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Using demographic models to manage Chinese privet (Ligustrum sinense Lour.)

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USING DEMOGRAPHIC MODELS TO MANAGE CHINESE PRIVET (*LIGUSTRUM SINENSE* LOUR.)

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DEDICATION

I would like to dedicate this thesis to my Grandpa Jack. I miss him greatly, and know that he is with me through every challenge I meet. He taught me to appreciate nature, live simply, and when all else fails, tell a dirty joke. I only hope to have a life as full as the one he led, and I hope always to make him proud of the person I am.

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ABSTRACT

Colonization of natural areas by Chinese privet (*Ligustrum sinense* Lour.) threatens biodiversity and preservation of native habitat in the southeastern United States. High rates of seed production and dispersal, coupled with clonal growth, result in a competitive advantage when introduced to novel areas. Land managers have attempted to control *L. sinense* through prolonged flooding, prescribed fire, and herbicide application with little success.

I determined presence of *L. sinense* invasion in four sites in Louisiana and assessed key reproductive, growth, and survivorship characteristics defining its life course. I used vegetation surveys, germination trials, dendrochronology, and demographic models to elucidate stages in *L. sinense*'s life cycle that contribute most to population growth.

Populations of *L. sinense* have the potential for rapid growth. I germinated seeds under growth chamber, greenhouse, and field conditions. Stage-based matrix projection models showed the finite rate of population increase (λ) ranged from 1.48 in the field to 2.26 in the growth chamber. I used elasticity analysis to identify the proportional contribution of remaining in a stage (P), growing to a subsequent stage (G), and fecundity (F) to population growth, and perturbed matrices to mimic management strategies. A 50% reduction in $P_{SEEDLING}$, $P_{JUVENILE}$, and $P_{SMALL\ ADULT}$ reduced λ to 1.66 in the growth chamber and 1.63 in the greenhouse. Under field conditions, a 50% reduction in all P_i was required to bring λ to 1, so that populations were stationary. Reductions in F_{ADULT} did not immediately cause a decline in population growth.

Approaches that target multiple life stages may be more successful for managing *L. sinense*. Using field germination rates, reduction of $F_{LARGE\ ADULT}$ by 50%, plus a 50% reduction of $G_{SEEDLING}$ and $G_{JUVENILE}$, and $P_{SMALL\ ADULT}$ and $P_{LARGE\ ADULT}$ made population growth stationary (λ = 1.04). Management techniques that increase annual mortality of specific life stages may be more cost effective than targeting all individuals within a population. This study has identified

transitions that contribute most to population growth over a range of growing conditions and indicated management options that may streamline control of this invasive plant.

INTRODUCTION

Non-native plant populations threaten native ecosystems when they expand rapidly. Increased transport of seeds and plant material has promoted invasion of natural areas by non-native plants (Mack et al. 2000). Plants are introduced intentionally for agricultural, fiber, or ornamental purposes, and many do not become invasive (Pimentel et al. 2000). The few that escape their intended use and colonize natural areas are recognized as major threats to preservation of biodiversity and as vehicles of accelerated global change (D'Antonio and Vitousek 1992, Vitousek et al. 1996, Mack et al. 2000, and Simberloff 2000). Colonization of natural areas by non-native invasive plants may result in the displacement of native species (Hobbs and Huenneke 1992, and Wilcove et al. 1998). Invasions threaten endangered plants, alter trophic structures, and change natural fire regimes (Mack and D'Antonio 1998, Lippincott 2000, Mack et al. 2000, and Brooks et al. 2004). In the United States alone, over one billion dollars are spent each year on the management and control of these organisms (Pimentel et al. 2000). Natural areas are threatened by the encroachment of invasive plant species.

Chinese privet (*Ligustrum sinense* Lour.) is a non-native shrub that is invasive in natural areas. It was first introduced in the United States from China in 1852 as a woody ornamental (Ward 2002). *Ligustrum sinense* is currently invasive in forests throughout the southeastern United States and is recognized as a weed in New Zealand, Australia, and Argentina (Cuda and Zeller 2000). It is commonly found in riparian areas, where it creates monospecific stands and outcompetes native species (Wilcox and Beck 2007). Characteristics of *L. sinense* that might contribute to successful invasion are prolific fruiting, clonal growth form, and high germination rates. It is also attractive to wildlife species, which disperse seeds to new areas, and it is tolerant of shady conditions (Swarbrick and Timmins 1999, Wilcox and Beck 2007). Shade-tolerance

allows *L. sinense* to proliferate on the edges and interiors of forests. These attributes make the spread of *L. sinense* difficult to control.

Various management techniques have so far failed to control *L. sinense* and stop its spread to new locations. Land managers have attempted to control *L. sinense* through prolonged flooding (Brown and Pezeshki 2000), prescribed fire (Faulkner et al. 1989), and herbicide application (Harrington and Miller 2005). Techniques combining the use of prescribed fire followed by herbicide application have also been tested (Faulkner et al. 1989). These techniques have not been successful controlling *L. sinense*. Evaluation of the basic life history of this plant may promote understanding of its population dynamics, which may lead to increased management success.

Demographic approaches may provide insight into effective control measures by elucidating life stages, which, when targeted for control, will reduce population growth. My study documented presence of *L. sinense* in Louisiana forests, described basic life history traits, and used matrix projection models to describe population growth. My goal was to determine the most effective methods of managing, controlling, and reducing populations of *L. sinense* in Louisiana by identifying the best life stages to remove. My first step was to describe the current extent of *L. sinense* invasion in four sites in Louisiana. I compared the presence of *L. sinense* to native species and other invasive species in the areas measured. Subsequently, I described the life history characteristics of *L. sinense*. I collected information on fecundity, time to first reproduction, survivorship, probability of survival at any given life stage, and maximum life span. I used this information to develop stage-based matrix projection models that described the growth dynamics of *L. sinense* populations. I used these models to predict the response of *L. sinense* to management regimes such as herbicide treatment, biological controls, and integrated

management techniques. Information gained from these models, combined with current management approaches, should lead to more effective and well-informed management plans.

LITERATURE REVIEW

This review presents research on various aspects of *L. sinense*, its taxonomy, life history, autoecology, ecological impacts, and management. Research describing the life history characteristics of *L. sinense* is somewhat limited, although more is known about its spread and how it negatively affects native species. *Ligustrum sinense* has been shown to outcompete native species and to be a *de facto* source of forage for wildlife. Several wildlife species use *L. sinense* as a food source, which may promote seed dispersal and expansion of *L. sinense* populations. Various attempts to manage *L. sinense* have been made, and I discuss these techniques and look at strengths and weaknesses in their application. Finally, this review presents the use of demographic models to describe growth dynamics of non-native invasive plant populations.

Taxonomy

Ligustrum sinense is a member of Oleaceae, which includes trees, shrubs, and woody vines. A recent molecular analysis of *L. sinense* placed it in the monophyletic tribe Oleeae and the subtribe Ligustrinae, which includes the genera *Syringa* and *Ligustrum* (Wallander and Albert 2000).

Life History Characteristics

Plants in the genus *Ligustrum* are widely planted as ornamentals, and many of these species are potentially invasive. There are approximately 50 species in the genus *Ligustrum*, 12 of which are cultivated for ornamental purposes (Swarbrick and Timmins 1999). Four of these species are considered naturalized in the United States (USDA 2008). *Ligustrum sinense* is considered one of the most problematic, and life history traits such as vigorous growth, high seed production, and long life expectancy may promote invasion.

The robust growth form of *L. sinense* allows it to shade out native competitors. *Ligustrum sinense* ranges from 4 – 10 m tall at maturity and can form a dense, closed-canopy shrub layer

that may suppress other plants. Individuals can also form tall thin-stemmed trees (USDA 2008) that capture more photosynthetic resources in low-light conditions in the mid-story. In its introduced range, *L. sinense* can be either evergreen or semi-deciduous. Retaining its leaves may enable *L. sinense* to capture more photosynthetic resources than plants that lose their leaves during winter. *L. sinense* may outcompete native species through space and light accrual. It is also extremely fecund, which may contribute to its spread and development of new populations.

Ligustrum sinense is a prolific fruiter and seeds have high germination rates. It produces purple-black to blue-black fruits ranging from 4 – 7 mm in diameter (USDA 2008), which ripen between October and December in Louisiana (personal observation). Fruits usually contain one seed, but occasionally two (3% of fruits; Burrows and Kohen 1983), and, rarely, three seeds (0.4% of fruits; van Aalst 1992). *Ligustrum sinense* is iteroparous, and mature plants can produce up to 1300 fruits per m^{-2} of canopy (Westoby et al. 1983), with germination rates ranging from 40% in the field (Panetta 2000) to 79% in the growth chamber (Burrows and Kohen 1983). *Ligustrum sinense* seeds germinate under low light intensity (1 – 5 % full sunlight) and in full sunlight (Swarbrick and Timmins 1999), which allows *L. sinense* to proliferate along forest edges (Figure 1) and interiors. Prolific seed production coupled with high germination rates allow *L. sinense* populations to grow and expand in natural areas.

Figure 1. *Ligustrum sinense* invading forest edge at Bottomland 1

Ligustrum sinense has a short-lived seed bank. In a study of *L. sinense* germination under irrigated and un-irrigated field conditions at different burial depths, most seeds germinated after six months and no seeds were viable after 12 months (Panetta 2000). While seeds may be short-lived, their sheer number, attractiveness to birds, and high germination rate contribute to the spread of *L. sinense* and its success in invading natural areas.

An additional mechanism that allows plant species to expand is clonal growth. *Ligustrum sinense* is capable of clonal growth (Swarbrick and Timmins 1999). Clonal plants have laterally expanding underground root systems. These horizontal roots can produce new stems that have their own root systems, called ramets, and can survive if severed from the parent plant. The entire plant is called the genet and is derived from one seed. All ramets, whether connected or separate from the parent plant, are part of the genet (Silvertown and Charlesworth 2001). When surface roots are damaged, *L. sinense* can produce new ramets (Swarbrick and Timmins 1999) (Figure 2). This makes it especially difficult to manage *L. sinense*, as plants that are cut down often resprout.

Figure 2. New ramets developing from the underground root system of *L. sinense*

Extent of Invasion

Ligustrum sinense is invasive in different parts of its introduced range and can encroach upon multiple habitat types. It has become naturalized in all southeastern states (USDA 1998) and is invasive in Argentina (Montaldo 1993), Australia, and New Zealand (Swarbrick and Timmins 1999). It grows in dense thickets along forests edges and forms monospecific stands along riparian zones (Merriam 2003). In Georgia's Upper Oconee River Basin, *L. sinense* invasion seems based primarily on changes in land use; as agriculture and grazing fields were abandoned, *L. sinense* expanded into these areas (Ward 2002). Native floodplain trees that colonized old fields at the same time as *L. sinense* were able to survive and grow. An absence of native saplings at the time of this study suggests that, once *L. sinense* populations became established, they suppressed further growth of native seedlings. In North Carolina, Merriam (2003) found that *L. sinense* occupied 7.5% of all forest edges, and it was particularly prevalent in riparian areas. Riparian zones are important areas for a wide range of wildlife, and increased presence of *L. sinense* may alter food sources and vegetation structure that is important to ecosystem functioning. Unmanaged populations may exert increasingly competitive pressures on native vegetation and wildlife.

Effects on Native Species

Ligustrum sinense outcompetes native plant species that are morphologically similar. In Tennessee, *L. sinense* has encroached upon cedar/glade and red cedar-oak-hickory stands, which have high rates of native plant endemism (Morris et al. 2002). To determine why *L. sinense* is a strong competitor, Morris et al. compared it to the morphologically and genetically similar native shrub, upland swamp privet (*Forestiera ligustrina*). They found that *L. sinense* grew vertically and more tree-like in shaded environments than *F. ligustrina* (Figure 3), which allowed *L. sinense* to capture more photosynthetic resources in low-light conditions. In addition, *L. sinense*

experienced less herbivory and produced more seeds than *F. ligustrina*, which likely contributed to its role as the superior competitor.

Figure 3. Tree-like form of *L. sinense* growing in shaded conditions

Reductions in *L. sinense* populations may help promote native species presence. In a North Carolina mixed hardwood forest, Merriam and Feil (2002) found that the presence of *L. sinense* was correlated with reduced herbaceous cover, and the removal of *L. sinense* from invaded plots led to an increase in native species. A vegetation survey in a Georgia floodplain also showed that increasing densities of *L. sinense* led to reductions in biodiversity (Wilcox and Beck 2007). Both studies indicated that *L. sinense* may readily outcompete native species.

Ligustrum sinense reduces biodiversity by outcompeting native species. The light and space-capturing advantages of *L. sinense* negatively affect native species both morphologically similar to and different from it. Ecologically similar species such as *F. ligustrina* are unable to compete with *L. sinense*, as are other species of smaller stature and less resource-accruing capabilities.

Wildlife Usage and Propagule Dispersal

Ligustrum sinense serves as supplemental food and habitat for some native wildlife. At Clyde Shepherd Nature Preserve in Decatur, Georgia, Wilcox and Beck (2007) found that high density *L. sinense* plots had similar abundance and richness of songbirds as low density plots in the spring and fall, but in the winter, high density *L. sinense* plots were visited more frequently. *Ligustrum sinense* retains its fruits during the winter, thus providing a food source for songbirds. High density *L. sinense* plots may also provide protection from predators.

Although *L. sinense* may be the most abundant food source during certain times of year, it is not necessary the first choice for native wildlife. In a study of winter fecal samples from Hermit Thrushes (*Catharus guttatus* Pallas) in southeastern Louisiana, researchers found that birds primarily chose the less abundant native plant, yaupon (*Ilex vomitoria* Ait.), over *L. sinense* as a food source (Strong et al. 2005). *Ligustrum sinense* seeds were the second-most abundant taken by the birds. Mammals also rely upon *L. sinense* were it is found.

Ligustrum sinense is a component of both songbird and mammal diets, which may contribute to seed dispersal. Birds appear to contribute most to dispersal. The removal of the fleshy mesocarp and exocarp by passage through their gut may serve to scarify seeds and increase germination success. White-tailed deer have also been recorded browsing and eating the fruits of *L. sinense*, particularly during the fall and winter months, as an alternative to acorns (Stromayer et al. 1998). While *L. sinense* browse may not have as much nutritional quality as acorns, deer may exert less energy foraging for it due to its abundance and thus select it preferentially (Stromayer et al. 1998). Seeds of *L. sinense*, after digested by possums (*Trichosurus vulpecula* Kerr), remain viable (Williams et al. 2000). Possums can have large home ranges and may serve as agents of seed dispersal for *L. sinense* expanding its range.

Because of their use of *L. sinense*, mammals and birds likely contribute to the expansion of *L. sinense* populations.

Management Techniques

Researchers have tested various management methods to control *L.* sinense. These include prescribed fire, herbicide trials, mechanical removal, flooding, and biocontrols. Prescribed fire alone is not successful in controlling *L. sinense*. In the Chickamauga and Chattanooga National Military Park in Tennessee, prescribed fire, post-burn herbicide application, and herbicide application alone were tested on *L. sinense* populations (Faulkner et al. 1989). Prescribed fire removed above-ground stems, but stimulated vigorous sprouting from the root crown. Burning, followed by application of the herbicide glyphosate (trade name Roundup) killed *L. sinense* plants effectively. There was no significant difference between plots that were burned and treated with glyphosate versus plots treated only with herbicide.

Herbicides alone have controlled *L. sinense*. Harrington and Miller (2005) tested different concentrations of foliar applications of two herbicides, glyphosate and triclopyr (trade name Garlon), at various times of the year to determine best rate and timing of application. They found that rates as low as 1.7 kg ae/ha applied during the spring and fall reduced *L. sinense* cover by up to 100%. Although herbicides are effective, they may translocate to desirable species and have negative environmental consequences. This has encouraged studies on non-herbicide control methods.

Non-chemical management techniques other than prescribed fire have been evaluated for *L. sinense*. Harrington and Miller (2005) found that manual removal reduced their target population by 38 – 57%. On average, one person was able to remove 1-m^2 of *L. sinense* in 14 minutes. While manual control may be the least environmentally harmful management technique, the expense and labor associated with it make it a prohibitive option.

Prolonged flooding has also been evaluated, but is not successful, at controlling *L. sinense*. Brown and Pezeshki (2000) subjected *L. sinense* seedlings to various flooding depths and found them to be relatively tolerant of flooding. The seedlings developed adventitious root systems that likely contributed to their survival. The lack of success in non-herbicide control techniques has led researcher to explore whether biocontrols can be used to control *L. sinense* populations.

Biocontrols are successful in controlling some invasive plants. *Argopistes tsekooni*, a leaf-mining flea beetle found in China, was studied for host specificity and as a biocontrol for *L. sinense* (Zhang et al. 2008). In choice experiments, *A. tsekooni* preferred *L. sinense*, but in non-choice experiments they oviposited and fed upon *Syringa oblata* Lindl. This may rule out *A. tsekooni* as a biocontrol for *L. sinense* because some plants in the genus *Syringa* are important ornamental species in the United States (Zhang et al. 2008).

A biocontrol for *L. sinense* may already be present in the United States. In Florida, larvae of the accidentally introduced seed weevil *Ochyromera ligustri* was found in *L. sinense* seeds (Cuda and Zeller 1998). The weevil was first found in the United States in 1959 feeding on Japanese privet seeds (*Ligustrum japonicum* Thunb.). Adult female weevils deposit their eggs in *L. sinense* fruits. As the larvae develop they eat the seeds. This weevil may be beneficial in reducing population expansion of *L. sinense* and warrants further research.

