INTEGRATING COMPLEX ECOLOGICAL INFORMATION TO DEVELOP A MANAGEMENT PLAN FOR CHINESE TALLOW (*SAPIUM SEBIFERUM* L. ROXB.) IN SOUTH GEORGIA

by

CHERYL MARIE MCCORMICK

(Under the Direction of C. RONALD CARROLL)

ABSTRACT

Managing pernicious invasive plant species is an essential component of maintaining biodiversity and restoring natural ecosystem structure and function. Chinese tallow (*Sapium sebiferum* L. Roxb.) is recognized as one of the most aggressive invaders of southeastern US wetland and coastal habitats. However, effective management of *S. sebiferum* is often obstructed by a lack of scientific information for management strategies, conflicting objectives, and a paucity of funding.

The first chapter is a comprehensive management plan for *S. sebiferum*, and includes a description of the biology and ecology of *S. sebiferum* and its history in the southeastern US. It provides a comprehensive overview of treatment methods for the species, including each method's advantages and disadvantages, timing, and case studies involving management of *S. sebiferum* on public lands.

In Chapter Two, I analyze the effects of feral hog (*Sus scrofa* L.) rooting behavior on *S. sebiferum* seedling recruitment and survivorship in island vs. mainland habitats as a function of hog density. I discuss the implications of tallow population regulation by hogs, and associated challenges to agencies mandated to eliminate both of these deleterious exotic species. My analysis indicates that at high densities of feral hogs such as occur on Ossabaw Island, feral hog rooting significantly increases the mortality of Chinese tallow seedlings; whereas at low densities such as occur in mainland ecosystems, there is little impact.

In Chapter Three, I present a scientific approach for prioritizing management objectives through the application of generalized linear models to predict seed crop quality based on morphological seed traits in 16 populations of *S. sebiferum* in mainland, coastal, and island habitats in south Georgia, USA. Based on analyses of generalized linear models (GLMs), I conclude that the use of such models to accurately predict seed crop quality of *S. sebiferum* populations is an ineffective tool for assisting land managers in developing priorities for tallow control. However, this technique does appear to be useful in identifying very high- and low-priority populations for management. The goal of this body of research is to merge sound science with judicious management strategies, resulting in effective conservation practices.

INDEX WORDS: Chinese tallow, *Sapium sebiferum*, management plan, invasive species, feral hog, rooting, *Sus scrofa*, Ossabaw Island, bottomland hardwood swamp, seed traits, generalized linear models, generalized linear mixed models

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M.A., The University of Georgia, 1998

A Dissertation Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2007

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DEDICATION

This work is dedicated to my grandfather, Francis G. McCormick (1920-1984), who inspired me to be inquisitive about the world and who instilled within me the values of unwavering loyalty, solid character and love of one’s family. In his understated and gentle manner, he embodied the guiding principles upon which I have humbly attempted to live my life. Rarely a day passes when I do not wonder whether “Poppy” would be proud of this small accomplishment on my part, and of the manner in which I’ve chosen to express joy, creativity and intellectual expression through my vocation.

“What is a scientist after all? It is a curious man looking through a keyhole,
the keyhole of nature, trying to know what's going on”

- Jacques Yves Cousteau

ACKNOWLEDGEMENTS

It has been an honor and a privilege to work under the direction of Ron Carroll, who has provided countless hours of invaluable mentoring, keen insight, and pragmatic management on this project. Ron will always be one of my greatest professional inspirations. Thank you, Ron, for everything. My deepest gratitude to Rebecca Sharitz, for whose endless patience and gentle encouragement I am forever indebted. It was a great honor to be mentored by a true paragon of wetlands research. Kathy Parker is a personal hero whose boundless energy, sharp, "big picture" intellect, and endearing personality inspires me in all realms of my life. All aspects of my work have greatly improved for her contribution. A special thanks to Laurie Fowler, who exudes positive energy and wisdom and without whom I am convinced the state of environmental policy in the State of Georgia would simply collapse. I have been inspired by the pragmatic, grounded research of Carl Jordan, whose logic, wisdom and cordiality I always appreciated. Thank you, Dr. Jordan for your review of my research; and for giving Institute graduate students the run of your farm. Lastly, Jim Hamrick elevated my research to levels I never imagined, through his high expectations, scientific rigor, and tremendous breadth and depth of plant ecology and genetics. Working with Jim was a professionally expansive and often very humbling experience. I am undoubtedly a higher-caliber scientist now than I was prior to working in your lab.

I would like to extend my gratitude to the Georgia Department of Natural Resources for providing funding that made this research possible. Mike Harris, Todd Holbrook, Jim Simmons, Andy Meadows, William "Darryl" Hartley, and Mark Dodd all ensured that my experiences on Ossabaw were positive, both personally and professionally.

My sincerest thanks go to Andrew Grosse and Jason Norman, without whose assistance throughout many seasons of field work on Ossabaw, I could not have sustained the data collection efforts. Their deep commitment to and passion for their vocation, coupled with an insatiable inquisitiveness about the natural world and determination to produce results of the very highest caliber, commands my respect and admiration. I consider each to be finest example of undergraduate student achievement that UGA has to offer, and the very brightest students with whom I have had the pleasure to work.

Though his influence appeared in the “11th hour”, Jim Sulentich, Executive Director of the Santa Lucia Conservancy, gave me one *very* compelling reason to complete my work. His good humor, gentle encouragement, and mastery in mentoring have already left an indelible mark on my professional career. Thanks, Jim.

I reserve my deepest expression of gratitude to Eleanor “Sandy” West (aka, “Moose”), the Grande Dame of Ossabaw Island, who made an indelible impression on me from our first introduction. I have never met a more passionate, hilarious, quirky, well-read, refined, intelligent woman. The years I spent on Ossabaw at “The Main House” were some of the most memorable and treasured in my life. Words cannot adequately express my gratitude to you for your irrepressible love of Ossabaw and all of its creatures, great and small. Thank you, Mrs. West, for giving us this unspoiled jewel. My greatest learning experience came from you.

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CHAPTER 1

CHINESE TALLOW (*SAPIUM SEBIFERUM* L. ROXB.) MANAGEMEN PLAN

INTRODUCTION

Chinese tallow, *Sapium sebiferum* (L.) Roxb. (Euphorbiaceae) is an aggressive woody invader of wetland, coastal, and disturbed habitats that has been shown to reduce native species diversity and richness, and alter ecosystem structure and function in natural areas (Jubinsky, 1993; Gordon, 1997; Simberloff *et al.,* 1997). Chinese tallow was introduced into the United States first as a seed oil crop in the late 18th century, and then later as an ornamental. Its colorful autumnal foliage and bird-dispersed arilite fruits contribute to its popularity with homeowners. Chinese tallow is an early successional tree with classic *r*-strategist life history traits, including high fecundity, relatively small size, short generation time, and the ability to disperse propagules widely, that enable it to thrive in unstable or unpredictable environments. Like many successful non-native plant species such as Melaleuca (*Melaleuca quinquenervia*), Brazilian pepper (*Schinus terebinthifolius*) and Australian pine (*Casuarina* spp.), Chinese tallow is a superior competitor in its new range, has virtually no specialist herbivore or pathogen loads, can readily occupy "vacant niches", and can alter ecosystem processes such as nutrient cycling and stand structure. In Texas, tallow has been shown to convert herbaceous coastal prairies into closed canopy tallow forests within a decade of establishment (Bruce *et al.,* 1995).

Chinese tallow was categorized as a Noxious Weed by the Florida Department of Agriculture and Consumer Services (FDACS) on June 30, 1996. Propagation was prohibited on July 1, 1996, and commerce and transport was prohibited by January 1, 1998 (Garland, *personal communication*). The species was added to the Florida Exotic Pest Plant Council's (EPPC)

Category I Invasive Species List in 1991. From 1998 to 2004, the Florida Department of Environmental Protection Bureau of Invasive Plant Management (DEP-BIPM) spent almost three quarters of a million dollars treating Chinese tallow on more than 4,000 acres of natural areas in north and central Florida (Leslie, *personal communication*). There have been no attempts to pass legislation in other states governing the commerce and transport of Chinese tallow.

The number of ecological studies of Chinese tallow has dramatically risen in the past decade, increasing our understanding of the mechanisms underlying the invasion process, and improving management strategies directed towards this species. Nevertheless, there is much work to be done in the future, particularly with regard to developing biological controls, experimenting with integrated management strategies, and increasing funding for management.

Jubinsky (1993) speculates that, based on its exponential growth rate, potential for rapid expansion into sensitive natural areas, and its deleterious effects on ecosystem structure and function, Chinese tallow may one day rival melaleuca in ecological and economic impact. Indeed, The Nature Conservancy has designated Chinese tallow as one of the “ten worst alien plant invaders” in the United States (Flack and Furlow, 1996), and the Invasive Species Specialist Group (ISSG) of the World Conservation Union (IUCN) has assigned Chinese tallow the dubious distinction of being one of “100 of the world’s worst invasive alien species” (IUCN, 2005).

This management plan has been developed to: 1) review the relevant literature concerning this species; 2) provide a comprehensive overview of the problem of Chinese tallow invasion; 3) develop a framework for agencies mandated to protect natural areas from Chinese tallow invasion, and; 4) inform land managers as to the most effective management techniques.

Species Background

Taxonomy

Synonyms include *Triadica sebifera* (L.) Small and *Croton sebiferum* (L.) Roxb. Vernacular names adopted from the horticulture trade are numerous, including Chinese tallow, popcorn tree, chicken tree, vegetable tallow, Florida aspen, and white wax berry.

The Euphorbiacaeae (spurge family) is a large and diverse taxonomic family comprising 326 genera and 7,750 species (Watson and Dallwitz, 1992). Of these, approximately 47 species are native to North America. Members of the Euphorbiaeae are herbs, lianas, shrubs, and trees, frequently characterized by milky latex that is irritating or toxic. Euphorbs are primarily located in moist tropical habitats, but a number are xerophytic and cactus-like. Members of the spurge family are often cultivated for ornamental (e.g., poinsettia), economic (e.g., tung oil) and medicinal (e.g., castor oil) purposes. Many species are highly poisonous. The genus *Sapium* contains 21 neotropical species, all of which are monoecious trees with trilocular fruits and seeds with an aril mantle, usually red.

Description

Sapium sebiferum (L.) Roxb. is a rapidly-growing, subtropical, monoecious, deciduous, polycarpic tree capable of attaining heights of 10 to 13 meters (Bruce *et al.*, 1997). Branches are slender, essentially glabrous, unarmed, arcuate and often drooping, the stems and branches brittle (Ridley, 1924). Bark is grayish-brown with extensive fissures and, when water stressed, is characterized by hypertrophied lenticels. Leaves are alternate; blades are rhombic, 3-7 cm long, basally biglandular and rounded to acute, marginally entire, apically acuminate; petioles are longer than their blades; stipules are subulate and caduceus (Correll and Johnson, 1970). The foliage exhibits a wide range of autumnal coloration, which enhances the species' appeal as an ornamental. Flowers are reduced, yellow-green, in terminal spiciform androgynous thyrses 5-15 cm in length, the minute bractlet at each node with two persistent bulbous-glandular stipules. Staminate flowers are clustered at the upper nodes, each on a pedicel approximately one mm long, with a cup-shaped irregularly three-toothed calyx approximately one mm in diameter. petals, glands, and rudiment are absent. Staminate flowers are characterized by three stamens. Pistillate flowers are few and solitary at the nodes. Calyx consists of three, triangular, nearly distinct sepals; petals, glands and disk absent. The ovary is subglobose, three-celled, and tri-ovulate. The three styles are free and spreading, and entire; the free portion being brown and papillate-fungoidal ventrally. The fruit is a trilocular capsule, approximately 1-2 cm long and two cm wide, the walls falling readily upon maturation. Seeds are 7-8 mm in length, long-persistent on the placenta after the dehiscence of the fruit, and enshrouded in a mantle of chalky-white aril (Chopra, 1970; Correll and Johnston, 1970; Bogler, 2000) (Figure 1.1).

Chinese tallow has a high degree of phenotypic plasticity, ranging from a “shrub-like” phenotype with low, multi-stemmed, laterally-spreading branches to tall, linear trees with pendant branch architecture (Scheld and Cowles, 1981; Jubinsky and Anderson, 1996). Trees attain maximum height within 10-12 years (Duke, 1983).

Distribution

Native Range

Chinese tallow is native to provinces along the Yangtze River Valley and throughout the southern half of the People’s Republic of China, where it is referred to by various names, the common Cantonese name being “u-kau-shu” or “wu-yau-shoe” (Howes, 1949). Tallow is especially abundant in the Anhui, Henan, Hubei, Sichuan, Guizhou, Gaunxi, and Zhehiang Provinces, where it typically occupies riparian habitats and sandy estuaries (Howes, 1949), and is actively cultivated for oil production (Scheld, 1983) (Figure 1.2). In addition to China, the native range of Chinese tallow extends to Japan, Indo-China, India, Vietnam, and the Korean Peninsula. Burkill (1935) reports that the species was intentionally established and cultivated in the United States, Singapore, southern Europe, Italy, Martinique, Mexico, Cuba, Brazil, and Jamaica. Distribution records from the Invasive Species Specialist Group (ISSG) of the World Conservation Union (IUCN) also indicate Chinese tallow as being present in Algeria, South Africa, Sri Lanka, and Sudan (IUCN, 2005).

Host Range - United States

The first documented evidence of intentional Chinese tallow introduction into the US territories was in 1772 by Benjamin Franklin, who forwarded seeds from "Cochin China" (now south Vietnam) to Mr. Noble Wimberly Jones, a gentleman farmer and fellow horticultural enthusiast residing in Darien, Georgia. In a letter addressed to Jones dated October 7, 1772, Franklin writes, "*… I send also a few seeds of the Chinese Tallow Tree, which will I believe grow &* (sic) *thrive with you. Tis a most useful plant*." (Bell, 1966). Franklin valued the Chinese tallow tree for its utility, anticipating that the aril-rich mantle would be extracted and fashioned into candles by enterprising Georgians. The first American botanical reference to Chinese tallow was by Michaux (1803), who stated that it had been "cultivated in Charleston and Savannah, but was then spreading spontaneously into the coastal forests." In 1826, Stephen Elliot protested that the Chinese tallow tree "*bears fruit in great abundance, but though they contain much oil, no use is yet made of them*." (Bell, 1966).

In 1906, the Foreign Plant Introduction Division of the USDA advocated extensive cultivation of Chinese tallow in coastal Louisiana and Texas in an effort to establish a commercial soap industry (Flack and Furlow, 1996). Since that time, range expansion of

Chinese tallow has been primarily attributed to multiple introductions throughout the southeast as a result of its use as an ornamental species in the horticulture industry, as well as its potential for oil seed production (Scheld and Cowles, 1981) and composite manufacturing (Lee *et al.*, 2004). Its current range in the conterminous US extends from Richmond County, North Carolina south through central Florida, west into eastern Texas, and north to northwestern Arkansas. Additionally, reports have documented tallow in California's Great Valley (CAL-IPC, 2007). Jubinsky and Anderson (1996) report that 57 percent of Florida's counties contained naturalized populations of Chinese tallow, with a range extending from Escambia County on the Florida/Alabama border eastward to Duval County (Jacksonville) and as far south as Hillsborough County (Tampa). Wunderlin (2000) has documented voucher specimens for 28 of the 38 counties listed by Jubinsky and Anderson, including one specimen from Miami-Dade County, indicating the possibility of significant expansion of the southern range of its distribution. Siemann and Rogers (2003a) note the existence of a voucher specimen from North Kohala, Hawaii; the plant was collected in 1927.

Although the potential for range expansion in the US remains unknown, Pattison (unpublished, described in Mlot, 2001), used CLIMEX™ models to predict suitable habitats where Chinese tallow might become established. The model demonstrated that the species showed potential for expansion well beyond its current distribution – as far north as Illinois and New Jersey and along the West Coast. The scenario appears unlikely, however, because although Chinese tallow is able to thrive within a wide range of environmental conditions, it is generally limited to frost-free latitudes (Draper, 1982; Bruce *et al.*, 1997).

Ethnobotanical Uses

The Chinese tallow tree has an extensive history in Chinese ethnobotany, providing medicinal products, fuel, and other commodities for over 15 centuries (Howes, 1949; Scheld, 1983; Jubinsky, 1993). Plants of the Euphorbiaceae family are rich in phenolic compounds (especially tannins), and Chinese tallow is no exception. Tannins have been shown to possess anti-cancer activity (Nonaka *et al.*, 1990), enhance nitrogen metabolism, and are often psychotropic (Nagasawa *et al.*, 1980). In addition to tannins, numerous biologically active compounds have been extracted from Chinese tallow (see Table 1).

Medicinal Uses

The Chinese have used the tallow tree extensively in traditional medicines, most generally as a preservative against contagious and infectious disease (an alexiteric), and as a remedy for treating wounds and sores in general (a vulnerary), especially skin ailments. The leaf and root tissues were traditionally used as a "blood purifying agent" (i.e., a depurative), diuretic, and laxative (Grieve, 1931). Duke and Ayensu (1985) report that the leaves are particularly effective as a suppurative (aids in the discharge of pus) in treating skin ailments, especially skin abscesses. The seeds, which can be lethal to humans and livestock when consumed in even modest quantities (Russell *et al.*, 1969), are used as a bowel purgative (hydrogogue) and an emetic (i.e., vomit-inducing) agent (Duke and Ayensu, 1985). The root bark resin is primarily used as a diuretic, tonic for indigestion, and is also useful as a topical treatment for snake bites and relief of swelling associated with skin ulcers (Duke and Ayensu, 1985). The latex (sap) is a caustic vesicant, with blistering similar to that caused by mustard gas (Chopra *et al.*, 1986). In a similar manner to castor oil, tallow tree oil is often employed as a purgative (Scheld, 1983). More recently, potent compounds have been isolated from tallow that have strong anti-viral

(Kane *et al.*, 1988) and anti-carcinogenic properties (Pradhan and Khastgir, 1973), and have been found to ameliorate symptoms of hypertension (Hsu *et al.*, 1994). It should be noted that not all chemical derivatives of tallow possess beneficial properties. Brooks *et al*. (1987) demonstrated that phorbol ester derivatives Sapinotoxins A and C, derived from Chinese tallow stillingia (seed kernel) oil, promoted tumor formation and inflammation in mice (Table 1.1).

Economic and Commercial Uses

The seed kernel is rich in lipids, consisting of approximately 40- to 60 percent fat by weight, and also contains roughly 10 percent protein (Duke and Ayensu, 1985). Holland and Meinke (1948) report that the defatted, dehulled seed meal may be used as a livestock feed supplement or to enrich baking flours. A refined oil referred to as “stillingia”, derived from the endosperm, is a drying oil used for paints and varnishes (Bolley and McCormack, 1950). Stillingia became more widely available for commercial use when the post World War II price of exported linseed and tung oils from Argentina and China became economically infeasible (Howes, 1949). Stillinga was also used at one time as a crude lamp oil. Ansari and Nand (1987) report that crushed foliage and fruit, when added to a body of water, is a highly effective piscicide (fish killer), but that the leaves can be consumed by sheep and goats, presumably with no ill effect. These conclusions contradict the findings of Russell *et al.* (1969). They report that, by the fifth day of a no-choice feeding trial of terminal leaves and unripened fruits by ruminants (steer and goat), five of seven animals were “severely emaciated” and by the sixth day, one animal had died. Seip *et al.* (1983) cautions against using the seed oil as a food additive for humans or livestock, based on isolation of skin irritants and tumor-promoting compounds from the kernel oil.

The opaque, waxy outer layer of the seeds is used in the production of soaps, cosmetics, candles, wax paper, and as a source of glycerine (Uphof, 1959; Scheld, 1983; Heywood, 1993), and is separated from the seed by emersion in hot water and skimming off the wax as it floats to the surface. The wax is solid at temperatures below 40 degrees Celsius, and has the consistency of lard. Subsequently, it is employed as a lard substitute in cooking and is used in cocoa butter production (Scheld, 1983; Facciola, 1999). "Tallow residue cake", produced with intact crushed seeds from which the stillingia has been extracted, is used as a green manure, and is particularly useful in enriching soils in tobacco fields (Duke, 1983).

During World War II, tallow tree was used by the Chinese as an emergency source of fuel for diesel equipment (Mason, 1997). More recently, Scheld (1983) and Scheld *et al.* (1984) have been active proponents for large-scale commercial production of tallow as a cash and petroleum-substitute crop. They have estimated that tallow is capable of annual yields equivalent to 4,500 pounds of oil per acre, making it "one of the most productive oil-seeds of the world, if not the most productive." Scheld (1983) cites the lack of a system for mechanical harvest as the "major technical barrier" to large-scale commercial production operations.

Black dye produced by boiling mature leaves in alum water was once used to color silk (Howes, 1949) and was also used as a hair coloring agent (Duke and Ayensu, 1985) and in printing inks (Scheld, 1983). The wood is similar to balsa in color, grain, and texture, and is well-suited for ornamental carving and the production of Chinese printing blocks. The wood is also suitable for limited furniture production and incense (Duke, 1983). Lee *et al.* (2004) report that tallow tree fiber, when combined with bagasse (compressed agricultural residue, usually sugar cane) has considerable potential for the production of medium-density fiberboard. Based on parameters such as coppice growth, seedling performance, germination, and survivorship, Rockwell and Devalerio (1986) described Chinese tallow, along with other pernicious invaders such as Brazilian pepper (*Schinus terebinthifolius*), lead tree (*Leucana leucocephala*), and mimosa (*Albizia julibrissin*) as "promising species" for large-scale biomass production in Florida. In its native range, Chinese tallow is often planted for soil stabilization and erosion control along canals and rivers.

Honey produced from Chinese tallow is reported to be similar in quality to that derived from goldenrod (*Solidago* spp.), but having more body, and is usually sold as "bakery grade." Though it lacks certain aspects of richness and complexity in palatability, tallow tree honey can be produced copiously and has proven to be an economic boon to beekeepers. In 2004, beekeepers in honey-producing states were paid $1.24 per pound of unprocessed, extracted "extra light amber" Chinese tallow honey, for quantities in excess of 10,000 pounds (USDA, 2004). In an article published in the American Bee Journal, Hayes (1979) states "(the Chinese tallow tree) has become the most successful tree nectar source ever introduced into the United States." Not surprisingly, many beekeeping associations have actively opposed legislative attempts to designate Chinese tallow on state noxious weed lists. For example, when the species was added to Mississippi's state noxious weed list in 2004, officials from the Mississippi Farm Bureau wrote that "should specific regulations affecting tallow tree be proposed, MBA (Mississippi Beekeepers Association) would have the opportunity to comment and have input" (MBA, 2004). Delaplane (1998) advocates extensive planting of tallow as a means of promoting bee conservation efforts in the southeastern US.

Life History

Phenology

In the southeastern US, the onset of new growth begins in February and flower production lasts from March through May (Cameron and LaPoint, 1978). Fruit set begins in July with asynchronous maturity lasting from October to November (Godfrey, 1988). Seeds typically persist on the plants for periods of up to six months (McCormick, *personal observation*). In the south central provinces of the Yangtze River Valley in China, tallow tree fruits normally ripen beginning in October and lasting through early November, which coincides with the second rice harvest. Consequently, with labor shifted to rice, tallow fruits remain on the trees until after rice harvest, resulting in considerable degradation of oil quality (Scheld, 1983). Long-term intensive selection programs in some provinces have resulted in entire populations of tallow that delay ripening until late November-December. The result is two annual crops (Scheld, 1983).

Flower and Fruit Production

Duke (1983) reports age to first reproduction as 3-8 years, after which trees may remain reproductively viable for 100 years. In Florida, flowers typically mature in April through June (Jubinsky, 1993). Chinese tallow is dichogamous, a strategy which promotes cross-pollination and genetic variability (Richards, 1986). Chinese tallow is pollinated by insects; a major pollinator is the introduced honey bee (*Apis mellifera*) (Duke, 1983). Although Grace (1997) reports that some individual tallow tree plants grown from seed in a greenhouse flowered during their first year, precocious flowering appears to be infrequent. Scheld *et al.* (1984) reports that nearly half of the tallow trees on the coastal plains of Texas flowered in their third year.

Seed Production and Dispersal

A mature stand of Chinese tallow can produce copious seed crops in excess of 10,000 lbs/acre/year (Potts, 1946; Bolley and McCormack, 1950; Conway *et al.*, 2000). Hsu (1928) and Lin *et al.* (1958) indicate that "useful" (i.e., high lipid content) seed crop production may be expected within five years, and that yields do not decline appreciably for 25-30 years. Echols (1983) provides evidence for a positive correlation between annual seed crop production and annual precipitation. The number of seed capsules per raceme may vary geographically. Scheld *et al.* (1980) observed that tallow trees in the Charleston, South Carolina area typically produced 2-3 capsules per raceme, whereas those in the Houston, Texas area produced 3-8 capsules per raceme. Though some populations in its native range have reportedly produced seeds up to 12.5 mm in diameter, average seed size appears to be much less than this (7-8 mm) (McCormick, *this publication*). Fruits are colloquially described as being approximately the size of a pea (Bruce *et al.*, 1997). In their effusive praise of the utility of Chinese tallow as a cash crop, Scheld *et al.* (1980) suggest that the tallow tree is readily adapted to, and even appears to facilitate, machine harvesting of seeds, as evidenced by the fact that the majority of harvestable crop is "*borne largely in the periphery of the crown, where it is readily accessible by hand or mechanical means*."

Toxic secondary compounds in the endosperm (stillingia) reduce its palatability to seed predators, although the aril-rich coating is an attractive source of energy for birds and possibly small rodents. Although the author has observed fire ants (*Solenopsis invicta*) consuming the aril, no dispersal of seeds by ants (myrmecochory) was documented. The aril coating is degraded by saprophytic fungi, most notably black mold of the genus *Pullularia* (Scheld *et al.*, 1980; Burns and Miller, 2004). Bruce (1993) reports that in advanced stages, *Pullularia* hyphae penetrate the seed kernel, resulting in embryo mortality.

Birds have been shown to be important dispersal agents in upland areas. Renne *et al.* (2000) demonstrated that birds in coastal South Carolina relied heavily on Chinese tallow as a food source, and that dispersal agent efficacy varied geographically as well as among habitat types. Whereas European Starlings proved to be the most important dispersal agent in South Carolina spoil areas, Northern Flickers were most important in South Carolina coastal forests, and Red-Bellied Woodpeckers contributed most significantly to dispersal of Chinese tallow along forest perimeters in Louisiana (Renne *et al.*, 2002). Arillite fruits are often preferred by birds as winter approaches and energy requirements increase (Herrera, 1982). The lipid-rich coating on tallow tree seeds makes them a highly attractive food source to some bird species, particularly at a time when few other native lipid-rich food sources are available. Baldwin (2005) found that the species richness of winter bird communities differed significantly between Chinese tallow woodlands and adjacent native bottomland hardwood forests in Louisiana. In general, bottomland hardwood forests supported a higher number of species and had a higher degree of species apportionment. Chinese tallow woodlands tended to support species associated with "edge habitats" whose population numbers were either stable or not declining significantly, and those species (e.g., Yellow-Rumped Warblers and American Robins) that were more efficient at metabolizing tallow tree fruit pulp relative to native species, such as wax myrtle (*Morella cerifera*), hackberry (*Celtis laevegata*), or deciduous holly (*Ilex decidua*).

Scheld *et al.* (1980) was vexed with the "problem" of high numbers of birds feeding on potentially valuable tallow oil crops, and commented that, "*the loss to birds could become a significant economic concern, and the attraction and sheltering of large numbers of birds would* *become a public health consideration. Techniques for dealing with birds will need to be developed*."

Seed Germination

A number of studies have investigated germination requirements of Chinese tallow in an effort to target the seed phase of its life history as a focus of control efforts, with highly variable results. Kuldeep *et al.* (1993) conducted germination trials under two sets of field conditions – permanently flooded and agricultural sites. They planted 500 tallow seeds (100 seeds with five replicates) at each site in February and May. Seed sown in February germinated on the 35th day, whereas seed sown in May germinated 5-8 days earlier, presumably due to an increase in ambient temperature. At the termination of the trials on the 60th day, germination success for the permanently flooded and agricultural sites were 60 and 62%, respectively. Conway *et al.* (2000) investigated whether imbibing and cold water treatments enhanced germination. Their results demonstrate that Chinese tallow seed is very difficult to germinate successfully under simulated natural conditions, and showed very low germination success across all treatments, ranging from 0-10%, whereas Cameron *et al.* (2000) and Renne *et al.* (2001) achieved higher germination success of 26 and 22.5%, respectively for seed sown in greenhouse environments and ambient temperature/light regimes.

Bruce (1993) reports germination rates of 20-65% in laboratory trials, and Bonner (1974) obtained a moderate germination rate of 38% over a 30-day period of hot-cold heat cycling on m moist Kimpak™ media. Nijjer *et al.* (2002) determined that oscillating temperatures (i.e., 16 hours of 32º C and 8 hours of 16 C º) resulted in a significantly higher proportion of tallow seed germination than either constant heat (24 hours of 32º C) or constant cold (hours of 16º C) treatments. Additionally, their studies suggest that Chinese tallow apparently has no specific light requirement for germination. A higher number of Chinese tallow seeds germinated in either constant (24 hours) light or constant dark, compared to oscillating light cycles (16 hours of light followed by 8 hours of darkness) (Nijjer *et al.*, 2002).

Donahue *et al.* (2004) found that the addition of mulch reduced tallow seed germination from 34% (217 germinants out of a total of 600 seeds) to approximately 0.06% (34 germinants). This suggests that mulching tallow tree stands may facilitate the elimination of Chinese tallow soil seed banks by reducing germination through the attenuation of day/night variation in surface soil temperatures. Indeed, oscillating soil temperatures may be a significant environmental cue for germination of Chinese tallow, and may be critical in breaking physical dormancy in soil seed banks (Baskin and Baskin, 1998). However, it is unclear to what depth mulch should be applied (Donahue *et al.*, 2004). Burns and Miller (2004) surveyed environmental characteristics around the perimeter of Lake Jackson, Florida in an effort to elucidate biotic and abiotic correlates of Chinese tallow invasion. They planted Chinese tallow seeds in buried pots along eight transects over an elevation gradient of more than one meter, and found that germination success was highest for medium and high elevations (4.5% and 3.2%, respectively) and lowest in low elevations (0.7%). In addition, their work suggests that controlled burning reduced the likelihood of germination (presumably through heat-induced embryo mortality), and may be used as an effective management tool for inhibiting seedling recruitment. However, there may be an unacceptable trade-off if burning increases coppicing and root shoots on mature trees.

Although absolute seed longevity is difficult to establish in orthodox (i.e., desiccation-tolerant) seeds with dormancy mechanisms, Zhang and Lin (1994) have speculated that Chinese tallow seed may remain dormant in soil seed banks for up to 100 years with little or no reduction in embryo viability. In a study of germination using Chinese tallow seeds collected over a period of seven years, Cameron *et al.* (2000) found that germination success peaked after two years, with little loss in germination (3%) by the seventh year. Additionally, they determined that among four collection sites in the southeastern US (Florida, Georgia, South Carolina, and Texas) and one in Taiwan, tallow populations in Florida exhibited the highest total percent germination across years (53.4% ± 5.9), followed by Georgia (30.9% ± 6.3), Taiwan (28.8% ± 3.3), Texas (24.3% ± 2.7) and South Carolina (5.7% ± 3.1 (Cameron *et al.*, 2000).

Cameron *et al.* (2000) determined that the highest proportion of Chinese tallow seeds germinated in January and February (average: 58-59%), with the lowest proportion germinating in the late fall (21-46%). Maximum germination during winter months may enhance Chinese tallow's ability to invade sites, because winter annual plants have died back and many overstory trees are deciduous (Harcombe *et al.*, 1993). Consequently, there is little competition from neighboring plants for resources, and few losses to seed predators and herbivores, which are generally less active during the winter (Cameron, 1977).

Vegetative Growth and Reproduction

Chinese tallow is capable of both vegetative reproduction and copious fruit production. Physiological stress resulting from environmental conditions, herbicide application, or mechanical damage typically result in profuse root coppicing (Scheld and Cowles, 1981; Bruce *et al.*, 1997). Jones and Sharitz (1990) documented substantial production of adventitious roots in Chinese tallow seedlings grown in persistently flooded conditions. Additionally, flooded tallow seedlings produced noticeably thicker roots than native water tupelo (*Nyssa aquatica*) and green ash (*Fraxinus pennsylvanica*) (Jones and Sharitz, 1990).

Genetic Traits

Scheld (1983) reports that the diploid chromosome count for “wild types” (i.e., non-cultivated) tallow trees is 36 (n=18), but that for cultivated trees under intense selection program, this number may be as high as 76. He goes on to state that this report by Chinese researchers “may be the result of a miscount, but it is not beyond the realm of possibility considering the strangeness of the Chinese tallow tree in other areas” (Scheld, 1983). No empirical evidence is cited to support this claim, although it is supported by the work of McCormick and Hamrick (*unpublished data*) who speculate that, based on allozyme banding patterns, the species may in fact be a tetraploid (4n). The ploidy level of a plant species is an important evolutionary trait that can reveal much about a species’ ability to respond rapidly to changing environmental conditions. Baker (1974) observed that polyploidy was a common trait in the evolution of weedy species. Bennett *et al.* (1998) analyzed DNA data from 39 weedy species and found that over half (51%) were polyploids. Consequently, ploidy levels may prove to be a valuable diagnostic feature for evaluating risks associated with the transportation, commerce, and use of potentially invasive plant species. While conducting surveys of Chinese tallow in the Yangtze River Valley, Scheld *et al.* (1984) conducted a survey of the Chinese literature. They reports that tallow is characterized by “extreme variability” within the species in its native range (Lin *et al.*, 1958; Shin, 1973). Scheld *et al.* (1984) also state that populations in the Houston, Texas area “appear to reflect a high degree of genetic variability”, though they do not report specifics of published research to support this claim.

