total seed weight produced by each individual each time interval making use of this regression. We used size in year t (*DBH*) to estimate total seed weight produced by plants at t and seed weight of plants at t+1 was estimated from *DBH* at t+1. Calculating the antilog, we obtained the seed weight, and multiplied by 1000 (to convert from kg to grams), and by 30,000 (number of seeds in 1 gram, Woodall 1982) to obtain the *seed crop*, which is the standing number of seeds that a tree of DBH *x* would have. Since most seeds are retained in the canopy from one year to the next and we are interested in the number of seed produced by a tree of size *x* during one year, we had to estimate both standing *seed crop* at t, and standing *seed crop* at t+1 as described above. A simple subtraction (*seed crop* at t+1 – *seed crop* at t) would seem like a straightforward way to estimate seed production, however we had to consider that a proportion of the seeds are not retained in the canopy and fall to ground as seed rain (SR) over one year. We estimated (based on Woodall 1982) that 7.4% of seeds in the canopy rain in one year; thus, 92.6% are held in the tree. The net number of _new_ seeds produced by a tree of size x within one year, could thus be estimated as:

seed production between time t and time t+1 =

standing seed crop at t+1 – (*standing seed crop* at t ×(1-0.074))

We estimated the probability of actually producing seeds ($f_s(x)$) using a logistic regression of ln (DBH) at time t, where the binary variable was whether or not there was positive seed production between time t and time t+1. It was necessary to make this estimation since some trees the upper section of the plant dries out and, from one year to the next, plants become too short. We refer to this phenomenon as *transition from tall to short trees* ($trans_{T\text{-}S}$). Simply applying the seed production equation above would have resulted in negative seed production for some individuals. The model was fit using a logistic regression with the linear link $\ln(s(x)/(1\text{-}s(x)) = a + bx$.

The number of seeds that a tree of size x would produce ($f_s(x)$) was estimated by a four parameter logistic regression of ln (DBH) at time t, as a function of ln number of seeds at time t. Since on average there are 264 seeds in one capsule (Woodall 1982), only plants producing at least 264 seeds were considered in this analysis. The four parameter logistic model was:

$$y = a + \left(\frac{b-a}{1+e^{\frac{c-x}{d}}} \right).$$

Since our data was log transformed, this model estimated the natural logarithm of the number of seeds, so we obtained the antilog ($e^{\text{number of seeds}}$) to obtain the actual number of seeds.

Finally, the number of new seeds produced by a tree of size x was estimated by multiplying the probability of producing seeds ($f_s(x)$) by a tree of size x, times the number of seeds produced by a tree of size x $f_n(x)$. Once this number was calculated we apportioned the new seeds produced in one year ($f_s(x)f_n(x)$) to either the canopy or the ground (Table 1). The proportion of new seeds that were held in the canopy was (1-SR), where seed rain (SR) was estimated as described before. Seed survival (SS) was set to be 9% based on the study by Rayachhetry *et al.* 1998 where they estimated changes in viability of *M. quinquenervia* seeds over time (in the canopy seed bank). The proportion of surviving seeds that remain alive as part of the seed bank on the ground (p_G) over one year was guesstimated to be 5%, and we assumed that the rest, 95%, become seedlings over one year (p_S).

The fate of seeds and seedlings, which correspond to the discrete parameters in the first three columns of the high dimensional matrix, was calculated as follows. The proportion of the seeds in the canopy that remain in the canopy after one year was 0.083 (SS × (1-SR)). The proportion of seeds in the canopy that rain and survive on the ground after one year was 0.0003 (SS × SR × p_G). The proportion of seeds in the canopy that become seedlings after one year was 0.006 (SS × SR × p_S). Seed stasis on the ground (seeds that remained dormant) was 0.0045 (SS × p_G), and seeds on the ground that become seedlings in one year was 0.0855 ($\mathrm{SS} \times p_{\mathrm{S}}$). The proportion of seedlings that become short trees in one year was 0.3, which we directly estimated in the field by counting and marking seedlings within 0.5 × 0.5m plots, and censusing them twice a year for over 2 years. These data showed that surviving seedlings after one year do not stay as seedlings (as defined in this study, <12cm tall), but either become short trees or die.

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