Demographic Modeling

The study of invasive plant demographics has been enhanced by the use of matrix projection models. These models use life history information to determine life stages that contribute most to population growth. They can be used for examining population growth of the same organism in response to different site conditions, as well as the response of organisms to different management techniques (Koop and Horvitz 2005).

Matrix projection models can be used to examine population growth for one species in multiple habitat types. Parker (2000) used stage-based matrix models to research population dynamics of the invasive plant Scotch or Scot's broom (*Cytisus scoparius* (L.) Link). She compared population growth rates in a well-established prairie site to those in an expanding urban field population, and found that population growth was more rapid in prairie sites, particularly when edge populations were compared (Parker 2000). Koop and Horvitz (2005) conducted a similar study with shoebutton ardisia (*Ardisia elliptica* Thunb.), which is invasive in a variety of habitat types in the Everglades National Park. They used stage-based matrix models to research spatial and temporal variation in five different populations and to predict the different rates at which populations were expanding. The finite rate of increase (λ) of *A. elliptica* among populations ranged from 0.99 to 1.30, and almost all populations had a $\lambda > 1$. This study suggested those populations that were capable of growing more rapidly, which may be principal targets for management. Along with describing growth dynamics across species and different environments, population models can be used to assess responses to management efforts.

Matrix projection models can be used to evaluate seed-eating biocontrols. Parker (2000) constructed matrices for *C. scoparius* that reflected reductions in fecundity, and found that 70 – 99.9% of seeds would have to be removed from the population to send the population into decline. Shea and Kelly (1998) looked at the use of the nodding thistle receptacle weevil (*Rhinocyllus conicus* Frölich, 1792) to control invasive nodding thistle (*Carduus nutans* L.) populations in New Zealand. This weevil has already been released in the field. The authors reduced seed production in their size-based matrix to simulate the effect of biocontrol. They found that *R. conicus* would have to reduce reproduction by almost 70% to send the population into decline. Biocontrols are not always effective enough to reduce population growth, and combining management tools may be of more use.

Integrated management techniques have been evaluated using stage-based matrix projection models. Shea and Kelly (1998) reduced seed production and germination in their matrix to mimic the combined use of grazing and biocontrol for control of *C. nutans*. They found that the integration of these techniques was a more effective method of reducing λ.

Matrix projection models allow researchers to describe population growth and provide a cost-effective method of evaluating a variety of management techniques. Models can be created for *L. sinense* to evaluate management regimes prior to on-the-ground implementation.

Ligustrum sinense is abundant in forests in the southeastern United States, and while there is understanding of its range and impact, knowledge of its basic life history is lacking. In colonized areas, *L. sinense* dominates mid-story canopy and outcompetes native species. Its presence in riparian zones is potentially disruptive to plants and wildlife that use these important ecosystems as habitat. *L. sinense* produces copious fruits that are dispersed to novel locations, primarily though bird dispersal, but also potentially by mammals. An evaluation of *L. sinense*'s life history traits can help researchers understand its invasion dynamics and rate of population growth. By collecting this information and using it to inform management, less time and resources may be required to control this invasive species.

MATERIALS AND METHODS

This study included three main components. The first was a vegetation survey to document invasion of southeastern Louisiana forests by *L. sinense* and to describe those forests. The second component was to describe the basic life history traits of *L. sinense*: fecundity, age to first reproduction, and life expectancy. The final component was the development of stage-based matrix projection models that yielded the finite rate of population increase (λ), and to perform elasticity analyses to identify life stages that contribute the most to λ.

Study Sites

My first step was to establish study sites in areas invaded by *L. sinense*. I set up four sites in southeastern Louisiana. Two of these sites were located in Baton Rouge, Louisiana: LSU AgCenter Burden Research Center (Bottomland 1) and the LSU AgCenter Aquaculture Research Station (Bottomland 2). The third site was located in Clinton, Louisiana at the LSU AgCenter Idlewild Research Station (Bottomland 3), and the fourth at Rosedown Plantation State Historic Park in St. Francisville, Louisiana (Upland 1) (Figure 4).

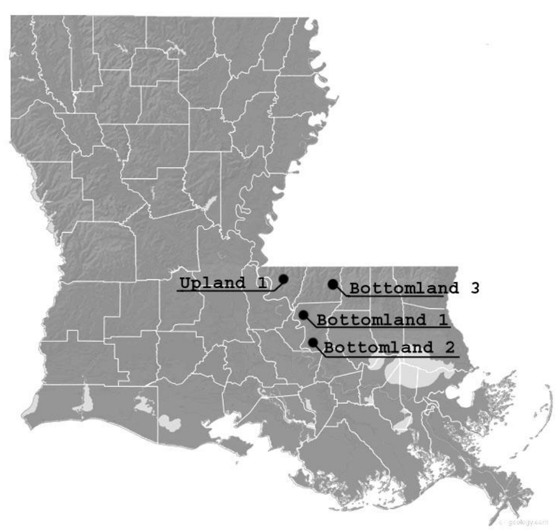

Figure 4. Study site locations

My sites had similar vegetation structures. All were dominated by a canopy composed primarily of oak (*Quercus* L.), southern magnolia (*Magnolia grandiflora* L.), sweet gum (*Liquidambar styraciflua* L.), American elm (*Ulmus americana* L.), hickory (*Carya* Nutt.), red maple (*Acer rubrum* var. *rubrum* L.), and cherrylaurel (*Prunus caroliniana* (P. Mill.) Ait.). *Ligustrum sinense* is a major component of the understory at all sites, and is accompanied by species such as American holly (*Ilex opaca* Ait.), winged elm (*U. alata* Michx.), hornbeam (*Carpinus caroliniana* Walt.), *I. vomitoria*, *L. japonicum*, red buckeye (*Aesculus pavia* L.), French mulberry (*Callicarpa americana* L.), Chinese tallow (*Triadica sebifera* (L.) Small), and dogwood (*Cornus* L.).

All study sites have been subjected to anthropogenic disturbance. Burden Research Center (Bottomland 1) covers 440 acres composed of row crops and unmanaged bottomland hardwood forest. It is bisected by a major highway and surrounded by urban development. It has been used to test ornamental and horticultural plant species (LSU 2007). The Aquaculture Research Station (Bottomland 2) is composed of 2,900 acres of pastureland and bottomland hardwood forest (Rupert 2006). This land has been used alternately for pasture grazing, row crops, and timber production. Idlewild Research Station (Bottomland 3) encompasses 1,760 acres of southern pine and bottomland hardwood habitat. Historically, it has been used to test forage crops, improve beef cattle production, research pine bark beetle management, study timber production, and develop horticultural plant species. Rosedown Plantation (Upland 1) has been farmed for over 100 years. In the 1800s most of the plantation's 3,455 acres were planted in cotton and indigo. Today, an 18-acre ornamental garden and upland forest habitat remain (Louisiana Department of Culture 2009).

Vegetation Composition Surveys

I conducted vegetation composition surveys at the study sites during the summer of 2007. I randomly set five 50 x 2 meter-long belt transects at each site (Figure 5) and recorded species name and number present in ten randomly placed 1-m^2 quadrats within each transect. I included only woody vegetation and vines in the survey. I counted individual plants at each site, identified them to species (in some cases to genus), and divided the number of individuals of each species by the number of total plants found at the site to calculate percent cover of each species at each site (Brower et al. 1989).

Figure 5. Transect set at the Bottomland 2

Life History Characteristics

Although *L. sinense* has been in the United States for more than a century, few of its life history traits are known, save for generalities on ease of reproduction from cuttings and seeds, early flowering, and longevity; most of these uncited descriptions are found in general horticulture texts and guides.

Specific quantitative life history information can be used to develop matrix projection models that describe population dynamics. I determined key maturational elements of *L.*

sinense's life history, including time to first reproduction, flower and fruit production, fecundity, and maximum life span, and used this information to develop stage-based matrix projection models.

Time to First Reproduction

Time to first reproduction is a critical component of a life history. I tracked the growth of juvenile *L. sinense* plants to determine time to first reproduction. In January 2008, I harvested 50 juvenile plants from Upland 1 in St. Francisville. I inspected the root ball to ensure that each specimen was a unique individual rather than part of a genet. I potted the plants in one-gallon containers using a soil mixture of composted pine bark. I maintained them in a shade house with 50% shade cloth factor for six months, after which I transplanted them to three-gallon pots and moved them to an area with full sunlight (Figure 6). This was done to maintain the transplants under light conditions similar to those in the collection site. I monitored the plants once a month over 18 months for health, survival, flowering and fruit production.

Figure 6. Juvenile transplants at Bottomland 1

At the time the study concluded, the transplants had not yet flowered, thus this experiment did not yield useful information. Instead, I was able to estimate time to first reproduction based on observations of the smallest reproductive adults found in the field trials. I used dendrochronology to determine the age of these individuals.

Flower Production

Fecundity is an important indicator of potential invasiveness and a key component of the matrix projection analysis. Fecundity is the number of viable offspring produced by an organism that has reached reproductive maturity. This information is currently unavailable and contributes to a greater understanding of *L. sinense*'s reproductive characteristics. To estimate fecundity, I first needed to estimate average flower production of *L. sinense*. I categorized reproductive plants in the field by size, assigning them the descriptors: small adult (diameter above the root collar 10.0 – 20.9 mm), medium adult (21.0 – 50.9 mm), and large adult (51 mm and above). I measured five small, five medium, and four large adults. I randomly selected three flower clusters on each individual and counted the number of flowers in each cluster (Figure 7). I then counted the number of clusters on each specimen. I took the mean flower number per cluster and

Figure 7. *Ligustrum sinense* flower clusters (Photograph by Robert Mirabello)

multiplied it by the number of clusters on each plant to estimate average flower production. Shapiro-Wilk test for normality revealed that the data were not normally distributed, so I log transformed the data to achieve a normal distribution ($W=0.91$, $p = 0.18$). I used simple linear regression to evaluate the correlation of flower production to plant size, with diameter at the root crown (mm) as the independent variable and number of flowers per plant as the dependent variable.

Fruit and Seed Production

Two other components of fecundity are fruit and seed production. I randomly selected 16 adult plants from Bottomland 1 and Camp Whispering Pines in Independence, Louisiana in October 2008[1]. I measured diameter at root crown of each sample and counted the number of fruits present on each plant (Figure 8). I multiplied the number of fruits by the average number of

Figure 8. *Ligustrum sinense* fruits (Photograph by Robert Mirabello)

seeds, first published by Burrows and Kohen (1983) and van Aalst (1992), to estimate average number of seeds per plant. According to their findings, approximately 3% of fruits contain two

[1] In September 2008, Hurricane Gustav hit Baton Rouge. , Seeds of many adult *L. sinense* were dislodged by the winds at all four study sites. Camp Whispering Pines, in Independence, Louisiana, was outside the direct path of the hurricane and contained adult *L. sinense* plants in fruit. I used individuals from this site to determine number of fruits produced by large adult *L. sinense*.

seeds (Burrows and Kohen 1983) and 0.4% contain three seeds (van Aalst 1992). Shapiro-Wilk test for normality indicated that the data were not normally distributed, so I log transformed the data to achieve a normal distribution ($W= 0.96$, $p = 0.71$). I then used simple linear regression to establish whether fruit production correlated with plant size, with diameter at root crown (mm) as the independent variable and number of fruits per plant as the dependent variable. I also used these data to estimate the percentage of flowers that successfully set fruit. I did not mark and track individual flowers to achieve this estimate.

Seed Viability

I used a combination of growth chamber, greenhouse, and field trials to determine seed viability and germination under different conditions. The growth chamber trial reflected germination rates under ideal growth conditions, and the field trials represented the most variable (e.g., least ideal) conditions. I set the growth chamber to 30°C for 13 hours and 10°C for 11 hours with no light (Figure 9). For all trials I processed fruits by hand to remove seeds from flesh and skin of fruit. I germinated the seeds in petri dishes on filter paper wetted with sterile water. I tracked 1,000 seeds, watered them as needed (approximately every other day), and monitored them for germination. After two days, 66 seeds developed mold. I washed them in a 10% bleach solution and returned them to the trial. After 31 days I counted the number of germinated seeds and divided this by the sample size to compute the germination rate.

The greenhouse trial reflected moderate growing conditions. I began this trial in November 2008. I set the greenhouse temperature to 21°C during the day and 16°C at night and watered the seeds daily. I monitored 1100 seeds every two weeks for germination (Figure 10). Once seeds germinated, I maintained them in the greenhouse for four months and monitored them monthly to determine whether survival changed over time. I determined germination rate by dividing the number of surviving seedlings by the sample size.

Figure 9. Growth chamber germination trials

Figure 10. Greenhouse germination trials

The field trial reflected germination under natural growing conditions. I began this trial in December 2008. I set eight 1-m^2 plots at Bottomland 1 and ten 1-m^2 plots at Bottomland 2 and Bottomland 3. I planted 100 seeds in each plot and marked their location to identify planted seeds at a future date (Figure 11). I marked an additional 100 locations within each plot to estimate the probability that a seed that germinated was one I planted, rather than one that came from another source. I monitored the sites monthly through April 2009 for emergence. I calculated seedling emergence at each plot by dividing the number of seeds germinating per site by the original sample size per site. I pooled the germination rates between the three sites to estimate average germination rate.

Figure 11. Field germination trial plot at Bottomland 1

Fecundity

I estimated fecundity of *L. sinense* by comparing the germination rates I acquired from the growth chamber, greenhouse, and field trials with average number of seeds produced by adult plants in different size stages. I multiplied the average number of seeds in each adult life stage (small, medium, and large) by the germination rate from the growth chamber, greenhouse, and field trials to obtain fecundity estimates for plants in different life stages under a variety of growing conditions.

Maximum Life Span

I estimated maximum life-span of *L. sinense*. I collected cross-sections from the root crown of ten plants at Bottomland 1 and sanded them with progressively finer sand paper, up to 1000-grit. I stained the cross-sections with ordinary yellow highlighter and used fluorescent light with magnification to read their growth rings (Lussier et al. 2004) (Figure 12). I estimated the age of three plants at Upland 1. These were the largest plants I found during my study. They had

the largest diameter at root crown observed and were approximately 10 meters tall. When harvested, they appeared to be suffering from heart rot. I used these samples as indicators of maximum age and size of *L. sinense*. I used simple linear regression to estimate whether age was correlated with size, with the independent variable as age in years and the dependent variable as diameter at root crown (mm).

Figure 12. Cross-sections of *L. sinense*

Stage-based Matrix Analysis

I used a density independent stage-based matrix model to evaluate growth of *L. sinense* populations. Stage-based matrix models are appropriate for species whose developmental stage or size better predicts population demography than age (Caswell 2001). I estimated annual survival (σ), and the probability of growth over one time step divided by survival (ρ). From σ and ρ, I calculated the probability of surviving and remaining in a stage, or stasis (P) and the yearly probability of surviving and transitioning to the next stage class (G) (Appendices E and F) using the following equations (Caswell 2001):

$$P_i = \sigma * (1 - \rho)$$

$$G_i = \sigma * \rho$$

Where $\rho = \sigma^D - \sigma^{D-1} / \sigma^D - 1$

I based fecundity (F) on a pre-reproductive census; seedlings were those seeds that germinated and survived their first year of life. I used a solution method that reached an unknown λ by assuming $\lambda = 1$.

Stage Assignment

I used *L. sinense*'s life history information to define stages for use in the matrix model. I categorized plants based on size (diameter above the root crown) and reproductive potential. Seedlings were first-year germinants ranging from 1.0 – 4.9 mm in diameter. Juveniles were older than one year and ranged in size from 5.0 – 9.9 mm. Fecundity of adult *L. sinense* varies with size, therefore I split the adult stage into three size classes, small adults (10.0 – 20.9 mm), medium adults (21.0 – 50.9 mm), and large adults (51 mm and above) (Figure 13). By estimating size-based stages for *L. sinense*, I approximated the number of years individual plants spend in each life stage. Estimating stage durations allowed me to calculate P_i and G_i. I also estimated F_i across adult stages.

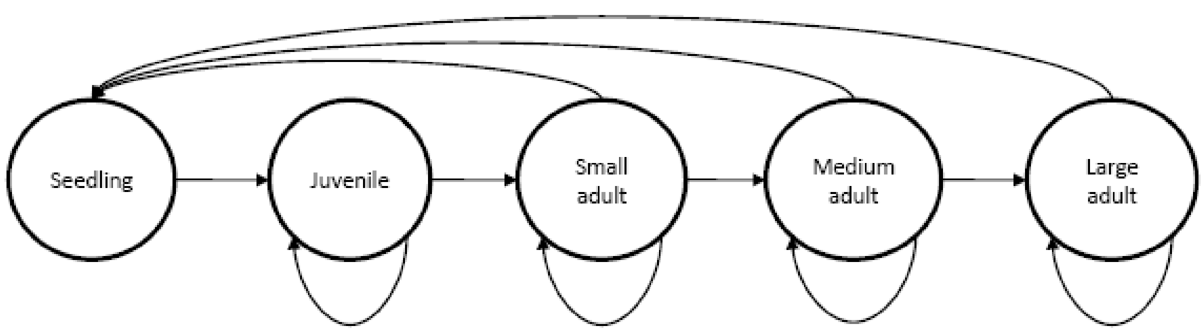

Figure 13. Life cycle graph for *L. sinense*. Horizontal arrows between stages represent the probability of transitioning from one stage to the next over the course of one year (G). Arched arrows on the lower half of the graph represent the probability of remaining in a stage after one year (P). Arched arrows on the top half of the graph represent the life stages that are capable of producing offspring and the reproductive investment of each life stage over the course of one year (F).