In a 14-year common garden experiment, Siemann and Rogers (2001) examined tallow tree plants originating from populations in China, Georgia, Louisiana, and Texas and compared plant size, foliage chemistry (an indicator of herbivore defenses), and annual seed crop abundance. They concluded that “native genotypes” (i.e., trees from China) were smaller in size, had intermediate seed production, and had the best defended foliage, whereas “invasive genotypes” were characterized by higher growth and low foliar defense. Their data support the hypothesis that, during their introduction phase, invasive plant species may allocate significant resources to growth and reproduction and less to defense (Strong, 1974).

Community and Ecosystem Dynamics

Post-Disturbance Effects

Leninger *et al.* (1997) examined impacts to vegetation structure, composition, and relative abundance in three sites in a bottomland hardwood forest of the Atchafalaya Basin four years following Hurricane Andrew. Their field surveys indicate that tallow trees suffered severe crown damage as a result of high winds, and were the most susceptible to hurricane damage of the 23 species surveyed (22 of which were native tree species). These results concur with those of Doyle *et al.* (1995), who also documented that Chinese tallow sustained the greatest proportion of stem damage, relative to native tree species, from Hurricane Andrew in coastal Louisiana. The implications of hurricane-induced mechanical damage on recruitment of tallow trees in coastal habitats remains unclear, and should be investigated further, particularly in light of recent high-frequency and magnitude storm events. Denslow and Battaglia (2002) described the composition and structure of woody species along a hydrologic gradient in Jean Lafitte National Park, Louisiana, and found that tallow recruitment was common in light gaps throughout the hydrologic gradient. They conclude that if hurricane damage creates light gaps by removing canopy cover and above-ground biomass, the site may experience high levels of recruitment from the soil seed bank.

One of the most alarming examples of the rapidity with which Chinese tallow expands its range in post-disturbance habitats is Bull Island, South Carolina. Prior to the arrival of Hurricane Hugo in 1989, much of Bull Island was considered old-growth maritime forest (Conner *et al.*, 2005). Pre-hurricane field surveys of vegetation communities on Bull Island by Helm *et al.* (1991) concluded that Chinese tallow was confined to "poorly drained swales" that live oak and laurel oak (*Quercus virginiana* and *Q. laurifolia*, respectively) and loblolly pine (*Pinus taeda*) could not exploit due to frequency of flooding. They conclude that "it is unlikely that this species (tallow tree) will occupy much more area than it does presently, since it is confined to moist soils." Interestingly, they found that richness and percent cover of the herbaceous layer subtending Chinese tallow stands were significantly higher than in either live oak or loblolly pine stands (Helm *et al.*, 1991). A follow-up vegetation survey of Bull Island by Smith *et al.* (1997) reports that stands of Chinese tallow were completely destroyed by winds and terminal salt damage from Hurricane Hugo (stem density per hectare decreased from 120 in 1988 to 0 in 1992). However, they noted aggressive recruitment of Chinese tallow seedlings into previously uninvaded vegetation communities, such as old growth loblolly forests. Conner *et al.* (2005) surveyed the Island in 1998, and compared data on vegetation parameters for pre-storm, 1991, and 1998 surveys. They found that Chinese tallow accounted for 9.8 (pre-storm), 4.1 (1991) and 22.6% (1998) of the tree density-frequency-dominance index. They speculate that light gaps stimulating the soil seed bank, coupled with a rise in the water table are responsible for an increase in tallow tree density 20 times that of estimated pre-Hugo density. As of July 2005, vegetation managers at Cape Romaine National Wildlife Refuge estimate that Chinese tallow is present on approximately 25% of Bull Island's terrestrial habitats (Dawsey, *personal* *communication*). These and other studies illustrate the potential role of disturbance as a stimulus for rapid population growth and expansion of Chinese tallow.

Effects on Ecosystem Structure and Function

Chinese tallow has become the dominant woody species of remnant Chenier woodlands in southwest Louisiana, significantly reducing species diversity and relative abundance in these old-growth maritime forests. Baseline surveys conducted by Neyland and Meyer (1997) revealed that the degree of tallow tree infestation in the chenieres was positively correlated with soil disturbance. The chenieres are unique coastal communities formed on the ridge of relic beach dunes, and serve as storm barriers limiting salt water intrusion. Additionally, they serve as important wildlife habitat, especially for migratory songbirds, shorebirds and butterflies. Chinese tallow has been shown to convert herbaceous coastal prairies into closed canopy tallow tree forests within a decade of establishment (Bruce *et al.*, 1995). Consequently, there is concern that this species will displace marsh habitats surrounding the chenieres, irrevocably altering ecosystem structure and function and dramatically changing seral stages of vegetation succession. Harcombe *et al.* (1993) measured above ground net primary productivity (ANPP) in a monontypic, 15-year old tallow stand and an adjacent wet coastal prairie dominated by native species and found that the tallow stand had significantly higher levels of ANPP. They also determined that maximum radial growth of tallow trees was 4.5 mm per year for a 17-cm dbh tree on the Texas coastal prairie. Harper (1995) measured radial growth of 6 mm per year in a river floodplain forest in Louisiana.

Bruce *et al.* (1995) examined tallow tree stands from four age classes (0-5, 6-10, 11-15 and 16-20 years old) ranging in size from 0.2 to 100 hectares in coastal graminoid/herbaceous prairies in eastern Texas. Their results confirm that Chinese tallow is self-regenerating up to 20 years and can form closed canopies within 10 years, demonstrating a rapid shift in dominance of vegetation structure as graminoids and forbs were replaced by trees and shrubs. Of the original coastal graminoid/herbaceous prairie, less than one percent remains (Smeins *et al.*, 1991), and this remnant has been designated as a "globally imperiled ecosystem" by The Nature Conservancy (Grossman *et al.*, 1994).

In many cases, the structural integrity of prairie vegetation communities can be maintained by the use of prescribed fire to prevent encroachment of woody species. Chinese tallow has been shown to significantly reduce fuel loads and inhibit the spread of fires that suppress woody vegetation and promote prairie ecosystems through shading and rapid leaf decay (Cameron and Spencer, 1989; Barrilleuax and Grace, 2000). Once naturalized, Chinese tallow forms monotypic canopies subtended by understories consisting of few if any native woody species (but see Helm *et al.*, 1991). Grace (1998) investigated whether prescribed fire can be employed to halt the encroachment of tallow tree invasion in coastal prairie ecosystems of Louisiana. He concluded that the use of fire to control Chinese tallow in coastal prairies is ineffective at best, and may in fact exacerbate infestations, in part due to a number of morphological and physiological adaptations to fire exhibited by the species (see "Management").

Effects on Nutrient Cycling and Soil Chemistry

Chinese tallow may have negative effects on leaf litter composition rates and species composition of aquatic macroinvertebrate reducer species. Cameron and LaPoint (1978) studied the effects of foliar tannins on reducers (i.e., shredders, sediment-deposit feeders, scrapers, and filter feeders) in grassland and ephemeral ponds in tallow tree forests in the Texas coastal wet prairie ecosystem. They showed that species richness and diversity were lower in ephemeral ponds of tallow forests, and that these ponds contained fewer shredders than the grassland ponds. Shredders have a critical ecological function in aquatic and terrestrial habitats and are primarily responsible for initiating decomposition of whole leaf organic matter in ephemeral ponds and the forest floor. The high tannin content in Chinese tallow foliage may inhibit feeding by reducers, either by binding to protein molecules and rendering them unusable ("tanning") or by preventing microbial growth on leaves. Tallow tree leaf litter cannot be utilized by reducers until tannins are leached by seasonal flooding and its physical structure is subsequently altered by microbial activity.

Fluctuating levels of resources are thought to play a pivotal role in facilitating the invasion process of pestiferous plant species (Dukes and Mooney, 1999; Davis *et al.*, 2000). Rapid decomposition of Chinese tallow litter often results in temporally pulsed releases of nitrogen. In areas of expansive tallow tree invasion, such as Gulf coastal Texas and Louisiana prairies, nutrient feedbacks may facilitate Chinese tallow invasion. Cameron and Spencer (1989) examined the rate of Chinese tallow leaf decomposition and the quantity and rate of nutrient inputs from decomposing leaves in a tallow tree forest. They determined that approximately 24% of biomass in Chinese tallow leaves was lost within the first week; 50% of leaf biomass was lost after four months, and total reduction occurred in approximately seven months. By comparison, some temperate deciduous trees take an average of 3.9 years to achieve total decay (Swift *et al.*, 1979). Soil analysis revealed that concentrations of P, K, NO3-, Zn, Mn, and Fe were significantly higher in soils subtending tallow tree forests than from prairie plots, whereas concentrations of Na and Mg were significantly lower. Levels of Ca and S did not vary significantly between sites. These results suggest that established populations of Chinese tallow appear to significantly alter nutrient distribution in subtending soils, and may contribute to enhanced productivity of invaded habitats.

Response to Waterlogging and Salinity

Chinese tallow can tolerate a wide spectrum of soil conditions. In the Gulf coast, where the species has exhibited rapid growth and range expansion over the past 40 years, soils typically range from moderately acidic at the epigeal surface to progressively alkaline with increasing depth (Crenweldge *et al.*, 1988; Bruce, 1993). Jones and Sharitz (1990) demonstrated that Chinese tallow seedlings are comparable to water tupelo (*Nyssa aquatica*) in their response to flooding and oxygen stress avoidance, such as hypertrophied lenticels and adventitious root formation. Conner and Askew (1993) demonstrated that Chinese tallow tree seedlings exhibited significantly higher survivorship when subjected to short-term inundation by saltwater (20-27 ppt) than either red maple (*Acer rubrum*) or redbay (*Pursea borbonia*). Similarly, Conner *et al.* (1997) found that Chinese tallow seedling survivorship was three times higher than that of baldcypress (*Taxodium distichum*), water tupelo (*N. aquatica*) and green ash (*Fraxinus pennsylvanicum*) under conditions of prolonged flooding with slightly saline water (10 ppm). Additionally, they demonstrated that Chinese tallow fully recovered from simulated storm surge events with 32 ppt saltwater; whereas all three native species experienced 100% mortality.

Butterfield *et al.* (2004) demonstrated that under a four-treatment water gradient ranging from permanently flooded to pulsed drought, Chinese tallow seedlings were able to thrive at any point along the water regime continuum, significantly outperforming loblolly pine (*P. taeda*), water tupelo (*N. aquatica*) and black gum (*N. sylvatica*). A single native species, sweetgum (*Liqudambar stryaciflua*), exhibited higher growth rate than Chinese tallow in drier treatments. Barrilleaux and Grace (2000) found significant effects of soil type and electrical conductivity (an indicator of soil salinity) on tallow tree seedling mortality in a Texas coastal prairie. In field trials, Chinese tallow suffered 73% mortality when grown on western soils (high sand/high conductivity), whereas tallow grown in central (clay/moderate conductivity) and eastern soils (silt-loamy/low conductivity) experienced only 3% and 0% mortality, respectively. Consequently, Chinese tallow appears to be able to tolerate short, infrequent pulses of saltwater flooding and may have a competitive advantage in coastal areas that may be subject to gradual or infrequent saltwater intrusion in the future and becoming a dominant species of southern coastal forests.

Growth Under Various Light Conditions

Chinese tallow is tolerant of a wide range of light conditions, and has growth rates comparable to or greater than, shade-tolerant and shade-intolerant species in both deep shade and full sun (Bruce, 1993). When compared to seedlings of American sycamore (*Platanus occidentalis*) and cherrybark oak (*Quercus falcata* var. *pagodifolia*) tallow tree seedlings attained greater height and biomass in deep shade (5% sun) than either of the natives, and equaled the growth of American sycamore in full sun (Jones and McLeod, 1989). In another study comparing Chinese tallow to green ash (*F. pennsylvanicum*), Jones and McLeod (1990) found that tallow had equal or greater growth rates (height and biomass) over a wide spectrum of light regimes relative to native ash (5-100% full sun) over a 100-day growing period. Furthermore, they estimate that a single, 15-year old tallow tree can reduce ambient light to 7%, and cast 80% or greater shade over a 30-m^2 area (Jones and McLeod, 1989; 1990).

Data by Rogers *et al.* (2000) showed that tallow tree seedlings exhibited a strong positive response to increased nutrients (specifically nitrogen) by increasing water-use efficiency (through reduction of stomatal conductance), and increasing leaf area, leaf number, leaf mass, and petiole length. Their data also support the results of previous studies by Jones and McLeod (1989; 1990) and suggest that Chinese tallow possesses significant physiological plasticity and can thrive under a wide range of natural light conditions. Under conditions of deep shade, Chinese tallow maintains high water-use efficiency and produces “shade leaves” by increasing leaf surface area (but not necessarily leaf mass) (Jones and McLeod, 1990). Furthermore, Chinese tallow maintains a high level of physiological activity in full sun (Rogers *et al.*, 2000). The broad amplitude of light conditions in which tallow is able to thrive undoubtedly contributes to its success in a number of habitats.

Competitive Interactions

There are abundant data to suggest that invasive plant species may expand their range as a result of competitive superiority (Gaudet and Keddy, 1988; Grace and Tilman, 1990; Callaway and Aschehoug, 2000). However, recent studies (Clark *et al.*, 1998; Hubbell *et al.* 1999) suggest that in some cases recruitment limitation may be more important than local competitive differences in determining the species composition of a given local patch. Consequently, observation that an invasive plant species is locally abundant does not necessarily indicate that it is competitively superior to native species in that patch. Rather, it may indicate high seed input by the non-native species (i.e., propagule pressure), such as when a small habitat is surrounded by habitats favoring the establishment of the non-native species (Smith and Knapp, 2001; Siemann and Rogers, 2003d). To investigate this hypothesis, Siemann and Rogers (2003d) added Chinese tallow seed to mesic and floodplain forests, and coastal prairie habitats, with and without soil disturbance. They predicted that (1) if low seed input limits local abundance, then experimentally added Chinese tallow and hackberry (*Celtis laevigata*) seed will readily germinate, grow, and survive, thereby increasing seedling abundance, and; (2) if a scarcity of suitable microsites limits invasion, then seed added on disturbed sites should grow and survive, thereby increasing seedling abundance (Siemann and Rogers, 2003d). They found relatively higher germination of hackberry vs. Chinese tallow at all three sites, but that Chinese tallow had overall higher survivorship in prairie and floodplain forest. Interestingly, tallow experienced moderate germination success in the mesic forest habitat, followed by 100% seedling mortality within approximately 1.5 years (~ 600 days) after planting. Soil disturbance had no effect on the germination rates of Chinese tallow, but increased germination success of hackberry seeds.

Jones (1993) examined the effects of soil temperature on intra- and interspecific root competition of Chinese tallow, sweetgum (*L. styraciflua*) and red maple (*A. rubrum*), and found that increasing soil temperature resulted in significantly higher root biomass in tallow tree seedlings, relative to that of natives when planted together; whereas below-ground competition was relatively less when Chinese tallow seedlings were planted with conspecifics. His results suggest that Chinese tallow may exhibit superior competitive ability relative to native species, in terms of resource acquisition in warmer temperatures.

Rogers and Siemann (2004) tested the competitive ability of invasive (Texas) and native (China) tallow tree seedlings against annual ryegrass (*Lolium multiflorum*) under conditions of increased soil fertilization. Chinese tallow seedlings were grown to four weeks, at which time 1.5 grams of *Lolium* seed was added to a 7.65 liter pot containing individual Chinese tallow seedlings of either genotype; the pots were treated with a 15:10:5 fertilizer. Data show that competition for soil resources increased the stem height growth of Chinese genotypes, but did not affect shoot or root mass. Competition did not significantly affect any measurable growth of Texas genotypes, suggesting that the invasive genotype is less effective in competition than the native genotype (Rogers and Siemann, 2004).

Microbial Interactions

The role of soil microbes and unique mycorrhizal associations in facilitating non-native pest plant invasions is an area of ecology that, though sorely neglected, may offer critical insight into the more subtle mechanism(s) that act as catalysts for plant invasions. Nijjer *et al.* (2004) examined the effects of mycorrhizal inoculation, fungicide application, and fertilization on the growth of Chinese tallow and five native species (sweetgum, *L. styraciflua*, water tupelo, *N. sylvatica*, loblolly pine, *P. taeda*, white oak, *Quercus alba*, and water oak, *Q. nigra*). They found a significant, positive growth response (65%) of Chinese tallow seedlings in response to mycorrhizal inoculation; whereas growth response in native species ranged from negative (*Q. alba* = 1% reduction), negligible (*Q. nigra* = 6%), minor (*P. taeda* = 17%, *L. styraciflua* = 24%), to large (*N. aquatica* = 46%). Unless a species is able to exploit mycorrhizal associations in an innovative fashion, it is unlikely that generalist mycorrhizae associations with low host fidelity would be the sole mechanism of invasion. Although numerous generalist fungal pathogens have been known to associate with Chinese tallow (Table 1.2), clearly, there are many knowledge gaps that exist in understanding the role of soil microbes and mycorrhizal associations in Chinese tallow invasions.

Herbivory

In its introduced range, Chinese tallow stands are noticeably depauperate in terms of specialist herbivore loads (Harcombe *et al.*, 1993; Bruce *et al.*, 1997). Perhaps not surprisingly, Liu *et al.* (1988) report that one of the biologically active compounds from tallow foliage [(-)-loliolide] is a potent ant repellent. The absence of an appreciable herbivore load on plants is usually attributed to foliage and other plant tissues being highly defended (unpalatable) or of nutritionally marginal quality (Price, 1997). Arthropods perform many ecosystem services, such as pollination, propagule dispersal, and nutrient cycling (Wilson, 1992; Jones *et al.*, 1994; Price, 1997). Consequently, they may be sensitive indicators of changes to vegetation structure, function, and diversity. Hartley *et al.* (2004) quantified arthropod communities in a Chinese tallow stand in coastal southeastern Texas and found that, of 811 individuals sampled, the orders Dipterans (flies), Acari (mites), and Araneida (spiders) comprised 78% of total species abundances. They concluded that Chinese tallow supports an unusual assemblage of arthropods of mostly predators and detritivores, with very few herbivores.

One of the prevailing theories explaining the success of invasive plant species is the Evolution of Increased Competitive Ability (EICA), proposed by Blossey and Nötzhold (1995). The EICA postulates that, in response to the absence of specialist herbivores (including pathogen loads), invasive plants evolve increased competitive ability (relative to native species) by shifting resources from defense to growth.

Siemann and Rogers (2003b) tested the EICA hypothesis by comparing growth and herbivory levels in tallow trees cultivated from native (Asian) and invasive (Texas and Hawaii) seed grown in competitive common gardens in Texas and Hawaii. Their results show that in the Texas garden, Asian genotypes were significantly smaller than North American genotypes, and both genotypes suffered very low levels of insect damage. However, in the Hawaiian garden, the situation was reversed. North American genotypes were significantly smaller than Asian genotypes. Additionally, North American genotypes experienced significantly more insect damage than Asian genotypes in the Hawaiian garden. The herbivore responsible for most foliar damage was *Adoretus sinicus* Burmsiter (Coleoptera: Scarabaeidae), a generalist chewing herbivore known to feed on more than 250 plant species in Hawaii (Habeck, 1963; Siemann and

Rogers, 2003b). The study demonstrates that invasive species liberated from herbivory may evolve greater competitive ability, allowing them to expand their ranges. However, in the presence of an abundant generalist herbivore from the native range, this did not occur.

In an experiment testing generalist herbivore choice between tallow and native hackberry (*Celtis laevigata*), Siemann and Rogers (2003d) planted tallow tree and hackberry seedlings in three habitats (mesic forest, coastal prairie, and floodplain forest). Each test plot was treated with insecticide and fungicide to reduce insect herbivores and foliage fungus. As predicted by the "enemy release hypothesis" (Keane and Crawley, 2002), Siemann and Rogers (2003d) hypothesized that, in absence of insecticide and fungicide application, hackberry seedlings will experience greater insect herbivory and fungal damage than Chinese tallow seedlings. Furthermore, in plots treated with insecticide and fungicide, hackberry seedlings would experience greater survival and growth rate than Chinese tallow, as a result of being liberated from specialist herbivores and fungal pathogens. Their results show that insect damage was lower on untreated Chinese tallow seedlings than untreated hackberry seedlings, as predicted. However, eliminating herbivores increased survivorship of tallow seedlings only, and fungicide application had no effect on survivorship of either species. They conclude that lower chronic herbivory on tallow compared to native plants is not responsible for tallow's success in Texas.

The role of subterranean herbivores in plant population dynamics and community structure has received considerably less attention than their above-ground phyllophagous counterparts (Andersen, 1987, Mortimer *et al.*, 1999). In a second test of the EICA hypothesis as it relates to root tissue, Rogers and Siemann (2004) assessed the effects of mechanical root damage and soil fertility on two Chinese tallow genotypes-invasive (seeds from Texas) and native (seeds from China), in a factorial experimental design. Herbivore damage was simulated by mechanically severing the entire root system of Chinese tallow seedlings five centimeters below the soil surface, after which a 15-5-10 fertilizer was applied to each treatment. Several tallow tree seedlings abscised all of their leaves during the week following root damage, but all had added new leaves by the termination of the 150-day experiment. Consistent with the EICA hypothesis, Chinese genotypes were negatively impacted by simulated root damage, whereas the Texas genotypes were able to completely compensate for root damage. Addition of fertilizer increased the growth of the Chinese genotypes, but not enough to compensate for root damage. Texas genotypes were not influenced by fertilization treatments (Rogers and Siemann, 2004).

Numerous studies show that plant species may enhance their growth and fitness by developing extrafloral nectaries (EFN) to attract pugnacious insects (e.g., predacious ants and parasitoid wasps) that discourage herbivores (Bentley, 1977; Tilman, 1978; Moya-Raygoza and Larsen, 2001). Despite the benefits gained from enhanced protection against herbivores, the production of EFN, the effluent of which is primarily composed of carbohydrates and amino acids (Baker *et al.*, 1978), may be detrimental to plants, particularly in the absence of a well developed community of specialist herbivores (Bentley, 1997). In the absence of ants, the uncollected sugary secretions support black sooty mold that can be harmful. In the absence of herbivores, such as on some islands, selection reduces the gland structure and function. Chinese tallow plants have a pair of swollen, glandular stipules at the leaf-petiole junction (Correll and Johnson, 1970; Urbatsch, 2000). However, the potential function of these EFN glands and conditions that stimulate their activity remains unknown. Rogers *et al.* (2003) tested the production of EFN on Chinese tallow seedlings in response to simulated foliar herbivory and nutrient enrichment. They hypothesized that tallow tree seedlings subject to simulated herbivory and those receiving nutrient (NPK) enrichment would have a greater number of active EFN than undamaged, unfertilized seedlings. They also predicted that Chinese genotypes would have significantly higher EFN production than Texas genotypes, as a consequence of higher specialist herbivore loads. They found that nutrient enrichment did not appear to stimulate EFN activity. Both invasive (Texas) and native (China) genotypes increased EFN activity following simulated herbivory, but there were no statistically significant differences between the two genotypes (Rogers *et al.*, 2003). The function and activity of EFN in tallow remain elusive.

Invasive plant species normally support diverse insect communities within 300 years of introduction (Strong, 1974). Until that time, potential herbivores may be behaviorally constrained because they do not recognize an invasive species as a potential food source under natural conditions, despite the fact that the host plant may be palatable. This is referred to as the Behavioral Constraint Hypothesis (Feeny, 1975; Abrahamson and Weis, 1997). The time lag may also be explained by the fact that introduced plant species may possess novel secondary compounds to which native herbivores are not physiologically adapted (the Novel Weapons Hypothesis) (Callaway and Ridenour, 2004). Both of these constraints require an evolutionary response from native insect fauna in order for generalist herbivores to utilize invasive plant species. These hypotheses were tested by Lankau *et al.* (2004) to determine whether feeding behavior is plastic or fixed by evolutionary constraints. They conditioned two species of acridid grasshoppers (*Melanoplus angustipennis* and *Orphullela pelidna*), an abundant and important herbivore of prairie ecosystems, with either Chinese tallow or hackberry (*C. laevigata*) seedlings, and then released them into a prairie ecosystem enclosure containing a single tallow tree seedling of either introduced (Texas) or native (China) genotype. They determined that grasshoppers consumed similar amounts of both genotypes, suggesting that Chinese tallow may have been a palatable host plant since its introduction, but that fixed behavioral avoidance by generalist herbivores may contribute to Chinese tallow's low herbivore load in its introduced range (Lankau *et al.*, 2004). In a similar experiment, Siemann and Rogers (2003a) conducted feeding trials whereby *M. angustipennis* grasshoppers were caged with a choice between Chinese tallow seedlings from Texas and China. Their data demonstrate that grasshoppers removed more foliage from introduced (Texas) foliage. They also found higher growth rates for the China seedlings compared to Texas seedlings, suggesting genetic variation in herbivore defense and growth responses (Siemann and Rogers, 2003b).

It is interesting to note that Johnson and Allain (1998) report observing "large concentrations of adult and juvenile leaf-footed bugs (*Leptoglossus zonatus*, Hemiptera: Coreidae) on Chinese tallow fruits at Brazoria National Wildlife Refuge (Texas). Densities of *L. zonatus* on fruits averaged approximately two individuals per fruit and approximately six individuals per fruit cluster." *L. zonatus* is known to feed on a wide range of native host plants; perhaps this species is in the initial stages of adapting, both behaviorally and physiologically, to feed on tallow tree seeds.

Rogers *et al.* (2000) examined growth and physiological responses of Chinese tallow foliage to various treatments of nitrogen, shade, and simulated herbivory. Contrary to their prediction that, under high levels of herbivory, Chinese tallow would show significant decreases in leave tissue growth and physiological activity, they found that tallow is extremely tolerant of foliar tissue damage and is capable of expedient morphological and physiological compensation to herbivore damage. These data concur with a later study by Rogers and Siemann (2003), who found that Chinese tallow seedlings were remarkably tolerant to both low-intensity, chronic defoliation and high-intensity acute foliation. Neither treatment negatively impacted tallow tree seedlings. Studies of simulated herbivory are often criticized because certain aspects of insect chewing cannot be accurately imitated by manual tearing or hole-punching foliage (Hendrix, 1988). Furthermore, many phytophagous insects release chemicals during chewing that elicit specialized responses from plants. Nevertheless, if performed carefully, it is assumed that simulated foliar herbivory provides an adequate representation of decreased leaf area and biomass experienced by insect herbivores (Hendrix, 1988; Rogers *et al.*, 2000). Studies investigating herbivore-plant interactions may reveal mechanisms by which pernicious pest plant species escape density-dependent regulation and provide insight into possible control and management.

Allelopathy

The lack of significant top-down regulation (i.e., herbivory, predation, pathogens) on aggressive non-indigenous plant species suggest that other mechanisms must be involved to contribute to the success of these species in their host range. One such mechanism is allelopathy, whereby non-indigenous plants release novel chemical compounds that have deleterious effects on neighboring native species. Chinese tallow is known to possess a suite of toxic secondary metabolites in every part of the plant, so it is possible that this species does in fact gain a competitive advantage through chemical mediation, either by suppressing the growth and fitness of neighboring plants or facilitating its own growth.

Keay *et al.* (2000) hypothesized that Chinese tallow invasion in coastal herbaceous grasslands may be mediated in part by chemical inhibition. They applied aqueous extracts of leaf tissue to seeds of little bluestem (*Schizachyrium scoparium*) sown in cups filled with potting soil. Results show that germination of *Schizachyrium* was neither reduced nor slowed. These results were corroborated by experiments by Conway and Smith (2002), who tested potential allelopathic effects of Chinese tallow on native black willow (*Salix nigra*) and baldcypress

(*Taxodium distichum*) seeds, as well as seeds of Chinese tallow. They applied aqueous extracts derived from tallow litter, woodland soil subtending tallow stands, and fresh tallow tree leaves, to seeds sown in Petri dishes.

Results show that aqueous extracts did not inhibit germination and seedling root mass and length of native species when compared to seeds treated with distilled water (control). However, germination rates and all seedling measurements of tallow were higher for seedlings receiving aqueous extracts than for controls. These patterns suggest that Chinese tallow may facilitate and perpetuate its own growth and survival rather than inhibit establishment and survivorship of native species.

Controlling Chinese Tallow in Natural Areas

An effective management strategy for long-term control of Chinese tallow requires an integrated pest management (IPM) plan, which involves the application of biological, chemical, mechanical, and physical control techniques. Prior to implementing an IPM plan, stewards of natural areas are encouraged to consider using an adaptive management approach, which requires establishing clear management goals, developing control programs based on those goals, and modifying the goals based on the outcome of post-treatment assessment (Randall, 1996).

Prior to implementing a Chinese tallow control program, vegetation managers should 1) establish management goals and objectives for their natural areas; 2) determine which populations threaten the most sensitive habitats and/or species, or have the potential to do so and assign priorities for control based on anticipated impacts; 3) determine what control methods are available and, if necessary, re-assign management priorities based on this information; 4) develop and implement an integrated management plan based on the aforementioned criteria; 5) monitor population dynamics and treatment efficacy in terms of originally stated goals and objectives, and; 6) re-evaluate, modify, or otherwise enhance the plan, as needed.

When establishing goals for a site-specific control plan, the following ecological, economic, social, and managerial factors should be considered (Thayer, 1997):

1) **Spatial Distribution**: The aerial extent of the invasion, plant density, and dispersion (i.e., clumped, random, uniform) of the species to be managed, as well other plant communities in the vicinity of treatment sites.

2) **Topography and Soil Types**: What is the spatial distribution of soils subtending target populations? Is there a relationship between soil type and elevation? What are the soil characteristics (e.g., marl, sand, loam, etc.)?

3) **Hydrology**: Has the site been altered by hydrologic features, such as remnant agriculture, canals, impoundments or wells that modify natural hydrologic regimes?

4) **Control Techniques**: Which treatment or combination of treatments will most likely be effective for the natural area being treated, based on available literature and practical experience? What is the most effective timing of treatments and what factors significantly influence treatment success?

5) **Economic Considerations**: What is the anticipated cost associated with initial treatment of sites, as well as re-treatment and monitoring? What time period will be required before the site reaches a “maintenance level” of population growth?

6) **Public Outreach**: Will the control program create negative public perception? Will a public awareness campaign increase awareness and foster support for control programs?

7. **Work Plan**: In order to plan for annual budgeting needs, labor, equipment, and logistics, establish a realistic schedule as an objective for initial treatment and follow-up/maintenance.

Mapping Chinese Tallow

Best management practices of non-indigenous invasive plant species requires spatially detailed assessments of species distribution and numbers, acquired at regular intervals (Turner et al., 2003). Such information can be prohibitively expensive and/or logistically impossible to collect directly in the field. Measuring the distribution and status of invasive species indirectly through remotely sensed data offers rapid data acquisition with relatively expedient generation of map products and spatial statistics at costs that are usually lower than direct field survey methods.

Determining spectrally unique responses from individual species in various phenological stages of a plant's life history is critical in detecting populations of invasive species among a mosaic of vegetation communities (McCormick, 1999). Ground reflectance measurements indicate that tallow is characterized by higher-than-average reflectance in the red portion (0.63-0.69μm) of the visible electromagnetic spectrum during autumn months when tallow tree foliage turns crimson prior to abscission. Everitt *et al.* (2000) evaluated the efficacy of large-scale color infrared and conventional ("true color") films to detect tallow among coastal prairie and marsh habitats in coastal Texas. They report that, although Chinese tallow could be distinguished on both film types, it was more accurately delineated on true color film. Their results concur with those of Ramsey *et al.* (2002), who used scanned 1:12,000-scale color infrared (CIR) aerial photographs acquired during leaf senescence to detect tallow in transition habitats of the Texas-Louisiana border. They conclude that high spatial (less than one meter) but low spectral resolution remote sensing data was most useful in detecting and mapping Chinese tallow to greater than 90% accuracy. They speculate that higher accuracy might be obtained by using true color photographs, as a consequence of Chinese tallow's asynchronous and highly variable autumnal foliage.

Ramsey and Nelson (2005) successfully applied an atmospheric correlation algorithm to hyperspectral image data to maximize the spectral uniqueness of tallow occurring within a mosaic of native upland and wetland vegetation forest communities (e.g., cypress-tupelo) and at low/scattered density. In a pilot study assessing the efficacy of coupling hyperspectral imagery with "precision farming" techniques, Mason (*pers. communication*) is mapping the distribution of Chinese tallow on lands owned by the St. John's River Water Management District, and using the resulting spatial data to determine specific herbicide treatment sites and quantities for District vegetation managers. Using canopy reflectance data sampled from 35 tallow trees, a "training set" was developed for spectral signature detection across 11 bands. Subsequent distribution maps were developed based on data in this "spectral library". Ground truth data based on 100 sample points estimated accuracy of thematic map products at 85% or better. This novel mapping service is currently being marketed by UAP Timberland and will assist vegetation managers in developing accurate annual management budgets and facilitate the coordination of labor, logistics, and treatment schedules.