Matrix Construction

I developed three matrices based on differences in germination rates in growth chamber, greenhouse, and field trials to reflect population growth under different conditions. I summarized differences in stage transitions using the population dynamics model:

$$\mathbf{n}(t + 1) = \mathbf{A}\mathbf{n}(t)$$

where n(t) is a vector of the number of individuals in a population at a given time and **A** is a population projection matrix (Koop and Horvitz 2005). The dominant eigenvalue of **A**, or λ, is an estimate of the finite rate of increase (λ) of *L. sinense* populations, and indicates the rate at which a population will grow if maintained under constant environmental conditions. For each matrix, I estimated λ using PopTools v. 3.0.3 (Hood 2008). Where $\lambda > 1$, the population is increasing. Where $\lambda < 1$, the population is declining. Where $\lambda = 1$, the population is stationary. I used the matrices to calculate the net reproductive rate (R_0) of *L. sinense* under each germinate rate, which is the mean number of seedlings an individual produces over its lifetime. I also calculated generation time (T), which is the time necessary for the population to grow by a factor of R_0 (Caswell 2001). I estimated the contribution of each life stage to population growth via reproductive input, which is given by the left eigenvector v of the population projection matrix (Caswell 2001). The stable stage distribution is the right eigenvector w of the population matrix **A**. It indicates the stage structure towards which the population will converge at a rate of λ. These calculations help describe the growth dynamics of *L. sinense* populations.

Elasticity Analysis

I performed an elasticity analysis on each matrix. This allowed me to ascertain how Gi, P_i, and F_i, as transitions associated with each life stage, varied in their contribution to population growth under each germination treatment. By determining the proportion that each transition

plays in finite population increase, I described those stages that, when targeted for management, may most effectively reduce population expansion.

The Impact of Various Control Techniques

I perturbed the original matrices by increasing annual mortality in transitions shown by the elasticity analysis to contribute most to population growth. I reported a new λ for each matrix. I developed multiple models based on germination condition (growth chamber, greenhouse, and field) and management technique (Table 1).

Table 1. Perturbations of P_i, G_i, and F_i across growth chamber, greenhouse, and field germination matrices to mimic the influence of different management options

Growth Chamber and Greenhouse

Perturbation
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, and $P_{SMALL\ ADULT}$ by 50%
Reduce all F_{ADULT} by 50%
Eliminate all F_{ADULT}
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, $P_{SMALL\ ADULT}$ by 50%, and $F_{SMALL\ ADULT}$ by 50%
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, $G_{SMALL\ ADULT}$ by 50%, $P_{SMALL\ ADULT}$ by 50%, and $F_{SMALL\ ADULT}$ by 50%
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, $P_{SMALL\ ADULT}$ by 50%, and all F_{ADULT} by 50%

Field

Perturbation
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, and $P_{SMALL\ ADULT}$ by 50%
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, and $P_{SMALL\ ADULT}$ by 50%, $P_{MEDIUM\ ADULT}$ by 50%, $P_{LARGE\ ADULT}$ by 50%
Reduce $F_{SMALL\ ADULT}$ by 50%, and eliminate $F_{MEDIUM\ ADULT}$ and $F_{LARGE\ ADULT}$
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, $P_{SMALL\ ADULT}$ by 50%, and $F_{LARGE\ ADULT}$ by 50%
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, $P_{SMALL\ ADULT}$ by 50%, $P_{LARGE\ ADULT}$ by 50%, and $F_{LARGE\ ADULT}$ by 50%
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, $P_{SMALL\ ADULT}$ by 50%, $P_{LARGE\ ADULT}$ by 50%, and $F_{SMALL\ ADULT}$ by 50%
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, $P_{SMALL\ ADULT}$ by 50%, $F_{SMALL\ ADULT}$ by 50%, and $F_{LARGE\ ADULT}$ by 50%
Reduce $G_{JUVENILE}$ by 50%, $P_{SMALL\ ADULT}$ by 50%, $P_{LARGE\ ADULT}$ by 50%, and $F_{LARGE\ ADULT}$ by 50%

By conducting perturbation analyses that altered P_i, G_i, and F_i in the life history of *L. sinense* I was able to describe which management options may be most successful in controlling this plant.

RESULTS

Vegetation Composition Survey

Ligustrum sinense has a strong presence at all of the sites I measured. At Bottomland 1, *L. sinense* plants composed 29.06% of all plants counted (Figure 14, Appendix A). At Bottomland 2, *L. sinense* composed 6.35% of individuals counted (Figure 15). Bottomland 3 had similar presence of *L. sinense* as Bottomland 1, 29.93% of the woody plants and vines surveyed (Figure 16). Upland 1 was the only site dominated by *L. sinense* seedlings (88.63%) (Figure 17). When seedling presence was included in the survey, adult *L. sinense* plants composed only 1.15% of vegetation measured. Removing *L. sinense* seedlings from the survey shifted the presence of adult *L. sinense* plants to 10.13% of surveyed vegetation at Upland 1 (Figure 18).

The number of species present at each site did not vary greatly. I found a total of 25 woody plant and vine species at Bottomland 1, 27 species at Bottomland 2, 20 species at Bottomland 3, and 21 species at Upland 1.

Species dominance differed among sites. At Bottomland 1, the most common species, other than *L. sinense*, were *Rubus* species (8.29%), *C. caroliniana* seedlings (6.74%), and the vines Virginia creeper (*Parthenocissus quinquefolia* (L.) Planch.) (6.22%) and common greenbrier (*Smilax rotundifolia* L.) (5.70%). At Bottomland 2, *U. americana* was the most common plant, composing 18.78% of woody plants and vines recorded. This was followed by the vines *P. quinquefolia* (12.96%), poison ivy (*Toxicodendron radicans* (L.)) (10.58%), Japanese honeysuckle (*Lonicera japonica* Thunb.) (10.05%), and *Rubus* species (9.52%). At Bottomland 3, the most common species, other than *L. sinense*, were the vines *T. radicans* (12.50%), *L. japonica* (11.80%), *Smilax* species (10.56%), and *P. quinquefolia* (8.27%). The second most common shrub I observed was *I. vomitoria* (5.28%). At Upland 1 the most common

species found in the survey (after excluding *L. sinense* seedlings) were *T. radicans* (30.38%), Chinese parasoltree (*Firmiana simplex* (L.) W. Wight) (18.78%), and *P. caroliniana* (15.93%).

The number of native species outweighed introduced species measured at all sites. At Bottomland 1, introduced species composed 37.31% of woody and vine species measured (Table 2). Along with *L. sinense*, these were *L. japonicum* (4.66%), *T. sebifera* (2.07%), Japanese climbing fern (*Lygodium japonicum* (Thunb. ex Murr.) Sw.) (1.04%), and coral ardisia (*Ardisia crenata* Sims) (0.52%). Native species composed 54.40% of counted plants.

Table 2. Native and introduced vegetation and percent of composition at Bottomland 1

Common name	**Scientific name**	**Native/introduce**	**Percent composition**
Chinese privet	*Ligustrum sinense*	Introduced	37.31%
Japanese privet	*Ligustrum japonicum*	Introduced	4.66%
Chinese tallow	*Triadica sebifera*	Introduced	2.07%
Japanese climbing fern	*Lygodium japonicum*	Introduced	1.04%
coral ardisia	*Ardisia crenata*	Introduced	0.52%
dewberry	*Rubus* sp.	Native	8.29%
american hornbeam (seedling)	*Carpinus caroliniana*	Native	6.74%
Virginia creeper	*Parthenocissus quinquefolia*	Native	6.22%
common greenbrier	*Smilax rotundifolia*	Native	5.70%
palmetto	*Sabal minor*	Native	5.18%
poison ivy	*Toxicodendron radicans*	Native	5.18%
water oak	*Quercus alba*	Native	4.15%
muscadine	*Vitis rotundifolia*	Native	3.11%
winged elm	*Ulmus alata*	Native	2.59%
water oak (seedling)	*Quercus alba* (seedling)	Native	1.55%
red buckeye	*Aesculus pavia*	Native	1.04%
American elm	*Ulmus americana*	Native	0.52%
swamp chestnut oak	*Quercus michauxii*	Native	0.52%
southern magnolia	*Magnolia grandiflora*	Native	0.52%
hornbeam	*Carpinus caroliniana*	Native	0.52%
unknown oak (seedling)	*Quercus* sp.	Native	0.52%
peppervine	*Ampelopsis arborea*	Native	0.52%
southern red oak	*Quercus falcata*	Native	0.52%
roughleaf dogwood	*Cornus drummondii*	Native	0.52%
sweetgum	*Liquidambar styraciflua*	Native	0.52%

At Bottomland 2, introduced species made up 18.78% of woody plants and vines counted (Table 3). Along with *L. sinense*, introduced species included *L. japonica* (10.05%), *T. sebifera* (0.79%), bamboo (*Bambusa* sp.) (0.79%), *L. japonicum* (0.53%) and nandina (*Nandina domestica* Thunb.) (0.26%). Native species composed 80.69% of plants surveyed.

Table 3. Native and introduced vegetation and percent of composition at Bottomland 2

Common name	**Scientific name**	**Native/Introduced**	**Percent composition**
Japanese honeysuckle	*Lonicera japonica*	Introduced	10.05%
Chinese privet	*Ligustrum sinense*	Introduced	6.35%
Chinese tallow	*Triadica sebifera*	Introduced	0.79%
bamboo	*Bambusa sp.*	Introduced	0.79%
Japanese privet	*Ligustrum japonicum*	Introduced	0.53%
nandina	*Nandina domestica*	Introduced	0.26%
American elm	*Ulmus americana*	Native	18.78%
Virginia creeper	*Parthenocissus quinquefolia*	Native	12.96%
poison ivy	*Toxicodendron radicans*	Native	10.58%
dewberry	*Rubus sp.*	Native	9.52%
sugarberry	*Celtis laevigata*	Native	7.14%
common greenbrier	*Smilax sp.*	Native	5.56%
trumpet creeper	*Campsis radicans*	Native	3.17%
muscadine	*Vitis rotundifolia*	Native	2.65%
red maple	*Acer rubrum var. rubrum*	Native	2.12%
crossvine	*Bignonia capreolata*	Native	1.59%
water oak	*Quercus nigra*	Native	1.32%
winged elm	*Ulmus alata*	Native	1.32%
southern red oak	*Quercus falcata*	Native	1.06%
boxelder	*Acer negundo*	Native	0.79%
swamp chestnut oak (tree)	*Quercus michauxii*	Native	0.53%
hickory	*Carya* sp.	Native	0.26%
palmetto	*Sabal minor*	Native	0.26%
pawpaw	*Asimina triloba*	Native	0.26%
peppervine	*Ampelopsis arborea*	Native	0.26%
sugarberry (tree)	*Celtis laevigata*	Native	0.26%
sweetgum	*Liquidambar styraciflua*	Native	0.26%

Native and introduced vegetation were almost equally represented in terms of number of individuals at Bottomland 3. Native vegetation composed 53.52% of surveyed species and

introduced species represented 44.37% of woody plants and vines measured. *Lonicera japonica* was the second-most abundant introduced species, composing 11.80% of the vegetation surveyed, followed by *L. japonicum* (1.76%) and *Bambusa* species (0.88%) (Table 4).

Table 4. Native and introduced vegetation and percent of composition at Bottomland 3

Common name	**Scientific name**	**Native/introduced**	**Percent composition**
Chinese privet	*Ligustrum sinense*	Introduced	29.93%
Japanese honeysuckle	*Lonicera japonica*	Introduced	1.76%
Japanese climbing fern	*Lygodium japonicum*	Introduced	1.76%
bamboo	*Bambusa sp.*	Introduced	0.88%
poison ivy	*Toxicodendron radicans*	Native	12.50%
common greenbrier	*Smilax* sp.	Native	10.56%
Virginia creeper	*Parthenocissus quinquefolia*	Native	8.27%
yaupon	*Ilex vomitoria*	Native	5.28%
southern red oak	*Quercus falcata*	Native	3.52%
water oak	*Quercus nigra*	Native	3.17%
muscadine	*Vitis rotundifolia*	Native	2.46%
American elm	*Ulmus americana*	Native	1.58%
red buckeye	*Aesculus pavia*	Native	0.35%
dewberry	*Rubus* sp.	Native	0.35%
loblolly pine	*Pinus taeda*	Native	0.35%
pawpaw	*Asimina triloba*	Native	0.18%
sweetgum	*Liquidambar styraciflua*	Native	0.18%
willow oak	*Quercus phellos*	Native	2.99%
French mulberry	*Callicarpa americana*	Native	0.88%
red maple	*Acer rubrum var. rubrum*	Native	0.88%

When *L. sinense* seedlings were included in the survey at Upland 1, introduced species composed 92.17% of the vegetation measured, and native species made up the remaining 7.8%. I removed *L. sinense* seedlings from the survey. Under these conditions, I found that introduced species made up 31.17% of the vegetation sampled at Upland 1. Introduced species, other than adult *L. sinense*, were *F. simplex* (18.78%), *A. crenata* (1.87%), *L. japonicum* (0.29%), and *L. japonica* (0.10%). Native vegetation made up the remaining 68.53% of vegetation sampled at this site (Table 5).

Table 5. Native and introduced vegetation and percent of composition at Upland 1 (*L. sinense* seedlings excluded)

Common name	Scientific name	Native/Introduced	Percent composition
Chinese parasoltree	*Firmiana simplex*	Introduced	18.78%
Chinese privet	*Ligustrum sinense* (adults)	Introduced	10.13%
coral ardisia	*Ardisia crenata*	Introduced	1.87%
Japanese privet	*Ligustrum japonicum*	Introduced	0.29%
Japanese honeysuckle	*Lonicera japonica*	Introduced	0.10%
poison ivy	*Toxicodendron radicans*	Native	30.38%
cherrylaurel	*Prunus caroliniana*	Native	15.93%
American holly	*Ilex opaca*	Native	4.72%
sugarberry	*Celtis laevigata*	Native	4.52%
Virginia creeper	*Parthenocissus quinquefolia*	Native	4.52%
winged elm	*Ulmus alata*	Native	3.05%
water oak	*Quercus nigra*	Native	2.56%
muscadine	*Vitis rotundifolia*	Native	0.98%
dewberry	*Rubus sp.*	Native	0.49%
peppervine	*Ampelopsis arborea*	Native	0.39%
southern red oak	*Quercus falcata*	Native	0.29%
yaupon	*Ilex vomitoria*	Native	0.29%
cherrybark oak	*Quercus pagoda*	Native	0.10%
crossvine	*Bignonia capreolata*	Native	0.10%
common greenbrier	*Smilax sp.*	Native	0.10%
oak (sp?)	*Quercus sp.*	Native	0.10%

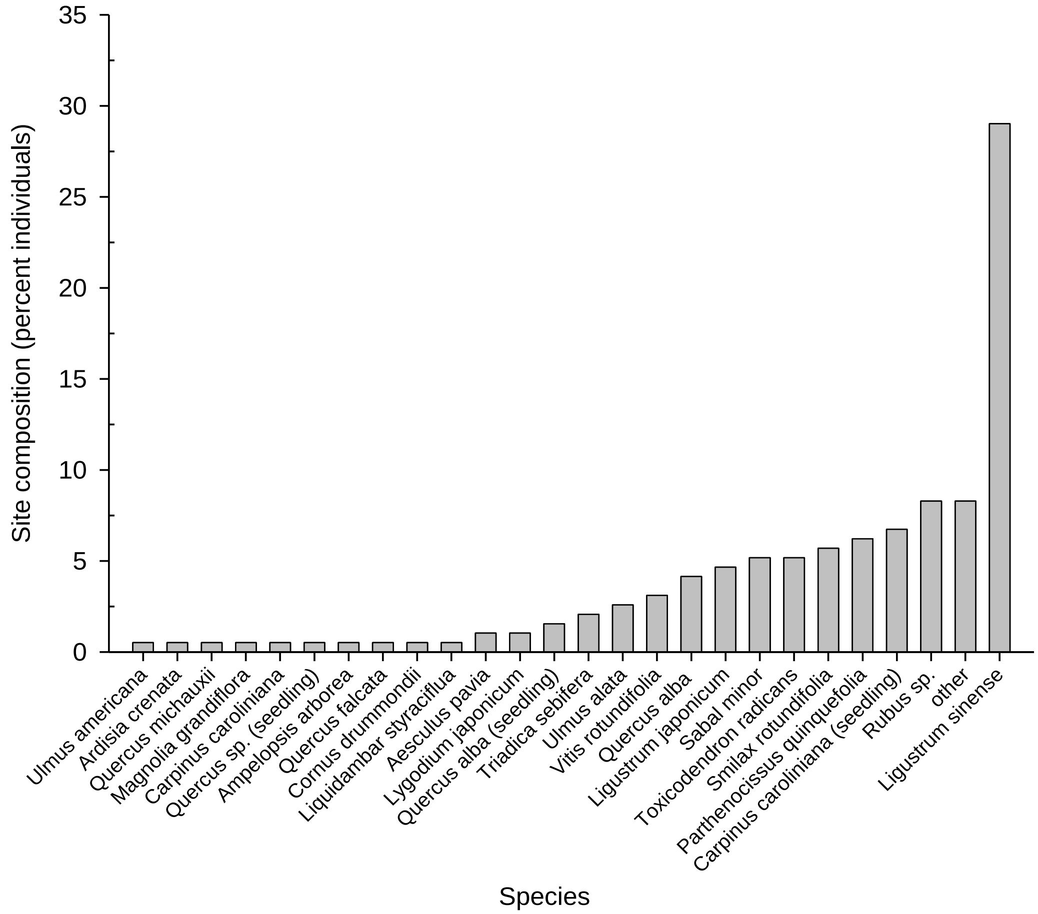

Figure 14. Woody species composition based on individual plants surveyed at Bottomland 1

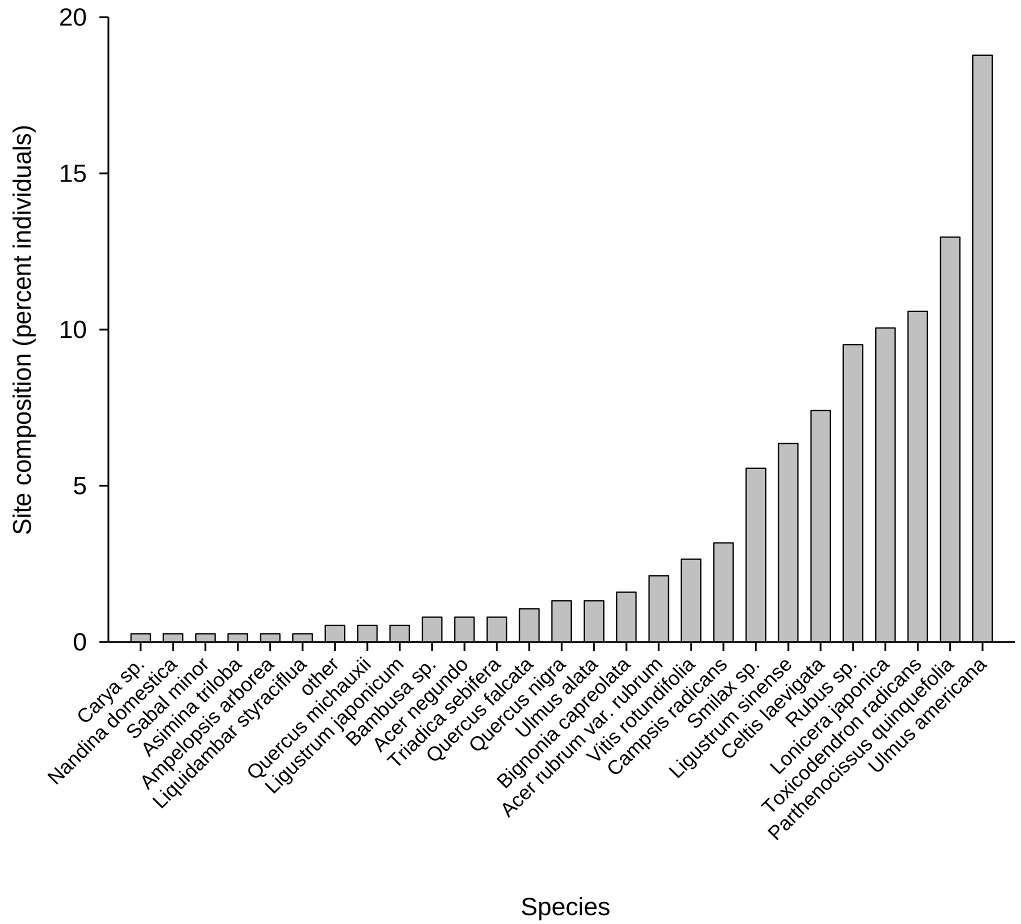

Figure 15. Woody species composition based on individual plants surveyed at Bottomland 2

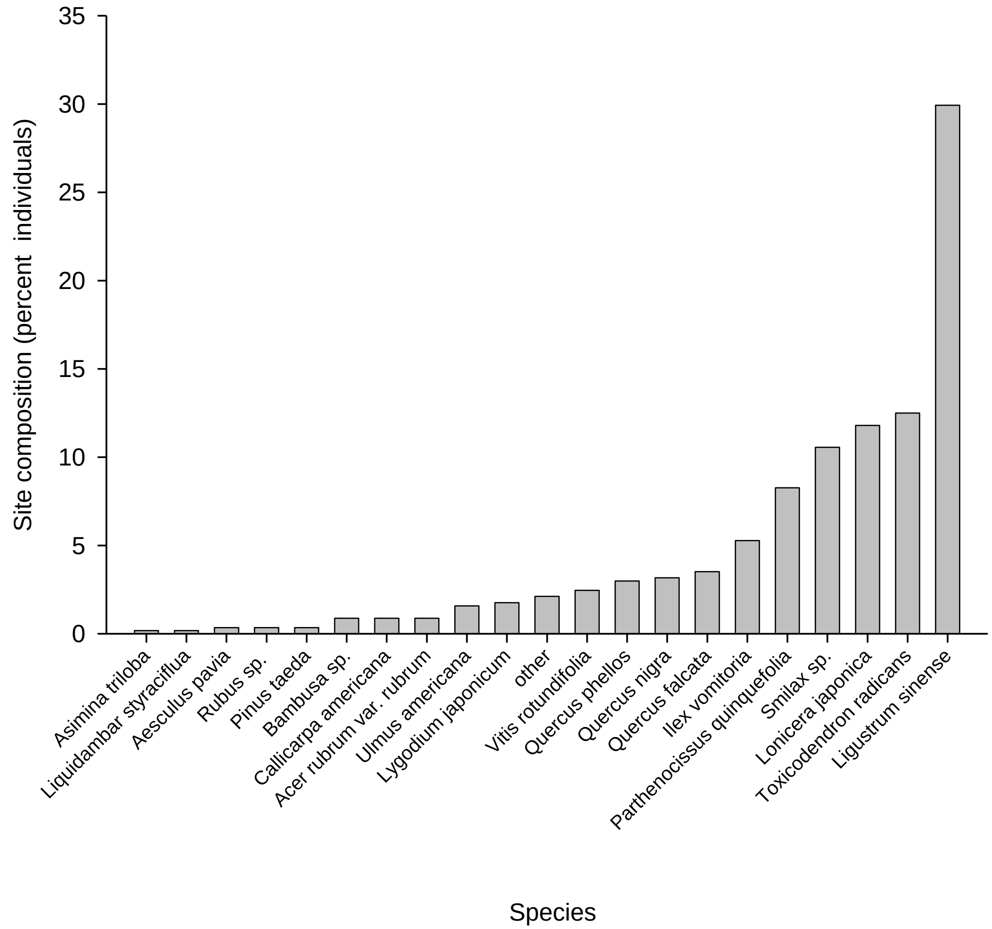

Figure 16. Woody species composition based on individual plants surveyed at Bottomland 3

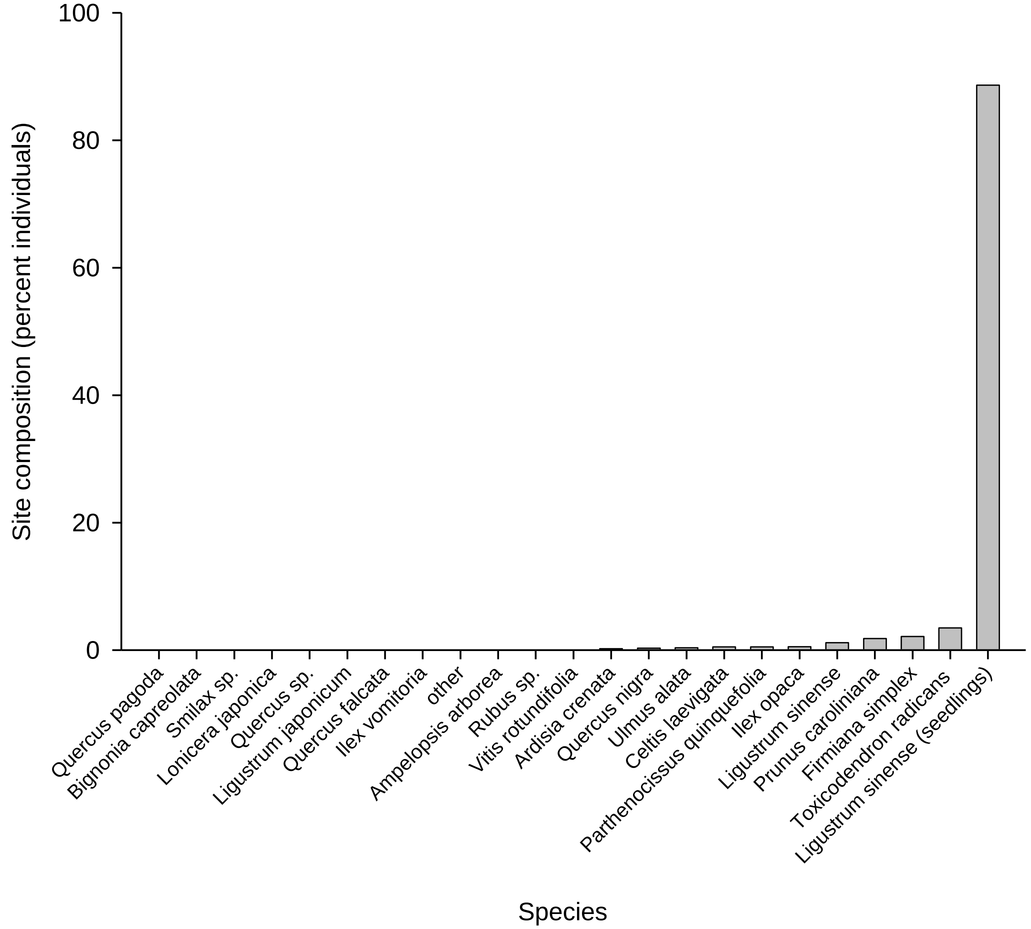

Figure 17. Woody species composition based on individual plants surveyed (including *L. sinense* seedlings) at Upland 1

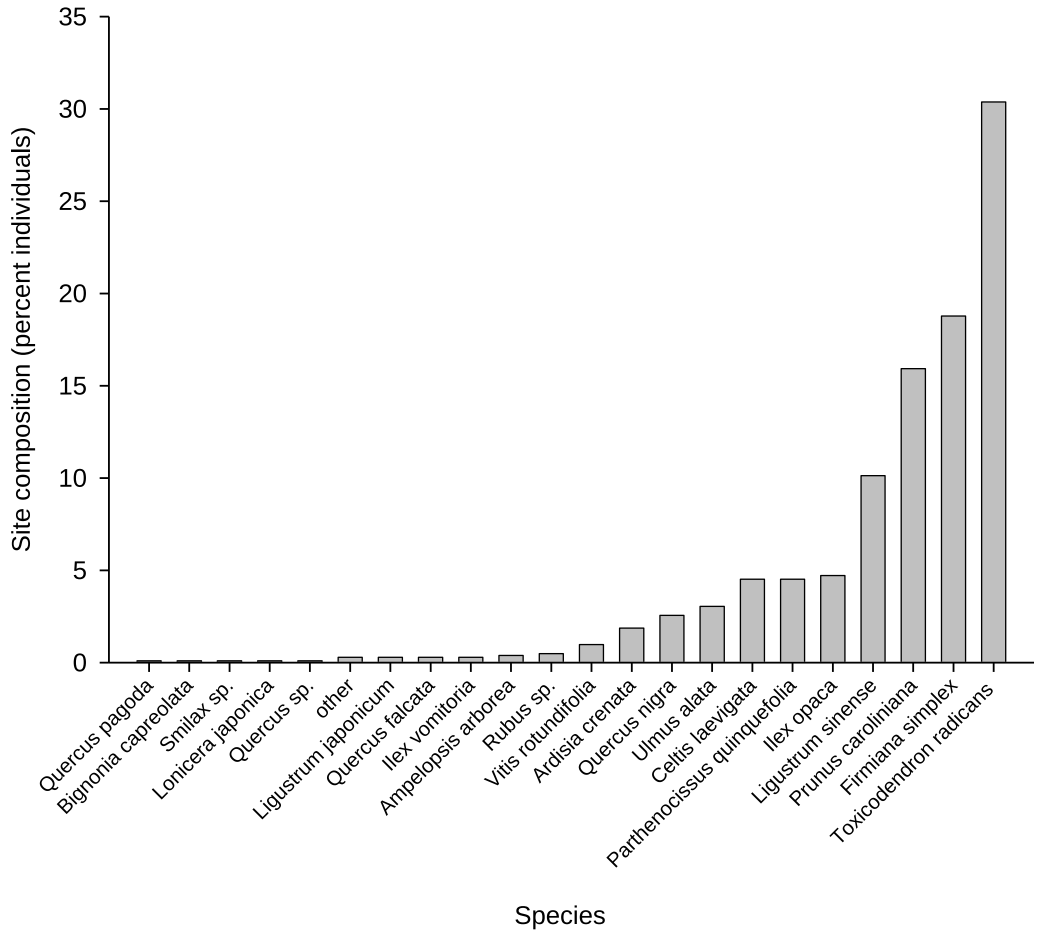

Figure 18. Woody species composition based on individual plants surveyed (excluding *L. sinense* seedlings) at Upland 1

Life History Characteristics

Time to First Reproduction

Ligustrum sinense becomes reproductive as young as four years of age. I based my estimate of time to first reproduction on size class observations made throughout the study. The smallest reproductive individual I observed was approximately 10 mm in diameter at root crown. This plant was approximately four years of age based on annual ring analysis. I used this individual to indicate age at first reproduction.

Flower Production

Flower production increased with plant size. As the diameter at root crown increased so did flower number (N = 14, r^2 = 0.7182, p = 0.0001) (Figure 19). Mean flower production was approximately 1,500 flowers for small adults, 5,000 flowers for medium adults, and 55,000 flowers for large adults (Appendix B).

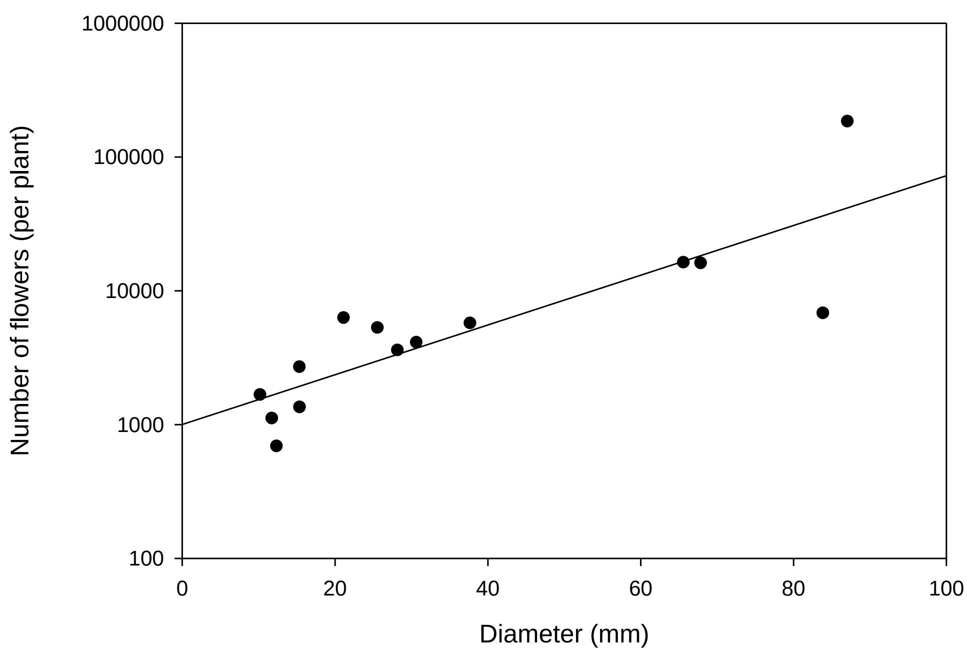

Figure 19. Flower production regression analysis (natural log)

Fruit Production

Larger *L. sinense* produced more fruits. As *L. sinense* increased in size so did the number of fruits per plant (N = 16, r^2 = 0.6085, p = 0.0004) (Figure 20). At the large adult stage fruit production varied, ranging from 1,291 – 15,352 fruits per plant. At the medium adult stage, fruit production ranged from 57 – 704 fruits per plant. Small adults ranged from 31 – 314 fruits per

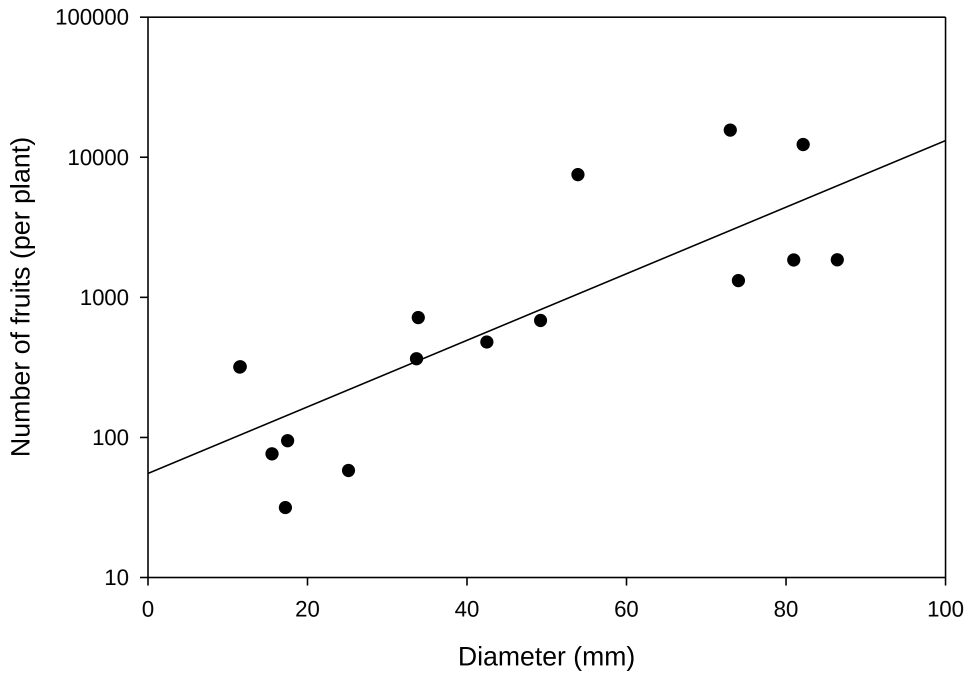

Figure 20. Size and number of fruits produced by *L. sinense* (natural log)

plant. The mean number of fruits for small adults was 165 fruits, for medium adults, 452 fruits, and for large adults, 6,626 fruits. On average, small adults produced 172 seeds, medium adults produced 470 seeds, and large adults produced 6,879 seeds per plant (Appendix C).