In addition to generating map products and spatial statistics, remotely sensed data can also used as a basis for developing predictive models regarding species distributions. Albright *et al*. (2004) are developing a cooperative agreement between the U.S. Geological Survey (USGS) and the Chinese State Bureau of Surveying and Mapping to document the current distribution of Chinese tallow in both its native and host ranges and determine the physiographic and biological parameters that facilitate or limit its distribution within these habitats. They are planning to utilize these data to develop predictive spatial models describing the potential future distribution of Chinese tallow if allowed to spread under current and various climate and land use change scenarios.

Integrated Pest Management Strategies

A successful control program for Chinese tallow will require an IPM approach - the integration of all available control techniques, including biological, mechanical, physical, and herbicidal methods. The current state of tallow control is not truly integrated, because biological control agents are not yet available. Furthermore, physical control methods, such as prescribed burning and hydrologic manipulation, remain either poorly understood or untenable to implement on large scale. Mechanical control typically involves felling trees and hand-pulling seedlings and saplings. Herbicide control presently offers the only pragmatic and cost-effective means of controlling range expansion of Chinese tallow into natural areas.

Biological Control

One hypothesis seeking to explain the success of invasive species in their host ranges is the “enemy release hypothesis” . First proposed by Darwin (1859) and later by Williams (1954), Elton (1958) and Gillett (1962), the underlying assumption of the enemy release hypothesis is that plants are suppressed in their native range by co-evolved, specialist natural enemies (herbivores and pathogens), and that release from these enemies provides a mechanism by which invasive populations expand and spread rapidly in ecosystems into which they are introduced (Maron and Vilà, 2001). Classical biological control involves the introduction, establishment, and dispersal of host-specific natural enemies in an attempt to suppress the population density of a pest species.

Successful biological control agents reduce pest species density and attenuate the rate of expansion into new habitats. Biological control cannot completely eradicate a pest species, and is usually used in conjunction with other management techniques, such as mechanical, physical, and herbicide applications (IPM). The National Academy of Sciences (1987) advocates the use of biological control agents as the primary pest control method in the United States. Unfortunately, the current forecast for the effective use of biological control agents for mitigating the spread of Chinese tallow in Florida appears bleak. Indeed, Chinese tallow would seem to be a prime candidate for biological control efforts. Its closest congeners have limited distribution outside of the conterminous United States, and it has no significant economic value, honey production notwithstanding. Furthermore, there is evidence to suggest that, in its native range, particularly in the Zhejiang Province, there are “numerous problems with insects” (Scheld, 1983; Zhang and Lin, 1994). The most significant of these pests are observed to be root-feeding grubs, moths (identified colloquially as the “poisonous caterpillar”), bagworms, and red spider mites (Scheld, 1983). During a visit to the Zhehiang Province Science Study Institute to study large-scale seed production of Chinese tallow, Scheld (1983) observed, “*there is a small larva(e)… either caterpillar or perhaps a beetle, which attacks and does considerable damage to the (seed) pods themselves. In the orchards observed this was apparently responsible for at least 10% loss in yield*.” Two bagworm species of the genus *Eumeta* (*E. japonica* and *E. mimuscula*), both native to Japan, are well-known pests of Chinese tallow (Nishida, 1983). These personal observations confirm the presence of a community of generalist and specialist herbivores, at least a few of which may be suitable candidates feeding trials (Table 1.3).

Paradoxically, the USDA reports that limited efforts have been initiated with regard to identification of biological control agents of Chinese tallow, primarily as a result of focusing resources on higher priority species, such as Old World climbing fern (*Lygodium microphyllum* (Cav.) R. Br.) and Brazilian pepper (*Schinus terebinthifolius* Raddi) or individual lack of research interest (B. Pemberton, *personal communication*). Even under the “best case” scenario whereby Chinese tallow became an immediate high-priority candidate species for biological control efforts, the process of foreign exploration, quarantine, mass culture, and release and colonization typically takes no less than a decade.

Mechanical Control

Mechanical removal involves the use of bulldozers and similar heavy equipment to remove vegetation. Mechanical control is usually ineffective when employed as the sole treatment of aggressive invasive plants, because soil disturbance may create conditions for regeneration from the (exposed) soil seed bank and from root fragments, and well as the possibility of invasion by pioneer exotic species. Additionally, mechanical removal is usually not appropriate in natural areas due to intense soil disturbance and damage to non-target vegetation caused by heavy equipment.

Mechanical control of Chinese tallow has proven to be ineffective and impractical at best, and in some cases may worsen invasion. The Northwest Florida Water Management District (NWFWMD) reports that efforts to manage Chinese tallow in Lake Jackson using mechanical methods have proven “impractical, and even counterproductive, as cutting results in the immediate production of multiple small, independent shoots” (Jubinsky, 1993;Thorpe, 1996). Efforts to control Chinese tallow infestations along canals at the Savannah National Wildlife Refuge (SNWR) using heavy equipment to sheer trees at a height of one meter above ground has also proven ineffective. Cut trees rapidly produced vegetative shoots and “runners” and exhibited phenotypic plasticity by assuming an extremely dense “shrub-like” growth form, with more branches to contribute to prolific seed production and significantly more leaf area for photosynthesis (C. McCormick, *personal observation*).

Physical Control

Woody vegetation can be physiologically stressed or sometimes killed by hydrologic manipulation or fire. Constraints, such as liability involved with burning, and effects on desired vegetation, often will limit the usefulness of these methods. Grace (1998) concluded that the use of fire to control Chinese tallow in coastal Louisiana prairies is ineffective at best, and may in fact exacerbate infestations. This is attributed, in part, to a number of morphological and physiological adaptations to fire exhibited by Chinese tallow, including the following:

- As tree diameter increases, thickening of the bark protects the cambium layer from damage to secondary growth. Above some minimum size, Chinese tallow appears resistant to top-kill (i.e., death of the above-ground portion of the plant) by fire.

- For smaller trees or trees subjected to extremely hot fires, response to top-kill is vigorous resprouting with the potential to produce up to 2 meters of regrowth within a single growing season. Consequently, tallow recovers from fire very quickly.

- As a consequence of damage by fire or mechanical cutting, Chinese tallow responds by root sprouting at some distance from the original plant, resulting in clonal spread for distances typically greater than five meters.

- Only the hottest fires are expected to ignite Chinese tallow, and trees typically neither carry nor transmit fire through the canopy, unlike many trees and shrubs.

- Chinese tallow stands are characterized by “low flammability” because it competitively excludes pyrogenic species that drive fire. Grace (1998) states, “it is common to watch a prescribed fire burn right up to the edge of a tallow stand and simply go out because of a lack of fuel.” As a consequence, fire-regulated prairie communities invaded by tallow shift from being fire-regulated to tallow-regulated.

Herbicide Control

Large areas: Prepare a basal bark application of a triclopyr ester-containing herbicide such as Garlon 4® or Pathfinder II® or cut stump application of triclopyr ester or triclopyr amine containing herbicide such as Garlon 3A®. Use at least 20% dilution in oil for basal bark application and at least 10% dilution (water for triclopyr amine) for cut stump application. For cut stump application, apply herbicide solution immediately after cutting. Coppicing may be reduced by addition of imazapyr-containing herbicide (e.g., 3% Stalker® or Arsenal®). Seedlings and saplings can be can controlled using foliar application (July to October) of imazapyr-containing herbicide (1% water-solution of Arsenal™ or Habitat™), fosamine-containing herbicide (30% water solution of Krenite S®), or triclopyr ester-containing herbicide (2% water-solution of Garlon 4®). For trees growing in water, aquatic labeled herbicides such as Habitat® (imazapyr) or Renovate® (triclopyr ester) must be used.

Private Property: Homeowners with one or a few trees should use Brush-B-Gon® or Brush Killer® herbicide. These diluted herbicide products (8.0% and 8.8% triclopyr amine, respectively) are available in quart-size containers from retail nursery supply stores. Property owners with larger stands of trees can use the more concentrated Garlon 3A® or Garlon 4® (44.4% triclopyr amine and 61.6% triclopyr ester, respectively), available in 2.5-gallon or larger containers from farm supply stores. If the dead trees will remain standing, Garlon 4® can be diluted at a rate of one part herbicide to five parts oil (i.e., 20%) and applied to the bark at the base of trees with stems less than 6 inches in diameter. Oil manufactured for this purpose is available from farm supply stores (Table 1.4). All herbicides are required to be clearly labeled with instructions regarding safe and accurate application of herbicides. If trees are treated during seed production, plant material should be disposed of in such a way that that seeds will not be dispersed to nearby habitats where they may germinate and produce new trees. Seedlings should be continually hand-pulled before they reach seed-producing age.

Physiological Considerations for Timing of Management

Conway *et al.* (1999) suggest applying foliar herbicides to Chinese tallow during its root replenishment period during leaf abscission, when root total non-structural carbohydrate (TNC) is highest and translocation of herbicides will be assimilated into perennating buds and organs, resulting in plant mortality. Root TNC levels are highest during seed maturation until leaf abscission. Contrary to herbicide application, where treatment should coincide with highest root TNC levels, mechanical treatments should be timed to coincide with lowest root TNC concentration (Conway *et al.*, 1999). If mechanical treatment is implemented during tallow's seed formation stage (i.e., a period of lowest root TNC levels), a higher percentage of stand mortality should be achieved than at other times of the year (Conway *et al.*,1999) (Table 1.5).

Cultural Control

Public Campaign: Tallow Tree Replacement Program (Gainesville, Alachua County)

A successful plan to address the issue of non-indigenous invasive plant species relies upon public support and the recognition that all sectors of society have a stake in protecting Florida's natural areas (National Invasive Species Council, 2001). However, informing the general public that not all trees are beneficial can be difficult. Putz et al. (1999) coordinated a

Chinese tallow tree replacement campaign in the City of Gainesville, Florida on Arbor Day, 1997, the goal of which was to garner public support for tallow control programs and increase awareness that individual horticultural choices may have environmental adverse consequences in neighboring natural areas (Figure 1.3). A number of stakeholders, including local, county, state, and federal governments, the University of Florida, garden clubs and native plant societies, and local commercial nursery growers, supported the efforts. Arbor Day ceremonies, which were attended by approximately 100 people, included presentations by Greg Jubinsky, a representative of FLEPPC and Jim Weimer, a biologist at Payne's Prairie Preserve. Events culminated in the felling of a Chinese tallow tree, followed by a cut stump treatment with herbicide. Three additional media events that highlighted the problem of tallow invasion were held, resulting in two articles in *The Gainesville Sun* (circulation 150,000) and coverage from local radio and television stations. As an incentive for removing a tallow tree their property, several Gainesville nurseries offered homeowners a 30% discount on replacement native species. Overall, the program was regarded as a success, and an estimated 75 seed-bearing tallow trees were felled and treated throughout Gainesville from January-March 1997.

The Arbor Day campaign elicited considerable public attention in the days following the event, including at least two "Letters to the Editor" of the *Sun* which were critical of the campaign, the city arborist, and those who cut tallow trees. The more vocal critics questioned the right of individuals to "kill" a tree, regardless of its ecological impact, while others complained that Arbor Day was an inappropriate day for a tree removal program (Figure 1.4).

Case Studies

Eglin Air Force Base (Niceville, Okaloosa County, Florida)

Eglin Air Force Base is one of the largest forested military reservations in the world, spanning some 464,000 acres in northwest Florida. The Eglin landscape contains almost half of the 83 natural community types recognized in Florida, providing habitat for more than 50 species on Florida's endangered species list and 12 federally listed species. In addition to containing one of the last major stands of long-leaf pine (*Pinus palustris*) on the Gulf coast, Eglin also contains sandhill pine, xeric hammock, upland hardwood and slope forest communities, as well as baygall, floodplain forest, wet prairie, and hydric hammock habitats.

On Eglin, the invasive species of greatest concern are Chinese tallow, cogon grass (*Imperata cylindrica*), torpedo grass (*Panicum repens*), and Japanese climbing fern (*Lygodium microphyllum*). Since its inception in 1995, the Eglin Invasive Non-native Species Control Program has removed more than 100,000 Chinese tallow trees from Air Force property. Additionally, all Chinese tallow trees planted decades ago in the base housing area and Eglin industrial areas for ornamental purposes have been removed.

Invasive species surveys are conducted by the Florida Natural Areas Inventory targeting at-risk high quality natural areas, as well as areas known to contain invasive non-native species. Survey information, maps, and GPS coordinates of these species can be provided to herbicide contractors, allowing rapid response and comprehensive treatment of large areas. Re-treatments are scheduled after two years or on an as required basis.

Santa Rosa Barrier Island

Chinese tallow was first documented in natural areas in the interdunal coastal swales (approximately five contiguous acres and scattered seedlings in surrounding areas) of Santa Rosa barrier island in 1995, after Hurricane Opal struck the Panhandle. The storm surge resulted in high mortality of mature slash pines and other native woody species due to saltwater inundation. Shortly after the water receded, thousands of tallow seeds germinated from the soil seed bank.

Staff ecologist Dennis Teague believes that these seeds likely came from undocumented seed producing trees in the area that were killed along with the slash pines and other woody natives. Initially, contractors attempted to hand-pull the rapidly emerging seedlings, but were quickly overwhelmed by their “carpet-like” density.

By 1999, the area was characterized by dense coverage of immature tallow trees (4-10’), which were treated that same year with a basal bark application with 18-20% Garlon 4® and the adjuvant JLB® Oil Plus Improved (or an equivalent oil carrier). Low-pressure sprays were applied with back-pack applicators to minimize drift and non-target mortality. Hand pulling small seedlings continued as necessary. Throughout 2000-2003, spot treatments were conducted to prevent sprouting, and on 21 December 2001, a restoration prescribed burn was conducted on three acres of the area with the dual objectives of removing dead woody debris and stimulating native plant growth. As of 2005, areas once infested with Chinese tallow have replaced by native groundcover. Spot treatments will be continue as required, in order to eliminate sprouting and regrowth. In 2002 and 2003, the entire area comprising Santa Rosa Island was treated for Chinese tallow and other woody invasive plant species. It is hoped that the Choctawatchee Bay will serve as a significant barrier to the continued dispersal of tallow seeds by avifauna from the mainland to Santa Rosa Island.

Eglin Main Base Property

The largest and most problematic infestation of Chinese tallow is located on the Main Base – a 50 acre site containing 15-20 year old trees of moderate to high density, surrounded by pine flatwoods. Vegetation surveys in 1999 revealed there was virtually no non-tallow species present in the herbacous layer. Thirty acres of the site had been cleared a number of years ago, but the project was abandoned and site was allowed to return to a semi-natural condition. Dennis

Teague suspects that, once cleared, the site became vulnerable to tallow invasion from seed originating from landscape debris.

In 1999 and 2000 the area was treated with 18-20% Garlon 4® and the adjuvant JLB® Oil Plus Improved (or an equivalent oil carrier) using cut stump and basal bark application methods. High density seedlings were hand-pulled when available labor permitted. Low pressure sprays were used to minimize drift and non-target mortality and marking dye was used in solution to indicate treated plants. Follow up treatments were conducted in 2002 and 2004. In winter 2003, a 20-acre parcel was subjected to a prescribed burn to reduce fuel loading, facilitate access for re-treatments, kill seedlings, and stimulate native plant recovery. In 2003, the previously cleared area was mechanically treated with a brown tree cutter, which removes dense native vegetation (e.g., vines/scrub) that emerges following elimination of the tallow overstory and seriously limits access of sites for re-treatment. Treatment of this area is considered a success and will be monitored for post-treatment changes to vegetation succession and ecosystem processes. Additionally, it is expected that long-term spot-treatments will be required due to the existence of a large soil seed bank that had developed prior to initial treatment.
Staff biologist Dennis Teague attributes the program’s success in controlling Chinese tallow on Eglin AFB with focusing attention on seed-producing trees, and prioritizing management areas such that sensitive habitats are treated first. “It may take a few years before you notice any success. After a while, though, treatments become quicker and cheaper and the areas recover with native species. The problem of dormant seeds in the soil still remains a challenge to long-term management.” The annual budget for controlling exotic invasive species on Eglin AFB is approximately $55,000.

Payne's Prairie Preserve State Park (Micanopy, Alachua County, Florida)

Payne's Prairie Preserve State Park is a 21,000 acre designated Wilderness State Park in Micanopy, located approximately 13 miles south of Gainesville. Payne's Prairie is characterized by a mosaic of habitats, including marsh, wet prairie, ponds, open water, grassy fields, pine flatwoods, and hardwood hammocks. Since it was first documented in Payne's Prairie in 1996, Chinese tallow has become the most problematic invasive species in the Preserve, infesting approximately 5,000 acres of seasonally flooded wet prairie and marsh habitats. The buoyant seed is thought to have been dispersed via stormwater drainage from nearby Gainesville, where it has been extensively planted as an ornamental throughout the Historic District of the City.

Management efforts began in 1998, and are based on a combination of chemical, mechanical and physical control. Infested sites are first cleared and delineated using a bulldozer. Herbicide control is achieved with a basal bark or cut-stump application of Garlon 4®, with an 18% basal oil concentration. Depending on their density, seedlings are either hand-pulled, or treated with a foliar application of 1% Garlon 3®. Following treatment of tallow, woody biomass, such as wax myrtle, salt bush, and box elder is chopped and crushed to prepare the site for a regular cycle of prescribed burning. Clearing infested sites in this manner makes Chinese tallow more conspicuous on the landscape, increasing re-treatment efficiency, and encourages the establishment of a diverse native herbaceous species composition. Although water levels are not directly manipulated in the Preserve, Chinese tallow trees are killed or at least physiologically stressed by prolonged flooding, depending on water depth (Jim Weimer, *pers. communication*). When funds and staff allow, treatment sites are revisited annually in November, when tallow trees are most conspicuous due to autumnal foliage. Control efforts are especially problematic in flooded sites because, although Chinese tallow thrives in these habitats, basal bark treatments cannot be applied in standing water, and field crew access to infestations are stymied.

Since FY 00-01, almost $300,000 has been budgeted for Chinese tallow control in Payne's Prairie, approximately one half of which is comprised of DEP-BIPM contracts. Despite removing an estimated 227,000 stems since the onset of their control program, there is currently more acreage invaded by Chinese tallow than in 1998. Although cost-sharing programs and DEP-BIPM-administered grants has been credited with much of the success of managing invasive plant species on state lands, greater results may be achieved by increasing funding for re-treatment programs, which ultimately dictate the long-term success of a invasive species control program. When asked if he considered the Chinese tallow control program a success, Payne's Prairie staff biologist Jim Weimer states, "The bottom line is… we're losing the battle.

St. John's River Water Management District, Palatka, Putnam County, Florida)

The St. John's River Water Management District (SJRWMD) jurisdiction covers approximately half a million acres, which is divided into conservation/restoration areas. While some of these areas contain no non-indigenous invasive plant species, most of them contain at least one problematic species – usually Chinese tallow, water hyacinth (*Eichornia crassipes*) or hydrilla (*Hydrilla verticillata*). The largest areas of tallow invasion are in Thomas Creek (Duval County) and Lake Jesup (Seminole County). The District's policy with regard to exotic species states that "… *established populations and isolated occurrences of plant and animal species not native to Florida will be monitored and either controlled, utilized, or eliminated*" (SJRWMD, 1990). Funding for and staffing of invasive species control programs are provided completely in-house. District Invasive Plant Manager Johnny Drew believes that the tallow on District lands was first introduced from surrounding nurseries.

Thomas Creek Conservation Area (Jacksonville, Duvall County)

Purchased by the District in 2001, the 6,000-acre Thomas Creek Conservation Area forms the boundary between Duvall and Nassau counties. Traveling east, the vegetation communities along the creek transition from a freshwater ecosystem of wax myrtle scrub, bald cypress swamps, loblolly pine flats and oak hammocks, to open expanses of salt marsh as the creek approaches the Nassau River. District vegetation mangers estimate that Chinese tallow current occupies 80% of Thomas Creek, much of it occurring as moderate density scattered individuals.

Herbicide control efforts began in 2003, consisting primarily of basal bark treatments of 25% Garlon 4® (75% Bark Oil). If the site is inundated, field crews apply a cut-stump treatment of Arsenal® and an oil-based surfactant with an SLN label (“Special Local Needs”, a 24-C). When treating dense tallow “islands” on higher elevations, field crews access sites using ATVs and apply a foliar treatment over the crowns of trees. Since the majority of tallow is comprised of moderate density individuals, the District refrains from using aerial foliar treatments with high non-target impacts. Tallow saplings, if present in low density (defined as less than 50 individuals per acre) are hand-pulled. In persistently flooded areas, seedling survivorship is generally low. Therefore, seedlings are neither treated nor hand-pulled in these areas. Invaded areas are prioritized for treatment and follow-up by seasonal hydrologic regimes as well as weather. For example, tallow foliage is usually vulnerable to frost in the northern portion of the District, whereas the growing season in the southern portion of the District (i.e., Seminole County) is year-round. In those areas where frost damage occurs, field crews treat tallow at the onset of the spring flush of foliage and continue until the winter months, when they shift their attention to tallow populations in the southern portion of the District.

Johnny Drew states that although he is confident that the District will meet its goal of achieving "manageable population levels" in Thomas Creek, total eradication of Chinese tallow is likely to be an unrealistic goal due to long-term soil seed bank recruitment, dispersal from surrounding seed sources, and difficulty in detecting outlying individuals.

Lake Jesup Conservation Areas (Sanford, Seminole County)

The Lake Jesup Conservation Area is a 5,257 acre floodplain along the eastern shore of Lake Monroe, providing flood protection, enhancing water quality, and protecting fish and wildlife habitat. Vegetation communities primarily include seasonally inundated prairie marshes and wooded hammocks. Chinese tallow is scattered throughout one-third of the site, much of it occurring as discrete, bell-shaped tree islands with numerous seed-bearing trees in persistently wet, low elevations areas (e.g., swales) and lower density saplings and seedlings colonizing the surrounding area.

Tallow treatment began in 1998-1999 and is confounded by persistent high water and difficulty of access by conventional means. To address this problem, the District employs an amphibious vehicle called a "marshmaster", equipped with an herbicide spray unit, to access tallow stands directly. Crews encircle tallow stands, and apply a foliar treatment of Arsenal™ with an oil surfactant to the canopy. Additional treatments and follow-up applications are performed in the same manner as the Thomas Creek site. According to Johnny Drew, he and his crew of nine field technicians have devoted a significant amount of resources to decreasing tallow populations to "manageable levels" in the Lake Jesup Conservation Area, and have successfully met their objective within two years of initial treatment. Assessment and monitoring of tallow population growth and range expansion on District property is carried out by visual observations made at regular intervals along a surveyed grid. Additionally, the District is participating in a pilot project involving the use of hyperspectral remote sensing data to quantify tallow distribution (described in the “Mapping” section of this document). A summary of expenditures, stems and area treated, and labor hours associated with controlling Chinese tallow within the Thomas Creek and Lake Jesup Conservation Areas are provided (Table 1.6).

St. Mark’s National Wildlife Refuge (St. Marks, Wakulla, Jefferson, & Taylor Counties, Florida)

The St. Mark’s National Wildlife Refuge was established in 1931 to provide wintering habitat for migratory birds, and is one of the oldest refuges in the National Wildlife Refuge System. It encompasses 68,000 acres spanning Wakulla, Jefferson, and Taylor counties along the Gulf Coast of northwest Florida. The Refuge contains expansive coastal marshes, key islands, tidal creeks and estuaries of seven north Florida rivers, and supports numerous species of flora and fauna, including seven federally-listed endangered species of birds, mammals, and reptiles. In accordance with its mandate to conserve, protect, and enhance native fish, wildlife, and their habitats, the U.S. Fish and Wildlife Service is obligated to take “all necessary measures to reduce and control biological threats to native plant and animal communities, including invasive species.” Chinese tallow is recognized as the most aggressive woody invader within St. Mark’s NWR.

The main infestation of Chinese tallow is a 12.5 acre portion of the former "Mounds Field", which was abandoned from seasonal millet cultivation in 1981. Tallow is present in Mounds Field as medium density seed-producing trees and saplings. Staff biologists noted that this population had expanded exponentially over the previous five years, and appeared to have potential to further expand its range if not immediately eradicated. Additionally, because the infestation was located immediately adjacent to the congressionally-designated St. Mark’s Wilderness Area, it was ranked as a high priority for control efforts.

There are no accounts of when tallow first colonized the site, but it was likely sometime after 1981. The site is now being actively managed by the FWS as pasture for migratory geese. The closest known significant infestation off-refuge is found on private lands and state road rights-of-way near Wakulla Station (S.R. 363). Infestations in that area persist despite recent land clearing for residential development. Since FY 2001, the St. Mark's NWR no longer receives annual federal funding specifically dedicated to exotics control, but continues to form productive inter-agency partnerships with the State of Florida Panhandle Uplands Invasive Working Group and the Florida Department of Environmental Protection-Bureau of Invasive Plant Management (DEP-BIPM).

In November 1998, the Mounds Field site was "walked down" with a D4 tractor, which crushes above-ground biomass without uprooting vegetation. At that time, the site was an "impenetrable tangle" of wax myrtle, tallow, palmetto, and smilax. The site is now primarily native herbaceous native high marsh vegetation (*Spartina patens*, *Spartina bakerii*, *Andropogon* spp., *Morella cerifera*, etc.) with occasional Chinese tallow less than 6' in height. Herbicide treatments (Garlon 4®, 20-25% basal bark application) and prescribe burning have been conducted at the site each year since 1999. Refuge biologist Michael Keys reports that, with a regular burning regime, native ground cover species are re-colonizing sites formerly occupied by monospecific tallow. Keys credits the DEP-BIPM as being a critical component to success in keeping tallow in St. Mark's NWR, and reports that "the worst of the Chinese tallow infestation is just about under control."

SUMMARY

Introduced in the late 18th Century by Benjamin Franklin for utilitarian purposes, Chinese tallow (*Sapium sebiferum*) has become an aggressive invader of natural areas (particularly wetland habitats) in southeastern U.S. from North Carolina to Texas within the past 50 years. Like many pernicious plant invaders, Chinese tallow possesses many life history traits that facilitate invasion, including rapid growth, early age to first reproduction, copious seed production, long-distance dispersal, vegetative and sexual reproduction, no specialist herbivores or disease pathogens, complex secondary chemistry, shade tolerance and persistent seed banks.

Increased research interest in tallow over the past two decades has lead to more comprehensive understanding of the ecology and invasive potential of the species. Of particular interest are variations in populations within the host- and native ranges of the species, such as differences in foliar chemistry, herbivore loads, and genetic profiles. Exploring these avenues of research further may be useful in developing biological controls for tallow, and a greater understanding of the mechanism(s) by which invaders become successful in their host ranges.

A variety of invasive plant control techniques have been shown to be effective in managing populations of tallow. These include the mechanical, chemical, and cultural strategies described in this management plan. However, it is evident that long-term successful control and management of tallow can only be achieved using an integrated pest management strategy, including the use of biological control agents. The objective of this management plan is to give land managers the advantage of currently accumulated information and data about tallow when they design and implement control and management plans for one of the most pernicious invasive plant species in the southeastern US.

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Table 1.1. Chemicals derived from various plant tissues of Chinese tallow and their medicinal properties.

PLANT PART	**CHEMICAL DERIVATIVE**	**CITATION**	**ADDITIONAL COMMENTS**
Stem bark resin	Baccatin	Pradhan (1985)	Taxol™, an anti-cancer drug, is derived from Baccatin III, a similar compound.
Stem bark resin	Methylated Ellagic Acid	Pradhan and Khastgir (1973)	Anti-carcinogen, anti-mutagen, and anticancer initiator. Ellagic acid is used in alternative medicine to prevent cancer.
Stem bark resin	Sebiferic Acid	Pradhan and Khastgir (1973)	---
Stem bark resin	Aleuritic Acid	Pradhan *et al.*, (1984)	Primarily used in the perfume industry, but is a potential substitute for alpha-hydroxy acids and valued for its antioxidant action on skin.
Stem bark resin	Sebiferenic Acid	Pradhan *et al.*, (1984)	---
Stem bark resin	Sebiferone	Liu and Kong (2002)	---
Stem (entire)	Geraniin	Neera and Ishimaru (1991)	Popular folk medicine and also an official anti-diarrhetic in Japan. Has anti-viral properties in the treatment of genital herpes.
Stem (entire)	β-glucogallin	Neera and Ishimaru (1991)	A co-enzyme whose bioactivity is not yet fully understood.
Stem (entire)	Chlorogenic Acid	Neera and Ishimaru (1991)	Major phenolic compound in coffee. An antioxidant in-vitro and may prevent heart disease. Inhibits tumor-promoting activity of phorbol esters.
Stem (entire)	Tercatain	Neera and Ishimaru (1991)	Analgesic properties
Stem (entire)	Chebulagic Acid	Neera and Ishimaru (1991)	May have immunosuppressive effects against cytotoxic T lymphocytes.
Foliage	Methyl-gallate	Kane *et al.*, (1988)	Shown to posses strong inhibitory effects on herpes-simplex virus.
Foliage	6-O-galloyl-d-glucose	Hsu *et al.*, (1994)	Reduces hypertension via intravenous administration in laboratory animal models.
Foliage	[(-)-loliolide]	Liu *et al.*, (1988)	Immunosuppressive activity; germination inhibitor and ant-repellent.
Foliage	Astragalin	Liu *et al.*, (1988)	Anti-dermatitis activity. Reduces severity of existing dermatitis; prevents development of atopical dermatitis when administered orally in mice.
Kernal Oil (Stillingia)	Sapinotoxins A&C	Brooks *et al.*, (1987)	Highly toxic compounds promoting tumor formation and inflammation in animal trials.
Kernal Oil (Stillingia) Roots (entire)	Factors S_1-S_8	Seip *et al.*, (1983)	Topical irritant and tumor-promoting activity manifested in mouse skin bioassays.

Table 1.2. Generalist fungal pathogens associated with Chinese tallow.

GROUP	SPECIFIC EPITHET	COMMON NAME	LOCATION	CITATION
Oomycete	*Pythium* spp.	Root Rot	Florida	Alfieri *et al*., 1994
Basiliomycete	*Armillaria mellea*	Oak Root Rot	California	Raabe, 1967
Basiliomycete	*Armillaria tabescens*	Root Rot	Florida	Alfieri *et al*., 1994
Hyphamycete	*Alternaria* spp.	Leaf Spot	Florida	Alfieri *et al*., 1994
Hyphamycete	*Phymatotrichopsis omnivore*	Root Rot	Texas	Alfieri *et al*., 1994
Hyphamycete	*Pseudocercospora stillingiae*	Leaf Spot	Florida & Louisiana	Alfieri *et al*., 1994
Coelomycete	*Diploidia* spp.	Dieback	Florida	Alfieri *et al*., 1994
Coelomycete	*Phomesis* spp.	Leave Tip Necrosis	Florida	Alfieri *et al*., 1994
Coelomycete	*Phyllosticta stillingiae*	Leaf Spot	Florida & Alabama	Alfieri *et al*., 1994

Table 1.3. Insect herbivores documented to consume Chinese tallow (Source: Zhang and Lin,1994; translated from Chinese to English and provided courtesy of Dr. William E. Rogers, Texas A&M University, 2002).

ORDER	FAMILY	GENUS	SPECIES	DISTRIBUTION	FEEDING MODE
Lepidoptera	Psychidae	*Acanthopsyche*			Bagworm
Lepidoptera	Saturniidae	*Actias*	*selene ningpoana*	China	Foliage
Coleoptera	Scarabaeidae	*Adoretus*	*tenuimaculatus*	Taiwan	Root/Leaf Eater
Lepidoptera	Noctuidae	*Agrostis*	*ypsilon*	Hawaii	Black Cutworm
Coleoptera	Scarabaeidae	*Anomala*	*corpulenta*	Paleoartic	Root/Leaf Eater
Coleoptera	Scarabaeidae	*Anomala*	*cupripes*	Paleoartic	Root/Leaf Eater
Coleoptera	Cerambycidae	*Batocera*	*Horfieldi*	China/India	Stem Borer
Orthoptera	Gryllidae	*Brachytrupes*	*portentosus*	Taiwan	Foliage
Lepidoptera	Psychidae	*Chaliodes*	*kondonis*	China/Japan	Bagworm
Lepidoptera	Psychidae	*Clania*	*minuscula*	China	Bagworm
Lepidoptera	Psychidae	*Clania*	*variegata*	China	Bagworm
Lepidoptera	Limacodidae	*Cnidocampa*	*flavescens*	Indoaustralia	Foliage
Lepidoptera	Lymantiadiidae	*Euproctis*	*bipunctapex*	China	Foliage
Lepidoptera	Eupterotidae	*Eupterote*	*saprivora*	China	Foliage
Coleoptera	Scarabaeidae	*Holotrichia*	*diomphalia*	Paleoartic	Root/Leaf Eater
Coleoptera	Scarabaeidae	*Madalera*	*orientalis*	Japan/Korea	Root/Leaf Eater
Coleoptera	Chrysomelidae	*Nodina*	*punctostriolata*	China	Foliage
Lepidoptera	Limacodidae	*Parasa*	*consocia*	Indoaustralia	Foliage
Lepidoptera	Hepialidae	*Phassus*	*excrescens*	China	Root Borer
Lepidoptera	Hepialidae	*Phassus*	*nodus*	China	Root Borer
Lepidoptera	Hepialidae	*Phassus*	*sinifer sinensis*	China	Root Borer
Lepidoptera	Saturniidae	*Philosamis*	*cynthia*	China	Root Borer
Coleoptera	Scarabaeidae	*Popillia*	*mutans*	French Indochina	Root/Leaf Eater
Lepidoptera	Limacodidae	*Thosea*	*sinensis*	Indoaustralia	Foliage
Lepidoptera	Limacodidae	*Thosea*	*Postornata*	Indoaustralia	Foliage
Heteroptera	Aphidadae	*Toxoptera*	*Odinae*	India/Taiwan	Foliage

Table 1.4. Herbicides for preventing sprouting of felled Chinese tallow trees (adapted from Langeland, 2002).