Compared to total flower production, a relatively small percentage of flowers matured. Flowering and fruiting measurements indicated that in all reproductive size classes 11% of flowers successfully matured to become fruits.

Seed Viability

Germination rates, and therefore fecundity, varied among growth chamber, greenhouse, and field trials. The growth chamber trial produced the highest germination rate of 62%. The greenhouse trial followed closely with 57% of seeds germinating three months after planting, and the field trial had the lowest germination rates. At Bottomland 1, 11% of seeds germinated. At Bottomland 2, 17% of seeds germinated. Seeds tested at Bottomland 3 were more successful, with 22% of seeds germinating. The average rate of germination across field sites was 16%. No seeds germinated in field plots other than ones I planted. Fecundity of *L. sinense* varied under different growing conditions (Table 6). Based on estimates of seeds per plant in each size class and germination rates, small adults, under growth chamber conditions, produced 106 viable seeds, under greenhouse conditions 99 viable seeds, and under field conditions 28 viable seeds. Medium adults, under growth chamber conditions, produced 289 viable seeds, greenhouse 270 viable seeds, and field 77 viable seeds. Large adults under growth chamber conditions produced 4,231 viable seeds, greenhouse 3,952 viable seeds, and field 1,132 viable seeds.

Table 6. Fecundity of *L. sinense* in different size classes based on germination rates in growth chamber, greenhouse, and field trials

Stage	**Seeds per plant**	**Fecundity Growth Chamber**	**Fecundity Greenhouse**	**Fecundity Field**
Small adult	172	106	99	28
Medium adult	470	289	270	77
Large adult	6,879	4,231	3,952	1,132

Maximum Life Span

Ligustrum sinense increase in size as they age. Due to the positive linear relationship documented between age and size, I was able to use dendrochronological measurements of smaller plants to approximate the age of larger plants ($N = 13$, $r^2 = 0.8121$, $p < 0.0001$)

(Appendix D). The largest individuals I encountered during this study were located at Upland 1 and ranged from 122 – 184 mm in diameter at the root collar. They were suffering from heart rot and a degenerating stem structure, which indicated that they were senescing. I used these individuals as indications of maximum life span for the Upland 1 population. The oldest plant at this site, based on my dendrochronological measurements, was 25 years old. From these measurements I estimated the age of *L. sinense* plants at different sizes (Figure 21).

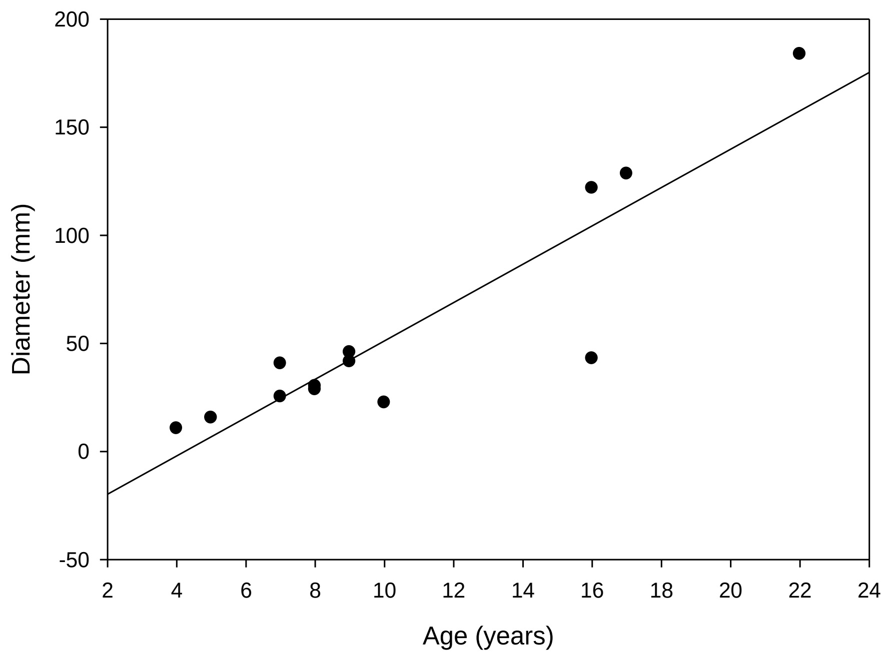

Figure 21. Age and size (diameter at root crown) of *L. sinense*

Analysis of Demographic Models

Ligustrum sinense populations have the potential for rapid growth. The finite rate of increase (λ) was greater than 1 across matrices, which indicates that *L. sinense* populations are growing. Models including germination rates obtained from growth chamber trials yield λ = 2.26, which was the highest rate of population growth among all trials. When seeds were germinated under greenhouse conditions, results were similar (λ = 2.20). Models using seed

viability from field germination tests gave the lowest rate of population growth (λ = 1.48) (Appendix G).

Net reproductive rate (R_0) and generation time (T) differed among germination trial conditions. Based on germination rates obtained from the growth chamber, R_0 = 1,774.35 and T = 9.20. Under these conditions, it takes approximately 9 years for the population to increase by a factor of 1,774. Under greenhouse germination rates, R_0 = 1,548.35 and T = 9.33, which is similar to growth chamber results. Under field conditions, R_0 = 126.95 and T = 12.37. The net reproductive rate (R_0) under field chamber conditions is much less than in the growth chamber or greenhouse; T is also longer. Under field conditions it takes longer for the population to grow by fewer individuals.

The stable stage distribution *w* showed the projected population structure. Under all germination conditions the projected population was dominated by seedlings (growth chamber 73%, greenhouse 73%; field 84%) (Table 7). This was followed by juveniles. Adult stages accounted for little of the population structure. Under greenhouse and growth chamber conditions, large adults accounted for only 0.01% of the total population. Reproductive values, conversely, showed that large adults contributed most to reproductive value *v* across germination trials (growth chamber 81%; greenhouse 81%; field 71%).

Interpretation of Elasticities

Elements of the matrix associated with specific stages differed in their contribution to λ. Elasticities indicated that $G_{SEEDLING}$ and $G_{JUVENILE}$, along with $P_{SMALL\ ADULT}$ and $F_{SMALL\ ADULT}$ contributed most to population growth when germination rates came from the growth chamber and greenhouse trials (Table 8). Targeting seedlings, juveniles and small adults in an effort to manage *L. sinense* thus may be most effective in reducing population growth. When seeds were

Table 7. Stable stage distribution (*w*) and reproductive values (*v*) for *L. sinense* matrix (adapted from Crowder et al. (1994))

Growth Chamber

Stage	Stable stage distribution	Reproductive value
Seedling	72.80%	0.03%
Juvenile	26.23%	0.10%
Small adult	0.87%	3.42%
Medium adult	0.08%	15.18%
Large adult	0.01%	81.28%

Greenhouse

Stage	Stable stage distribution	Reproductive value
Seedling	73.41%	0.03%
Juvenile	25.60%	0.10%
Small adult	0.89%	3.50%
Medium adult	0.09%	15.51%
Large adult	0.01%	80.86%

Field

Stage	Stable stage distribution	Reproductive value
Seedling	83.82%	0.04%
Juvenile	14.82%	0.33%
Small adult	1.07%	6.39%
Medium	0.22%	22.59%
Large adult	0.07%	70.66%

germinated in field conditions, $P_{SMALL\ ADULT}$, $P_{MEDIUM\ ADULT}$, and $P_{LARGE\ ADULT}$, along with $G_{SEEDLING}$ and $G_{JUVENILE}$ contributed most to λ. This suggests that removal of a fraction of plants in all life stages will contribute to a reduction in population growth.

Table 8. Results of elasticity analyses for stage-based matrices reflecting germination rate obtained from growth chamber, greenhouse, and field trials. Stages and transitions that contribute most to population growth are in **bold**

Growth chamber

	Seedling	**Juvenile**	**Sm adult**	**Med adult**	**Lrg adult**
Seedling	0	0	**0.112**	0.030	0.057
Juvenile	**0.199**	0.064	0	0	0
Sm adult	0	**0.199**	**0.112**	0	0
Med adult	0	0	0.087	0.047	0
Lrg adult	0	0	0	0.057	0.038

Greenhouse

	Seedling	**Juvenile**	**Sm adult**	**Med adult**	**Lrg adult**
Seedling	0	0	**0.106**	0.029	0.059
Juvenile	**0.194**	0.065	0	0	0
Sm adult	0	**0.194**	**0.115**	0	0
Med adult	0	0	0.088	0.049	0
Lrg adult	0	0	0	0.059	0.041

Field

	Seedling	**Juvenile**	**Sm adult**	**Med adult**	**Lrg adult**
Seedling	0	0	0.031	0.017	0.077
Juvenile	**0.125**	0.074	0	0	0
Sm adult	0	**0.125**	**0.153**	0	0
Med adult	0	0	0.095	**0.107**	0
Lrg adult	0	0	0	0.077	**0.118**

Management Options

Reductions in the proportional contribution of P_i and G_i reduced λ. For the growth chamber matrix, a 50% reduction in $G_{SEEDLING}$, $G_{JUVENILE}$, and $P_{SMALL\ ADULT}$ brought λ to 1.66 (Table 9). The same perturbation for the greenhouse matrix brought λ to 1.63. For the field matrix, a

reduction in $G_{SEEDLING}$ and $G_{JUVENILE}$ of 50%, as well as a 50% reduction in $P_{SMALL\ ADULT}$, $P_{MEDIUM\ ADULT}$, and $P_{LARGE\ ADULT}$ brought λ to 1.0.

Table 9. Reductions in P_i, G_i, and F_i and associated lambdas

Growth Chamber

Perturbation	**λ**
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, and $P_{SMALL\ ADULT}$ by 50%	1.66
Reduce all F_{ADULT} by 50%	1.98
Eliminate all F_{ADULT}	0.89
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, $P_{SMALL\ ADULT}$ by 50%, and $F_{SMALL\ ADULT}$ by 50%	1.62
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, $G_{SMALL\ ADULT}$ by 50%, $P_{SMALL\ ADULT}$ by 50%, and $F_{SMALL\ ADULT}$ by 50%	1.50
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, $P_{SMALL\ ADULT}$ by 50%, and all F_{ADULT} by 50%	1.50

Greenhouse

Perturbation	**λ**
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, and $P_{SMALL\ ADULT}$ by 50%	1.63
Reduce all F_{ADULT} by 50%	1.93
Eliminate all F_{ADULT}	0.89
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, $P_{SMALL\ ADULT}$ by 50%, and $F_{SMALL\ ADULT}$ by 50%	1.59
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, $G_{SMALL\ ADULT}$ by 50%, $P_{SMALL\ ADULT}$ by 50%, and $F_{SMALL\ ADULT}$ by 50%	1.47
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, $P_{SMALL\ ADULT}$ by 50%, and all F_{ADULT} by 50%	1.47

Field

Perturbation	**λ**
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, and $P_{SMALL\ ADULT}$ by 50%	1.00
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, and $P_{SMALL\ ADULT}$ by 50%, $P_{MEDIUM\ ADULT}$ by 50%, $P_{LARGE\ ADULT}$ by 50%	1.19
Reduce $F_{SMALL\ ADULT}$ by 50%, and eliminate $F_{MEDIUM\ ADULT}$ and $F_{LARGE\ ADULT}$	1.04
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, $P_{SMALL\ ADULT}$ by 50%, and $F_{LARGE\ ADULT}$ by 50%	1.13
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, $P_{SMALL\ ADULT}$ by 50%, $P_{LARGE\ ADULT}$ by 50%, and $F_{LARGE\ ADULT}$ by 50%	1.04
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, $P_{SMALL\ ADULT}$ by 50%, $P_{LARGE\ ADULT}$ by 50%, and $F_{SMALL\ ADULT}$ by 50%	1.09
Reduce $G_{SEEDLING}$ by 50%, $G_{JUVENILE}$ by 50%, $P_{SMALL\ ADULT}$ by 50%, $F_{SMALL\ ADULT}$ by 50%, and $F_{LARGE\ ADULT}$ by 50%	1.12
Reduce $G_{JUVENILE}$ by 50%, $P_{SMALL\ ADULT}$ by 50%, $P_{LARGE\ ADULT}$ by 50%, and $F_{LARGE\ ADULT}$ by 50%	1.13

A seed-eating biocontrol was not a viable option for *L. sinense* control. For matrices using the growth chamber and greenhouse germination rates, I reduced all F_{ADULT} by 50% and obtained $\lambda = 1.98$ (growth chamber) and $\lambda = 1.93$ (greenhouse), respectively. To obtain $\lambda < 1$, I had to eliminate all F_{ADULT} ($\lambda = 0.89$). To reduce population growth for the field matrix, I reduced $F_{SMALL\ ADULT}$ by 50% and eliminated $F_{MEDIUM\ ADULT}$ and $F_{LARGE\ ADULT}$ ($\lambda = 1.04$).

Integrated management techniques reduced λ, but did not cause population growth to decline. For the growth chamber and greenhouse matrices, I reduced $F_{SMALL\ ADULT}$ by 50%, reduced $G_{SEEDLING}$ and $G_{JUVENILE}$ by 50%, and reduced $P_{SMALL\ ADULT}$ by 50%, which lowered population growth but did not cause it to decline (growth chamber $\lambda = 1.62$; greenhouse $\lambda = 1.59$). I added a reduction in $F_{MEDIUM\ ADULT}$ and $F_{LARGE\ ADULT}$ by 50% (growth chamber $\lambda = 1.50$; greenhouse $\lambda = 1.47$). I achieved the same λ by reducing $G_{SEEDLING}$, $G_{JUVENILE}$, and $G_{SMALL\ ADULT}$ by 50%, reducing $P_{SMALL\ ADULT}$ by 50%, and eliminating half of $F_{SMALL\ ADULT}$.

Integrated management options for reducing population growth were more successful with the field trial matrix (i.e., lowest germination rates). I reduced $G_{SEEDLING}$ and $G_{JUVENILE}$ 50%, and reduced $P_{SMALL\ ADULT}$ by 50%, to achieve λ of 1.19. I reduced $F_{LARGE\ ADULT}$ by 50%, which brought λ to 1.13. Reducing $P_{LARGE\ ADULT}$ by 50% lowered λ to 1.04. Additional reductions in matrix elements achieved similar results (Appendix H).

DISCUSSION

Vegetation Composition Surveys

I evaluated natural areas in Louisiana to determine the presence of *L. sinense* and the proportion of *L. sinense* individuals compared to native plants counted at each site. By assessing the presence of *L. sinense*, I gained an understanding of the extent to which this invasive plant has outcompeted native species within parts of the state.

Ligustrum sinense is established as an invasive component of Louisiana bottomland and upland forests. At two of the study sites (Bottomland 1 and Bottomland 3), of the plants I measured, *L. sinense* was the most prevalent species, dominating the understory vegetation sampled. At these sites *L. sinense* was also the most common invasive species. Upland 1 and Bottomland 2 experienced less invasive pressure from *L. sinense*.

Differences in disturbance regimes among sites may explain why some areas are more invaded by *L. sinense*. Both Bottomland 1 and Bottomland 3 have been used extensively to research horticultural species, and Bottomland 3 has also been used for timber production and to research livestock. Both Bottomland 1 and Bottomland 3 may have at one time tested or planted *L. sinense* as a horticultural species, which may have facilitated its invasion in these areas. Human and natural disturbances often promote non-native species invasions (Hobbs and Huenneke 1992), and it can be assumed that both Bottomland 1 and Bottomland 3 have been subjected to significant anthropogenic alteration. Bottomland 1 was at one time a homestead and was used by landowners for agricultural purposes. When it was purchased by LSU in the 1980s, one of the conditions of the acquisition was that the forest would be left untouched (LSU 2007). Prolonged disturbance followed by cessation of management likely allowed *L. sinense* populations to expand at Bottomland 1.

I found the largest numbers of seedlings at Upland 1. My survey showed that *L. sinense* seedlings composed 80.69% of counted plants, which inflated the estimate of introduced versus native species at this site. At the time of this survey in the summer of 2007, the area beneath adult *L. sinense* plants was blanketed with seedlings. Upland 1 has been established as a home for over 150 years, with an extensive ornamental garden. Ownership of the site changed in 1956 and Louisiana State Parks purchased the area in 2004 (Louisiana Department of Culture 2009). Archeological digs and some logging have recently occurred in the forested area of the plantation (Dozier, personal communication), which may have increased light availability and promoted disturbance. These recent disturbances may explain why Upland 1 had a greater presence of *L. sinense* seedlings than the other sites.