HERBICIDE	**APPLICATION**	**DILUTION**	**AVAILABILITY**
Brush-B-Gon™	Cut Stump Treatment	Undiluted	Retail Stores
Brush Killer ™	Cut Stump Treatment	Undiluted	Retail Stores
Garlon 3A™	Cut Stump Treatment	1 Herbicide: 10 Water	Farm Supply Stores
Garlon 4™	Cut Stump Treatment	1 Herbicide: 5 Water	Farm Supply Stores
Garlon 4™	Basal Bark Treatment	1 Herbicide: 5 Oil	Farm Supply Stores

Table 1.5. Chinese tallow root TNC levels from roots collected from trees in Texas (adapted from Conway *et al*., 1999).

PHENOLOGICAL STAGE	**DATES**	**OVERALL TNC LEVELS**
Dormancy	November 1995-January 1996	47.94%
Bud Break	February 1996	47.3%
Leaf Development	March-April 1996	41.11%
Seed Formation	May-June 1996	36.71%
Seed Maturation	July-August 1996	51.69%
Leaf Abscission	September –October 1996	60.72%

Table 1.6. Summary of Chinese tallow management efforts in Lake Jesup and Thomas Creek, (1998-2004). Data provided by the St. John’s River Water Management District.

FISCAL YEAR	**HERBICIDE COST ($)**	**AGENCY LABOR (HOURS)**	**# STEMS TREATED**	**AREA TREATED (ACRES)**
98-99	9,356	758	23,057	2,417
99-00	938	68	6,357	985
00-01	6,350	362	12,350	1,789
01-02	1,618	36	11,360	1,235
02-03	13,885	320	20,234	2,400
03-04	8,876	492	22,856	2,239
Total	41,023	2,036	96,214	11,065

Figure 1.1. Autumnal foliage, flowers, and mature fruits of the Chinese tallow tree. Because these attractive features are popular with homeowners, the tallow tree remains a valued ornamental tree throughout the southeastern US.

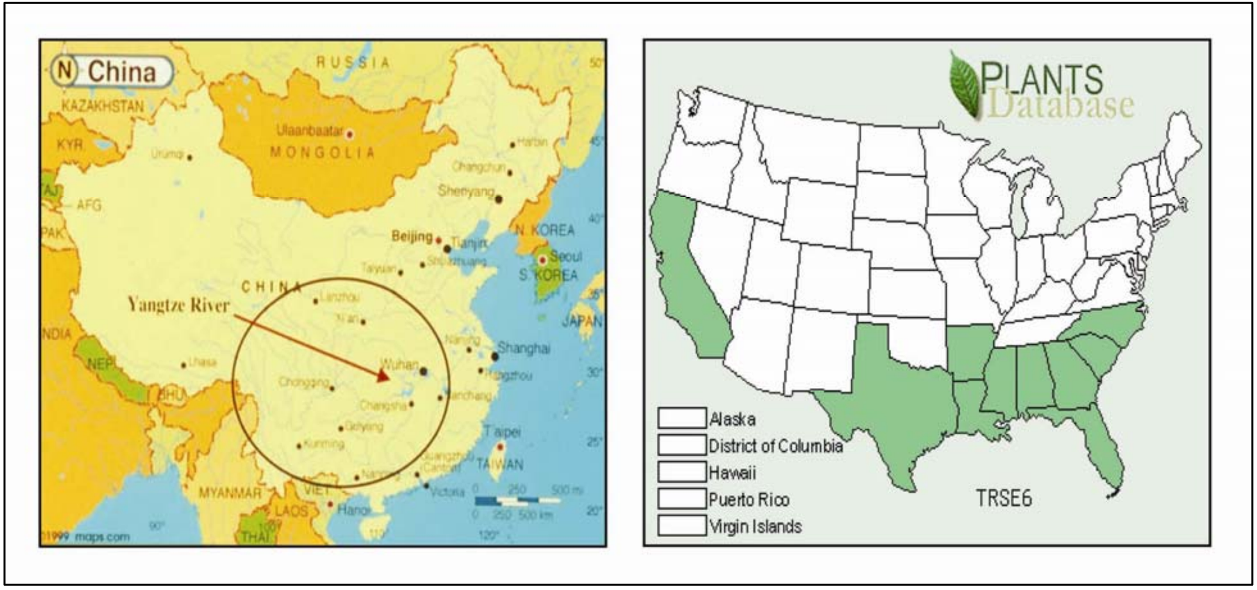

Figure 1.2. The native range of Chinese tallow (left) and its host range in the southeastern US and California (right). Images courtesy of USDA (2005) and Wunderlin (2000).

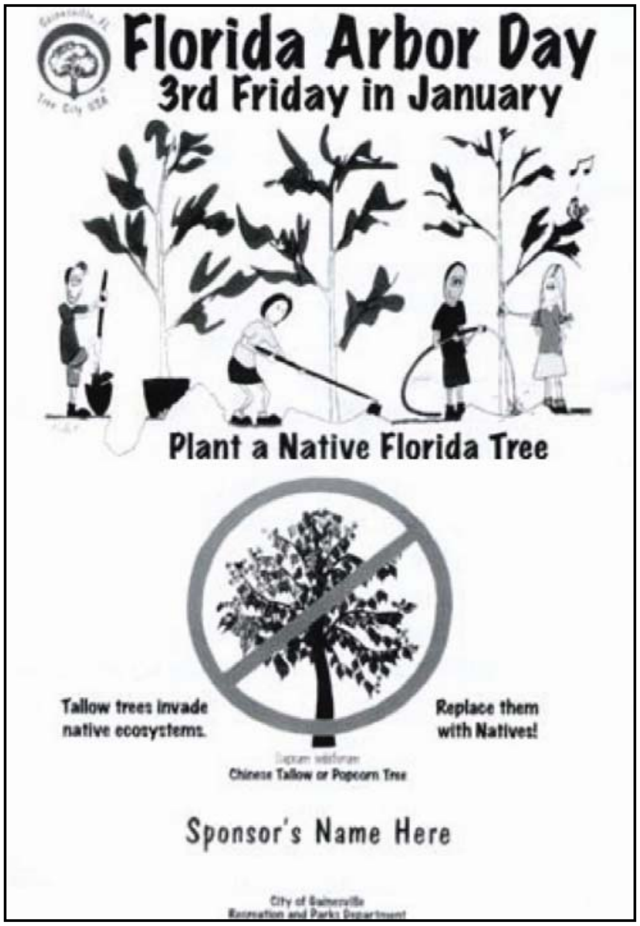

Figure 1.3. Promotional poster used for the Arbor Day Chinese tallow tree replacement program (from Putz *et al*., 1999).

Wrong Tool For Arbor Day

"*I was quite disappointed to see the city arborist's decision to celebrate Arbor Day with a chainsaw (guest column, Jan. 16). I certainly support the effort to replace tallow trees with native trees. However, the marking of a day dedicated to that important symbol of life and beauty – trees – by a tree killing binge strikes me as way off the mark. It has been my understanding that Arbor Day celebrates the positive role trees play in nature and the community. There certainly is the understanding that some trees can become predators and dominate an ecosystem; therefore, it is good to remove them and replace them with more integrated species. Let us continue as long as there is replanting – not just removal. Nonetheless, I think it is objectionable of the arborist to celebrate Arbor Day with a chain saw*."

Figure 1.4. Duplication of a "Letter to the Editor" published in *The Gainesville Sun* on January 20, 1997 (author name withheld).

CHAPTER 2

EFFECTS OF FERAL HOG (*SUS SCROFA* L.) ROOTING ON CHINESE TALLOW (*SAPIUM SEBIFERUM* L. ROXB.) SEEDLING SURVIVORSHIP IN A SOUTHEASTERN BARRIER ISLAND AND BOTTOMLAND HARDWOOD SWAMP

INTRODUCTION

Feral hogs (*Sus scrofa* L.) influence the distribution and demography of plant species through their behaviors, such as wallowing, digging, and rooting, that result in mechanical disturbance (Alexiou, 1983) as well as direct consumption of seedlings and seeds. Quantifying ecological impacts due to feral hog rooting is confounded by the fact that some impacts are direct, such as destruction of the last individuals of an endangered plant, while other impacts are indirect, such as erosion and subsequent siltation of aquatic habitats adjacent to areas of intense hog wallowing and rooting (Hone, 1988). In addition, the frequency of disturbance may be chronic, as in the constant rooting of forest floor litter, or seasonal, as in the case of differential impacts resulting from wet and dry seasons (Arrington *et al*., 2003).

There are numerous reports of severe problems with feral hog activities occurring in parks, recreational areas, national seashores, refuges, wildlife management areas, and forest districts across the United States (Lipscomb, 1989; Jacobi, 1981; Lacki and Lancia, 1986; Willy, 1987; Ralph and Maxwell, 1984; Singer *et al*., 1984; Ray, 1988). Feral hogs pose an especially high risk on islands, where population levels are high and dispersal opportunities may be limited. Additionally, many island flora and fauna are endemic and/or have evolved in the absence of predators and significant mechanical disturbance.

Through their rooting activities, hogs dramatically increase levels of disturbance in the habitats in which they reside by homogenizing soil horizons and uprooting vegetation while selectively foraging on plants with high carbohydrate root tissues or searching for invertebrates, eggs of ground-nesting vertebrates, mast, and other food items (Bratton, 1975; Barrett, 1978; Cushman *et al*., 2004). Hog rooting influences vegetation community structure by reducing the abundance of understory vegetation, including ground cover species and woody seedlings and saplings, influencing regeneration of seeds in the soil seed bank, and modifying soil characteristics by reducing litter and increasing mineral leaching (Singer *et al*., 1984; Eberhardt, 1968).

The impacts of feral hog rooting on native plant communities and associated ecosystem properties is well-documented, including beech forests (Bratton, 1975), montane rain forests (Ralph and Maxwell, 1984), tropical rain forests (Ickes *et al*., 2005), herbaceous species (Royo and Carson, 2005), oak forests (Sweitzer and Van Vuran, 2002), deciduous mixed forests (Welander, 2000), grasslands (Cushman *et al*., 2004; Wilson, 2004), coastal prairie (Kotanen, 1995), monsoon wetlands (Bowman and McDonough, 1991), floodplain marshes (Arrington *et al*., 1999), high-elevation vernal flora (Bratton, 1974) longleaf pine forests (Wahlenber 1946; Wakely (1954), and dune communities (Baron, 1982). Several studies have documented a positive correlation between vegetation damage and feral hog densities (Katahira *et al*., 1993; Hone, 1995). The objective of this study is to assess the impact of feral hog rooting on the survivorship of Chinese tallow (*Sapium sebiferum* L. Roxb.) seedlings in barrier island and bottomland hardwood swamps characterized by varying hog densities.

Feral Hogs (*Sus scrofa*) in Georgia

Feral hogs on Georgia's sea islands were originally of Eurasian descent introduced in the 1540's by Spanish exploration parties as a reliable island larder to missionaries and subsequent visitors (Mayer and Brisbin, 1991). In some locations, the descendents of the Eurasian animals have maintained a portion of their genetic integrity. In Georgia, however, Eurasian boars have freely interbred with free-ranging domestic swine in the state since the 19th Century (Mayer and Brisbin, 1991). As a consequence of extensive hybridization, it is unlikely that individuals of the pure Eurasian strain exist in Georgia. However, hybrid offspring possess many phenotypic traits of their Eurasian progenitors (Kammermeyer *et al*., 2003). Mayer and Brisbin (1991) report that feral hogs have been documented in Georgia throughout the coastal plain and in the Blue Ridge Mountains, as well as limited areas within the Piedmont. Additionally, feral hogs inhabit Georgia's barrier islands, including Cumberland, St. Simons, St. Catherine's, Ossabaw, and Wassaw. Bottomland hardwood swamps and marshes are preferred habitat within the coastal plain. Golley *et al*. (1965) and Gaines *et al*. (2005) report that feral hogs prefer hardwoods and are found infrequently in upland pineland and scrub habitats. On barrier islands, such as Cumberland and Ossabaw, saw palmetto-live oak forests and salt marshes are preferred (J. Simmons, *personal communication).* In the southeastern US, hogs are predators of eggs of ground-nesting avifauna (including game and shorebirds), sea turtles, gopher tortoises, and alligators (Cox, 1999).

Feral hogs currently do not possess legal game status in Georgia; they are considered "domestic animals". Consequently, the animals are considered the private property of the landowner on whose property they reside (Mayer and Brisbin, 1991). Feral hogs may be hunted year-round without limit on private lands. On state wildlife management areas (WMAs) and federal lands, the hunting season for feral hogs is coincident with that of white-tailed deer (Kammermeyer *et al*., 2003).

Impacts of Feral Hogs in Island Ecosystems

Feral hogs occur on numerous oceanic and barrier islands throughout the world where their population densities frequently attain very high levels relative to continental populations, primarily due to the absence of major predators and competitors. For example, on the Channel Islands off the coast of California, feral hog densities are reported to commonly exceed 20 hogs/ km^2 (Baber and Coblenz, 1986; Sterner, 1990). Alternatively, an ecologically similar site on the nearby mainland supports hog densities of just 3-4 hogs/ km^2 (Sweitzer *et al*., 1997; Sweitzer, 1998).

Contrary to mainland ecosystems, where hog rooting may be less overt, depending on population densities, the impacts of hog rooting on vegetation communities in island ecosystems by feral hogs is overwhelmingly negative, particularly with regard to endemic and/or endangered plant species. Campbell and Rudge (1984) measured changes in vegetation as a result of hog rooting and browsing over a ten year period on endemic tussock (*Chionocloa antartica*) grasslands at Port Ross, Aukland Islands. They determined that tussock was greatly reduced or eliminated in areas where rooting and browsing by feral hogs occurred, and that woody vegetation replaced *Chionocloa* grasslands in areas where tussock had been removed (Campbell and Rudge, 1984). Challies (1975) concluded that, as a result of heavy foraging and rooting of endemic broad-leaved plant species on Aukland Island by feral hogs, the spatial distribution of these vegetation communities is now exclusively confined to steep, inaccessible slopes and cliffs. In surveys of soapbush (*Clidemia hirta*) invasion patterns in tropical forests of Maylasia, Peters (2001) observed that the spatial distribution of *C. hirta* invasion foci in forest gaps was highly correlated with previous soil disturbance from feral pigs, and that these invasion foci may potentially modify forest regeneration dynamics through competition with native plant species. Kastadalen (1982) reported that hogs consumed endemic herbs, grasses, and rhizomes of bracken fern (*Pteridium aquilinum*) on Santa Cruz Island in the Galapagos Archipelago. Van de Werff (1982) documented that the distribution of the terrestrial orchids *Prescottia oligantha* and *Liparis nervosa* on Santa Cruz Island have both been severely restricted as a consequence of feral hog foraging and rooting. Excessive rooting at the base of large trees on Santiago Island, Galapagos, has resulted in many falling over (Eliasson, 1968). Nevertheless, Coblenz and Baber (1987) conclude that habitat modification by feral hogs on Santiago Island is negligible, in part because they consume many of the same food items formerly consumed by giant tortoises (Schofield, 1989). Similarly, Baron (1982) found no significant differences among vegetation patterns between Horn Island, a barrier island with hogs present and an island without a resident population of hogs. Results suggested that rooting activity was strongly seasonal with greater activity during the winter months when above-ground food items were scarce. Furthermore, rooting-induced damage recovered rapidly, supporting Baron's conclusions.

Impacts of Hog Rooting on Mainland Vegetation

Bratton (1975) determined that hog rooting reduced the abundance and diversity of herbaceous native vegetation by 90% or more in gray beech forests in the Great Smoky Mountains National Park. Tisdell (1982) reported that natural resource managers of national parks in New South Wales, Australia document that hog rooting provides ideal seed beds for burrs, thistles, and other noxious weed species. In addition, they note that pigs "completely destroy" burrawang shrubs (*Macrozamia communis*) because their root stock contains high levels of starch and are therefore a preferred food item.

In some cases, hog foraging may enhance native vegetation. In a study of effects of hog rooting in the Tullgarn Nature Reserve in Stockholm, Welander (2000) found that plant species diversity increased by approximately 30% in disturbed patches. Furthermore, he reports that feral hogs enhanced seed dispersal through pelage adhesion. The impacts of hog foraging may have important seasonal components. Bowman and McDonough (1991) found that disturbance from feral hog rooting varied spatially and temporally in monsoon forest-wetland ecosystems in Northern Australia. During the dry season, sedgelands and melaleuca forests were exploited heavily by feral hogs, whereas at the onset of the wet season, hogs shifted use to eucalypt and lophostemon forests.

Effects on Native Species Regeneration

In a two-year exclosure study examining the effects of feral hog rooting on oak tree regeneration and forage availability (i.e., acorns) for native wildlife in oak-woodlands in California, Sweitzer and Van Vuren (2002) found that rooting disturbance by feral hogs ranges between 35 and 65 percent annually in areas of high density hog populations, and that rooting activities significantly reduced oak tree seedling survival. Additionally, they found that acorn consumption by feral hogs contributes dually to decreased acorn survivorship and subsequent germination as well as reduced forage availability for native wildlife (Sweitzer and Van Vuren, 2002). Conversely, Groot Bruinderink and Hazebroek (1996) found no evidence that intense foraging had any effect on the regeneration of several tree species in the Netherlands, including European black cherry (*Prunus padus*), American black cherry (*P. serotina*), birch (*Betula pubescens* and *B. pendula*), rowan (*Sorbus aucuparia*), holly (*Ilex aquifolium*), Scots pine (*Pinus sylvestris*), Douglas fir (*Pseudotsuga menziesii*), Norway fir (*Picea abies*) and Japanese larch (*Larix kaempferi*). However, they did determine that regeneration of oak (*Quercus robur*, *Q.*

petraea, and *Q. rubra*) and beech (*Fagus sylvestris*) were negatively correlated with hog rooting frequency. Kotanen (1995) evaluated the effects of feral hog rooting on plant assemblages in northern California meadow communities containing both native and non-native plant species using thirty 25 x 25 cm permanent plots at randomly selected sites and evaluated changes for three years. He found that feral pigs overturned an average of 74% of the area in five meadow communities. In contrast, all other native animals (e.g., moles, pocket gophers, ground squirrels, skunks, gray squirrels, and ants) accounted for less than 1% of soil disturbance (Kotanen, 1995). Fiedler and Keever (2003) documented direct negative impacts to 34% of endangered Suisun thistle (*Cirsium hydrophilum* var. *hydrophilum*) populations at Rush Ranch in Solano County, California.

Effects on Ecosystem Structure

In Malaysia tropical forests, indigenous female feral hogs construct nests primarily from woody saplings that hogs either break or uproot, resulting in significant localized damage. In their assessment of impacts of feral hog nest construction on lowland rainforest saplings in Malaysia, Ickes *et al*. (2005) determined that a single pig nest contained an average of 267 ± 86 woody saplings, 45% of which had been uprooted and the remaining 55% snapped at the primary stem. Furthermore, they estimated that the understory affected by a single pig nest comprised an area of 244 ± 112 m^2, in which 53% of the woody plants were either uprooted or snapped. They estimate that nest construction by feral hogs was responsible for 29% of tree mortality in saplings of 1-2 cm dbh, and 43% of sapling mortality and damage combined (Ickes *et al*., 2005).

Arrington *et al*. (1999) constructed fenced exclosures in Florida’s Kissimmee River floodplain and found that rooting-induced microtopographic and soil moisture variation significantly increased plant species richness as well as plant-defined microhabitats.

Additionally, they speculated that hog rooting may be a disturbance that creates small-scale habitats for numerous fish and bird species as marshes are reflooded, thereby enhancing species diversity and richness in wetland habitats.

Enhancing Non-Native Plant Populations

There are numerous studies to suggest that foraging and digging by feral hogs reduces the dominance of native plant species and increases the abundance of invasive taxa (Baker and Stebbins, 1965; Bratton, 1975; Spatz and Mueller-Dombois, 1975; Baker, 1979; Russell-Smith and Bowman, 1992). Akanda *et al*. (1996) report that rooting by feral hogs facilitates the dispersal and subsequent germination of tropical soda apple (*Solanum viarum*), an invasive shrub in central and south Florida. They also speculate that feral hogs may be a significant dispersal vector of hydrilla (*Hydrilla verticillata*) by shedding resistant turions (i.e., fleshy axillary buds) in feces of pigs that have consumed the plants (Langeland and Burks, 1999). In Britain, where feral hogs have been re-introduced as a result of escaping from "wild boar farms" after having been eradicated over three hundred years ago, Goulding (2003) records that "thistles are the only plant species I have noticed to survive the rooting experience". Extensive rooting in moist gullies in the Strzelecki National Park in Australia led to significant erosion and loss of native forest plant species, which were replaced by dense, monotypic understories of bracken fern (*Pteridium esculentum*). In Hawaii, dispersal of seeds of invasive banana poka (*Passiflora mollissima*) and guava (*Psidium cattleianum*) is facilitated by feral hogs, which forage heavily on these fruits (Aplet *et al*., 1991; Stone and Loope, 1987; Smith, 1985). Aplet *et al*. (1991) found that invasive plant species were much more likely to be associated with the soil disturbance resulting from feral hog rooting in a Hawaiian montane forest, including kahili ginger

(*Hedychium gardenerianum*), firetree (*Myrica faya*), Vasey grass (*Paspalum urvillei*), and palmgrass (*Setaria palmifolia*).

The extent to which feral hogs consume or serve as dispersal vectors of seeds of invasive plant species is poorly understood. Low (2002) reports that in wet tropical habitats of Australia, feral hogs are responsible for dispersing and facilitating the occurrences of the vigorous invasive buffalo grass (*Paspalum conjuctatum*). In contrast, Tisdell (1982) reported that selective foraging on the root stock of cattail (*Typha latifolia*) and Patterson's curse (*Echium lycopsis*) by feral hogs controlled the abundance of these invasive species on some of Australian public lands. Hone (1980) found conflicting data on the impact of hog rooting on weedy species in Australian pasturelands. On introduced pasture rooted by feral hogs, he noted a 74% reduction in native grass biomass and a ten-fold increase in non-native invasive cogon-grass (*Imperata cylindrica*) and in broad-leaved weedy species, particularly bracken fern (*Pteridium esculentum*). Feral hog rooting and wallowing has been implicated in spreading lantana (*Lantana camara*), one of the "worlds' worst weeds" (Foy and Inderjit, 2001) by opening forest canopies and creating light gaps and germination microsites (Low, 2002). In a four year exclosure experiment documenting the effects of foraging by feral hogs in a California grassland, Cushman *et al*. (2004) found that rooting activity and subsequent soil disturbance led to a 62% increase of exotic annual grasses in short-grass prairie communities. Drawing on field interviews with members of the indigenous Jawoyn tribe in Australia's Kakadu National Park, Robinson *et al*. (2005) reports that feral pigs root and wallow extensively in the vicinity of patches of giant sensitive plant (*Mimosa pigra*), a highly invasive shrub, and that the seed is transported to other habitats by adhesion on the mud-encrusted pelage of wallowing pigs, although this phenomenon has not been quantified. McIlroy *et al*. (1993) reported that, although feral pigs likely consume a wide range of fruits and seeds, the viability of seeds in hog feces may be related to seed size. For example, fruits containing small seeds (i.e., < 5 mm diameter) from species such as umbrella tree (*Schefflera actinophylla*) and guava (*Psidium guajava*) appear to suffer little physical damage. There is conflicting evidence regarding the fate of larger, easily masticated seeds (McIlroy, *et al*., 1993). Guava seeds have been observed germinating in hog feces, but their viability appears to be low (Pavlov *et al*., 1992). Because invasive non-woody plants frequently have small sized seeds as part of their "weedy" phenotype, these weedy plant seeds may be successfully dispersed by hogs while the larger seeds of non-weedy phenotypes are destroyed.

The objectives of this research address the following questions: 1) how does feral hog rooting influence the mortality of Chinese tallow (*Sapium sebiferum* L. Roxb.), an invasive, subtropical tree of coastal, wetland, and island habitats, and; 2) are there significant differences between island and mainland ecosystems with respect to *S. sebiferum* seedling mortality as a direct consequence of feral hog rooting?

MATERIALS AND METHODS

Study Sites

Ossabaw Island

Ossabaw Island is owned by the State of Georgia and managed by the Department of Natural Resources, Wildlife Resources Division (DNR-WRD). Located in Chatham County, Ossabaw is the second largest barrier island on the Georgia coast, consisting of approximately 25,000 acres of which 11,800 is upland forest. In 1978, Ossabaw was designated as Georgia's first Natural Heritage Site, a designation which ensures that the Island is utilized solely for "natural, scientific, and cultural study, research and education, and environmentally sound preservation, conservation, and management of the island's ecosystem…" (GDNR, 2000).

The vegetation communities of Ossabaw Island are typical of Georgia barrier islands and consist primarily of freshwater ephemeral wetlands, salt marshes of smooth cordgrass (*Spartina alterniflora*) and pine forests dominated by loblolly and slash pine (*Pinus taeda* and *P. elliotti*, respectively), and maritime forests dominated by live oak (*Quercus virginiana*), cabbage palm (*Sabal palmetto*), saw palmetto (*Serenoa repens*), red bay (*Pursea borbonia*), and wax myrtle (*Morella cerifera*). Subtending soils are generally infertile, porous, acidic, and subject to leaching. Soils at higher elevations are very well drained, while soils in low elevations are poorly drained (GDNR, 2000).

Chinese tallow (*S. sebiferum*) is widespread on the Island and typically present in densities ranging from scattered individuals in wet prairies and marshes (≤ 1 tree/100m^2) to dense, self-thinning, monotypic stands in low-lying areas in intermittently flooded areas (≥ 30 trees/100m^2). Although accurate records documenting the introduction history and subsequent spread of Chinese tallow on Ossabaw do not exist. However, based on the spatial distribution of current populations in and along the periphery of ephemerally flooded wet areas, it seems likely that the buoyant seeds traveled along river corridors and were deposited in low-lyling areas during seasonal and/or episodic flooding events. The aril-rich mantle of the seed is utilized by birds such as red-bellied woodpeckers (*Melanerpes carolinus*) and northern flickers (*Colaptes auratus*) (Renne *et al*., 2002). Consequently, birds may serve as secondary dispersal vectors into upland maritime forests of Ossabaw. Extensive ground surveys conducted along east-west transects in upland habitats in 2002 by the author confirm that solitary mature or sapling-sized tallow individuals are virtually nonexistent. This suggests that dispersal by avifauna is not the primary means of long-distance dispersal for this species on Ossabaw Island. Though its management and control is acknowledged as being a significant and ever-increasing challenge to

DNR-WRD resources, the goal of tallow control efforts, as indicated by the Ossabaw Island Comprehensive Management Plan (CMP) is “eventual elimination”.

Pigs were reportedly introduced to Ossabaw Island during the 1500’s when the Spanish were attempting to settle coastal areas of Georgia (Mayer and Brisbin, 1991). Various breeds have been introduced in attempts to enhance the stock. Nevertheless, the animals have retained morphological and behavioral characteristics typical of feral hogs throughout the southeastern US, including long guard hairs, mid-dorsal “mane” of hair, split grey-brown hair tips, agouti coloration, and longitudinally-striped piglets (Fletcher *et al*., 1990).

As stated by the CMP produced by the DNR-WRD, the continued existence of feral swine on Ossabaw Island directly impedes the agency’s mission of “environmentally sound preservation, conservation, and management of the Island’s ecosystem”. Consequently, the primary objective of the DNR-WRD is the eradication of all feral hogs from Ossabaw (DNR, 2000). Despite annual culling of between 1,000- to 1,500 animals through trapping, sharp-shooting, and hunting, the population density remains extremely high and is estimated to be at least 24.7 hogs/km^2, based on field trials of bait trapping techniques (Fletcher *et al*., 1990).

Jesup, Georgia

The floodplain along the Altamaha River in Jesup is seasonally flooded, with water levels reaching depths of up to two meters during the fall and winter seasons (Figure 2.1A). Vegetation communities are characterized by seasonally inundated bottomland hardwood swamps dominated by tupelo (*Nyssa aquatica* or *N. sylvatica* var. *biflora*) and baldcypress (*Taxodium distichum*) with seasonally sparse herbaceous understories dominated by lizard’s tail (*Saururus cernuus*), false nettle (*Boehmeria cylindrica*) and trumpet creeper (*Campsis radicans*). Less frequently flooded mixed hardwoods are also common and are dominated by overcup and southern red oak (*Quercus lyrata* and *Q. falcata*, respectively), coastal plain willow (*Salix caroliniana*), red maple (*Acer rubrum*) and sweetgum (*Liquidambar styraciflua*). The area also contains numerous creeks, tributaries, and oxbow lakes. Population densities of feral hogs have not been determined systematically for the Jesup site. However, the Georgia DNR-WMD estimates that, based on qualitative assessments of populations in nearby Wildlife Management Areas (WMAs) in Long County, GA, the feral hog population is described as “good” (i.e., stable or increasing, from a game management perspective) on an ordinal scale of “poor, fair, good, and excellent” (W. Abler, *personal communication*). There are no quantitative measurements associated with these categorical classes. *Sapium* is distributed in these bottomlands in a clumped distribution, typically as one or a few large seed-producing trees. During the summer months, these trees are subtended by a profusion of seedlings in densities as high as 250/m^2 (Figure 2.1B).

Seed Collection and Germination

A total of 5,000 mature tallow seeds were collected from randomly selected mature tallow trees from the Jesup site in November of 2000 and from Ossabaw in November 2001. Seeds were sown in flats in December and placed in a greenhouse subject to ambient light conditions. Seeds were allowed to germinate until May, at which time a total of at least 1,000 germinated tallow seedlings with an average height of 27 cm, were selected for field experiments.

Experimental Design

Five circular (0.5-meter diameter) exclosures were randomly placed within each site on Ossabaw Island and the Jesup site. Exclosures were constructed using 14-guage 2” x 4” mesh welded wire fencing with a height of 48”. Exclosures were anchored into the substrate using four, two-foot sections of 5/8” diameter rebar, one end of which was hooked to secure the exclosure wire. To discourage exclosure structural damage by excessive rooting and toppling by feral hogs, the bottom 12” of the exclosures were wrapped with barbed wire. Ten seedlings were planted within and outside of each of the exclosures (Figure 2.2). To minimize mortality due to transplanting, seedlings were watered every other day from May 19th through August 30th in both years. Exclosures in the Jesup site were established at 10 locations, each of which was characterized by the same vegetation community. Exclosures at Ossabaw Island were also established at 10 sites (Figure 2.3).

Every other day, between May 19th and August 30th, 2000, each exclosure and its paired control was visited at the Jesup site. At each pair (i.e., exclosure and nearby plot), the presence or absence of hog rooting was noted, and the number of uprooted seedlings in the plot was counted. The same protocol was used at the Ossabaw site during May 19th through August 30th, 2001. Each experiment lasted 103 days. Mortality data from the outside plots were entered into an Excel spreadsheet, pooled by site and location, and analyzed by one-way Analysis of Variance (ANOVA).

RESULTS

Tallow seedling mortality was significantly higher and more immediate on Ossabaw Island than at the Jesup site ($p = < 0.001$). The average time required to achieve 50 percent tallow seedling mortality as a direct result of hog rooting was 37.8 days on Ossabaw Island. Only one population in Jesup experienced ≥ 50% mortality, and that was achieved in 97 days (Table 1). At the end of the 103-day experiment, the average *Sapium* seedling mortality for Ossabaw and Jesup populations was 90% and 34.6%, respectively (Figure 2.4). Mortality of

Sapium seedlings inside the exclosures was negligible. Throughout the duration of the study, two seedlings within exclosures on Ossabaw (one on North Bradley Beach and another in North Central) died from what appeared to be water stress and were replaced immediately. In Jesup, a single seedling showed evidence of foliar damage due to insect herbivory, and all seedlings within the exclosures survived. The average height of *Sapium* seedlings on Ossabaw and Jesup at the beginning of the experiments were 27 cm and 29.2 cm, respectively.

Ossabaw Island

There were no significant differences among sites with regard to *Sapium* seedling mortality at the 0.05 alpha level (p= 0.6984). Overall, seedling mortality was lowest in Cane Patch and Mule Run Road (82%) and highest in Gator Hole South (100%). There appear to be similar temporal relationships with regard to rooting activities among sites in close proximity. For example, in the Hog Pond and North Bradley Beach sites, seedling mortality declined precipitously in early-to-mid June and then remained constant at approximately 90% for both populations beyond late June (Figure 2.5).

Populations in the north and central portions of the Island (Cane Patch, Cabbage Garden East, Cabbage Garden West, North Central, and Pine Barren Road) exhibited similar temporal patterns of rooting. However, in Cabbage Gardens East and West, hogs began rooting *Sapium* seedlings and investigating exclosures immediately, whereas seedlings and exclosures in sites in Cane Patch, North Central, and Pine Barren Road weren’t encountered until at least three days after the experiment began. Once discovered by hogs, all planted populations experienced steady mortality over the summer months, resulting in an average seedling mortality of 88.4% at the end of the study.

Populations in the southern portion of Ossabaw (Mule Run Road, South End Beach, and Gator Hole South) experienced similar temporal patterns of rooting. Initial encounter of exclosures and seedlings by hogs occurred after four days. Once encountered, hogs rooted the area intensively for short periods of time, and then did not disturb seedlings for up to several days later (Figure 2.5). Mortality of *Sapium* seedlings at the Gator Hole South site experienced 100% mortality by the end of the study period.

Jesup

Distinct spatial and temporal patterns of seedling mortality due to feral hog rooting are more difficult to discern, but the general trend appears to be a protracted period prior to discovery of exclosures and seedlings, followed by rooting activities resulting in low levels of seedling mortality, after which time sites are either intermittently or completely undisturbed during the summer months. Sites characterized by this pattern of rooting include First Ridge, Second Ridge, High Ridge South, High Ridge North, Clear Cut East, Clear Cut West, and River Edge (Figure 2.6). Exceptions to this temporal pattern include Clear Cut North and Moccasin Cross. These two sites were not discovered and rooted by hogs until 31 and 59 days, respectively, after which each site experienced a single event of intense rooting resulting in at least 25% seedling mortality, followed by intermittent revisits and low levels of rooting and subsequent seedling mortality. In contrast, Back Forty was discovered within two days, resulting in 8% seedling mortality, followed by almost three months of inactivity.

DISCUSSION

Sapium seedling mortality was both higher and occurred more rapidly on Ossabaw Island than in Jesup sites, most likely a result of much higher pig densities on islands compared to mainland ecosystems. This observation has been made by other researchers (Sweitzer and Van Vuren, 2002) and is important because rooting disturbance may potentially alter competitive relationships among plants to a greater degree in areas where hog populations are high. *Sapium* seedlings are known to contain a number of noxious secondary compounds in foliage, stem, and root tissues (Seip *et al*., 1983; Pradhan *et al*., 1984; Hsu *et al*., 1994). Consequently, the seedlings are likely unpalatable, of little nutritional value, and not a sought-after food item. In neither the Jeup nor the Ossabaw site did we observe evidence of hogs eating seedlings, only mechanical uprooting. On Ossabaw Island, *Sapium* seedlings (or those of any woody species) are rarely encountered. Conversely, in the Jesup bottomland hardwood swamp, *Sapium* seedlings establish and grow in densities as high as 250 plants/m^2 with relatively low levels of hog rooting and associated mortality. High hog density may mean the population is close to limiting food resources and this may cause individuals to investigate any plants as possible food. Rooting activity and associated predation is so intense on Ossabaw that Wild Turkey (*Meleagris gallopavo*), normally a ground-nesting species, have been observed nesting in live oak trees probably in an attempt to avoid nest predation (Fletcher, 1994).

Ossabaw

There appeared to be few definitive spatial and temporal patterns associated with feral hog rooting on Ossabaw. Cane Patch and Mule Run Road experienced the lowest levels of *Sapium* seedling mortality (82%). The former is a small “satellite island” located to the northwest of Ossabaw proper and, though easily accessed by a ¼ mile dirt road from the northern part of Ossabaw, remains significantly less accessible than other sites on the main portion of the Island.

Intensive rooting activity and associated seedling mortality on Ossabaw Island in sites located in back-dune communities (i.e., Hog Pond and North Bradley Beach) beginning in mid-to-late June may in part be explained by their proximity to dunes in which female loggerhead sea turtles (*Caretta caretta*) build nests containing up to 150 eggs (GDNR, 2004). Hogs frequently traverse the Hog Pond and North Bradley Beach site to gain access to this high value food source.

With the exception of a single site (Gator Hole South), which was located within 100 meters of a heavily-utilized, artificial water hole, there were no instances where seedling mortality reached 100%. Rather, once seedling density reached approximately 90% mortality, hogs either ignored or avoided uprooting them during their rooting activities. There may be several explanations for why this may occur. First, though their visual acuity is known to be poor, hogs may be stimulated by a high density patch of vegetation and subsequently compelled to investigate the patch as a palatable food item. Single seedlings or very low density vegetation may be ignored until they are happened upon by chance. Second, hogs may simply be responding to a novel item on the landscape containing possible food items (i.e., the exclosure structure) and *Sapium* seedlings are uprooted merely as an "incidental take" while investigating the structure. Despite barbed wire reinforcement at the base of the structures, a number of exclosures were moderately- to severely collapsed (though none were destroyed) due to pushing and rooting (Figure 2.7). Density-dependent rooting of vegetation "patches" may explain why hogs tended to uproot seedlings rapidly and intensively, at least at sites on Ossabaw Island. Alternatively, high hog density coupled with subsequent resource limitation may compel hogs to investigate any plant material as a possible food item.

Jesup

No attempts are made to control feral hogs at the Jessup sites and, though densities are likely to be much less than on Ossabaw, they are typical of many mainland feral hog densities in the southeast (Mayer and Brisbin, 1991). The large dense patches of tallow seedlings at the Jesup patch are further evidence, though circumstantial, that facultative rooting by hogs may reduce tallow seedlings. There is simply a low hog-tallow encounter rate because hog densities are low. The lack of hog damage also provides evidence that hogs are not feeding on tallow seedlings. If hogs were consuming tallow seedlings, one would expect to see a pattern of extensive damage within discovered patches. At the Jesup site there are many tallow seedlings and dense stands of mature tallow trees but intermediate size classes are rare. This suggests enhanced mortality on these intermediate size classes. Although further investigation is needed, the high energy of the river's flood stage may be a major source of mortality to the intermediate size classes. As an indication of the force of these flood waters, 5/8" diameter rebar that was used to mark plot corners was bent flat during the winter high waters. Tallow seedlings are flexible and may simply bend with the current while the more woody and relatively weak saplings are more easily broken or uprooted.

Impacts of Feral Hog Rooting on the Composition of Plant Communities on Ossabaw

The current population density of feral hogs on Ossabaw Island, conservatively estimated at over 27 hogs/km^2 (Fletcher, 1990), poses an immediate and significant threat to the structure and functional characteristics of vegetation communities on Ossabaw. For example, live oak regeneration is extremely limited on the Island due to consumption of virtually all available mast and seedling herbivory. Indeed, with the exception of root sprouts, no discrete live oak seedlings (or any woody seedlings or saplings) were discovered during the study period, despite intense surveys. Feral hog rooting appears to have significant, negative impacts on the growth and development of *Sapium* seedlings on the Island. Because feral hogs are known to eat oak seedlings and acorns, we would expect an even greater impact of high hog densities on oak seedlings. It should be noted, as in the case of *Sapium* seedlings, feral hogs are not known to actively select *Sapium* seeds as food sources. The seed kernel contains highly toxic compounds (Seip *et al*., 1983) and no traces of intact or masticated *Sapium* seeds were observed in hog scat on the Island. Maybe move this back to where you talk about toxins in plant leaves. While *Sapium* plants reproduce vegetatively much like root sprouts of live oaks, it is unclear to what degree the species reproduces asexually on Ossabaw. The author, having observed *Sapium* populations throughout its southeastern and in California range, has not observed seedling recruitment as low as on Ossabaw Island (Figure 2.8).

MANAGEMENT IMPLICATIONS

In accordance with Georgia state legislation, feral hogs are removed from state-owned land when possible. In many natural areas, though not in Georgia, large scale exclosures have been constructed to protect native vegetation communities and to allow recovery from intense hog rooting activities (Stone and Loope, 1987). Haleakala National Park (Maui, Hawaii) is completely fenced against feral hogs. In some areas, native plants once believed to be locally extinct reappeared, and new species were discovered, apparently through germination of dormant seeds in the soil seed bank (Hone and Stone, 1989). Several exclosures in Hawaii protect the last known individual plants from destruction by feral hog rooting (Stone and Loope, 1987).

The Ossabaw Island Management Plan states that “the WRD will continue to remove feral hogs to result in no measurable ecological impact”, through a combination of lethal techniques, including trapping, shooting by WRD personnel, and managed hunts (GDNR, 2000).

However, GDNR personnel concede that to achieve zero-population growth (ZPG) would require culling no less than 2,500 hogs annually (GDNR, 2000). Actually, based on their estimate of the number of hogs on Ossabaw this would represent culling 100% of the population.

The dual goals of eliminating feral hogs and tallow represent a dilemma. Reducing the number of hogs may reduce mortality on tallow seedlings and lead to an increase in tallow populations. Leaving the hog (and deer) populations high may impose unacceptable levels of mortality on live oak seeds and seedlings. There is only one resolution for this dilemma, which is to reduce populations of both hogs and tallow. Since it is unlikely that sufficient resources will be available to eliminate hogs and tallow, the question becomes, "to what levels do these populations need to be reduced"? In other words, what are *acceptable* population densities for hogs and tallow? To begin to answer this question, it is useful to turn to the Jesup site and other mainland sites that contain tallow populations. On many mainland sites, tallow forms dense stands of small and large trees that exclude native vegetation. There is no question that tallow has a large and negative impact on native biodiversity. The picture on Ossabaw is quite different. Tallow occurs as a rare tree in uplands, in scattered populations around the edges of depressional wetlands, and in dense stands of mostly small trees near the coast. If it were possible to "freeze" this tallow picture on Ossabaw the ecological impact of tallow would remain fairly small. A critical question then becomes, "if hogs were removed, would tallow populations increase to the extent of mainland populations?"

To address the question experimentally, I recommend establishing a series of large (1 ha) exclosures, one meter in height, to exclude hogs. Their location is critically important. Because we want to know how tallow populations will respond in the absence of hogs, the exclosures need to include sizable stands of tallow that are capable of reproduction. In order to assess the impact of hogs and deer on oaks and other upland trees, a series of exclosures smaller in size could be placed in oak woodlands. Some exclosures should be sized to exclude hogs exclusively, while others exclude both hogs and deer. These exclosures will answer two questions that are fundamental to the development of a cost-effective management plan. First, is tallow population growth limited by hogs? Second, are oaks and other upland trees limited by hogs and are deer also important? If tallow populations do not expand significantly in the absence of hog rooting activity, then tallow management can be considered independently of feral hog management. Tallow management may then consist of little more than spot treatment of relatively few high density tallow sites on Ossabaw. If the absence of hogs and/or deer does not influence the recruitment of upland tree seedlings then other environmental factors need to be investigated and hog management can proceed independently.

The Ossabaw Island Comprehensive Management Plan calls for the complete eradication of feral hogs. This may be impractical given realistic resource constraints. The exclusion experiments in the uplands will provide a benchmark for setting a population control target. Culling efforts could be increased slowly until oak seedling survival begins to equal that observed within the exclosures. Any further increase in culling efforts would not be cost-effective because no more protection would be provided to the oak seedling population. Finally, long-term monitoring of plants within and near the exclosures will be necessary in order to capture any external effects created by changing abiotic (i.e., weather) patterns.

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Table 2.1. Number of days required to achieve 50% mortality for Ossabaw Island and Jesup sites.

OSSABAW POPULATIONS	50% MORTALITY	JESUP POPULATIONS	50% MORTALITY
Cabbage Garden West	31	High Ridge North	0
Cabbage Garden East	29	High Ridge South	0
Hog Pond	23	Clear Cut East	0
North Bradley Beach	35	Clear Cut West	0
Pine Barren Road	35	Clear Cut North	97
Mule Run Road	35	First Ridge	0
Cane Patch	57	Second Ridge	0
South End Beach	47	River Edge	0
North Central	49	Moccasin Cross	0
Gator Hole South	37	Back Forty	0
Average # days:	**37.8**	Average # days:	n/a

Figure 2.1. A) Seasonally flooded bottomland hardwood swamp in Jesup, Georgia. B) *Sapium* seedlings attain very high densities beneath parent plants.

Figure 2.2. Exclosure design used in both island and mainland sites.

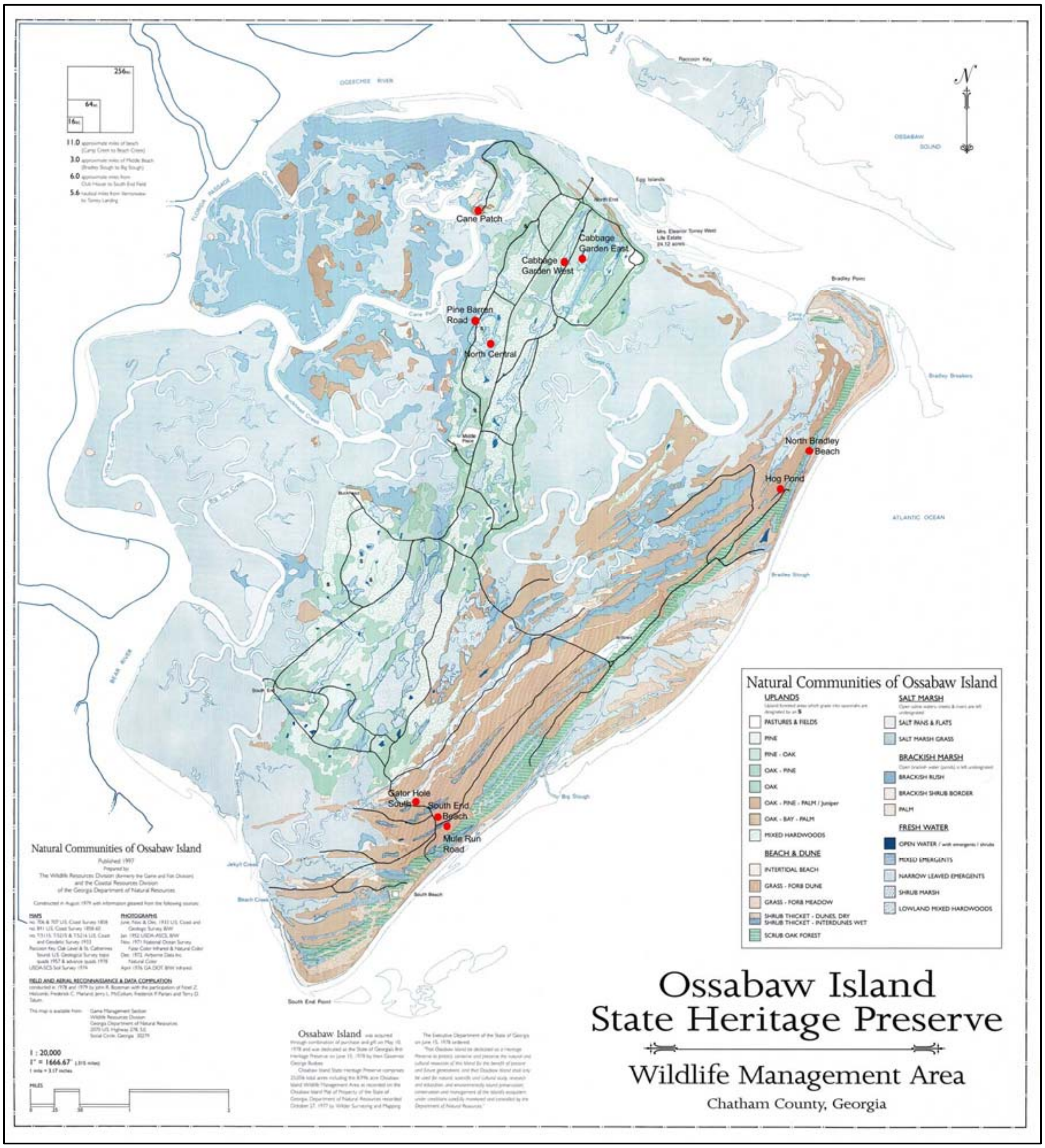


Figure 2.3. Location of exclosure sites on Ossabaw Island, Georgia. Vegetation map courtesy of the Georgia Department of Natural Resources, Wildlife Management Division, Brunswick, Georgia.

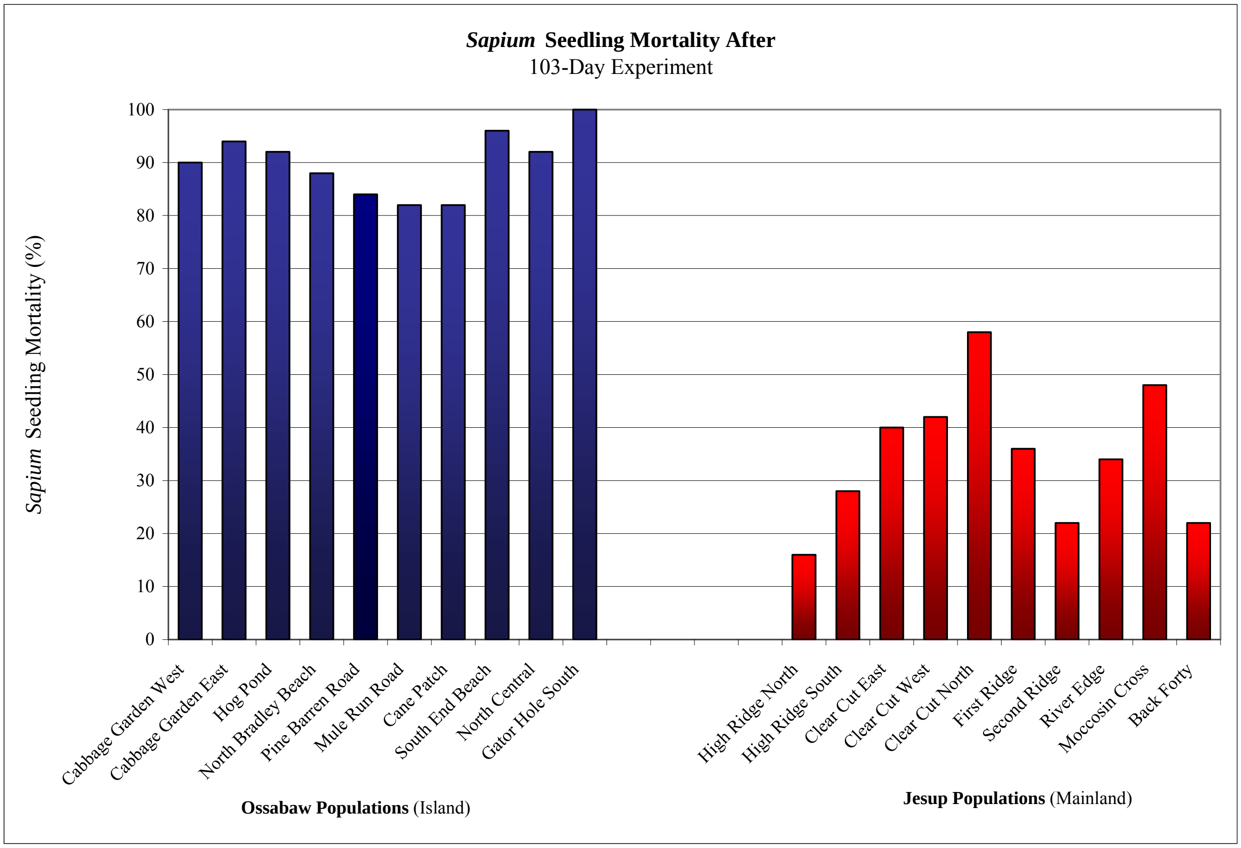
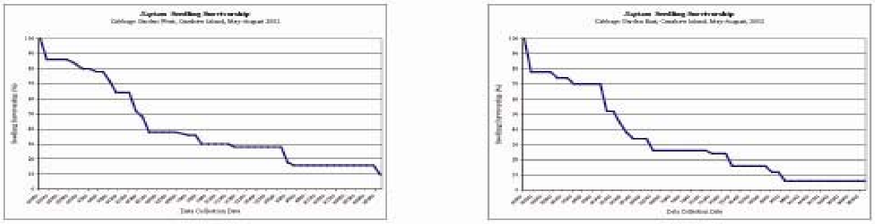
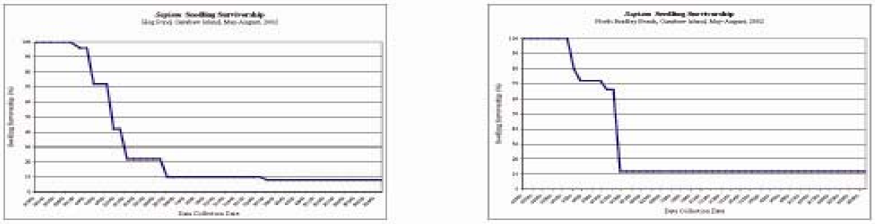


Figure 2.4. *Sapium* seedling mortality on Ossabaw Island occurs more rapidly and to a much higher degree relative to sites located in a bottomland hardwood swamp on the mainland (Jesup).



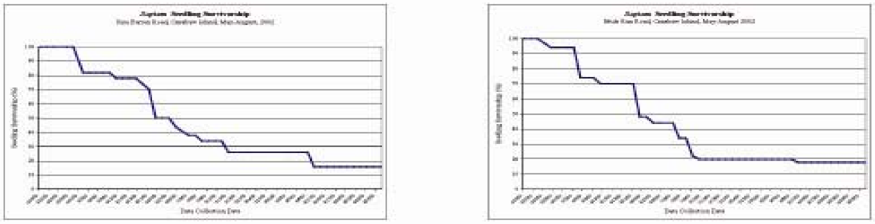
Cabbage Garden West

Cabbage Garden East



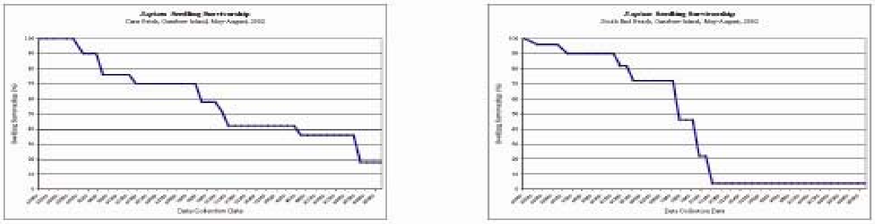
Hog Pond

North Bradley Beach



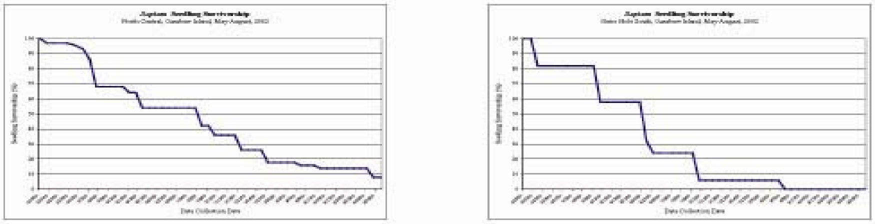
Pine Barren Road

Mule Run Road



Cane Patch

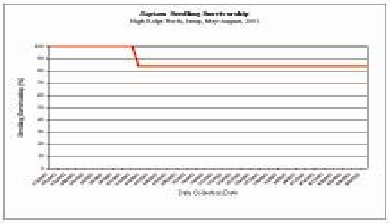
South End Beach



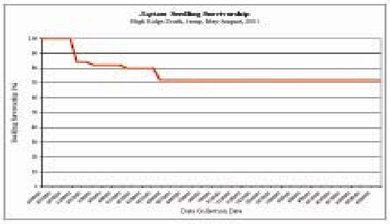
North Central

Gator Hole South

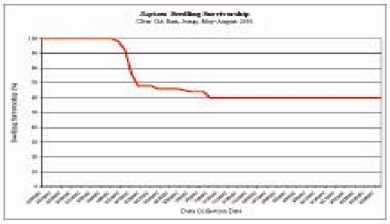
Figure 2.5. *Sapium* survivorship over a 103-day period in 2001 (May 19th through August 30th) for 10 populations on Ossabaw Island, Georgia.



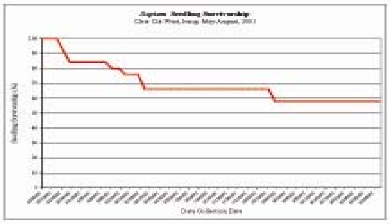
High Ridge North



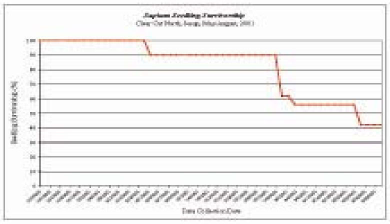
High Ridge South



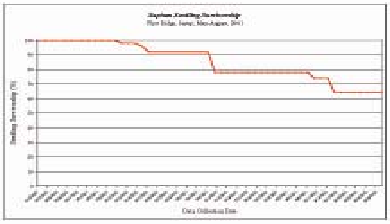
Clear Cut East



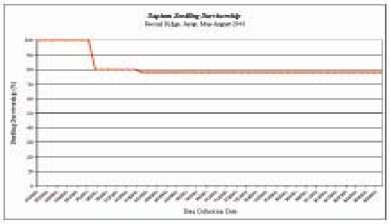
Clear Cut West



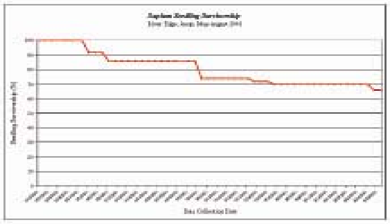
Clear Cut North



First Ridge

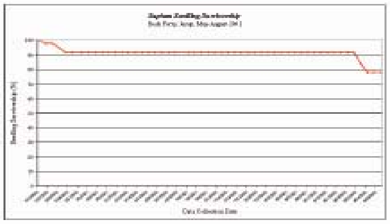


Second Ridge



River Edge

Moccasin Cross



Back Forty

Figure 2.6. *Sapium* survivorship over a 103-day period in 2000 (May 19th through August 30th) for 10 populations in a bottomland hardwood swamp in Jesup, Georgia.

Figure 2.7. Despite reinforced construction, including barbed wire, feral hogs damaged a number of exclosure structures. It is unclear whether hogs were investigating the structure itself, attempting to access enclosed seedlings, or both.

Figure 2.8. Stands of *Sapium* on Ossabaw are typically characterized by little or no seedling recruitment. Note the lack of seedlings and/or saplings in the understory.

CHAPTER 3

USING GENERALIZED LINEAR MODELS TO PREDICT SEED TRAITS OF CHINESE TALLOW (*SAPIUM SEBIFERUM* L. ROXB.), AN INVASIVE, SUBTROPICAL TREE

ABSTRACT

Chinese tallow (*Sapium sebiferum* L. Roxb.) is recognized as one of the most pernicious invaders of southeastern US wetland and coastal habitats. Control efforts are ongoing in some areas, but are hampered by a lack of information on the most effective means of prioritizing resources for eradicating large-scale infestations. I investigated whether it was feasible to prioritize populations of *S. sebiferum* for eradication on the basis of simple seed traits, namely seed mass and shape.

I used general linear models (GLMs) and general linear mixed models (GLMMs) to examine the reliability of simple morphological seed traits - mass, length, breadth, and the product of length and breadth ('seed shape') – to serve as reliable predictors of viability and germination in over 22,500 seeds collected from 16 populations of *S. sebiferum* in southern Georgia from 2001 to 2003.

Results indicate that in general, seed mass was not a significant predictor of seed viability in any of the three years of the study. When random effects due to seed-producing trees within a population are removed, the variables mass and seed shape do vary among populations for each year, though the variation is not pronounced. Year is a significant predictor for seed mass, shape, and the probabilities of viability and germination. This was true both for all trees from all populations, and, in general, for all populations. In any given year, both viability and germination vary among populations. In addition, neither seed length nor seed breadth were

reliable indicators of viability or germination. I conclude that targeting and prioritizing populations of *S. sebiferum* for eradication based solely on a rapid assessment of seed traits is an inappropriate tool for prioritization of all populations of *S. sebiferum.* However, this technique does appear to be useful in identifying very high- and low-priority populations for management.

INTRODUCTION

Seed traits, through their pronounced and various fitness effects, are a critical element in the ecology and evolution of plant life histories (Simons and Johnston, 2000; Harper, 1977; Janzen, 1969). Seed traits that directly influence fitness are seed mass, seed shape (i.e., length and breadth), viability, and germination success.

Seed mass is a critical trait of plant fitness and influences the regeneration process of a population (Fenner, 1992; Leishmann, 2001). Seed mass represents a fundamental trade-off within the life history strategy of a species, between producing more small seeds versus fewer larger seeds from a given quantity of resource allocated to reproduction (Fenner, 2000; Baskin and Baskin, 1998). Furthermore, seed mass links plant reproductive ecology and seedling establishment, and is one element of a coevolving complex of traits, including dormancy, dispersal, plant size, longevity, niche specialization, and competition among species, and can also influence seed predation, as well as seedling growth and survival (Michaels *et al*., 1988; Venable and Brown, 1988; Rees, 1997; Weller, 1985; Gross, 1984; Jordano, 1984; Fenner, 1983). The most commonly cited advantages of large seed mass through greater reserves are drought resistance, early shade tolerance, and other direct effects of larger (initial) seedling size (Westoby *et al*., 1992). Thus, seed mass has significant ecological consequences.

Germination, survival, and seedling development are greatly influenced by the amount of food reserves within seeds, which generally increases with increasing seed mass (Fenner, 2000).

Conflicting evidence exists on interspecific variation in seed mass and germination. Small seeds may germinate at higher percentages than larger seeds (Murali, 1997; Marshall, 1986), larger seeds may germinate at higher percentages than smaller seeds (Seltmann *et al*., 2007; Cordazzo, 2002; Khan and Shanker, 2001; Bhuyan *et al*., 2000; Vera, 1997), or germination success may be independent of seed mass (Khan *et al*., 1999; Perez-Garcia, 1995).

Researchers in agriculture, forestry, and horticulture commonly evaluate seed characteristics to identify superior genotypes. The effects of seed mass and dimensions on progeny vigor and fitness in tree species have been studied by many researchers (Kandya, 1978; Kahlil, 1981; Scheld *et al*., 1984; Toon *et al*., 1991; Abdul-Assis *et al*., 1994; Negi and Todaria, 1997). It follows that, at a landscape level, some populations of a species will, depending on genetics and environmental effects, produce higher quality (i.e., higher viability and germination success) seed crops than others.

Intraspecific variation in shape components (i.e., length and breadth) of simple seeds are heritable traits and may differ widely (Harper *et al*., 1970). Several investigations found seed shape and seed mass to be a predictor of persistence in the soil (Thompson *et al*. 1993, Thompson, 1992, Cerabolini *et al*., 2003, Peco *et al*., 2003). Alone or in combination with other seed traits, seed mass and seed shape are also believed to be reliable predictors of buoyancy and hydrochory (Römermann *et al*., 2004). Peñaloza *et al*. (2005) measured several morphological and physiological parameters of lettuce seed (*Lactuca sativa* L.) using the seed vigour imaging system (SVIS), followed by greenhouse germination studies, and found no correlation between seed shape and germination success. In an attempt to investigate whether beechnut (*Fagus sylvatica* L.) seeds could be separated mechanically based on seed shape, Tylek and Walczyk (2002) analyzed several geometric properties and found a positive relationship between viability and linear dimension. Cosyns *et al*. (2005) found that small, elongated seeds, rather than heavy, ovate seeds had a higher relative germination success after passage through ungulate and rabbit guts.

The objective of this study is to develop general linear models to determine whether seed mass and seed shape can be used as a rapid assessment tool in predicting viability and germination of *S. sebiferum* seeds within and among 16 populations in south Georgia, USA, and the utility of technique in developing priorities for management.

METHODS

Study Species

Sapium sebiferum (L.) Roxb. (Euphorbiaceae), commonly referred to as "Chinese tallow", is a rapidly-growing, subtropical, monoecious, deciduous, polycarpic tree capable of attaining heights of 10 to 13 meters (Bruce *et al.*, 1997). Flowers are small, yellow, borne on spikes, and mature in late-spring (Broschat and Merrow, 1991). Fruits are a trilocular capsule, approximately one cm in width, turning brown and dehiscing at maturity to reveal three white- to cream colored seeds, which persist on the parent plant and are dispersed by birds (zoochory) and water (hydrochory) (Jubinsky, 1993). Chinese tallow is also capable of vegetative reproduction and produces shoots profusely from root tissue.

Once established, Chinese tallow aggressively displaces native species and forms monotypic woodland thickets (Bruce *et al*., 1997; Grace, 1998), alters soil chemistry and nutrient cycling (Cameron and Spencer, 1989), dramatically impacts net primary production (Harcombe *et al*., 1993), modifies soil faunal communities (Cameron and LaPoint, 1978), and quickly colonizes post-disturbance gaps (Helm *et al*., 1991). The geographic range of Chinese tallow in the conterminous US extends from Richmond County, North Carolina south through central Florida, west into eastern Texas, and north to northwestern Arkansas (Langeland and Craddock Burks, 1998). Recently, Chinese tallow has been documented in California's Great Valley (CAL-IPC, 2007).