Bottomland 2 was the least invaded of all sites. Further analysis of light availability and soil characteristics may lend information as to why this site is less dominated by *L. sinense* than other areas evaluated. It is by far the wettest of the four sites, and it experiences extended periods of seasonal flooding. Although *L. sinense* tolerates prolonged flooding once it has established, perhaps repeated inundation over successive years has acted as a deterrent to colonization, and has helped keep this plant at bay. In September 2008, winds from Hurricane Gustav severely damaged many canopy species at Bottomland 2. Future vegetation surveys may elucidate whether increased light availability due to the thinned canopy and gap formation will promote invasion of *L. sinense* at this site.

With the strong presence that *L. sinense* has in Louisiana forests and its ability to outcompete native species, it is likely that wildlife have come to rely upon it at a food source. As populations of *L. sinense* grow, native plants may become scarcer. Animals are likely to rely upon food sources that are abundantly available, which, in many cases are plant species that have invaded natural areas. Wildlife may then disperse invasive species to novel locations. Further

evaluation of the relationship between wildlife and *L. sinense* proliferation may elucidate mechanisms of its spread.

Life History Characteristics

The reproductive potential of *L. sinense* increases as plants grow larger. Key reproductive and maturational elements in the life history of *L. sinense* showed that flower, fruit, and seed production are all positively correlated with plant size. Size of plant is also positively correlated with age. In essence, as *L. sinense* plants grow larger, their reproductive capability increases, to a point. Visual observation of the largest plants indicated a thinning canopy and many broken limbs. The largest plants were also suffering from heart rot. When plants battle disease and herbivory, they allocate fewer resources towards reproduction and growth. It is likely that the largest *L. sinense* plants produce fewer fruits and seeds than those of moderate size.

L. sinense is a long-lived species. The fast-slow continuum hypothesis says that species with short life spans grow more rapidly than those that live longer (Silvertown and Charlesworth 2001). My research is consistent with this hypothesis, as *L. sinense* remains in the juvenile stage for at least three years before becoming reproductively mature. By being larger at reproductive maturity, *L. sinense* can contribute more resources to fruit and seed production.

Clonal growth is a life history trait that many plant species possess, and can be a tradeoff for sexual reproduction. *Ligustrum sinense* contributes resources to clonal growth and seed production, which likely enhances its ability to invade natural areas. By expanding laterally and developing new ramets, *L. sinense* may readily outcompete native species in its general vicinity. The combined effect of sexual reproduction and clonal growth make *L. sinense* a double threat and that much more difficult to manage in natural settings.

Long-lived, iteroparous species influence population expansion by repeatedly donating propagules to existing populations. This study shows that *L. sinense* at Upland 1 have a life-span

of approximately 25 years. *Ligustrum sinense* fruits yearly, and as it ages it produces more seeds. A single large adult ramet can produce up to 15,000 seeds. While germination rates in the field were lower than I expected, previous studies have found germination rates of 40% in the field (Panetta 2000). Due to the high rate of seed production, and potentially high germination rates, each cohort is capable of contributing large numbers of new individuals to existing populations, a fraction of which, in turn, grow and become reproductive themselves. If *L. sinense* is not targeted at stages that contribute most to population growth, it will continue to expand and impact ecosystem functioning.

Demographic Modeling

Ligustrum sinense populations have the potential for rapid growth. G_i and P_i remained the same in all the matrices except for $G_{SEEDLING}$. F_i also changed among matrices, based on differences in seed viability estimates obtained from growth chamber, greenhouse, and field trials. Despite the differences, all matrices I developed indicated that *L. sinense* populations are increasing in size ($\lambda > 1$). Under ideal germination conditions, populations of *L. sinense* are capable of producing large numbers of seedlings over the course of one year ($\lambda = 2.26$). Germination rates in the field trial, designed to reflect natural growing conditions, were significantly less. Still, the field analysis suggested that *L. sinense* populations are capable of growing by almost 50% each year.

Ligustrum sinense populations have a relatively low T and a high R_0. Generation time (T) ranged from approximately 9 years, based on growth chamber germination rates, to 12 years, based on field germination rates. Net reproductive rate (R_0) ranged from approximately 127, based on field germination rates, to 1,774, based on growth chamber germination rates. This indicates that *L. sinense* populations have the potential for rapid population growth. Under ideal growth chamber growing conditions, a single seedling may be replaced with 1,774 individuals

over the course of 9 years. This further underscores the importance of developing effective methods of managing *L. sinense* populations.

Elasticity analysis indicated those transitional elements that contribute most to λ. In the growth chamber and greenhouse, $G_{SEEDLING}$ and $G_{JUVENILE}$, $P_{SMALL\ ADULT}$, and $F_{SMALL\ ADULT}$ contributed most to λ. Because germination rates were different in the field, the elasticity analysis showed different matrix elements as contributing most to population growth. The field germination matrix indicated that $G_{SEEDLING}$ and $G_{JUVENILE}$, and $P_{SMALL\ ADULT}$, $P_{MEDIUM\ ADULT}$, and $P_{LARGE\ ADULT}$ contributed most to population growth. These transitions may affect population growth most significantly when targeted for management.

Using these matrices, I evaluated the effectiveness of different management regimes. Herbicide application has been the most useful method of controlling *L. sinense*. By adjusting the matrices to reflect reductions in the proportional contributions of P_i and G_i, I described which life stages, when targeted by a management tool such as herbicide and removed from the population, would cause the population growth rate to decline. The growth chamber and greenhouse matrices both indicated that reductions in $P_{SEEDLING}$, $P_{JUVENILE}$, and $P_{SMALL\ ADULT}$ would reduce population growth; the only stasis transitions that did not contribute considerably to population growth were $P_{MEDIUM\ ADULT}$ and $P_{LARGE\ ADULT}$. This information may help land managers streamline control programs. Rather than targeting all *L. sinense* individuals in a population, managers can focus their efforts on seedlings, juveniles, and small adults, which may be easier and less costly to remove than medium and large adults.

Germination rates were much lower in the field, therefore elasticity elements as well as potential management options differed. $G_{SEEDLING}$ and $G_{JUVENILE}$, as well as $P_{SMALL\ ADULT}$, $P_{MEDIUM\ ADULT}$, and $P_{LARGE\ ADULT}$ contributed most to λ. While this essentially demonstrates that all stages contribute significantly to λ, reductions of select transitions led to declines in population growth

that neared equilibrium ($\lambda = 1$). Managers may have success by first removing half of the seedlings, juveniles, and small adults in a population to near a point where populations are stationary.

Biological control may be used as part of an integrated management plan for controlling *L. sinense*. The seed weevil, *O. ligustri*, has been found attacking *L. sinense* (Cuda and Zeller 2000). A biological control that negatively affects seed production may contribute to limiting the spread of this plant, but is not a practical option for controlling *L. sinense* alone. To send populations into decline ($\lambda = 0.89$), I had to eliminate all F_{ADULT}, and elimination of all seeds of adult *L. sinense* is effectively impossible.

Integrated management techniques that combine reduction of fecundity and removal of individuals to control *L. sinense* provided more realistic options. I found that a seed-eating biocontrol coupled with eradication of plants in specific life stages led to reductions in and possible stabilization of population growth. Under growth chamber and greenhouse conditions, I found that reducing all F_{ADULT}, $G_{SEEDLING}$ and $G_{JUVENILE}$, and $P_{SMALL\ ADULT}$ lowered population growth, but did not cause it to decline. My field matrix delivered more optimistic options, indicating one method of becoming stationary (reducing $G_{SEEDLING}$ and $G_{JUVENILE}$, and all P_{ADULT} by half brought λ to 1.0), and other methods of nearing stationary (e.g., reducing $G_{SEEDLING}$ and $G_{JUVENILE}$, $P_{SMALL\ ADULT}$, and $F_{LARGE\ ADULT}$ by half brought λ to 1.13). If a biocontrol agent is introduced that is capable of removing half of viable seeds from the population, and land mangers target seedlings, juvenile, and small adult plants, my field model indicates that these efforts will cause *L. sinense* populations to become static. Although a stable population may not be the ideal condition, preventing invasive populations from growing and expanding under circumstances where management resources are limited may be the most practical control option at this time.

This is the first study to use matrix projection analysis to look at λ of *L. sinense* populations. Other studies have tracked the rate of population expansion through yearly observation (Merriam 2003) and long-term aerial photography (Ward 2002). Merriam's study showed that *L. sinense* populations are expanding at a rate of roughly 5% per year in North Carolina. My study shows that populations have the capacity to double over the course of one year under ideal growing conditions. *Ligustrum sinense* populations have already established in natural areas of the southeastern United States and are exerting competitive pressure on native plant species in Louisiana. Any rate of population growth may be destructive for native ecosystems.

The next step is to field test model predictions to determine whether they reflect natural conditions and will be effective in controlling *L. sinense*. Although I attempted to develop models that reflect multiple growing conditions, the variability of different ecosystems limits the unadulterated use of control techniques as suggested by my models. Ideally, models would be constructed that reflect the nuances of a specific population. Demographic modeling is limited by the conditions under which data were collected.

The benefit of these models is that they provide a low-cost method of describing population growth and the effects of different management options prior to on-the-ground application. While it is unlikely that *L. sinense* will be eradicated from the southeastern United States, methods to control it as suggested by demographic models may provide ways to keep populations from growing and expanding to new locations.

CONCLUSION

Non-native invasive plants are a growing problem and pose challenges to those who attempt to manage them. Questions arise about the best methods towards removing invasive species, ethical dilemmas present themselves regarding the use of different management techniques, and sociological challenges abound. Can we, for example, use prescribed fire to manage an invasive species in an area where local residents fear potential threats to their homes? If we remove invasive species, what will take their place? Will it be a plant that is more harmful, or do we need to actively revegetate areas with native species? Managing invasive species is more than a biological question; it fosters discourse in a wide variety of arenas and therefore becomes an increasingly difficult challenge.

There is no doubt that *L. sinense* as a species of study incorporates these points of tension. Herbicide application is the most effective method of removing it, but there may be other options that are less potentially harmful to the surrounding vegetation. If we remove all the *L. sinense* in sight, what will take its place? My thesis suggests that targeting a fraction of the population as opposed to all plants will provide land managers with more effective ways of reducing population expansion of *L. sinense*.

Non-native invasive species pose huge challenges to maintaining the diversity and functioning of ecosystems in our world today. Tools such as life history analysis and demographic modeling may provide keys towards understanding how best to manage and prevent the expansion of growing invasive plant populations.

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APPENDIX A: VEGETATION SURVEY DATA

Bottomland 1

Summer 2007

Transect	Plot	Common name	Number in plot
1	1	Virginia creeper	2
1	1	winged elm	1
1	1	poison ivy	5
1	1	Chinese privet	3
1	1	dewberry	1
1	2	poison ivy	3
1	2	palmetto	2
1	2	rough-leafed dogwood	1
1	3	Chinese privet	2
1	3	palmetto	2
1	4	bare dirt	–
1	5	water oak (seedling)	3
1	5	Virginia creeper	3
1	5	oak sp. (seedling)	1
1	5	unknown	2
1	6	water oak (seedling)	3
1	6	unknown	1
1	7	unknown	1
1	8	water oak (seedling)	1
1	8	unknown vine	1
1	9	palmetto	1
1	10	Chinese tallow	4
1	10	dewberry	2
1	10	water oak	1
1	10	poison ivy	2
2	1	sweet gum	1
2	1	palmetto	1
2	1	poison ivy	3
2	2	bare dirt	–
2	3	tree privet	2
2	3	palmetto	2
2	4	poison ivy	4
2	4	unknown vine	2
2	5	Chinese privet	4
2	5	palmetto	1
2	5	winged elm	2
2	6	water oak	1
2	6	Virginia creeper	2
2	6	Chinese privet	2
2	6	poison ivy	1
2	6	unknown vine	1
2	7	buckeye	2
2	7	Chinese privet	1
2	7	palmetto	1

Transect	Plot	Common name	Number in plot
2	8	winged elm	1
2	9	winged elm	1
2	9	unknown	1
2	10	tree privet	1
2	10	Chinese privet	2
3	1	palmetto	1
3	1	cow oak	1
3	2	water oak	1
3	2	Chinese privet	1
3	2	unknown vine	1
3	3	water oak	1
3	3	muscadine	1
3	4	common greenbrier	2
3	4	water oak	2
3	4	dewberry	1
3	5	Chinese privet	3
3	6	muscadine	1
3	7	Chinese privet	2
3	7	tree privet	1
3	8	palmetto	1
3	8	water oak	1
3	9	Chinese privet	1
3	10	Japanese climbing fern	1
3	10	unknown vine	1
3	10	dewberry	1
3	10	Chinese privet	6
4	1	Chinese privet	6
4	1	water oak	1
4	1	dewberry	1
4	1	red oak	1
4	1	ardisia	1
4	2	magnolia	1
4	2	peppervine	1
4	2	Virginia creeper	3
4	2	Chinese privet	1
4	2	common greenbrier	2
4	3	Chinese privet	3
4	3	Virginia creeper	3
4	3	common greenbrier	2
4	4	muscadine	1
4	4	common greenbrier	1
4	4	Chinese privet	2
4	5	Chinese privet	1
4	6	tree privet	1
4	6	muscadine	1
4	6	poison ivy	2
4	6	dewberry	3
4	7	muscadine	1
4	8	bare dirt	–

Transect	Plot	Common name	Number in plot
4	9	tree privet	1
4	9	Virginia creeper	4
4	9	Chinese privet	1
4	9	common greenbrier	1
4	9	unknown vine	1
4	10	Chinese privet	8
4	10	Virginia creeper	1
5	1	dewberry	4
5	1	Japanese climbing fern	1
5	1	poison ivy	11
5	1	unknown vine	2
5	1	common greenbrier	1
5	1	Chinese privet	1
5	2	Chinese privet	1
5	2	tree privet	1
5	3	Virginia creeper	2
5	3	common greenbrier	1
5	3	water oak	1
5	3	muscadine	1
5	4	Virginia creeper	4
5	4	musclewood (seedling)	13
5	4	poison ivy	1
5	5	bare dirt	–
5	6	palmetto	1
5	6	winged elm	4
5	6	Chinese privet	1
5	7	Virginia creeper	2
5	7	American elm	1
5	8	tree privet	1
5	8	musclewood	1
5	8	Virginia creeper	3
5	8	unknown vine	1
5	9	Chinese privet	2
5	9	Virginia creeper	1
5	9	tree privet	1
5	10	dewberry	3
5	10	poison ivy	16
5	10	Chinese privet	2
5	10	common greenbrier	1
5	10	tree privet	1

Bottomland 2
Summer 2007

Transect	Plot	Common name	Number found
1	1	winged elm	5
1	1	Virginia creeper	2
1	1	tree privet	1
1	1	Chinese privet	1
1	2	bare dirt	–
1	3	dewberry	3
1	3	greenbrier sp.	1
1	3	honeysuckle	1
1	3	Virginia creeper	2
1	4	muscadine	1
1	4	dewberry	3
1	4	Chinese tallow	1
1	4	Virginia creeper	3
1	4	greenbrier sp.	1
1	5	American elm	4
1	5	honeysuckle	1
1	5	Virginia creeper	1
1	5	poison ivy	1
1	5	muscadine	1
1	6	dewberry	3
1	6	poison ivy	1
1	6	honeysuckle	2
1	6	hickory	1
1	6	American elm	1
1	7	American elm	4
1	7	poison ivy	1
1	7	muscadine	1
1	7	Chinese privet	1
1	8	Virginia creeper	1
1	8	poison ivy	1
1	8	muscadine	1
1	8	honeysuckle	1
1	9	nandina	1
1	9	greenbrier sp.	1
1	9	Virginia creeper	1
1	10	dewberry	1
1	10	Chinese tallow	2
1	10	American elm	11
1	10	Chinese privet	1
1	10	tree privet	1
1	10	Virginia creeper	1
1	10	poison ivy	1
2	1	red oak	1
2	1	honeysuckle	1
2	1	dewberry	1
2	1	Chinese privet	1

Transect	Plot	Common name	Number in plot
2	2	honeysuckle	1
2	2	poison ivy	1
2	3	water oak	1
2	3	poison ivy	1
2	3	honeysuckle	1
2	3	Chinese privet	4
2	3	Virginia creeper	1
2	4	cow oak (tree)	1
2	4	honeysuckle	1
2	4	crossvine	1
2	5	honeysuckle	1
2	5	poison ivy	1
2	5	trumpet creeper	1
2	5	red oak	2
2	6	crossvine	1
2	6	trumpet creeper	1
2	6	water oak	1
2	6	honeysuckle	1
2	6	unknown vine	1
2	6	poison ivy	1
2	7	water oak	1
2	7	greenbrier sp.	2
2	7	crossvine	1
2	8	American elm	4
2	8	muscadine	2
2	8	honeysuckle	1
2	8	red maple	1
2	9	honeysuckle	1
2	9	poison ivy	3
2	9	trumpet creeper	1
2	9	greenbrier sp.	2
2	9	Virginia creeper	1
2	10	poison ivy	1
2	10	honeysuckle	1
2	10	Virginia creeper	1
2	10	water oak	1
2	10	dewberry	1
3	1	muscadine	1
3	1	Chinese privet	3
3	1	red oak	1
3	1	American elm	2
3	1	poison ivy	1
3	2	red maple	2
3	2	boxelder	1
3	2	American elm	4
3	3	palmetto	1
3	3	Virginia creeper	1
3	3	American elm	1
3	3	crossvine	1