Study Sites

Seeds were collected from 16 *S. sebiferum* populations collected from four geographic areas ranging from inland riparian floodplain, to tidally influenced coastal wetlands and barrier islands (Figure 3.1).

Ossabaw Island: Owned by the State of Georgia and managed by the Department of Natural Resources, Wildlife Resources Division (DNR-WRD), Ossabaw Island is located in Chatham County, GA. Ossabaw is the second largest barrier island on the Georgia coast, consisting of approximately 10,100 hectares (~ 25,000 acres) of which 4,775 hectares (~ 11,800 acres) is upland forest. The vegetation communities of Ossabaw Island are typical of Georgia barrier islands and consist primarily of freshwater ephemeral wetlands, salt marshes of smooth cordgrass (*Spartina alterniflora*) and pine forests dominated by loblolly and slash pine (*Pinus taeda* and *P. elliotti*, respectively), and maritime forests dominated by live oak (*Quercus virginiana*), cabbage palm (*Sabal palmetto*), saw palmetto (*Serenoa repens*), red bay (*Pursea borbonia*), and wax myrtle (*Morella cerifera*).

Jesup: The site is located in a seasonally flooded bottomland hardwood swamp in the floodplain of the Altamaha River in Long County, GA. Vegetation communities are characterized by tupelo (*Nyssa aquatica* or *N. sylvatica* var *biflora*) and baldcypress (*Taxodium distichum*) with seasonally sparse herbaceous understories dominated by lizard's tail (*Saururus cernuus*), false nettle (*Boehmeria cylindrica*) and trumpet creeper (*Campsis radicans*). Less frequently flooded mixed hardwoods are also common and are comprised of overcup and southern red oak (*Quercus lyrata* and *Q. falcata*, respectively), coastal plain willow (*Salix caroliniana*), red maple (*Acer rubrum*) and sweetgum (*Liquidambar styraciflua*). The area also contains numerous creeks, tributaries, and oxbow lakes. Seeds were collected from a single population (n= 1).

Savannah NWR: The site is a National Wildlife Refuge consisting of over 10,900 hectares (~ 27,000 acres), located in Chatham and Effingham Counties, GA and Jasper County, SC. Vegetation communities on the Refuge include cypress-tupelo bottomland hardwood swamps, palustrine, estuarine and tidal freshwater wetlands, and upland forests dominated by water oak (*Quercus nigra*), black gum (*N. sylvatica*), red maple (*Acer rubrum*), sycamore (*Platanus occidentalis*), and sweetgum (*L. styraciflua*). Managed freshwater impoundments (pools) make up about 1,124 hectares (~ 3,000 acres).

Wassaw Island: A 4,068 hectare (~10,053 acre) National Wildlife Refuge located 14 miles southeast of Savannah, GA in Chatham County, GA. The Refuge is comprised of 76% *Spartina alterniflora*-dominated salt marsh and 24% beach dune and upland forest communities dominated by live oak (*Q. virginiana*) and slash pine (*P. elliotti*).

Seed Collection

Sampling protocols were developed with the goal of ensuring that seeds were collected at peak quality, such that their longevity is optimal. Many plant populations will naturally have fruits of varying maturity at any point in time (Hay and Smith, 2003). As Schmidt (2000) notes, natural dispersal in itself is a reliable field indicator of seed maturity and collectors can safely assume that seeds in the process of natural dispersal are suitable for collection. *S. sebiferum* seeds begin ripening in October and often remain in the canopy for months. However, field indicators such as peak bird visitation, complete dehiscence of fruit husks, white-to-creamy seed coat coloration, and absence of saprophytic fungi, suggest that peak pre-dispersal ripening occurs in late fall for this species.

Each of 16 populations was visited in November-December of 2001, 2002, and 2003 (with the exception of Wassaw Island, which was not visited in 2001). From each site, 24 mature, seed-bearing *S. sebiferum* trees were randomly selected from the population and marked with a numeric designation (i.e., 1 through 24) using a bark application of Wet Coat™ tree marking paint to ensure that the same trees were sampled in subsequent years. Five-to ten randomly selected seed-bearing branches were removed from various portions of the canopy of each parent tree using a 14' pole pruner (Figure 3.2). *S. sebiferum* seed clusters were individually assessed for damage and maturity and secured in labeled, cotton draw-string bags. Once transported to a field station, seeds were cleaned using a sieve and cool running water, and spread out on filter paper to surface-dry prior to storage in labeled cloth bags. Twenty seeds from each seed tree were randomly selected for analysis. Each seed was weighed using a digital scale, and dimensions of shape (i.e., length and breadth) were measured with digital calipers. Seeds were sown in flats with 50-50 perlite/vermiculite potting mix and placed in a greenhouse subject to ambient light and temperature conditions. Seeds were not pre-treated (i.e., scarified or stratified) in an effort to enhance or accelerate overall germination success (which was defined as emergence of the radicle). Flats were watered every other day, or as needed, for six months and monitored for germination. Immediately following the termination of the six-month germination study, the ungerminated fraction was tested for viability using a 0.1 percent solution of 2,3,5-triphenyl tetrazolium chloride ("TZ"). Seeds that failed to stain positively after a 36 hour incubating period were deemed non-viable (AOSA, 2000). Measurements and observations of seed traits were entered into an Excel™ spreadsheet and imported into SAS™ for analysis and model development.

Five variables were measured or observed and recorded for each seed collected in 2001, 2002, and 2003: length, breadth, weight, viability, and germination. One site (Wassaw) was not visited in 2001. Consequently, there are then:

3 (years) x 15 (populations) x 24 (seed trees) x 20 (seeds) +
2 (years) x 1 (population) x 24 (seed trees) x 20 (seeds) = 22,560 observations

For each observation, the following were recorded: the year, the population (i.e., 1 of 16), the index *i* of the seed tree at that population (*i* = 1,… 24), and the index *j* of the seed sampled from tree *i* (*j* = 1,… 20).

Missing and Outlying Data

Almost all observations were complete. There were three observations for which the recorded value of size was '.'. There were also several observations for which the recorded values of length, breadth, or mass were improbably large (Table 3.1). If the six largest values of *length* are omitted from the dataset, the quantiles for the remaining values are as follows:

Min	**Q_1**	**Median**	**Q_3**	**Max**
3.75	6.81	7.39	7.96	12.49

If the five largest values are omitted, the quantiles for the remaining values of *breadth* are as follows:

Min	**Q_1**	**Median**	**Q_3**	**Max**
2.75	5.09	5.44	5.84	9.56

In reviewing the outlier values in Table 3.1, it seems probable that the six large values of length and the five large values for breadth were the result of a misplaced or omitted decimal point. For example, a length of 708 was recorded for seed tree 16, seed 13, at Middle Beach in 2003, but the actual measurement most likely was 7.08.

Values for mass also contained numerous outliers. There were 22,516 recorded values between 30 and 300 grams. There were 18 recorded values larger than 300 grams, and 26 less than 30 grams, including 15 less than 1. The length and breadth of those seeds with recorded mass less than 30 grams were not particularly small, relative to length and breadth of seeds with recorded weights larger than 30 grams.

It is almost certain that recorded weights less than 30 grams (particularly those less than 1) were recorded erroneously. Additionally, recorded lengths larger than 15 mm and recorded breadths larger than 10 mm were eliminated from the dataset and attributed to recording error. For analyses involving length and breadth, the 11 observations with large values of these variables were omitted from the dataset. Similarly, for analyses involving weight, the 44 observations with recorded weights outside of the range of 30-300 grams were omitted from the analysis. Quantiles for values of *mass* between 30 and 300 grams are as follows:

Min	**Q_1**	**Median**	**Q_3**	**Max**
39.5	127.4	150.3	175.0	279.5

The derived quantity ‘shape’ was defined as the product of length x breadth. For most observations, the recorded shape was equal or almost equal to the product of recorded length and recorded breadth. For 20,864 observations, length is less than 15 mm, breadth is less than 10 mm, and their product differs from recorded shape by an amount of between 6×10^{-3} and zero. These observations were included in the dataset, since the discrepancy is very small. There were

61 observations in which recorded size was less than 1, and apparently unrelated to the product of length and breadth. These 61 observations were omitted from calculations involving size.

A seed may germinate only if it contains a viable embryo. That is, the variable ‘viability’ is a binary response. Consequently, if viability for a given seed is ‘*N*’ (‘no’), germination was not considered for this seed. When fitting a model for germination, only those observations were used for which viability was ‘*Y*’ (‘yes’) and shape was recorded. Of a total of 22,560 data points, there were 16,829 for which viability was ‘Y’ and shape was recorded. Consequently, overall germination success was 75%.

Variation of Seed Mass Across Populations

Observations with unacceptable recorded values of seed mass were not used in the analysis. For each year *y*, a model was fitted using the following equation.

$$\widehat{mass}_{ijy} = \mu_y + \sum_{i'\in S} \alpha_{i'y} I_{i=i'} + \in^T_{ijy} \qquad (1)$$

$$\left\{\in^T_{ijy} : 1 \le i \le 16, 1 \le j \le 24,\ y \in \{2001, 2002, 2003\}\right\} \text{ i.i.d.} \sim N(0,\sigma^2_{T,y})$$

Tables 3.2, 3.3, and 3.4 show the estimated least squares means, for each site and year, when the ANOVA model is fitted. The least squares means are shown in descending order, with columns of letters indicating sets of least squares that are not significantly different.

Variation of Seed Shape Among Populations

Observations with erroneous recorded values of seed shape were not incorporated in the following analysis. For year *y*, estimates of mean seed shape by population were determined using a model identical to that in Equation 1. Let $\widehat{\text{shape}}_{ijy}$ denote the mean shape of seeds for tree *j* in population *i* in year *y*. The model is:

$$\widehat{shape}_{ijy} \;=\; \mu_y \;+\; \textstyle\sum_{i'\in S} \alpha_{i'y} I_{i=i'} \;+ \in^{T}_{ijy} \tag{2}$$

$$\left\{\in^{T}_{ijy} : 1 \le i \le 16, 1 \le j \le 24,\; y \in \left\{ 2001, 2002, 2003 \right\}\right\} \; i.i.d. \sim N(0, \sigma^{2}_{T,y})$$

"2" indicates that the expected mean shape of seeds for tree *j* in population *i* is given by an overall mean μ_y plus a population-specific amount. The amount α_i added varies as population *i* varies. $\in^{T}_{ijy}$ is a random error for tree *j* in population *i* in year *y*. "i.i.d." is a contraction to indicate "independent and identically distributed". An ANOVA model was fitted to the set of mean shape by tree. The resulting estimated least squares means are shown in Table 3.5. The least squares means are shown in descending order, with columns of the same letters indicating populations that are not significantly different.

Variation of Viability and Germination Among Populations

A generalized linear model was used to fit the probability P(V) that a given seed would be viable. This analysis was performed separately for each year:

$$\log\left(\frac{P(V_{ijky})}{1 - P(V_{ijky})}\right) = \mu_y + \sum_{i'\in S} \alpha_{i'y} I_{i=i'} \tag{3}$$

V_{ijky} denotes the value of viability (T or F) for seed *k* from tree *j* at population *i* in year *y*. Population is a categorical variable; for regression, there must be a separate indicator variable for each distinct value (except one) of population. Each population has its own mean level. An intercept μ_y is incorporated into the model, and is the mean for one of the populations (i.e., the "baseline" population). For every other population *i*, we must add quantity α_i. One of the populations must be selected to serve as the baseline, but the actual choice may be arbitrary. SAS selects the site which appears last in an alphabetized list of names.

The analysis was performed using PROC GENMOD in SAS. According to equation 3, there is a separate predicted value (least squares mean) for the logit of P(V) for each value of 'population'. These logits and their associated values of P(V) are shown in Table 3.6, in descending order, for each year. Columns of letters indicating sets of least squares represent populations for which logit P(V) are not significantly different. Two sites are significantly different if the 95% confidence interval for logit $(P(V_i))$ – logit $(P(V_j))$ does not include 0.

A generalized linear model similar to that of Equation 3 was also fitted for germination. The resulting least squares means and probabilities of germination are shown in Table 3.7.

Variation of Predicted Quantiles Across Years

I examined whether the predicted value of a quantity varies significantly over time. For the variable 'mass', the model is:

$$mass_{ijky} = \mu_y + \alpha_{2002}\, I_{y=2002} + \alpha_{2003}\, I_{y=2003} + \in^{S}_{iy} + \in^{T}_{ijy} + \in^{r}_{ijky} \qquad (4)$$

$$\left\{\in^{S}_{iy} : 1 \le i \le 16\right\}\ i.i.d. \sim N(0, \sigma^2_{i,S,y})$$

$$\left\{\in^{T}_{ijy} : 1 \le i \le 16, 1 \le j \le 24\right\}\ i.i.d. \sim N(0, \sigma^2_{i,T,y})$$

$$\left\{\in^{r}_{ijky} : 1 \le i \le 16, 1 \le j \le 24,\ 1 \le k \le 20\right\}\ i.i.d. \sim N(0, \sigma^2_{i,r,y})$$

$\in^{S}_{iy}$ is a random error for population *i* in year y; $\in^{T}_{ijy}$ is a random error for tree *j* in population *i* in year *y*; and $\in^{r}_{ijky}$ is a residual error term for seed *k* from tree *j* in population *i* in year *y*. The estimated least square means from the model in Equation 4 are given in Table 3.8. In this table (and all tables pertaining to this section), two expected probabilities are considered significantly different if the 95% confidence internal for the difference of the expected probabilities does not include zero. Table 3.5 shows that mean seed mass for years 2001 and 2003 are not significantly different, but the mean mass for year 2002 is significantly different from the other two means.

We conclude, then, that seed mass does vary significantly between years. To examine this relationship more closely, seed mass was regressed on year separately for each population. The model describing this relationship is as follows:

$$mass_{ijky} = \mu_{iy} + \alpha_{2002} I_{y=2002} + \alpha_{2003} I_{y=2003} + \in^{T}_{ijy} + \in^{r}_{ijky} \tag{5}$$
$$\left\{ \in^{T}_{ijy} : 1 \le i \le 16, 1 \le j \le 24 \right\} \ i.i.d. \sim N(0, \sigma^2_{i,T,y})$$
$$\left\{ \in^{T}_{ijky} : 1 \le i \le 16, 1 \le j \le 24,\ 1 \le k \le 20 \right\} \ i.i.d. \sim N(0, \sigma^2_{i,r,y})$$

The estimated least square means from the model in Equation 5 are given in Table 3.9.

I also analyzed seed shape across years. The model that has year as a predictor of seed shape, for all data, is almost identical to Equation 4, with the substitution of 'mass' with 'shape'. The least squares means from the model are shown in Table 3.10. As with seed mass, I regressed seed shape on year for each population, using a model nearly identical to Equation 5 (i.e., substituting 'mass' with 'shape'). The estimated least square means from this model are given in Table 3.11.

To determine if viability or germination vary according to year, I used generalized linear mixed models, using the variable 'year' as a predictor of the probability of viability. The actual model takes 'tree' as subject; the variable to predict is the number of viable seeds out of all seeds from a tree: (#viable seeds from tree *i*)/(# seeds from tree *i*). Population is taken to be a random effect, since the probability of viability will vary from population to population.

$$\log\left(\frac{P(V_{ijy} = 'Y')}{1 - P(V_{ijy} = 'Y')}\right) = \mu_y + \alpha_{2002} I\{y = 2002\} + \alpha_{2003} I\{y = 2003\} + \in_{ij} \tag{6}$$
$$\left\{ \in_{i,}\ 1 \le i \le 16, 1 \le j \le 20 \right\} \ i.i.d. \sim N(0, \sigma^2)$$

The results from the model in Equation 6 are presented in Table 3.12. As with seed mass and shape, the analysis across years for viability was also performed for each population. The model describing this relationship is as follows:

$$\log\left(\frac{P(V_{ijy}='Y')}{1-P(V_{ijy}='Y')}\right) = \mu_y + \alpha_{i2002} I\{y=2002\} + \alpha_{i2003} I\{y=2003\} + \in_{ij} \qquad (7)$$

$$\{\in_{i,}\ 1 \le i \le 16, 1 \le j \le 20\}\ i.i.d. \sim N(0,\sigma_i^2)$$

The results for this model are given in Table 3.13. As with viability, germination was evaluated across years. The model that has ‘year’ as a predictor of probability of germination for the data is nearly identical to Equation 6, with “V” (i.e., viability) replaced by “G” (i.e., germination). The model is applied to the subset of data for which viability is “Y”. The least square means for logits of P(G) from the model are show in Table 3.14. The analysis for germination across years was also performed for each population. The model describing this relationship is nearly identical to that in Equation 7, with the variable “V” (viability) replaced with “G” (germination). The results for analysis of germination across years by population are given in Table 3.15.

Association of Seed Mass to Viability and Germination

The number of viable and non-viable seeds for mass categories of 20 are shown in Table 3.16, and indicates that viability is not associated with mass over most of the range for that variable. The probability that a seed will be viable is higher for seeds having mass values greater than 240 grams. Indeed, of 17 seeds with a mass value of greater than 264 g, only one seed was not viable. There is a definite trend in germination rates related to mass in that the probability that a viable seed will be germinable decreases as mass increases.

A fitted model can test the association of seed mass with viability and germination. Initially, generalized linear models were fit with the SAS procedure GENMOD. For viability, the model is:

$$\log\left(\frac{pv}{1-pv}\right)=\mu+\alpha w \qquad (8)$$

where pv = P(*viability* = Y) and w is seed mass. This model was fit separately for each year. The SAS output includes the *p*-value of the hypothesis that $\alpha \neq 0$. Analysis performed using the GENMOD procedure did not take into account the structure of the data. Seeds that were sampled form 'clusters' at two levels: 'tree' and, at a larger scale, 'population'. We might expect two seed trees from the same population to be more similar than two seed trees from different populations. Additionally, within a population, one might expect two seeds from the same tree to be more similar than two seeds from different trees. In the terminology of mixed models, there is a "random effect" arising from populations, and another random arising from trees within a population. These random effects can be incorporated into a *generalized linear mixed model* (GLMM).

In defining indices, let *i* be the population index, *j* the index for trees within a population, *k* the index for seeds sampled from one tree, and *y* the year. V_{ijky} is the value of viability for seed *k* from tree *j* in population *i* in year *y*. A separate GLMM is fit for each year. The model for $P(V_{ijky} = \text{'Y'})$ is:

$$\log\left(\frac{P(V_{ijky}='Y')}{1-P(V_{ijky}='Y')}\right)=\mu_y+\alpha_y w_{ijky}+\in_{ijy}+\eta_{iy} \qquad (9)$$

$$\{\in_{ijy}: 1\le i\le 16, 1\le j\le 24\}\, i.i.d. \sim N(0,\sigma_y^2)$$

$$\{\eta_{iy}: 1\le i\le 16\}\, i.i.d.\, N(0,\zeta_y^2)$$

$\in_{ijy}$ is the value of the random effect of tree within population, for tree *j* in population *i*; η_{iy} is the value of the random effect of population, for population *i*.

A generalized linear mixed model can be fitted with the SAS procedure GLIMMIX. GLIMMIX uses an iterative algorithm and stops when a certain criterion converges to a value near zero. GLIMMIX had difficulty in fitting models when all available data were given. The criterion did not converge within a reasonable number of iterations, and evidently did not converge at all for some years. If a model is fitted with a representative subset of the data, however, the result does not deviate from that fitted with the full dataset. Consequently, the GLMM was fitted to various subsets of the data. One subset consists of all seed trees with index $j \in \{7,\dots, 19\}$ and seeds with index $k \in \{5,\dots, 14\}$, across all populations and years. The *p*-values for α_y in Equation 6 are shown in Table 3.7. GLIMMEX was also used to fit a GLMM for germination. Again, GLIMMIX did not converge for the entire dataset. GLIMMIX did converge for the subset of all seed trees with index $j \in \{7,\dots, 19\}$ and seeds with index $k \in \{5,\dots, 14\}$, across all populations and years. The *p*-values for α_y in Equation 9 are shown on the second line of Table 3.17. Table 3.18 shows the *p*-values for the coefficient of mass for these models.

Additionally, germination was regressed on seed mass, using those observations for which viability = ‘Y’. A generalized linear model with logistic regression, similar to Equation 5, was fitted for each combination of year and population. Table 3.19 shows the *p*-values for the coefficient of mass for these models.

Association of Seed Length and Breadth with Viability and Germination

Prior to fitting a model, a preliminary examination was performed to determine whether an obvious association of seed length and breadth existed for viability and/or germination. Results indicate that no clear association existed for either viability or germination with length and/or breadth exclusively (Table 3.20). Generalized linear models were fit to elucidate the relationship of the binary variables (viability and germination) to length and breadth. Models included the product between seed length and breadth – the variable 'shape'.

$$\log\left(\frac{pv}{1-pv}\right) = \mu + \alpha \cdot length + \beta \cdot breadth + \gamma \cdot length * breadth \qquad (10)$$

Where pv = P(viability = 'Y'). This model was fitted separately for each year. Similar models were fitted for the response variable 'germination'. Table 3.21 shows the estimated coefficients, for each year and effect, with *p*-values. Estimates of the intercept term (μ) are omitted. In order to gain a better understanding of the relationship of length and breadth to the probability that a seed will be viable or germinate, a more robust generalized linear model was fitted to the data. This model included the predictors 'length', 'breadth', and their product ('shape'), but also incorporated 'population' as a predictor. Population is a categorical variable with 16 levels (15 levels in year 2001), so this new model has 16 (or 15) new indicator predictors for each year. The coefficients and their *p*-values are shown in Tables 3.22, 3.23 and 3.24. It is notable that the coefficients for populations are mostly larger, in absolute value, than the coefficients for length, breadth, and their interaction (shape). Even for 2001, when the *p*-values for length, breadth, and shape are small, the coefficients for these predictors are smaller in absolute value than most of the population coefficients. This indicates that, even if length and breadth have predictive power, it is *more* helpful to know from which population a seed originated. Next, a generalized linear mixed model was fit to the data:

$$\log\left(\frac{P(V_{ijky}='Y'}{1-P(V_{ijky}='Y')}\right)=\mu_y+\alpha_y\cdot length_{ijky}+\beta\cdot breadth_{ijky} \tag{11}$$

$$+\gamma\cdot length_{ijky}*breadth_{ijky}+\in_{ijy}+\eta_{iy}$$

$$\left\{\eta_{iy},1\le i\le 16,\right\} i.i.d.\ N(0,\varsigma_y^2)$$

$$\left\{\in_{ijy},1\le i\le 16,1\le j\le 24\right\} i.i.d.\ N(0,\sigma_y^2)$$

As in Equation 3, $\in_{ijy}$ is the random effect for seed tree within population, and η_{iy} is the random effect for population. The model was fitted for each year. Three additional models were fitted for response germination, using the subset of data for which viability = 'Y'. Again, the SAS procedure GLIMMIX would not converge when the full dataset was utilized, but did converge when smaller subsets of the dataset were used. One such subset consisted of observations for which seed tree had index in {7,…, 18) and seed index in {6,…, 15}. Resulting coefficients and *p*-values of the model are shown in Table 3.25. Tables 3.26, 3.27, and 3.28 show the estimated coefficients and *p*-values of these models for viability. Tables 3.29, 3.30, and 3.31 show the estimated coefficients and *p*-values of these models for germination. The intercepts are omitted; for the purposes of this analysis, it is not relevant whether or not the intercept is zero.

RESULTS

Of all sites, the expected seed mass of Jesup is well above the expected mass of any other site in each year. The expected seed mass for the Jesup site is nearly 200 grams in all three years. The minimum expected seed mass is less than 125 grams for each year. The minimum occurs at North Central in 2001 and in 2002. In 2003, the mean seed mass for North Central is also low (approximately 138 grams), but the minimum occurs at Savannah NWR. The mean seed mass for other sites may vary greatly from year to year. For example, in 2001 and 2002, the mean seed mass for Cane Patch was quite low – 125.3 and 134 grams, respectively. In 2003, however, the mean seed mass for Cane Patch was over 176 grams. The mean seed mass for Savannah NWR decreased from 150.88 grams in 2001, to 122.6 grams in 2003.

With regard to variation of viability among populations, there are 9 into groupings of populations in 2001 and 2002, and ten groups in 2003. A group is a set of populations whose least square means are not significantly different. The groups overlap, but not to the extent of the groups in Table 3.2. This indicates that viability varies among populations. In any year, if two populations are selected at random, it is most likely that their viability will differ significantly.

The Jesup population has the highest probability that a randomly selected seed will be viable. The probability of viability for Jesup is always significantly larger than that of any other population. Wassaw has the second highest probability during the two years for which there is data for that population (i.e., 2002 and 2003). North Bradley Beach has the lowest probability in every year, although in 2002, the probability for North Bradley Beach was not significantly different from that of two other populations. Gator Hole South, South End Beach, and Hog Pond West also rank consistently near the bottom. The relative rankings of the remaining populations tend to vary from year to year.

North Bradley Beach has the highest rate of germination in two of three years, and ranked second in the third year. South End Beach and Cabbage Garden West also rank high every year. Jesup has the lowest rate each year. Gator Hole South is second or third from the bottom every year. Other sites tend to vary more in their ranking. Pine Barren Road has the highest rate in

2002, but is ranked number ten in 2001. It is notable that germination (given viability) does not appear to be related to viability. North Bradley Beach has the lowest viability rate every year, but a very high rate of germination. Jesup has the highest viability rates, as well as the lowest germination rates. It is interesting to note that seeds collected from the Jesup population also had the heaviest seeds in each year (Figure 3.3). High viability and low germination suggests that seeds from this population have a relatively high level of dormancy, and that dormancy is positively associated with seed mass.

Populations fall into eight groups in 2001, six in 2002, and nine in 2003. The groups do not overlap appreciably; most population-year combinations belong to only one or two groups and indicate that, in most cases, germination rates do vary among populations. In any given year, if two sites are selected at random, it is most likely that their germination rates will be significantly different.

For most sites, seed mass does vary significantly according to year. There are six populations in which the maximum seed mass occurs in 2002 and the minimum in 2003; there are four populations in which the means increase steadily from 2001 to 2003. There are seven populations for which the means for the three years are all significantly different, and one population (North Bradley Beach) for which no two of the means are significantly different. The pattern shown in Table 3.5, of a sharp peak in 2002, does not hold for most individual populations. For the variable ‘shape’, the means varied significantly across years, and increased steadily from 2001 to 2003. This significant short-term variation in shape features may be a local adaptation to environmental conditions (maternal effects). The expected rate of viability is significantly higher in 2003 than in the previous two years. However, the expected values are close – they are slightly above 0.75. While 2003 has the highest probability of viability overall, there are seven populations for which the highest probability of viability did not occur in 2003. There are eight populations for which the three yearly probabilities are not significantly different. There is a single population (Pine Barren Road) for which the three annual rates are significantly different.

The expected rate of germination increases steadily from 2001 to 2003. The rate for each year is significantly higher than the rate of the previous year. The probability of germination (given viability) is always well below the probability of viability; the probability of germination increases from about 0.49 to 0.6, while the overall probability of viability is over 0.75 for each year. Results indicate that there are nine populations for which the estimated probability of germination increases from 2001 to 2003, as the overall rate increases. At the North Central and Jesup populations, however, the 2003 value is significantly lower than one of the two previous yearly rates. The 2003 *p* value was the lowest for both Cane Patch and Jesup populations.

I conclude that there is a significant effect of year on expected mean values of seed mass and seed shape, as well as the expected probabilities of viability and germination. This is true for the set of all seeds from all trees at all populations; it is also true for most populations. The pattern across years for a single population is quite often very different from the pattern for the data set for all populations. For example, the expected probability of germination increases steady from 2001 to 2003 for the data of all populations, but for some sites (i.e., Jesup) there is not a steady increase in germination.

When random effects of variation across populations and variation among seed trees within a population are removed, seed mass is not a reliable predictor for either viability or germination. Seed shape components, including length, breadth, and their product (i.e., ‘shape’) do not appear to be effective predictors of either viability or germination, except for year 2002.

DISCUSSION

The Jesup population has the highest mean seed mass of all populations in all years. High seed mass has been correlated with shade tolerance, and this may be a contributing factor for this site relative to the other 15 populations, as the site receives considerable shade from canopy trees such as cypress and tupelo. The seeds from the Jesup population were significantly more elliptical in shape (i.e., length was significantly higher) and the ends appear tapered, resulting in a more 'aerodynamic' shape relative to seeds of any other population sampled. This may be a local adaptation to facilitate long-distance dispersal efficiency by increasing laminar flow across the surface of the seed through water. Recruitment potential from Jesup site is higher and may be a result of maternal effects, microsite conditions (e.g., soil nutrients, shadier, lack of salt stress), or genetic adaptation. That said, the germination of seeds from this site is consistently lower than all other populations in all three years sampled. The high viability but low germination suggests that seed dormancy is an important strategy in the life history of seeds at this site. The onset of seed maturity for *S. sebiferum* (i.e., late fall) is marked by the beginning of seasonal flooding. It is possible that physical dormancy is an adaptation to facilitate long-distance dispersal via hydrochory to more suitable microsites for germination – possibly to areas well beyond the Altamaha floodplain. Water levels recede in the spring and soon after, tallow seedlings are encountered in high densities. Additionally, seedlings are also found in great numbers under parent trees in the spring and summer, suggesting asynchronous ripening. That is, seeds are retained on the parent tree for several months and the seed crop may have a protracted period during which peaks of optimal germination may occur as a means of "bet hedging" in stressful environments.

Traits of seed collected from the Wassaw Island site resemble those of the Jesup site, with the exception of high average seed mass. The mechanisms underlying these patterns on Wassaw are difficult to determine. It was expected that seed traits on Wassaw would be more similar to those of Ossabaw Island, which is located due south of Wassaw, rather than to the inland Jesup site. However, Wassaw Island does differ from Ossabaw in its historical land use, vegetation community structure, and degree of herbivore pressure. The maritime forests on Wassaw are characterized by larger (diameter) trees and more vertical stratification of vegetation types; the subcanopy is a dense shrub/scrub layer, and there are fewer canopy gaps. The single population of *S. sebiferum* on Wassaw is sheltered from direct salt spray and wind sheer stress, and the site is subtended by Holocene deposited soils. On Ossabaw Island, all but two populations are underlain by Holocene soils.

Ossabaw Island – Implications for Management

Of the 13 populations on Ossabaw Island, five have trends in seed traits that merit further consideration. A noteworthy trend is evident for North Bradley Beach. Results suggest that seed from this site have the lowest probability of being viable. However, those that are viable, germinate readily. In terms of seed mass, the population ranks 7th overall across all years. The North Bradley Beach population is located in a back dune community, where it is subject to frequent flooding, salt spray, and wind sheer effects. Although the population is larger in terms of aerial extent than all other populations sampled, this population appears to produce fewer fruits/tree than any other population sampled (although this should be verified experimentally), perhaps as a direct result of physiological stress (McCormick, *pers. observation*). High germination probability (and subsequent recruitment and range expansion potential) for this site may be negated by very intense feral hog (*Sus scrofa*) rooting in and around the North Bradley

Beach population. Feral hogs often traverse this site, particularly during summer months, in order to gain access to loggerhead sea turtle (*Caretta caretta*) nests. Feral hog rooting resulted in 88% mortality of *S. sebiferum* seedlings in a 3-month exclosure study at this site (McCormick, *unpublished data*). Consequently, from a management perspective, since very local little recruitment actually occurs, and those seeds that are dispersed long-distance have a relatively low probability of being viable, the DNR may opt to concentrate resources on other populations of *S. sebiferum* on Ossabaw. Despite the fact that North Bradley Beach is the largest population on the Island, physically speaking, the potential for range expansion appears to be limited for this site.

A similar relationship exists for South End Beach, which ranked very low in terms of probability of viability in all years, but high in all years for germination (given viability). Additionally, there was only one population on Ossabaw (North Central) that ranked lower than South End Beach in terms of seed mass. Consequently, as with the North Bradley Beach population, in a hierarchical framework for decision-making, the DNR may opt to focus resources aimed at eradication efforts toward other populations, and assign the South End Beach population a low ranking.

The Pine Barren Road population ranked sixth overall in terms of seed mass (fifth among Ossabaw populations). Although it ranked ninth in 2001 for probability of viability, it increased to sixth in 2002, and finally to third in 2003. It should be noted that even though its ranking was relatively low for 2001, the probability of viability for that year was estimated at approximately 73 percent. More compelling is the pattern of germination exhibited by this population. From 2001 to 2003, the probability of germination (given viability) of seeds from Pine Barren Road increased steadily from 46.2 percent in 2001; 59.4 percent in 2002, to 86.4 percent in 2003. This population was ranked first in 2003 for germination. This response may be partially explained by a combination of unique local site conditions (Pine Barren Road is the only *S. sebiferum* population to be underlain with higher mineral content Pleistocene soils rather than Holocene substrate) and/or a rapid response to local precipitation patterns. From 2001 to 2003, average annual rainfall on Ossabaw was 42.9”, 50.7”, and 57.9”, respectively (Southeast Regional Climate Center, 2007). “Normal” annual precipitation is considered 50.8”, which indicate that 2001 and 2002 were below-average years – 2001 significantly so. It is possible that local site conditions at Pine Barren Road reflect a response by individual seed trees to local site conditions (i.e., maternal effects). It would be useful to incorporate precipitation records into long-term analysis of maternal effects on seed traits in order to predict seed crop quality. The combination of moderately high probability of viability, high germination, relatively high seed mass, richer mineral soils and possible positive response to higher-than-average annual rainfall events, suggests that Pine Barren Road has the potential to expand its range through seed production and dispersal events. Therefore, from a management perspective, the DNR should consider assigning this population a high priority for control and eradication.

A less strongly pronounced relationship exists for traits of seed collected at Cabbage Garden West. This population consistently ranked in the lower third of all populations in all years for probability of viability. However, it terms of germination, this population ranked fourth in 2001, and third in 2002 and 2003. Overall, Cabbage Garden West ranked third (second among Ossabaw populations) in seed mass. Moderate viability probability, coupled with relatively high germination (given viability) and high seed mass, suggests that this population may have potential to expand into adjacent un-invaded areas in a relatively short amount of time. Therefore, it warrants a higher prioritization than most other populations on Ossabaw.

Gator Hole South ranks low for both probability of viability AND germination (given viability). This suggests that the DNR should rank this population last, in terms of priority for controlling tallow on Ossabaw, and not invest limited resources toward eliminating this population until all others have been eliminated, as its potential for growth and expansion appears to be relatively low.

For the vast majority of *S. sebiferum* populations on Ossabaw, seed trait analysis does not appear to be a useful tool in establishing priorities for controlling this species. However, the models do appear to be effective in identifying those populations with the strongest relationships among traits. That is, those populations that should receive the highest and lowest priorities for management. Since judicious use of limited resources (funds, time, labor, equipment, etc.) is critical in any invasive species management program, simply knowing "where to start" and "where to end" in order to optimize success, may be useful.

CONCLUSIONS

From the various GLMs and GLMMs developed to analyze relationships among various traits of *S. sebiferum* seeds collected from 16 populations in southern Georgia from 2001-2003, the following conclusions may be drawn:

When random effects due to trees within a site are removed, seed mass does vary among sites for each year. However, the variation from site to site is not pronounced. In any given year, if two sites are selected at random, the expected values of seed mass for the two sites will usually not be significantly different.

When random effects due to seed trees within a population are removed, the variable 'seed shape' (defined as length x breadth) does vary among populations for each year. However, the variation among populations is not pronounced. In any given year, if two populations are randomly selected, the expected value of seed shape for the two populations will usually not be significantly different.

Year is a significant predicator for seed mass, shape, and the probabilities of viability and germination. This is true for both all trees from all populations, and, in general, for all populations. This does not indicate that, for example, the expected mass for 2001 is significantly different from that of 2003. Rather, that there is at least one significant difference among all three years.

In any given year, viability and germination rates vary among populations. This is the case even when we take into account that seeds from a single tree will tend to have similar probabilities of viability and germination. In any year, if two populations are selected at random, their estimated probabilities of viability or germination will usually be significantly different. Germination rates tend to increase from 2001 to 2002, often by a significant amount. Viability rates do not show a strong trend over the three year sample period.

In general, seed mass is not a significant predictive variable of viability. Mass is not significant if population and seed tree are considered as ‘random effects’, in any of the three years. Attempts to fit the model using mass as a predictor for each combination of year and population, yields the result of mass not being significant for most year-population combinations. There are a few year-population combinations for which mass is significant, but viability (or germination) is positively correlated with mass for some of these combinations, and negatively in others. If mass is significant, it is usually due to a small number of unusual observations – a few seeds with large values of mass that are all viable, for instance. Mass may appear to be negatively correlated with germination, overall. However, this seems to be due to the fact that seed mass varies significantly among populations. The data indicate that in each year, mean seed mass is positively associated with overall germination among populations. It is impossible to separate the overall negative association of seed mass with germination, from the association of mass with population; mass and germination may both be influenced by environmental conditions expressed through maternal effects.

Overall, length and breadth are not significant reliable predictors of viability or germination. When either viability or germination are modeled with length and breadth for each year and population, length and breadth do appear to have some predictive power for a few population-year combinations. However, the *p*-values are not very small, and the predictive power of length and breadth, even when apparently significant, is much less than random variation.

Suggested Research

The seed stage of a plant is complex and generally, the least well-understood life history stage of invasive plant species. Ultimately, management plans that incorporate strategies of dealing with the seed phase of pernicious invasives have greater long-term success than those that concentrate exclusively on the removal of above-ground biomass. Consequently, research that bridges knowledge gaps in basic seed ecology of invasive plant species may contribute greatly to our understanding of the population dynamics and invasion mechanisms of aggressive plant species. For Chinese tallow, I suggest the following lines of investigation to enhance the long-term successful control and eradication of this species in the southeastern US.

- Genetic studies to elucidate patterns of relatedness among populations and to trace possible sources of invasion and dispersal mechanisms.

- Physiological experiments to determine type(s) of dormancy (i.e., physical, physiological, chemical, etc.) which may elucidate the *potential* longevity period of dormancy. Although it is generally believed that tallow has physical dormancy, there may be additional mechanisms responsible for inhibition of germination.

- Long-term soil seed bank dynamic experiments to elucidate patterns of in-situ dormancy periods, seed viability, and mortality may be useful in determining long-term allocation of resources for invasive plant control.

- An examination of the relationship between viability/germination vs. soil types may be useful in prioritizing and identifying potentially vulnerable habitats where invasion has not yet occurred and where monitoring efforts can be focused.

- Common Garden experiments with seeds collected from a gradient of “inland to island” population to decipher genetic vs. environmental factor influencing population dynamics.

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Table 3.1. Observations of improbably large values of length or breadth.

POPULATION	SEED TREE	YEAR	SEED ID	LENGTH	BREADTH
Hog Pond West	20	2002	4	87.26	5.42
Middle Beach	16	2002	13	708	5.14
Middle Beach	17	2003	14	772	6.08
Middle Beach	22	2001	2	65	5.45
North Central	10	2002	14	64.7	5.68
South Bradley Beach	24	2002	10	724	5.43
Cane Patch	12	2003	8	9.48	65.56
Jesup	4	2001	3	7.02	50.4
Jesup	20	2001	16	7.83	572
Savannah NWR	8	2002	10	6.87	55.83
Savannah NWR	13	2003	9	7.09	45.46

Table 3.2. Least squares means for seed mass, by population and sampling year (2001). Letters indicate sets of least squares means that are not significantly different.

SAMPLING	POPULATION	ESTIMATE								
2001	Jesup	197.23	A							
2001	Hog Pond West	160.43		B						
2001	South Bradley	159.78		B						
2001	Gator Hole	157.89		B						
2001	Hog Pond	156.91		B	C					
2001	Mule Run Road	155.25		B	C					
2001	North Bradley	155.02		B	C					
2001	Pine Barren	151.55		B	C	D				
2001	Savannah NWR	150.88		B	C	D				
2001	Cabbage Garden	148.17		B	C	D	E			
2001	Cabbage Garden	139.18			C	D	E	F		
2001	Middle Beach	134.09				D	E	F		
2001	South End Beach	130.85					E	F		
2001	Cane Patch	125.30						F		
2001	North Central	124.69						F		

Table 3.3. Least squares means for seed mass, by population and sampling year (2002). Letters indicate sets of least squares means that are not significantly different.

SAMPLING	**POPULATION**	**ESTIMATE**								
2002	Jesup	201.09	A							
2002	Hog Pond West	163.36		B						
2002	Cabbage Garden	162.12		B						
2002	South Bradley	160.71		B	C					
2002	South End Beach	160.08		B	C					
2002	Hog Pond	157.38		B	C	D				
2002	North Bradley	154.69		B	C	D	E			
2002	Wassaw	152.41		B	C	D	E			
2002	Pine Barren	152.01		B	C	D	E			
2002	Mule Run Road	151.78		B	C	D	E			
2002	Gator Hole	151.61		B	C	D	E			
2002	Cabbage Garden	150.17		B	C	D	E			
2002	Middle Beach	139.39			C	D	E	F		
2002	Savannah NWR	138.11				D	E	F		
2002	Cane Patch	134.07					E	F		
2002	North Central	123.93						F		

Table 3.4. Least squares means for seed mass, by population and sampling year (2003). Letters indicate sets of least squares means that are not significantly different.

SAMPLING	POPULATION	ESTIMATE								
2003	Jesup	194.11	A							
2003	Cane Patch	176.47	A	B						
2003	Cabbage Garden	170.28		B	C					
2003	Hog Pond West	168.32		B	C					
2003	Middle Beach	159.86		B	C	D				
2003	Hog Pond	153.72			C	D	E			
2003	Wassaw	151.86			C	D	E			
2003	North Bradley	151.18			C	D	E			
2003	Pine Barren	147.25				D	E	F		
2003	Cabbage Garden	146.72				D	E	F		
2003	Mule Run Road	144.77				D	E	F	G	
2003	South Bradley	141.41				D	E	F	G	H
2003	North Central	138.17					E	F	G	H
2003	South End Beach	127.07						F	G	H
2003	Gator Hole	126.18							G	H
2003	Savannah NWR	122.61								H

Table 3.5. Least squares means for seed shape, by population and sampling year. Letters indicate sets of least squares means that are not significantly different.

SAMPLING YEAR	POPULATION	ESTIMATE				
2001	Jesup	52.8329	A			
2001	Cane Patch	49.7171	A	B		
2001	Cabbage Garden West	43.0004	A	B	C	
2001	South End Beach	42.4777	A	B	C	
2001	Hog Pond West	42.1049	A	B	C	
2001	Middle Beach	41.8190	A	B	C	
2001	North Bradley Beach	41.0265	A	B	C	
2001	Savannah NWR	40.7588	A	B	C	
2001	South Bradley Beach	40.7451	A	B	C	
2001	Hog Pond	38.3634		B	C	
2001	Gator Hole South	38.1776		B	C	
2001	Pine Barren Road	37.4219		B	C	
2001	Mule Run Road	36.3932			C	
2001	North Central	34.1686			C	
2001	Cabbage Garden East	33.9274			C	
2002	Middle Beach	56.8217	A			
2002	South Bradley Beach	51.2276	A	B		
2002	Cane Patch	48.8233	A	B	C	
2002	South End Beach	46.9399	A	B	C	
2002	Jesup	46.0814	A	B	C	
2002	Cabbage Garden West	42.3791	A	B	C	
2002	Hog Pond West	42.3139	A	B	C	
2002	Wassaw	40.4031		B	C	
2002	North Bradley Beach	40.1400		B	C	
2002	Hog Pond	38.2279		B	C	
2002	Gator Hole South	37.8379		B	C	
2002	Savannah NWR	37.7069		B	C	
2002	Pine Barren Road	37.1567		B	C	
2002	Cabbage Garden East	36.8098		B	C	
2002	North Central	36.2421			C	
2002	Mule Run Road	36.0762			C	
2003	Middle Beach	54.9950	A			
2003	Cane Patch	54.3589	A	B		
2003	South End Beach	47.9567	A	B	C	
2003	Jesup	44.7970	A	B	C	D
2003	North Bradley Beach	44.7074	A	B	C	D
2003	Wassaw	44.4473	A	B	C	D
2003	South Bradley Beach	44.4125	A	B	C	D
2003	Cabbage Garden West	43.5524	A	B	C	D
2003	Mule Run Road	42.5814	A	B	C	D
2003	Hog Pond West	40.9433		B	C	D
2003	Savannah NWR	40.7287			C	D
2003	Hog Pond	38.4640			C	D
2003	Pine Barren Road	38.3330			C	D
2003	Gator Hole South	37.7606			C	D
2003	North Central	35.1488			C	D
2003	Cabbage Garden East	33.9392				

Table 3.6. Logits of probability of viability, and probability of viability, as predicted by a generalized linear model, by population, in descending order. A column of letters indicates a lack of significant difference.

YEAR	**POPULATION**	**LOGIT (P($V_i = y$))**	**P($V_i = y$)**										
2001	Jesup	2.6730	0.93542	A									
2001	Hog Pond	1.6094	0.83333		B								
2001	North Central	1.3863	0.80000		B	C							
2001	Middle Beach	1.3733	0.79792		B	C							
2001	Cabbage Garden East	1.3477	0.79375		B	C							
2001	Savannah NWR	1.3171	0.78870		B	C							
2001	South Bradley Beach	1.2852	0.78333			C	D						
2001	Cane Patch	1.0986	0.75000			C	D	E					
2001	Pine Barren Road	0.9906	0.72921				D	E	F				
2001	Mule Run Road	0.8572	0.70208					E	F	G			
2001	Gator Hole South	0.7120	0.67083						F	G			
2001	Hog Pond West	0.6713	0.66180							G			
2001	Cabbage Garden West	0.6652	0.66042							G			
2001	South End Beach	0.3108	0.57708								H		
2001	North Bradley Beach	-0.0921	0.47699									I	
2002	Jesup	2.7442	0.93958	A									
2002	Wassaw	2.2444	0.90417		B								
2002	Hog Pond	1.6245	0.83542			C							
2002	North Central	1.5362	0.82292			C	D						
2002	South Bradley Beach	1.4801	0.81458			C	D	E					
2002	Pine Barren Road	1.3994	0.80208			C	D	E					
2002	Mule Run Road	1.3224	0.78958			C	D	E	F				
2002	Savannah NWR	1.2799	0.78243				D	E	F				
2002	Cane Patch	1.1896	0.76667					E	F				
2002	Middle Beach	1.0410	0.73904						F				
2002	Cabbage Garden West	0.6931	0.66667							G			
2002	Gator Hole South	0.6745	0.66250							G			
2002	Cabbage Garden East	0.6282	0.65208							G			
2002	Hog Pond West	0.6282	0.65208							G			
2002	South End Beach	0.3279	0.58125								H		
2002	North Bradley Beach	0.0335	0.50837									I	
2003	Jesup	3.0358	0.95417	A									
2003	Wassaw	2.2912	0.90814		B								
2003	Pine Barren Road	1.9246	0.87265		B	C							
2003	Savannah NWR	1.8015	0.85833			C	D						
2003	South Bradley Beach	1.5506	0.82500				D	E					
2003	Hog Pond	1.5079	0.81875				D	E					
2003	North Central	1.4125	0.80417					E	F				
2003	Mule Run Road	1.3863	0.80000					E	F				
2003	Middle Beach	1.1210	0.75417						F	G			
2003	Cane Patch	1.0010	0.71325							G	H		
2003	Cabbage Garden East	0.8974	0.71042							G	H		
2003	Cabbage Garden West	0.7982	0.68958								H	I	
2003	South End Beach	0.5826	0.64167									I	J
2003	Gator Hole South	0.5555	0.63542									I	J
2003	Hog Pond West	0.4931	0.62083										J
2003	North Bradley Beach	0.4666	0.61458										J

Table 3.7. Logits of probability of germination, and probability of germination as predicted by a generalized linear model, by population, in descending order. A column of letters indicates a lack of significant difference.

YEAR	POPULATION	LOGIT ($P(G_i = y)$)	$P(G_i = y)$									
2001	North Bradley Beach	1.1945	0.76754	A								
2001	South End Beach	0.7149	0.67148		B							
2001	Middle Beach	0.5290	0.62924		B	C						
2001	Cabbage Garden West	0.2345	0.55838			C	D					
2001	Mule Run Road	0.0059	0.50148				D	E				
2001	Cabbage Garden East	-0.0473	0.48819				D	E	F			
2001	Cane Patch	-0.1001	0.47500					E	F			
2001	Hog Pond	-0.1302	0.46750					E	F			
2001	South Bradley Beach	-0.1492	0.46277					E	F			
2001	Pine Barren Road	-0.1523	0.46199					E	F			
2001	North Central	-0.2091	0.44792					E	F	G		
2001	Savannah NWR	-0.2399	0.44032					E	F	G		
2001	Hog Pond West	-0.3766	0.40694						F	G	H	
2001	Gator Hole South	-0.4811	0.38199							G	H	
2001	Jesup	-0.6402	0.34521								H	
2002	North Bradley Beach	1.3010	0.78601	A								
2002	South End Beach	0.9825	0.72760	A	B							
2002	Cabbage Garden West	0.7595	0.68125		B							
2002	Pine Barren Road	0.3839	0.59481			C						
2002	North Central	0.3634	0.58987			C						
2002	Hog Pond	0.3271	0.58105			C						
2002	Mule Run Road	0.2493	0.56201			C	D					
2002	Middle Beach	0.1358	0.53390			C	D	E				
2002	Cabbage Garden East	0.1344	0.53355			C	D	E				
2002	South Bradley Beach	0.0460	0.51151				D	E				
2002	Cane Patch	-0.0544	0.48641					E				
2002	Savannah NWR	-0.1071	0.47326					E				
2002	Hog Pond West	-0.1087	0.47284					E				
2002	Gator Hole South	-0.1133	0.47170					E				
2002	Wassaw	-0.4693	0.38479						F			
2002	Jesup	-0.5310	0.37029						F			
2003	Pine Barren Road	1.8458	0.86364	A								
2003	North Bradley Beach	1.4076	0.80339		B							
2003	Cabbage Garden West	1.1434	0.75831		B	C						
2003	South End Beach	1.0986	0.75000		B	C						
2003	Mule Run Road	0.9254	0.71615			C						
2003	Cabbage Garden East	0.8938	0.70968			C						
2003	Middle Beach	0.4262	0.60497				D					
2003	South Bradley Beach	0.4097	0.60101				D					
2003	Hog Pond	0.2921	0.57252				D	E				
2003	Savannah NWR	0.2341	0.55825				D	E	F			
2003	Hog Pond West	0.1210	0.53020				D	E	F	G		
2003	North Central	0.0726	0.41813					E	F	G		
2003	Wassaw	-0.0874	0.47816						F	G	H	
2003	Cane Patch	-0.1198	0.47009							G	H	
2003	Gator Hole South	-0.2438	0.43934								H	
2003	Jesup	-1.5229	0.17904									I

Table 3.8. Least squares means of seed mass, for each year. Letters in a column indicates a set of means that are not significant.

YEAR	ESTIMATE		
2001	151.10	A	
2002	156.99		B
2003	150.58	A	

Table 3.9. Least square means of seed mass, by year, for every population. Letters indicate lack of significant differences.

POPULATION	YEAR	ESTIMATE	RANK			
Cabbage Garden East	2001	148.17	2	A	B	
	2002	150.17	1	A		
	2003	146.72	3		B	
Cabbage Garden West	2001	139.18	3	A		
	2002	162.12	2		B	
	2003	170.28	1			C
Cane Patch	2001	125.30	3	A		
	2002	134.07	2		B	
	2003	176.47	1			C
Gator Hole South	2001	157.89	1	A		
	2002	151.61	2		B	
	2003	126.18	3			C
Hog Pond	2001	156.91	2	A	B	
	2002	157.38	1	A		
	2003	153.72	3		B	
Hog Pond West	2001	160.43	3	A		
	2002	163.36	2	A		
	2003	168.32	1		B	
Jesup	2001	197.23	2	A		
	2002	201.09	1		B	
	2003	194.11	3			C
Middle Beach	2001	134.09	3	A		
	2002	139.39	2		B	
	2003	159.86	1			C

Table 3.9. Least square means of seed mass, by year, for every population. Letters indicate lack of significant differences (continued from previous page).

POPULATION	YEAR	ESTIMATE	RANK			
Mule Run Road	2001	155.25	1	A		
	2002	151.78	2	A		
	2003	144.77	3		B	
North Bradley Beach	2001	155.02	1	A		
	2002	154.69	2	A		
	2003	151.18	3	A		
North Central	2001	124.69	2	A		
	2002	123.93	3	A		
	2003	138.17	1		B	
Pine Barren Road	2001	151.55	2	A		
	2002	152.01	1	A		
	2003	147.25	3		B	
Savannah NWR	2001	150.88	1	A		
	2002	138.11	2		B	
	2003	122.61	3			C
South Bradley Beach	2001	159.78	2	A		
	2002	160.71	1	A		
	2003	141.41	3		B	
South End Beach	2001	130.85	2	A		
	2002	160.08	1		B	
	2003	127.07	3	A		
Wassaw	2002	152.41	1	A		
	2003	151.86	2	A		

Table 3.10. Least squares means of seed shape, for each year. Letters in a column indicate a set of means that are not significantly different.

YEAR	ESTIMATE			
2001	40.0293	A		
2002	41.6253		B	
2003	42.8186			C

Table 3.11. Least squares means of seed shape, by year, for every population. Letters indicate lack of significant differences.

POPULATION	YEAR	ESTIMATE	RANK			
Cabbage Garden East	2001	33.9274	3	A		
	2002	36.8098	1		B	
	2003	33.9392	2	A		
Cabbage Garden West	2001	43.0004	2	A	B	
	2002	42.3791	3	A		
	2003	43.5524	1		B	
Cane Patch	2001	49.7171	2	A		
	2002	48.8233	3	A		
	2003	53.1749	1		B	
Gator Hole South	2001	38.1776	1	A		
	2002	37.8379	2	A		
	2003	37.7606	3	A		
Hog Pond	2001	38.3634	2	A		
	2002	38.2279	3	A		
	2003	38.4640	1	A		
Hog Pond West	2001	42.1049	1	A		
	2002	41.3330	2	A	B	
	2003	40.9433	3		B	
Jesup	2001	42.9439	3	A		
	2002	46.0814	1		B	
	2003	44.7970	2			C
Middle Beach	2001	41.1667	3	A		
	2002	49.3166	1		B	
	2003	45.3108	2			C

Table 3.11. Least square means of seed shape, by year, for every population. Letters indicate lack of significant differences (continued from previous page).

POPULATION	YEAR	ESTIMATE	RANK			
Mule Run Road	2001	36.3932	2	A		
	2002	36.0762	3	A		
	2003	42.5814	1		B	
North Bradley Beach	2001	41.0265	2	A		
	2002	40.1400	3	A		
	2003	44.7074	1		B	
North Central	2001	34.1686	3	A		
	2002	35.5186	1		B	
	2003	35.1488	2		B	
Pine Barren Road	2001	37.4129	2	A	B	
	2002	37.1567	3	A		
	2003	38.3330	1		B	
Savannah NWR	2001	40.7588	1	A		
	2002	36.9819	3		B	
	2003	40.1408	2	A		
South Bradley Beach	2001	40.7451	3	A		
	2002	43.1272	2		B	
	2003	44.4125	1			C
South End Beach	2001	42.4777	3	A		
	2002	46.9399	2		B	
	2003	47.9568	1		B	
Wassaw	2002	40.4031	2	A		
	2003	44.4473	1		B	

Table 3.12. Least squares means for logits of probability of viability, and expected probability of viability, for each year. Letters in a column indicate a set of means that are not significantly different.

YEAR	ESTIMATE	*p* VALUE		
2001	1.1472	0.7590	A	
2002	1.1681	0.7628	A	
2003	1.2826	0.7829		B

Table 3.13. Predicted μ and probability of viability, by year, for every population. Letters indicate lack of significant differences.

POPULATION	YEAR	ESTIMATE	ESTIMATED *p*	RANK			
Cabbage Garden East	2001	1.3477	0.79375	1	A		
	2002	0.6282	0.65208	3		B	
	2003	0.8974	0.71042	2	A		
Cabbage Garden West	2001	0.6652	0.66042	3	A		
	2002	0.6931	0.66667	2	A		
	2003	0.7982	0.68958	1	A		
Cane Patch	2001	1.0986	0.75000	2	A		
	2002	1.1896	0.76667	1	A		
	2003	1.0010	0.73125	3	A		
Gator Hole South	2001	0.7120	0.67083	1	A		
	2002	0.6745	0.66250	2	A		
	2003	0.5555	0.63542	3	A		
Hog Pond	2001	1.6094	0.83333	2	A		
	2002	1.6245	0.83542	1	A		
	2003	1.5079	0.81875	3	A		
Hog Pond West	2001	0.6713	0.66180	1	A		
	2002	0.6282	0.65208	2	A		
	2003	0.4931	0.62083	3	A		
Jesup	2001	2.6730	0.93542	3	A		
	2002	2.7442	0.93958	2	A		
	2003	3.0358	0.95417	1	A		
Middle Beach	2001	1.3733	0.79792	1	A		
	2002	1.0410	0.73904	3		B	
	2003	1.1210	0.75417	2	A	B	

Table 3.13. Predicted μ and probability of viability, by year, for every population. Letters indicate lack of significant differences (continued from previous page).

POPULATION	YEAR	ESTIMATE	ESTIMATED *p*	RANK			
Mule Run Road	2001	0.8572	0.70208	3	A		
	2002	1.3224	0.78958	2		B	
	2003	1.3863	0.80000	1		B	
North Bradley Beach	2001	-0.0921	0.47699	3	A		
	2002	0.0335	0.50837	2	A		
	2003	0.4666	0.61458	1		B	
North Central	2001	1.3863	0.80000	3	A		
	2002	1.5362	0.82292	1	A		
	2003	1.4125	0.80417	2	A		
Pine Barren Road	2001	0.9906	0.72921	3	A		
	2002	1.3994	0.80208	2		B	
	2003	1.9246	0.87265	1			C
Savannah NWR	2001	1.3171	0.78870	2	A		
	2002	1.2799	0.78243	3	A		
	2003	1.8015	0.85833	1		B	
South Bradley Beach	2001	1.2852	0.78333	3	A		
	2002	1.4801	0.81458	2	A		
	2003	1.5506	0.82500	1	A		
South End Beach	2001	0.3108	0.57708	3	A		
	2002	0.3279	0.58125	2	A	B	
	2003	0.5826	0.64167	1		B	
Wassaw	2002	2.2444	0.90417	2	A		
	2003	2.2912	0.90814	1	A		

Table 3.14. Least squares means of logits of probability of germination, and expected probability of germination, for each year. Based on observations for which viability was “Y”. Letters in a column indicate a set of means that are not significantly different.

YEAR	ESTIMATE	*p* VALUE			
2001	-0.02847	0.4928	A		
2002	0.2071	0.5516		B	
2003	0.4153	0.6024			C

Table 3.15. Predicted μ and probability of germination, by year, for every population, based on observations for which viability was "Y". Letters indicate lack of significant differences.

POPULATION	**YEAR**	**ESTIMATE**	**ESTIMATED *p***	**RANK**			
Cabbage Garden East	2001	-0.0473	0.48819	3	A		
	2002	0.1344	0.53355	2	A		
	2003	0.8938	0.70968	1		B	
Cabbage Garden West	2001	0.2345	0.55836	3	A		
	2002	0.7595	0.68125	2		B	
	2003	1.1434	0.75831	1			C
Cane Patch	2001	-0.1001	0.47500	2	A		
	2002	-0.0544	0.48641	1	A		
	2003	-0.1198	0.47009	3	A		
Gator Hole South	2001	-0.4811	0.38199	3	A		
	2002	-0.1133	0.47170	1		B	
	2003	-0.2438	0.43934	2	A	B	
Hog Pond	2001	-0.1302	0.46750	3	A		
	2002	0.3271	0.58105	1		B	
	2003	0.2921	0.57252	2		B	
Hog Pond West	2001	-0.3766	0.40694	3	A		
	2002	-0.1087	0.47284	2	A	B	
	2003	0.1210	0.53020	1		B	
Jesup	2001	-0.6402	0.34521	2	A		
	2002	-0.5310	0.37029	1	A		
	2003	-1.5229	0.17904	3		B	
Middle Beach	2001	0.5290	0.62924	1	A		
	2002	0.1358	0.53390	3		B	
	2003	0.4262	0.60497	2	A	B	

Table 3.15. Predicted μ and probability of viability, by year, for every population, based on observations for which viability was "Y". Letters indicate lack of significant differences (continued from previous page).

POPULATION	YEAR	ESTIMATE	ESTIMATED *p*	RANK			
Mule Run Road	2001	0.0059	0.50148	3	A		
	2002	0.2493	0.56201	2	A		
	2003	0.9254	0.71615	1		B	
North Bradley Beach	2001	1.1945	0.76754	3	A		
	2002	1.3010	0.78601	2	A		
	2003	1.4076	0.80339	1	A		
North Central	2001	-0.2091	0.44792	3	A		
	2002	0.3634	0.58987	1		B	
	2003	0.0726	0.51813	2	A		
Pine Barren Road	2001	-0.1523	0.46199	3	A		
	2002	0.3839	0.59481	2		B	
	2003	1.8458	0.86364	1			C
Savannah NWR	2001	-0.2399	0.44032	3	A		
	2002	-0.1071	0.47326	2	A		
	2003	0.2341	0.55825	1		B	
South Bradley Beach	2001	-0.1492	0.46277	3	A		
	2002	0.0460	0.51151	2	A		
	2003	0.4097	0.60101	1		B	
South End Beach	2001	0.7149	0.67148	3	A		
	2002	0.9825	0.72760	2	A	B	
	2003	1.0986	0.75000	1		B	
Wassaw	2002	-0.4693	0.38479	2	A		
	2003	-0.0874	0.47816	1		B	

Table 3.16. Categorization of viability and germination rates, by mass classes, for all data.

RANGE	VIABILITY			GERMINATION		
	N	Y	probY	N	Y	probY
20-40	1	0	0	0	0	-
40-60	14	48	0.774	18	30	0.625
60-80	72	215	0.749	83	132	0.614
80-100	286	788	0.731	344	434	0.558
100-120	667	2005	0.750	911	1094	0.546
120-140	1243	3316	0.727	1468	1848	0.557
140-160	1304	3722	0.741	1604	2118	0.569
160-180	1054	3132	0.748	1427	1705	0.544
180-200	599	2084	0.777	1094	990	0.475
200-220	311	970	0.757	505	465	0.479
220-240	111	357	0.763	192	165	0.462
240-260	30	137	0.820	74	63	0.460
260-280	5	32	0.865	17	15	0.469

Table 3.17. *p*-values for mass coefficient, in generalized linear mixed models (GLMMs) for viability and germination.

	2001	**2002**	**2003**
Viability	0.4100	0.3640	0.2613
Germination	0.3500	0.2771	0.3271

Table 3.18. Coefficients of mass, standard errors, and *p*-values, after fitting GLM of viability~weight for all combinations of year and population.

YEAR	POPULATION	COEFFICIENT	STANDARD ERROR	P-VALUE
2001	Cabbage Garden East	0.0065	0.0028	0.0199
2001	Cabbage Garden West	0.0064	0.0048	0.1833
2001	Cane Patch	-0.0048	0.0059	0.4227
2001	Gator Hole South	-0.0039	0.0043	0.3685
2001	Hog Pond	0.0033	0.0057	0.5599
2001	Hog Pond West	0.0008	0.0040	0.8397
2001	Jesup	0.0041	0.0056	0.4659
2001	Middle Beach	-0.0013	0.0044	0.7779
2001	Mule Run Road	-0.0045	0.0038	0.2327
2001	North Bradley Beach	-0.0013	0.0021	0.5329
2001	North Central	0.0076	0.0046	0.1001
2001	Pine Barren Road	0.0010	0.0042	0.8089
2001	Savannah NWR	0.0056	0.0042	0.1792
2001	South Bradley Beach	0.0062	0.0035	0.0749
2001	South End Beach	-0.0047	0.0036	0.1982
2002	Cabbage Garden East	-0.0009	0.0036	0.8004
2002	Cabbage Garden West	-0.0027	0.0040	0.4923
2002	Cane Patch	-0.0047	0.0033	0.1589
2002	Gator Hole South	-0.0030	0.0050	0.5415
2002	Hog Pond	0.0056	0.0055	0.3057
2002	Hog Pond West	0.0006	0.0044	0.8892
2002	Jesup	0.0108	0.0058	0.0602
2002	Middle Beach	0.0085	0.0087	0.3288
2002	Mule Run Road	-0.0003	0.0039	0.9396
2002	North Bradley Beach	-0.0040	0.0031	0.1967
2002	North Central	0.0004	0.0040	0.9201
2002	Pine Barren Road	0.0056	0.0038	0.1431
2002	Savannah NWR	0.0094	0.0072	0.1952
2002	South Bradley Beach	0.0043	0.0054	0.4245
2002	South End Beach	-0.0089	0.0041	0.0283
2002	Wassaw	0.0009	0.0040	0.8143
2003	Cabbage Garden East	0.0048	0.0071	0.5014
2003	Cabbage Garden West	0.0003	0.0028	0.9266
2003	Cane Patch	-0.0023	0.0027	0.3898
2003	Gator Hole South	0.0030	0.0118	0.7989
2003	Hog Pond	0.0023	0.0050	0.6473
2003	Hog Pond West	-0.0035	0.0052	0.4982
2003	Jesup	-0.0194	0.0146	0.1847
2003	Middle Beach	0.0082	0.0071	0.2456
2003	Mule Run Road	0.0096	0.0043	0.0263
2003	North Bradley Beach	0.0002	0.0036	0.9509
2003	North Central	0.0055	0.0057	0.3329
2003	Pine Barren Road	-0.0086	0.0044	0.0525
2003	Savannah NWR	-0.0091	0.0056	0.1028
2003	South Bradley Beach	0.0001	0.0034	0.9807
2003	South End Beach	-0.0162	0.0038	<.0001
2003	Wassaw	0.0020	0.0041	0.6157

Table 3.19. Coefficients of mass, standard errors, and *p*-values, after fitting GLM of germination~ seed mass for all combinations of year and population.