Transect	Plot	Common name	Number in plot
3	3	greenbrier sp.	1
3	4	dewberry	1
3	4	poison ivy	3
3	4	muscadine	1
3	4	Virginia creeper	1
3	4	greenbrier sp.	1
3	4	pawpaw	1
3	5	honeysuckle	3
3	5	Virginia creeper	5
3	6	trumpet creeper	1
3	6	Virginia creeper	2
3	6	honeysuckle	3
3	7	honeysuckle	2
3	7	trumpet creeper	2
3	7	dewberry	1
3	7	greenbrier sp.	1
3	7	American elm	1
3	8	Chinese privet	1
3	8	greenbrier sp.	2
3	8	peppervine	1
3	8	American elm	19
3	9	muscadine	2
3	9	American elm (tree)	6
3	9	boxelder	1
3	9	Chinese privet	1
3	9	red maple	1
3	10	Chinese privet	4
3	10	American elm	2
3	10	Virginia creeper	1
3	10	crossvine	1
3	10	trumpet creeper	2
4	1	Virginia creeper	1
4	1	honeysuckle	1
4	1	dewberry	1
4	1	poison ivy	2
4	1	sugarberry	1
4	2	American elm (tree)	2
4	2	Virginia creeper	1
4	2	red maple	1
4	2	poison ivy	2
4	3	Virginia creeper	1
4	3	honeysuckle	1
4	3	Chinese privet	1
4	3	American elm	1
4	3	poison ivy	1
4	4	greenbrier sp.	1
4	4	Virginia creeper	2
4	4	honeysuckle	1
4	4	poison ivy	1

Transect	Plot	Common name	Number in plot
4	5	dewberry	1
4	5	trumpet creeper	1
4	5	honeysuckle	2
4	5	sugarberry	13
4	6	sugarberry	13
4	6	water oak	1
4	7	Chinese privet	1
4	7	trumpet creeper	1
4	7	American elm	1
4	7	Virginia creeper	3
4	7	greenbrier sp.	4
4	7	crossvine	1
4	7	poison ivy	2
4	8	poison ivy	4
4	8	dewberry	1
4	8	Virginia creeper	1
4	8	greenbrier sp.	1
4	9	sweetgum	1
4	9	Virginia creeper	1
4	9	poison ivy	1
4	9	Chinese privet	1
4	10	American elm (tree)	1
4	10	Virginia creeper	2
4	10	boxelder	1
5	1	sugarberry (tree)	1
5	1	dewberry	1
5	1	bamboo	1
5	1	trumpet creeper	1
5	2	poison ivy	1
5	2	red maple	2
5	2	Virginia creeper	4
5	2	honeysuckle	1
5	3	poison ivy	2
5	3	honeysuckle	2
5	3	Virginia creeper	1
5	4	cow oak	1
5	4	poison ivy	1
5	4	Virginia creeper	3
5	4	honeysuckle	1
5	4	dewberry	1
5	4	Chinese privet	1
5	5	dewberry	5
5	5	poison ivy	2
5	5	American elm	2
5	5	honeysuckle	1
5	5	bamboo	1
5	6	Chinese privet	2
5	6	honeysuckle	1
5	6	American elm	2

Transect	Plot	Common name	Number in plot
5	7	red maple	1
5	7	dewberry	3
5	7	honeysuckle	1
5	7	Virginia creeper	5
5	7	poison ivy	1
5	8	bamboo	1
5	8	dewberry	1
5	8	honeysuckle	2
5	8	poison ivy	3
5	8	American elm	3
5	9	greenbrier sp.	2
5	9	dewberry	5
5	9	honeysuckle	1
5	10	Chinese privet	1
5	10	honeysuckle	1
5	10	dewberry	3
5	10	trumpet creeper	1
5	10	greenbrier sp.	1

Bottomland 3
Summer 2007

Transect	Plot	Common name	Number found
1	1	loblolly pine	2
1	1	honeysuckle	1
1	1	greenbrier sp.	1
1	2	greenbrier sp.	1
1	2	poison ivy	4
1	2	honeysuckle	3
1	2	Virginia creeper	1
1	3	poison ivy	3
1	3	Virginia creeper	1
1	3	honeysuckle	1
1	3	Chinese privet	7
1	3	muscadine	1
1	4	muscadine	3
1	4	yaupon	1
1	4	Chinese privet	1
1	4	Virginia creeper	2
1	4	greenbrier sp.	2
1	4	poison ivy	2
1	5	greenbrier sp.	2
1	5	poison ivy	5
1	5	honeysuckle	2
1	5	Chinese privet	1
1	5	unknown	1
1	5	willow oak	1
1	6	greenbrier sp.	6
1	6	poison ivy	9
1	6	Chinese privet	1
1	6	dewberry	1
1	7	Chinese privet	3
1	7	poison ivy	6
1	7	honeysuckle	1
1	7	water oak	1
1	7	unknown	1
1	7	willow oak	1
1	7	greenbrier sp.	5
1	8	unknown	1
1	8	Chinese privet	5
1	8	muscadine	5
1	8	poison ivy	6
1	8	honeysuckle	2
1	9	Chinese privet	7
1	9	greenbrier sp.	3
1	9	poison ivy	1
1	9	Virginia creeper	2
1	9	honeysuckle	2
1	10	Chinese privet	1

Transect	Plot	Common name	Number found
1	10	poison ivy	3
1	10	greenbrier sp.	2
1	10	yaupon	1
2	1	water oak	1
2	1	pawpaw	1
2	1	red oak	1
2	1	honeysuckle	6
2	1	willow oak	2
2	1	Japanese climbing fern	2
2	2	yaupon	12
2	2	honeysuckle	2
2	2	red oak	1
2	3	Chinese privet	2
2	3	bamboo	1
2	3	willow oak	1
2	3	poison ivy	1
2	3	Japanese climbing fern	1
2	4	greenbrier sp.	1
2	4	red oak	1
2	4	Chinese privet	3
2	4	honeysuckle	2
2	4	greenbrier sp.	1
2	4	poison ivy	2
2	5	willow oak	5
2	5	Chinese privet	2
2	5	greenbrier sp.	1
2	5	sweetgum	1
2	5	red oak	3
2	5	muscadine	1
2	5	poison ivy	1
2	6	buckeye	2
2	6	greenbrier sp.	2
2	6	Chinese privet	2
2	6	willow oak	3
2	7	yaupon	13
2	7	willow oak	1
2	8	willow oak	1
2	8	honeysuckle	2
2	8	red maple	1
2	8	Virginia creeper	1
2	9	Chinese privet	1
2	9	yaupon	1
2	9	red oak	1
2	9	greenbrier sp.	1
2	9	honeysuckle	5
2	10	water oak	2
2	10	willow oak	2
2	10	red oak	1
2	10	honeysuckle	7

Transect	Plot	Common name	Number found
2	10	Virginia creeper	1
3	1	Virginia creeper	5
3	1	Japanese climbing fern	1
3	1	poison ivy	1
3	1	French mulberry	2
3	1	honeysuckle	1
3	1	Chinese privet	1
3	2	Chinese privet	4
3	2	greenbrier sp.	2
3	2	honeysuckle	3
3	2	red oak	1
3	2	Japanese climbing fern	3
3	3	poison ivy	3
3	3	Virginia creeper	2
3	3	Chinese privet	5
3	3	French mulberry	1
3	3	honeysuckle	1
3	4	water oak	1
3	4	yaupon	1
3	4	Chinese privet	1
3	5	Chinese privet	5
3	5	poison ivy	1
3	6	Chinese privet	4
3	6	French mulberry	1
3	7	honeysuckle	3
3	7	Chinese privet	6
3	7	greenbrier sp.	2
3	7	Virginia creeper	1
3	8	Chinese privet	5
3	8	red maple	1
3	8	Virginia creeper	1
3	9	American elm	1
3	9	greenbrier sp.	1
3	9	Chinese privet	9
3	9	Virginia creeper	1
3	9	red oak	1
3	10	Chinese privet	1
3	10	French mulberry	1
3	10	honeysuckle	2
4	1	Chinese privet	5
4	1	poison ivy	1
4	1	Japanese climbing fern	1
4	1	water oak	1
4	2	greenbrier sp.	3
4	2	poison ivy	1
4	2	Chinese privet	5
4	3	Virginia creeper	1
4	3	greenbrier sp.	1
4	3	Chinese privet	2

Transect	Plot	Common name	Number found
4	3	dewberry	1
4	3	honeysuckle	2
4	4	Virginia creeper	2
4	4	Chinese privet	6
4	5	Chinese privet	7
4	5	honeysuckle	1
4	6	red maple	1
4	6	unknown	1
4	6	Chinese privet	2
4	6	bamboo	1
4	7	unknown vine	1
4	7	Chinese privet	5
4	7	poison ivy	1
4	7	greenbrier sp.	3
4	7	unknown woody	1
4	8	Chinese privet	8
4	8	Virginia creeper	1
4	8	honeysuckle	1
4	8	Japanese climbing fern	1
4	8	water oak	1
4	9	Chinese privet	4
4	9	greenbrier sp.	1
4	9	bamboo	1
4	9	unknown	1
4	10	Chinese privet	8
4	10	bamboo	2
4	10	greenbrier sp.	1
5	1	greenbrier sp.	2
5	1	Chinese privet	2
5	1	honeysuckle	1
5	2	Virginia creeper	5
5	2	Chinese privet	6
5	2	red oak	2
5	2	unknown	1
5	2	honeysuckle	2
5	2	greenbrier sp.	1
5	3	Chinese privet	9
5	3	Virginia creeper	3
5	3	honeysuckle	1
5	3	poison ivy	2
5	3	greenbrier sp.	2
5	3	Japanese climbing fern	1
5	3	water oak	2
5	4	American elm	1
5	4	muscadine	1
5	4	water oak	1
5	4	yaupon	1
5	4	Chinese privet	2
5	4	honeysuckle	5

Transect	Plot	Common name	Number found
5	4	Virginia creeper	4
5	4	greenbrier sp.	3
5	4	red oak	1
5	5	poison ivy	2
5	5	Virginia creeper	3
5	5	greenbrier sp.	1
5	5	red oak	1
5	5	American elm	1
5	5	Chinese privet	3
5	6	American elm	1
5	6	water oak	1
5	6	red oak	1
5	6	honeysuckle	1
5	6	poison ivy	8
5	6	Virginia creeper	3
5	6	muscadine	1
5	6	Chinese privet	4
5	7	American elm	1
5	7	poison ivy	4
5	7	muscadine	2
5	7	honeysuckle	1
5	7	red oak	4
5	7	Chinese privet	1
5	8	American elm	2
5	8	red oak	1
5	8	water oak	4
5	8	Chinese privet	6
5	8	unknown	3
5	8	greenbrier sp.	4
5	8	Virginia creeper	3
5	8	honeysuckle	1
5	8	red maple	1
5	8	poison ivy	2
5	9	Chinese privet	4
5	9	American elm	1
5	9	red maple	1
5	9	water oak	3
5	9	greenbrier sp.	2
5	9	unknown	1
5	9	honeysuckle	1
5	9	Virginia creeper	2
5	10	Chinese privet	4
5	10	American elm	1
5	10	honeysuckle	4
5	10	greenbrier sp.	3
5	10	poison ivy	2
5	10	Virginia creeper	2

Upland 1

Summer 2007

Transect	Plot	Common name	Number found
1	1	American holly	8
1	1	virginia creeper	2
1	1	greenbrier	1
1	1	sugarberry	1
1	1	Chinese privet	2
1	1	Chinese privet (seedlings)	~780
1	2	Chinese privet	2
1	2	muscadine	1
1	2	American holly	4
1	2	Chinese privet (seedlings)	~ 500
1	3	sugarberry	4
1	3	American holly	13
1	3	Chinese privet (seedlings)	~700
1	4	Chinese privet	1
1	4	sugarberry	7
1	4	American holly	7
1	4	Chinese privet (seedlings)	~300
1	4	poison ivy	1
1	5	sugarberry	5
1	5	American holly	4
1	5	virginia creeper	1
1	5	chinese privet	1
1	5	Chinese privet (seedlings)	~80
1	6	American holly	4
1	6	poison ivy	1
1	6	sugarberry	5
1	6	Chinese privet (seedlings)	~300
1	7	poison ivy	1
1	7	American holly	4
1	7	virginia creeper	1
1	7	sugarberry	1
1	7	Chinese privet (seedlings)	~250
1	8	sugarberry	9
1	8	Chinese privet (seedlings)	~100
1	9	virginia creeper	2
1	9	sugarberry	12
1	9	Chinese privet (seedlings)	~280
1	10	chinese privet	2
1	10	American holly	4
1	10	poison ivy	1
1	10	Chinese privet (seedlings)	~500
2	1	chinese privet	15
2	1	poison ivy	3
2	1	peppervine	3
2	1	water oak	2
2	1	cherrybark oak	1

Transect	Plot	Common name	Number found
2	1	cherrylaurel	4
2	1	Chinese privet (seedlings)	~260
2	2	cherrylaurel	15
2	2	water oak	1
2	2	virginia creeper	2
2	2	sugarberry	2
2	2	Chinese privet (seedlings)	~160
2	3	muscadine	1
2	3	cherrylaurel	14
2	3	Chinese privet (seedlings)	~30
2	3	chinese parasol tree	3
2	4	chinese parasol tree	11
2	4	cherrylaurel	6
2	4	ardisia	1
2	4	chinese privet	2
2	4	Chinese privet (seedlings)	~10
2	5	cherrylaurel	2
2	5	chinese privet	2
2	5	water oak	2
2	5	chinese parasol tree	22
2	5	ardisia	1
2	6	sandy bottom	–
2	7	ardisia	12
2	7	Chinese privet (seedlings)	~20
2	7	chinese parasol tree	26
2	8	chinese privet	2
2	8	cherrylaurel	17
2	8	chinese parasol tree	6
2	8	Chinese privet (seedlings)	~50
2	8	ardisia	1
2	9	chinese privet	5
2	9	cherrylaurel	11
2	9	chinese parasol tree	4
2	9	Chinese privet (seedlings)	8
2	10	cherrylaurel	10
2	10	water oak	3
2	10	chinese privet	3
2	10	ardisia	1
2	10	Chinese privet (seedlings)	11
3	1	chinese privet	11
3	1	cherrylaurel	7
3	1	chinese parasol tree	11
3	1	Chinese privet (seedlings)	~170
3	2	cherrylaurel	5
3	2	winged elm	1
3	2	chinese privet	6
3	2	chinese parasol tree	26
3	2	virginia creeper	1
3	2	Chinese privet (seedlings)	~140

Transect	Plot	Common name	Number found
3	3	virginia creeper	3
3	3	ardisia	2
3	3	chinese parasol tree	34
3	3	poison ivy	12
3	3	cherrylaurel	3
3	3	winged elm	1
3	3	Chinese privet (seedlings)	~110
3	3	red oak sp.	1
3	4	cherrylaurel	13
3	4	virginia creeper	8
3	4	chinese privet	2
3	4	chinese parasol tree	3
3	4	poison ivy	6
3	4	winged elm	5
3	4	Chinese privet (seedlings)	~70
3	5	cherrylaurel	8
3	5	winged elm	13
3	5	chinese parasol tree	4
3	5	red oak sp.	1
3	5	Chinese privet (seedlings)	~110
3	6	chinese parasol tree	16
3	6	Chinese privet (seedlings)	~380
3	6	chinese privet	3
3	6	cherrylaurel	3
3	6	water oak	1
3	6	poison ivy	3
3	6	virginia creeper	1
3	6	winged elm	2
3	7	cherrylaurel	6
3	7	chinese privet	5
3	7	chinese parasol tree	17
3	7	Chinese privet (seedlings)	~85
3	8	chinese parasol tree	8
3	8	poison ivy	6
3	8	virginia creeper	4
3	8	cherrylaurel	7
3	8	winged elm	2
3	8	Chinese privet (seedlings)	~130
3	9	ardisia	1
3	9	cherrylaurel	7
3	9	japanese privet (tree)	3
3	9	chinese privet	4
3	9	Chinese privet (seedlings)	~180
3	9	virginia creeper	1
3	9	winged elm	2
3	10	chinese privet	4
3	10	yaupon holly	1
3	10	virginia creeper	1
3	10	cherrylaurel	7

Transect	Plot	Common name	Number found
3	10	Chinese privet (seedlings)	~270
4	1	peppervine	1
4	1	virginia creeper	2
4	1	cherrylaurel	1
4	1	Chinese privet (seedlings)	~330
4	2	poison ivy	~100
4	2	water oak	1
4	2	chinese privet	1
4	2	Chinese privet (seedlings)	~90
4	2	cherrylaurel	1
4	2	virginia creeper	2
4	3	poison ivy	~90
4	3	oak sp.	1
4	3	chinese privet	1
4	3	Chinese privet (seedlings)	30
4	4	Chinese privet (seedlings)	~300
4	4	poison ivy	3
4	4	dewberry	1
4	4	red oak sp.	1
4	4	honeysuckle	1
4	5	chinese privet	3
4	5	winged elm	2
4	5	unknown vine	2
4	5	poison ivy	1
4	5	Chinese privet (seedlings)	~200
4	6	cherrylaurel	1
4	6	Chinese privet (seedlings)	~360
4	7	winged elm	2
4	7	virginia creeper	4
4	7	water oak	1
4	7	chinese privet	2
4	7	Chinese privet (seedlings)	~190
4	8	chinese privet	5
4	8	virginia creeper	1
4	8	Chinese privet (seedlings)	~120
4	8	dewberry	3
4	9	water oak	3
4	9	poison ivy	~60
4	9	winged elm	1
4	9	cherrylaurel	1
4	9	virginia creeper	1
4	9	chinese privet	5
4	9	Chinese privet (seedlings)	~140
4	10	chinese privet	7
4	10	Chinese privet (seedlings)	~120
5	1	water oak	7
5	1	chinese privet	2
5	1	virginia creeper	2
5	1	Chinese privet (seedlings)	~50

Transect	Plot	Common name	Number found
5	1	poison ivy	2
5	1	cherrylaurel	2
5	2	cherrylaurel	2
5	2	muscadine	2
5	2	chinese privet	2
5	2	virginia creeper	2
5	3	muscadine	3
5	3	crossvine	1
5	3	cherrylaurel	5
5	3	yaupon holly	2
5	3	poison ivy	10
5	4	chinese privet	2
5	4	water oak	2
5	4	virginia creeper	2
5	4	poison ivy	2
5	5	Chinese privet (seedlings)	3
5	5	muscadine	1
5	6	water oak	2
5	6	Chinese privet (seedlings)	4
5	7	cherrylaurel	2
5	7	poison ivy	3
5	8	muscadine	2
5	8	poison ivy	4
5	8	virginia creeper	2
5	9	Chinese privet (seedlings)	2
5	9	virginia creeper	1
5	9	dewberry	1
5	10	cherrylaurel	2
5	10	water oak	1
5	10	chinese privet	1
5	10	Chinese privet (seedlings)	1

APPENDIX B: FLOWER PRODUCTION MEASUREMENTS

Observation	Stage	Diam (mm)	Clusters/plant	Flrs/cluster 1	Flrs/cluster 2	Flrs/cluster 3	Avg flrs/cluster	Avg flrs per plant
1	Sm adult	11.82	26	29	43	55	42.33	1100.67
2	Sm adult	10.29	45	29	50	31	36.67	1650.00
3	Sm adult	15.44	50	50	38	72	53.33	2666.67
4	Sm adult	12.45	14	55	46	45	48.67	681.33
5	Sm adult	15.46	31	40	40	49	43.00	1333.00
6	Med adult	30.75	79	46	58	50	51.33	4055.33
7	Med adult	21.22	110	48	61	60	56.33	6196.67
8	Med adult	28.26	67	44	74	41	53.00	3551.00
9	Med adult	25.65	100	55	57	45	52.33	5233.33
10	Med adult	37.77	104	48	41	74	54.33	5650.67
11	Lrg adult	87.15	2819	81	54	59	64.67	182295.33
12	Lrg adult	67.95	289	43	41	81	55.00	15895.00
13	Lrg adult	83.95	114	56	79	42	59.00	6726.00
14	Lrg adult	65.68	347	57	31	51	46.33	16077.67

APPENDIX C: FRUIT PRODUCTION MEASUREMENTS

Observation	Site	Stage	Diam (mm)	Number of fruits/plant
1	Bottomland 1	Small adult	11.62	312
2	Bottomland 1	Small adult	11.69	314
3	Bottomland 1	Small adult	15.66	75
4	Bottomland 1	Small adult	17.35	31
5	Bottomland 1	Small adult	17.62	93
6	Bottomland 1	Medium adult	25.26	57
7	Bottomland 1	Medium adult	33.78	358
8	Bottomland 1	Medium adult	34.00	704
9	Bottomland 1	Medium adult	42.60	470
10	Bottomland 1	Medium adult	49.35	671
11	Camp Whispering Pines	Large adult	54.04	7380
12	Camp Whispering Pines	Large adult	73.12	15352
13	Bottomland 1	Large adult	74.15	1291
14	Camp Whispering Pines	Large adult	81.09	1814
15	Camp Whispering Pines	Large adult	82.28	12097
16	Camp Whispering Pines	Large adult	86.55	1820

APPENDIX D: AGE AND SIZE MEASUREMENTS

Observation	Site	Diam 1 (mm)	Diam 2 (mm)	Diam 3 (mm)	Avg diam (mm)	Age
1	Bottomland 1	41.08	50.36	−	45.72	9
2	Bottomland 1	10.80	10.23	−	10.52	4
3	Bottomland 1	26.12	34.12	−	30.12	8
4	Bottomland 1	37.47	45.31	−	41.39	9
5	Bottomland 1	41.18	44.56	−	42.87	16
6	Bottomland 1	23.38	21.53	−	22.46	10
7	Bottomland 1	45.67	35.38	−	40.53	7
8	Bottomland 1	14.37	16.53	−	15.45	5
9	Bottomland 1	27.03	23.27	−	25.15	7
10	Bottomland 1	24.90	32.18	−	28.54	8
11	Upland 1	190.00	161.00	200.00	183.67	22
12	Upland 1	132.00	122.00	131.00	128.33	17
13	Upland 1	132.00	110.00	123.00	121.67	16

APPENDIX E: LIFE HISTORY TABLE

Stage	Duration (yrs)	Number alive (*Nx*)	Survival (*lx*)	Mortality (*dx*)	Mortality rate (*qx*)	Survival rate (*px*)	Annual survivorship (σ)	Seeds/plant (*mx*)
Seedling	1	1000	1.000	0.385	0.385	0.615	0.615	0
Juvenile	3	615	0.615	0.394	0.641	0.359	0.710	0
Sm adult	6	221	0.221	0.051	0.230	0.770	0.957	172
Med adult	5	170	0.170	0.026	0.150	0.850	0.968	470
Lrg adult	10	145	0.145	0.022	0.150	0.850	0.984	6879

APPENDIX F: EQUATIONS GENERATING MATRIX ELEMENTS

Equations, definitions, formulas, and calculations for matrix transition parameters used in *L. sinense* stage-based matrix projection model; adapted from Crowder et al. (1994)

Parameter	Definition	Formula
P	Probability of surviving and remaining in stage *i*	$P_i = \sigma * (1 - \rho)$
G	Probability of surviving and growing to stage *i* + 1	$G_i = \sigma * \rho$

Seedling P and G

$m = -\ln(0.615) = 0.4861$

$\frac{0.4861}{1} = 0.4861$

$m_2 = e^{-0.4861} = 0.615$

$\rho = \frac{(0.615)^1 - (0.615)^0}{(0.615)^1 - 1} = \frac{0.615 - 1}{0.615(1)} = 1$

$P_{SEEDLING} = 0.615\ (1 - 1) = 0$

$G_{SEEDLING} = 0.615\ (1) = \ 0.615$

Juvenile P and G

$m = -\ln(0.359) = 1.023$

$\frac{1.023}{3} = 0.341$

$m_2 = e^{-0.341} = 0.71$

$\rho = \frac{(0.71)^3 - (0.71)^2}{(0.71)^3 - 1} = \frac{0.3579 - 0.5041}{.3579 - 1} = \frac{-0.1462}{-0.6421} = 0.227$

$P_{JUVENILE} = 0.71\ (1 - 0.227) = 0.54883$

$G_{JUVENILE} = 0.71\ (.227) = \ 0.04767$

Small Adult P and G

$m = -\ln(0.770) = 0.261$

$\frac{0.261}{6} = 0.0436$

$m_2 = e^{-0.0436} = 0.957$

$\rho = \frac{(0.957)^6 - (0.957)^5}{(0.957)^6 - 1} = \frac{0.7682 - 0.8027}{.7682 - 1} = \frac{-0.0345}{-0.2318} = 0.1488$

$\mathrm{P}_{\text{SMALL ADULT}} = 0.957\ (1 - 0.1488) = 0.8146$

$\mathrm{G}_{\text{SMALL ADULT}} = 0.957\ (0.1488) = 0.1424$

Medium Adult P and G

$m = -\ln(0.85) = 0.1625$

$\frac{0.1625}{5} = 0.0325$

$m_2 = e^{-0.0325} = 0.968$

$\rho = \frac{(0.968)^5 - (0.968)^4}{(0.968)^5 - 1} = \frac{0.8499 - 0.878}{.8499 - 1} = \frac{-0.0281}{-0.1501} = 0.1872$

$\mathrm{P}_{\text{MEDIUM ADULT}} = 0.968\ (1 - 0.1872) = 0.7868$

$\mathrm{G}_{\text{MEDIUM ADULT}} = 0.968\ (0.1872) = 0.1812$

Large Adult P

$m = -\ln(0.85) = 0.1625$

$\frac{0.1625}{10} = 0.01625$

$m_2 = e^{-0.01625} = 0.9839$

$\rho = \frac{(0.984)^{10} - (0.984)^9}{(0.984)^{10} - 1} = \frac{0.851 - 0.8649}{0.851 - 1} = \frac{-0.0139}{-0.149} = 0.0933$

$\mathrm{P}_{\text{LARGE ADULT}} = 0.984\ (1 - 0.0933) = 0.8922$

APPENDIX G: STAGE-BASED MATRICES

Growth chamber

	Seedling	Juvenile	Sm adult	Med adult	Lrg adult
Seedling	0	0	105.780	289.050	4230.585
Juvenile	0.615	0.549	0	0	0
Sm adult	0	0.048	0.815	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	0.892

λ = 2.26

Greenhouse

	Seedling	Juvenile	Sm adult	Med adult	Lrg adult
Seedling	0	0	98.814	270.015	3951.986
Juvenile	0.575	0.549	0	0	0
Sm adult	0	0.048	0.815	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	0.892

λ = 2.20

Field

	Seedling	Juvenile	Sm adult	Med adult	Lrg adult
Seedling	0	0	28.294	77.315	1131.596
Juvenile	0.165	0.549	0	0	0
Sm adult	0	0.048	0.815	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	0.892

λ = 1.48

APPENDIX H: PERTURBATION ANALYSIS

Growth chamber

Reduce seedling and juvenile transitions by 50% and small adult stage by 50%

	Seedling	Juvenile	Sm adult	Med adult	Lrg adult
Seedling	0	0	105.780	289.050	4230.585
Juvenile	**0.308**	0.549	0	0	0
Sm adult	0	**0.024**	**0.408**	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	0.892

λ = 1.66

Reduce adult fecundity by 50%

	Seedling	Juvenile	Sm adult	Med adult	Lrg adult
Seedling	0	0	**52.890**	**144.525**	**2115.293**
Juvenile	0.615	0.549	0	0	0
Sm adult	0	0.048	0.815	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	0.892

λ = 1.98

Eliminate adult fecundity

	Seedling	Juvenile	Sm adult	Med adult	Lrg adult
Seedling	0	0	**0**	**0**	**0**
Juvenile	0.615	0.549	0	0	0
Sm adult	0	0.048	0.815	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	0.892

λ = 0.89

Reduce seedling and juvenile transitions by 50%, small adult stage by 50%, and small adult fecundity by 50%

	Seedling	Juvenile	Sm adult	Med adult	Lrg adult
Seedling	0	0	**52.890**	289.050	4230.585
Juvenile	**0.308**	0.549	0	0	0
Sm adult	0	**0.024**	**0.408**	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	0.892

λ = 1.62

Reduce seedling, juvenile, and small adult transitions by 50%, small adult stage by 50%, and small adult fecundity by 50%

	Seedling	**Juvenile**	**Sm adult**	**Med adult**	**Lrg adult**
Seedling	0	0	**52.890**	289.050	4230.585
Juvenile	**0.308**	0.549	0	0	0
Sm adult	0	**0.024**	**0.408**	0	0
Med adult	0	0	**0.071**	0.787	0
Lrg adult	0	0	0	0.181	0.892

λ = 1.50

Reduce seedling and juvenile transitions by 50%, small adult stage by 50%, and adult fecundity by 50%

	Seedling	**Juvenile**	**Sm adult**	**Med adult**	**Lrg adult**
Seedling	0	0	**52.890**	**144.525**	**2115.293**
Juvenile	**0.308**	0.549	0	0	0
Sm adult	0	**0.024**	**0.408**	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	0.892

λ = 1.50

Greenhouse

Reduce seedling and juvenile transitions by 50% and small adult stage by 50%

	Seedling	Juvenile	Sm adult	Med adult	Lrg adult
Seedling	0	0	98.814	270.015	3951.986
Juvenile	**0.288**	0.549	0	0	0
Sm adult	0	**0.024**	**0.408**	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	0.892

λ = 1.63

Reduce adult fecundity by 50%

	Seedling	Juvenile	Sm adult	Med adult	Lrg adult
Seedling	0	0	**49.407**	**135.008**	**1975.993**
Juvenile	0.575	0.549	0	0	0
Sm adult	0	0.048	0.815	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	0.892

λ = 1.93

Eliminate adult fecundity

	Seedling	Juvenile	Sm adult	Med adult	Lrg adult
Seedling	0	0	**0.000**	**0.000**	**0.000**
Juvenile	0.575	0.549	0	0	0
Sm adult	0	0.048	0.815	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	0.892

λ = 0.89

Reduce seedling and juvenile transitions by 50%, small adult stage by 50%, and small adult fecundity by 50%

	Seedling	Juvenile	Sm adult	Med adult	Lrg adult
Seedling	0	0	**49.407**	270.015	3951.986
Juvenile	**0.288**	0.549	0	0	0
Sm adult	0	**0.024**	**0.408**	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	0.892

λ = 1.59

Reduce seedling, juvenile, and small adult transitions by 50%, small adult stage by 50%, and small adult fecundity by 50%

	Seedling	**Juvenile**	**Sm adult**	**Med adult**	**Lrg adult**
Seedling	0	0	**49.407**	**135.008**	**1975.993**
Juvenile	**0.288**	0.549	0	0	0
Sm adult	0	**0.024**	**0.408**	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	0.892

λ = 1.47

Reduce seedling and juvenile transitions by 50%, small adult stage by 50%, and adult fecundity by 50%

	Seedling	**Juvenile**	**Sm adult**	**Med adult**	**Lrg adult**
Seedling	0	0	**49.407**	270.015	3951.986
Juvenile	**0.288**	0.549	0	0	0
Sm adult	0	**0.024**	**0.408**	0	0
Med adult	0	0	**0.071**	0.787	0
Lrg adult	0	0	0	0.181	0.892

λ = 1.47

Field

Reduce seedling and juvenile transitions by 50% and small adult stage by 50%

	Seedling	Juvenile	Sm adult	Med adult	Lrg adult
Seedling	0	0	28.294	77.315	1131.596
Juvenile	**0.083**	0.549	0	0	0
Sm adult	0	**0.024**	**0.407**	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	0.892

λ = 1.19

Reduce seedling and juvenile transitions by 50% and small, medium and large adult stages by 50%

	Seedling	Juvenile	Sm adult	Med adult	Lrg adult
Seedling	0	0	28.294	77.315	1131.596
Juvenile	**0.083**	0.549	0	0	0
Sm adult	0	**0.024**	**0.407**	0	0
Med adult	0	0	0.142	**0.394**	0
Lrg adult	0	0	0	0.181	**0.446**

λ = 1.00

Reduce small adult fecundity by 50% and elminiate medium and large adult fecundity

	Seedling	Juvenile	Sm adult	Med adult	Lrg adult
Seedling	0	0	**14.147**	**0**	**0**
Juvenile	0.165	0.549	0	0	0
Sm adult	0	0.048	0.815	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	0.892

λ = 1.04

Reduce seedling and juvenile transitions by 50%, small adult stage by 50%, and large adult fecundity by 50%

	Seedling	Juvenile	Sm adult	Med adult	Lrg adult
Seedling	0	0	28.294	77.315	**565.798**
Juvenile	**0.083**	0.549	0	0	0
Sm adult	0	**0.024**	**0.407**	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	0.892

λ = 1.13

Reduce seedling and juvenile transitions by 50%, small and large adult stages by 50%, and large adult fecundity by 50%

	Seedling	**Juvenile**	**Sm adult**	**Med adult**	**Lrg adult**
Seedling	0	0	28.294	77.315	**565.798**
Juvenile	**0.083**	0.549	0	0	0
Sm adult	0	**0.024**	**0.407**	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	**0.446**

λ = 1.04

Reduce seedling and juvenile transitions by 50%, small and large adult stages by 50%, and small adult fecundity by 50%

	Seedling	**Juvenile**	**Sm adult**	**Med adult**	**Lrg adult**
Seedling	0	0	**14.147**	77.315	1131.596
Juvenile	**0.083**	0.549	0	0	0
Sm adult	0	**0.024**	**0.407**	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	**0.446**

λ = 1.09

Reduce seedling and juvenile transitions by 50%, small adult stage by 50%, and small and large adult fecundity by 50%

	Seedling	**Juvenile**	**Sm adult**	**Med adult**	**Lrg adult**
Seedling	0	0	**14.147**	77.315	**565.798**
Juvenile	**0.083**	0.549	0	0	0
Sm adult	0	**0.024**	**0.407**	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	0.892

λ = 1.12

Reduce juvenile transition by 50%, small and large adult stages by 50%, and large adult fecundity by 50%

	Seedling	**Juvenile**	**Sm adult**	**Med adult**	**Lrg adult**
Seedling	0	0	28.294	77.315	**565.798**
Juvenile	0.165	0.549	0	0	0
Sm adult	0	**0.024**	**0.407**	0	0
Med adult	0	0	0.142	0.787	0
Lrg adult	0	0	0	0.181	**0.446**

λ = 1.13

VITA

Metha Klock was born and raised in northern California where she first discovered her love of native plants and the outdoors. She received a Bachelor of Arts from Sarah Lawrence College in New York in 2001 and returned to California shortly after to pursue a job in publishing. She soon realized that her calling was in working to preserve natural areas, and obtained an internship with the Marin Headlands Native Plant Nursery, a park partner of the National Park Service. This led to a job as Restoration Coordinator at the Arastradero Preserve, an area that has been degraded though anthropogenic disturbances such as fire, ranching, and logging, and whose native plant composition is impacted by the encroachment of non-native invasive species. Questions about non-native invasive plant management and habitat restoration generated by these experiences led Metha to pursue a Master of Science in forestry at Louisiana State University. Metha plans to continue researching non-native invasive plant demography and contributing her knowledge of plant population biology to protecting native habitat.