YEAR	POPULATION	COEFFICIENT	STANDARD ERROR	P-VALUE
2001	Cabbage Garden East	0.0065	0.0036	0.8125
2001	Cabbage Garden West	0.0064	0.0041	0.7298
2001	Cane Patch	-0.0048	0.0037	0.2277
2001	Gator Hole South	-0.0039	0.0032	0.0998
2001	Hog Pond	0.0033	0.0039	0.9101
2001	Hog Pond West	0.0008	0.0042	0.1678
2001	Jesup	0.0041	0.0038	0.3726
2001	Middle Beach	-0.0013	0.0045	0.1971
2001	Mule Run Road	-0.0045	0.0050	0.4054
2001	North Bradley Beach	-0.0013	0.0037	0.8849
2001	North Central	0.0076	0.0037	0.8529
2001	Pine Barren Road	0.0010	0.0035	0.7831
2001	Savannah NWR	0.0056	0.0026	0.0287
2001	South Bradley Beach	0.0062	0.0042	0.4650
2001	South End Beach	-0.0047	0.0053	0.5784
2002	Cabbage Garden East	-0.0009	0.0033	0.2707
2002	Cabbage Garden West	-0.0027	0.0047	0.3529
2002	Cane Patch	-0.0047	0.0039	0.3131
2002	Gator Hole South	-0.0030	0.0054	0.3531
2002	Hog Pond	0.0056	0.0032	0.8554
2002	Hog Pond West	0.0006	0.0027	0.2267
2002	Jesup	0.0108	0.0061	0.5784
2002	Middle Beach	0.0085	0.0035	0.1804
2002	Mule Run Road	-0.0003	0.0032	0.4505
2002	North Bradley Beach	-0.0040	0.0045	0.6918
2002	North Central	0.0004	0.0042	0.9776
2002	Pine Barren Road	0.0056	0.0034	0.5165
2002	Savannah NWR	0.0094	0.0050	0.9563
2002	South Bradley Beach	0.0043	0.0058	0.9003
2002	South End Beach	-0.0089	0.0046	0.6191
2002	Wassaw	0.0009	0.0033	0.4507
2003	Cabbage Garden East	0.0048	0.0103	0.6849
2003	Cabbage Garden West	0.0003	0.0044	0.0608
2003	Cane Patch	-0.0023	0.0031	0.7338
2003	Gator Hole South	0.0030	0.0085	0.4311
2003	Hog Pond	0.0023	0.0040	0.1363
2003	Hog Pond West	-0.0035	0.0047	0.6149
2003	Jesup	-0.0194	0.0087	0.3751
2003	Middle Beach	0.0082	0.0028	0.2422
2003	Mule Run Road	0.0096	0.0054	0.0032
2003	North Bradley Beach	0.0002	0.0037	0.3040
2003	North Central	0.0055	0.0049	0.4199
2003	Pine Barren Road	-0.0086	0.0049	0.2096
2003	Savannah NWR	-0.0091	0.0053	0.9276
2003	South Bradley Beach	0.0001	0.0037	0.3648
2003	South End Beach	-0.0162	0.0024	0.3328
2003	Wassaw	0.0020	0.0043	0.0541

Table 3.20. Categorization of viability and germination. (A): By length categories, (B) By breadth categories.

		VIABILITY			GERMINATION		
	Range	N	Y	ProbY	N	Y	ProbY
A	3-4	2	4	0.667	3	1	0.25
	4-5	23	62	0.729	26	36	0.581
	5-6	258	746	0.743	370	376	0.504
	6-7	1525	4660	0.754	2112	2548	0.547
	7-8	2579	7279	0.738	3344	3935	0.5406
	8-9	1045	3236	0.759	1490	1746	0.5396
	9-10	219	666	0.753	321	345	0.518
	10-11	39	124	0.761	59	65	0.524
	11-12	13	40	0.755	20	20	0.500
	12-13	0	3	1.000	1	2	0.667
B	2-3	0	3	1	0	3	1
	3-4	21	58	0.734	29	29	0.500
	4-5	1050	3334	0.7605	1532	1802	0.500
	5-6	3606	10291	0.7405	4760	5531	0.5405
	6-7	893	2731	0.7536	1238	1493	0.5375
	7-8	126	369	0.7455	167	202	0.5467
	8-9	7	32	0.8205	20	12	0.547
	9-10	0	2	1.00	0	2	1.000

Table 3.21. *p*-values for generalized linear model with length, breadth, and their interaction (product = 'shape') as predictors, by year, for the variables 'viability' and 'germination'.

YEAR	**EFFECT**	**VIABILITY**		**GERMINATION**	
		ESTIMATE	P	ESTIMATE	P
2001	Length	0.2753	0.384	-0.1771	0.482
	Breadth	0.1886	0.659	-0.1992	0.517
	Length * Breadth	-0.0395	0.4995	0.0264	0.557
2002	Length	0.5639	0.0217	-0.4921	0.0013
	Breadth	0.9520	0.0044	-0.6328	0.0027
	Length * Breadth	-0.1136	0.0114	0.0859	0.0018
2003	Length	0.1762	0.5355	0.4121	0.1050
	Breadth	0.4044	0.3162	0.3851	0.2519
	Length * Breadth	-0.0411	0.3960	-0.0552	0.1890

Table 3.22. Coefficients for generalized linear model with length, breadth, and their interaction (product = ‘shape’) as predictors, by year, for the variables ‘viability’ and ‘germination’ (2001).

YEAR	**POPULATION**	**VIABILITY**		**GERMINATION**	
		Estimate	p	Estimate	P
2001	Cabbage Garden East	-1.0779	<0.0001	0.74267	0.00146
2001	Cabbage Garden West	-0.3566	0.0210	0.48883	0.01343
2001	Cane Patch	-0.7514	0.0003	0.81378	0.00002
2001	Gator Hole South	-0.4348	0.0912	1.19461	0.00000
2001	Hog Pond	-1.3275	<0.0001	0.84784	0.00007
2001	Hog Pond West	-0.3762	0.0434	1.09496	0.00000
2001	Jesup	-2.3538	<0.0001	1.35319	0.00000
2001	Middle Beach	-1.0825	<0.0001	0.17868	0.29702
2001	Mule Run Road	-0.5793	0.0018	0.69635	0.00084
2001	North Bradley Beach	0.3920	0.0201	-0.48536	0.00947
2001	North Central	-1.1218	0.0001	0.90353	0.00001
2001	Pine Barren Road	-0.7199	0.0004	0.85028	0.00011
2001	Savannah NWR	-1.0283	<0.0001	0.95703	0.00000
2001	South Bradley Beach	-0.9836	<0.0001	0.85391	0.00039
2001	Length	0.2622	0.2786	-0.16494	0.49976
2001	Breadth	0.2905	0.3889	-0.26278	0.41477
2001	Length * Breadth	-0.0499	0.2567	0.03049	0.48647

Table 3.23. Coefficients for generalized linear model with length, breadth, and their interaction (product = 'shape') as predictors, by year, for the variables 'viability' and 'germination' (2002).

YEAR	POPULATION	VIABILITY		GERMINATION	
		Estimate	p	Estimate	p
2002	Cabbage Garden East	1.5796	<0.0001	-0.64809	0.00034
2002	Cabbage Garden West	1.5001	<0.0001	-1.21798	0.00000
2002	Cane Patch	1.0896	<0.0001	0.35305	0.12106
2002	Gator Hole South	1.5228	<0.0001	-0.36882	0.17536
2002	Hog Pond	0.5849	0.0263	-0.80539	0.00008
2002	Hog Pond West	1.5978	<0.0001	-0.34226	0.06811
2002	Jesup	-0.5256	0.1692	0.06247	0.76387
2002	Middle Beach	1.1979	<0.0001	-0.63478	0.00250
2002	Mule Run Road	0.8847	0.0002	-0.78226	0.00042
2002	North Bradley Beach	2.1937	<0.0001	-1.79020	0.00000
2002	North Central	0.6746	0.0018	-0.89265	0.00000
2002	Pine Barren Road	0.8381	0.0006	-0.87031	0.00000
2002	Savannah NWR	0.9064	0.0028	-0.38587	0.03550
2002	South Bradley Beach	0.7620	0.0034	-0.50534	0.06870
2002	South End Beach	1.9062	<0.0001	-1.43147	0.00000
2002	Length	0.3952	0.0567	-0.54005	0.00016
2002	Breadth	0.6818	0.0101	-0.60048	0.00049
2002	Length * Breadth	-0.0830	0.0190	0.08363	0.00060

Table 3.24. Coefficients for generalized linear model with length, breadth, and their interaction (product = ‘shape’) as predicators, by year, for the variables ‘viability’ and ‘germination’ (2003).

YEAR	POPULATION	VIABILITY		GERMINATION	
		Estimate	p	Estimate	P
2003	Cabbage Garden East	1.4516	<0.0001	-1.01683	0.00233
2003	Cabbage Garden West	1.5170	<0.0001	-1.28028	0.00000
2003	Cane Patch	1.3257	<0.0001	0.06776	0.73287
2003	Gator Hole South	1.7617	<0.0001	0.10965	0.70878
2003	Hog Pond	0.8043	0.0002	-0.40112	0.05407
2003	Hog Pond West	1.8110	<0.0001	-0.21905	0.41319
2003	Jesup	-0.7370	0.0002	1.44607	0.00000
2003	Middle Beach	1.2303	<0.0001	-0.53426	0.02958
2003	Mule Run Road	0.9227	<0.0001	-1.04261	0.00000
2003	North Bradley Beach	1.8416	<0.0001	-1.52291	0.00000
2003	North Central	0.9285	0.0002	-0.17919	0.36227
2003	Pine Barren Road	0.3907	0.2212	-1.93041	0.00000
2003	Savannah NWR	0.5295	0.1349	-0.39080	0.13698
2003	South Bradley Beach	0.7382	0.0005	-0.49154	0.00933
2003	South End Beach	1.7813	<0.0001	-1.22410	0.00000
2003	Length	0.4474	0.1859	0.10452	0.67954
2003	Breadth	0.5037	0.2774	0.34193	0.29497
2003	Length * Breadth	-0.0741	0.1964	-0.03095	0.46114

Table 3.25. Estimated coefficients and *p*-values, for coefficients of length, breadth, and interaction (product = ‘shape’), in GLMMs for viability and germination.

YEAR	EFFECT	VIABILITY		GERMINATION	
		Estimate	p-value	Estimate	p-value
2001	Length	0.7865	0.1071	-0.4900	0.2746
2001	Breadth	1.3363	0.0496	-0.6874	0.2701
2001	Length * Breadth	-0.1726	0.0558	0.08972	0.2691
2002	Length	0.2850	0.5675	-0.6424	0.1793
2002	Breadth	0.6677	0.3350	-0.4776	0.4786
2002	Length * Breadth	-0.07263	0.4219	0.08732	0.3105
2003	Length	0.3262	0.4884	0.1789	0.6597
2003	Breadth	0.4138	0.5171	0.2632	0.6319
2003	Length * Breadth	-0.06492	0.4228	-0.03276	0.6335

Table 3.26. Coefficients, standard errors, and *p*-values for GLMs of viability, length, breadth, and length * breath ('shape') as predictors, by year and population (2001).

YEAR	POPULATION	PARAMETER	ESTIMATE	STD ERROR	PROB CHI SQ
2001	Cabbage Garden East	Length	-1.3515	0.9866	0.1707
2001	Cabbage Garden East	Breadth	-2.1611	1.3034	0.0973
2001	Cabbage Garden East	Length * Breadth	0.3180	0.1871	0.0891
2001	Cabbage Garden West	Length	-1.4848	1.0134	0.1429
2001	Cabbage Garden West	Breadth	-1.5132	1.2646	0.2315
2001	Cabbage Garden West	Length * Breadth	0.2354	0.1643	0.1521
2001	Cane Patch	Length	-1.7392	0.8004	0.0298
2001	Cane Patch	Breadth	-2.0882	1.0803	0.0532
2001	Cane Patch	Length * Breadth	0.2510	0.1255	0.0455
2001	Gator Hole South	Length	3.9009	2.0642	0.0588
2001	Gator Hole	Breadth	5.0363	2.7077	0.0629
2001	Gator Hole	Length * Breadth	-0.7634	0.3796	0.0443
2001	Hog Pond	Length	1.0453	1.7070	0.5403
2001	Hog Pond	Breadth	0.9687	2.2813	0.6711
2001	Hog Pond	Length * Breadth	-0.1938	0.3182	0.5426
2001	Hog Pond West	Length	1.4992	1.1424	0.1894
2001	Hog Pond West	Breadth	1.7817	1.6494	0.2801
2001	Hog Pond West	Length * Breadth	-0.2528	0.2112	0.2314
2001	Jesup	Length	1.0643	1.3910	0.4442
2001	Jesup	Breadth	0.6974	1.6497	0.6807
2001	Jesup	Length * Breadth	-0.1712	0.2362	0.4686
2001	Middle Beach	Length	0.8202	1.1637	0.4809
2001	Middle Beach	Breadth	1.1314	1.6901	0.5032
2001	Middle Beach	Length * Breadth	-0.1560	0.2058	0.4483
2001	Mule Run Road	Length	0.4807	1.0802	0.6563
2001	Mule Run Road	Breadth	0.9529	1.2092	0.4307
2001	Mule Run Road	Length * Breadth	-0.1454	0.1912	0.4469
2001	North Bradley Beach	Length	0.1808	0.4898	0.7131
2001	North Bradley Beach	Breadth	-0.1097	0.6878	0.8733
2001	North Bradley Beach	Length * Breadth	-0.0200	0.0903	0.8249
2001	North Central	Length	0.7631	1.2954	0.5558
2001	North Central	Breadth	1.1918	1.8637	0.5225
2001	North Central	Length * Breadth	-0.1268	0.2571	0.6218
2001	Pine Barren Road	Length	0.0053	0.8911	0.9952
2001	Pine Barren Road	Breadth	-0.1452	1.3438	0.9139
2001	Pine Barren Road	Length * Breadth	-0.0021	0.1768	0.9904
2001	Savannah NWR	Length	4.1940	2.5936	0.1059
2001	Savannah NWR	Breadth	5.6854	3.0255	0.0602
2001	Savannah NWR	Length * Breadth	-.7881	0.4346	0.0698
2001	South Bradley Beach	Length	0.1957	0.6495	0.7632
2001	South Bradley Beach	Breadth	-0.4135	0.7814	0.5967
2001	South Bradley Beach	Length * Breadth	0.0200	0.1148	0.8615
2001	South End Beach	Length	0.2112	1.0576	0.8417
2001	South End Beach	Breadth	0.5609	1.4527	0.6994
2001	South End Beach	Length * Breadth	-0.0501	0.1871	0.7887

Table 3.27. Coefficients, standard errors, and *p*-values for GLMs of viability, length, breadth, and length * breath (‘shape’) as predictors, by year and population (2002).

YEAR	POPULATION	PARAMETER	ESTIMATE	STD ERROR	PROB CHI SQ
2002	Cabbage Garden East	Length	0.6183	0.9594	0.5192
2002	Cabbage Garden East	Breadth	1.7443	1.3239	0.1877
2002	Cabbage Garden East	Length * Breadth	-0.1913	0.1882	0.3094
2002	Cabbage Garden West	Length	7.0172	2.8488	0.0138
2002	Cabbage Garden West	Breadth	9.4265	3.9492	0.0170
2002	Cabbage Garden West	Length * Breadth	-1.2367	0.5053	0.0144
2002	Cane Patch	Length	0.2337	1.0439	0.8228
2002	Cane Patch	Breadth	0.3840	1.5830	0.8083
2002	Cane Patch	Length * Breadth	-0.0445	0.1804	0.8053
2002	Gator Hole South	Length	-0.3546	1.8607	0.8488
2002	Gator Hole	Breadth	-0.5875	2.4851	0.8131
2002	Gator Hole	Length * Breadth	0.0370	0.3456	0.9148
2002	Hog Pond	Length	1.0421	1.8939	0.5822
2002	Hog Pond	Breadth	0.8889	2.4016	0.7113
2002	Hog Pond	Length * Breadth	-0.1335	0.3267	0.6829
2002	Hog Pond West	Length	-8491	2.0303	0.6758
2002	Hog Pond West	Breadth	-2.1410	2.8018	0.4448
2002	Hog Pond West	Length * Breadth	0.1896	0.3655	0.6040
2002	Jesup	Length	0.6298	1.3402	0.6384
2002	Jesup	Breadth	1.8320	1.7987	0.3084
2002	Jesup	Length * Breadth	-0.2045	0.2326	0.3793
2002	Middle Beach	Length	1.9379	1.0595	0.0674
2002	Middle Beach	Breadth	3.3192	1.2967	0.0105
2002	Middle Beach	Length * Breadth	0.1590	0.0181	0.0181
2002	Mule Run Road	Length	1.0158	1.1170	0.3631
2002	Mule Run Road	Breadth	1.9065	1.4136	0.1774
2002	Mule Run Road	Length * Breadth	-0.2352	0.2029	0.2463
2002	North Bradley Beach	Length	0.6587	0.5909	0.2650
2002	North Bradley Beach	Breadth	0.3002	0.8005	0.7077
2002	North Bradley Beach	Length * Breadth	-0.0973	0.1040	0.3498
2002	North Central	Length	1.3757	1.1508	0.2319
2002	North Central	Breadth	2.1684	1.5088	0.1507
2002	North Central	Length * Breadth	-0.2676	0.1995	0.1799
2002	Pine Barren Road	Length	-1.4808	0.7520	0.0489
2002	Pine Barren Road	Breadth	-1.1973	1.1314	0.2899
2002	Pine Barren Road	Length * Breadth	0.2503	0.1455	0.0854
2002	Savannah NWR	Length	-1.2862	1.9057	0.4997
2002	Savannah NWR	Breadth	-0.5074	2.2687	0.8230
2002	Savannah NWR	Length * Breadth	0.1381	0.3406	0.6851
2002	South Bradley Beach	Length	0.7165	1.3649	0.5996
2002	South Bradley Beach	Breadth	0.0529	1.7398	0.9757
2002	South Bradley Beach	Length * Breadth	-0.0612	0.2486	0.8057
2002	South End Beach	Length	0.8834	1.2875	0.4926
2002	South End Beach	Breadth	0.9559	1.5926	0.5484
2002	South End Beach	Length * Breadth	-0.1293	0.2056	0.5292
2002	Wassaw	Length	1.7783	0.9986	0.0750
2002	Wassaw	Breadth	2.6509	1.4687	0.0711
2002	Wassaw	Length * Breadth	-0.3824	0.1992	0.0549

Table 3.28. Coefficients, standard errors, and *p*-values for GLMs of viability, length, breadth, and length * breath ('shape') as predictors, by year and population (2003).

YEAR	POPULATION	PARAMETER	ESTIMATE	STD ERROR	PROB CHI SQ
2003	Cabbage Garden East	Length	-2.3361	3.084	0.4482
2003	Cabbage Garden East	Breadth	-3.3356	3.9259	0.3955
2003	Cabbage Garden East	Length * Breadth	0.5119	0.6246	0.4125
2003	Cabbage Garden West	Length	-1.5930	1.5780	0.3128
2003	Cabbage Garden West	Breadth	-1.7829	1.9949	0.3715
2003	Cabbage Garden West	Length * Breadth	0.2498	0.2606	0.3378
2003	Cane Patch	Length	1.0397	1.0006	0.2988
2003	Cane Patch	Breadth	1.3316	1.4775	0.3675
2003	Cane Patch	Length * Breadth	-0.1631	0.1599	0.3078
2003	Gator Hole South	Length	0.5747	1.6928	0.7343
2003	Gator Hole	Breadth	-0.6798	2.1519	0.7521
2003	Gator Hole	Length * Breadth	-0.0193	0.3002	0.9487
2003	Hog Pond	Length	0.8276	1.8416	0.6532
2003	Hog Pond	Breadth	0.8181	2.7352	0.7649
2003	Hog Pond	Length * Breadth	-0.1043	0.3599	0.7720
2003	Hog Pond West	Length	-0.0579	1.3877	0.9667
2003	Hog Pond West	Breadth	0.6158	2.0021	0.7584
2003	Hog Pond West	Length * Breadth	-0.0193	0.2629	0.9414
2003	Jesup	Length	3.4151	2.1447	0.1113
2003	Jesup	Breadth	4.4827	2.9915	0.1340
2003	Jesup	Length * Breadth	-0.6263	0.3872	0.1058
2003	Middle Beach	Length	1.4967	1.2596	0.2348
2003	Middle Beach	Breadth	1.9216	1.5633	0.2190
2003	Middle Beach	Length * Breadth	-0.2299	0.1769	0.1938
2003	Mule Run Road	Length	0.4411	1.0822	0.6836
2003	Mule Run Road	Breadth	0.7763	1.4009	0.5795
2003	Mule Run Road	Length * Breadth	-0.0735	0.1887	0.6969
2003	North Bradley Beach	Length	-3.6558	2.1006	0.0818
2003	North Bradley Beach	Breadth	-4.4822	2.8450	0.1151
2003	North Bradley Beach	Length * Breadth	0.6027	0.3568	0.0911
2003	North Central	Length	0.4170	1.3146	0.7511
2003	North Central	Breadth	0.7635	1.7433	0.6614
2003	North Central	Length * Breadth	-0.0686	0.2401	0.7751
2003	Pine Barren Road	Length	0.5648	1.3509	0.6758
2003	Pine Barren Road	Breadth	0.3677	1.6856	0.8273
2003	Pine Barren Road	Length * Breadth	-0.1417	0.2539	0.5767
2003	Savannah NWR	Length	2.4937	2.7485	0.3642
2003	Savannah NWR	Breadth	4.6502	3.8580	0.2281
2003	Savannah NWR	Length * Breadth	-0.5863	0.5341	0.2723
2003	South Bradley Beach	Length	-2.2678	2.2817	0.3203
2003	South Bradley Beach	Breadth	-4.5996	3.4590	0.1836
2003	South Bradley Beach	Length * Breadth	0.5045	0.4207	0.2304
2003	South End Beach	Length	1.4387	1.0697	0.1786
2003	South End Beach	Breadth	1.1406	1.3133	0.3851
2003	South End Beach	Length * Breadth	-0.1949	0.1657	0.2393
2003	Wassaw	Length	-2.1685	2.5135	0.3883
2003	Wassaw	Breadth	-4.0902	3.5633	0.2510
2003	Wassaw	Length * Breadth	0.4139	0.4469	0.3544

Table 3.29. Coefficients, standard errors, and p-values for GLMs of germination, length, breadth, and length * breath ('shape') as predictors, by year and population (2001).

YEAR	POPULATION	PARAMETER	ESTIMATE	STD ERROR	PROB CHI SQ
2001	Cabbage Garden East	Length	1.8901	0.8369	0.0239
2001	Cabbage Garden East	Breadth	1.7539	1.2081	0.1466
2001	Cabbage Garden East	Length * Breadth	-0.3428	0.1673	0.0405
2001	Cabbage Garden West	Length	-1.3652	1.1423	0.3337
2001	Cabbage Garden West	Breadth	-1.5916	1.8533	0.3905
2001	Cabbage Garden West	Length * Breadth	0.2263	0.2376	0.3408
2001	Cane Patch	Length	-0.9676	1.1868	0.4149
2001	Cane Patch	Breadth	-1.4843	1.5924	0.3516
2001	Cane Patch	Length * Breadth	0.1639	0.1885	0.3845
2001	Gator Hole South	Length	-0.8861	1.8817	0.6377
2001	Gator Hole	Breadth	-1.1327	2.5960	0.6266
2001	Gator Hole	Length * Breadth	0.1703	0.3451	0.6215
2001	Hog Pond	Length	-3.435	1.4698	0.0175
2001	Hog Pond	Breadth	-3.7120	1.8584	0.0458
2001	Hog Pond	Length * Breadth	0.5689	0.2597	0.0285
2001	Hog Pond West	Length	1.3280	1.3869	0.3383
2001	Hog Pond West	Breadth	1.5178	1.7885	0.3961
2001	Hog Pond West	Length * Breadth	-0.2397	0.2494	0.3364
2001	Jesup	Length	0.5896	1.0860	0.5872
2001	Jesup	Breadth	0.9572	1.4538	0.5103
2001	Jesup	Length * Breadth	-0.0985	0.1935	0.6107
2001	Middle Beach	Length	-0.0873	1.4876	0.9532
2001	Middle Beach	Breadth	0.1479	1.9213	0.9386
2001	Middle Beach	Length * Breadth	-0.0019	0.2588	0.9941
2001	Mule Run Road	Length	0.5122	0.9956	0.6069
2001	Mule Run Road	Breadth	1.0086	1.4337	0.4818
2001	Mule Run Road	Length * Breadth	-0.1223	0.2086	0.5575
2001	North Bradley Beach	Length	1.6429	1.1151	0.1407
2001	North Bradley Beach	Breadth	1.1907	1.3530	0.3788
2001	North Bradley Beach	Length * Breadth	-0.2513	0.1936	0.1944
2001	North Central	Length	0.2031	1.3122	0.8770
2001	North Central	Breadth	-0.6897	1.6807	0.6815
2001	North Central	Length * Breadth	0.0067	0.2483	0.9784
2001	Pine Barren Road	Length	0.2280	0.7126	0.7490
2001	Pine Barren Road	Breadth	-0.1769	0.7853	0.8218
2001	Pine Barren Road	Length * Breadth	-0.0252	0.1204	0.8343
2001	Savannah NWR	Length	-3.4868	1.5315	0.0228
2001	Savannah NWR	Breadth	-4.3527	2.0616	0.0347
2001	Savannah NWR	Length * Breadth	0.5965	0.2738	0.0293
2001	South Bradley Beach	Length	-0.8535	0.9417	0.3648
2001	South Bradley Beach	Breadth	-0.7541	1.1514	0.5125
2001	South Bradley Beach	Length * Breadth	0.1585	0.1714	0.3549
2001	South End Beach	Length	-0.7368	1.4011	0.8673
2001	South End Beach	Breadth	-0.7368	1.8088	0.6838
2001	South End Beach	Length * Breadth	0.0442	0.2362	0.8517

Table 3.30. Coefficients, standard errors, and *p*-values for GLMs of germination, length, breadth, and length * breath (‘shape’) as predictor, by year and population (2002).

YEAR	POPULATION	PARAMETER	ESTIMATE	STD ERROR	PROB CHI SQ
2002	Cabbage Garden East	Length	1.1202	1.7319	0.5178
2002	Cabbage Garden East	Breadth	1.1791	2.3044	0.4557
2002	Cabbage Garden East	Length * Breadth	-0.2133	0.3364	0.5259
2002	Cabbage Garden West	Length	-2.3093	2.4947	0.3546
2002	Cabbage Garden West	Breadth	-2.1850	3.3027	0.5082
2002	Cabbage Garden West	Length * Breadth	0.3192	0.4391	0.4672
2002	Cane Patch	Length	1.2323	0.8088	0.1276
2002	Cane Patch	Breadth	2.0362	1.1896	0.0869
2002	Cane Patch	Length * Breadth	-0.2138	0.1326	0.1069
2002	Gator Hole South	Length	0.6448	1.4357	0.6534
2002	Gator Hole	Breadth	0.8166	1.9438	0.6744
2002	Gator Hole	Length * Breadth	-0.1025	0.2615	0.6950
2002	Hog Pond	Length	0.6354	1.4527	0.6618
2002	Hog Pond	Breadth	0.9886	1.9529	0.6217
2002	Hog Pond	Length * Breadth	-0.1318	0.2785	0.6359
2002	Hog Pond West	Length	-0.7006	1.7063	0.6814
2002	Hog Pond West	Breadth	-1.5704	2.4775	0.5262
2002	Hog Pond West	Length * Breadth	0.1530	0.3212	0.6339
2002	Jesup	Length	-2.3460	0.8328	0.0048
2002	Jesup	Breadth	-2.7959	1.1588	0.0158
2002	Jesup	Length * Breadth	0.3919	0.1400	0.0051
2002	Middle Beach	Length	-1.3745	0.6932	0.0474
2002	Middle Beach	Breadth	-1.0439	0.9817	0.2867
2002	Middle Beach	Length * Breadth	0.1663	0.1102	0.1313
2002	Mule Run Road	Length	-0.3563	0.7287	0.6248
2002	Mule Run Road	Breadth	-0.5125	0.9845	0.6026
2002	Mule Run Road	Length * Breadth	0.0662	0.1327	0.6182
2002	North Bradley Beach	Length	0.4986	1.0349	0.6300
2002	North Bradley Beach	Breadth	0.5109	0.8926	0.5671
2002	North Bradley Beach	Length * Breadth	-0.0998	0.1608	0.5350
2002	North Central	Length	0.3876	0.8700	0.6559
2002	North Central	Breadth	0.7891	1.2344	0.5227
2002	North Central	Length * Breadth	-0.1197	0.1610	0.4571
2002	Pine Barren Road	Length	-0.8861	0.9351	0.3434
2002	Pine Barren Road	Breadth	-0.9198	1.5305	0.5478
2002	Pine Barren Road	Length * Breadth	0.1401	0.1953	0.4729
2002	Savannah NWR	Length	-2.4823	1.3080	0.0577
2002	Savannah NWR	Breadth	-3.9674	1.8013	0.0276
2002	Savannah NWR	Length * Breadth	0.5050	0.2505	0.0438
2002	South Bradley Beach	Length	-1.8303	1.2550	0.1447
2002	South Bradley Beach	Breadth	-2.4500	1.7240	0.1553
2002	South Bradley Beach	Length * Breadth	0.3306	0.2317	0.1537
2002	South End Beach	Length	1.2124	1.8083	0.5026
2002	South End Beach	Breadth	1.3328	2.4464	0.5859
2002	South End Beach	Length * Breadth	-0.1965	0.3077	0.5231
2002	Wassaw	Length	-0.3945	0.5530	0.4755
2002	Wassaw	Breadth	-0.7036	0.9149	0.4419
2002	Wassaw	Length * Breadth	0.0445	0.1148	0.6985

Table 3.31. Coefficients, standard errors, and *p*-values for GLMs of germination, length, breadth, and length * breath (‘shape’) as predictor, by year and population (2003).

YEAR	POPULATION	PARAMETER	ESTIMATE	STD ERROR	PROB CHI SQ
2003	Cabbage Garden East	Length	-3.1444	2.1571	0.1449
2003	Cabbage Garden East	Breadth	-3.8024	2.9332	0.1949
2003	Cabbage Garden East	Length * Breadth	0.6184	0.4260	0.1466
2003	Cabbage Garden West	Length	-3.8061	3.5140	0.2788
2003	Cabbage Garden West	Breadth	-4.2804	4.6860	0.3610
2003	Cabbage Garden West	Length * Breadth	0.6033	0.6184	0.3293
2003	Cane Patch	Length	0.6216	0.7929	0.4331
2003	Cane Patch	Breadth	1.0991	1.1594	0.3431
2003	Cane Patch	Length * Breadth	-0.1098	0.1276	0.3892
2003	Gator Hole South	Length	0.8075	1.3499	0.5497
2003	Gator Hole	Breadth	1.2069	1.7470	0.4897
2003	Gator Hole	Length * Breadth	-0.1556	0.2462	0.5273
2003	Hog Pond	Length	-0.4430	1.5399	0.7736
2003	Hog Pond	Breadth	-0.1015	2.1885	0.9630
2003	Hog Pond	Length * Breadth	0.0564	0.2963	0.8489
2003	Hog Pond West	Length	3.6511	1.8912	0.0535
2003	Hog Pond West	Breadth	3.8071	2.5444	0.1346
2003	Hog Pond West	Length * Breadth	-0.5761	0.3390	0.0893
2003	Jesup	Length	0.3004	1.0643	0.7777
2003	Jesup	Breadth	0.6878	1.6968	0.6852
2003	Jesup	Length * Breadth	-0.0720	0.1805	0.6899
2003	Middle Beach	Length	0.2717	0.7756	0.7261
2003	Middle Beach	Breadth	0.3703	0.9930	0.7092
2003	Middle Beach	Length * Breadth	-0.0365	0.1113	0.7427
2003	Mule Run Road	Length	0.2432	1.6619	0.8836
2003	Mule Run Road	Breadth	0.3349	2.3729	0.8878
2003	Mule Run Road	Length * Breadth	-0.0469	0.3164	0.8823
2003	North Bradley Beach	Length	-1.7582	2.5385	0.4885
2003	North Bradley Beach	Breadth	-1.9609	3.3466	0.5579
2003	North Bradley Beach	Length * Breadth	0.2646	0.4351	0.5431
2003	North Central	Length	0.6263	1.2753	0.6234
2003	North Central	Breadth	-0.4297	1.5257	0.7782
2003	North Central	Length * Breadth	0.1116	0.2318	0.6302
2003	Pine Barren Road	Length	-0.5069	1.2132	0.6761
2003	Pine Barren Road	Breadth	-1.8154	1.8476	0.3258
2003	Pine Barren Road	Length * Breadth	0.1351	0.2423	0.5770
2003	Savannah NWR	Length	3.4735	2.2406	0.1211
2003	Savannah NWR	Breadth	5.5342	2.8357	0.0510
2003	Savannah NWR	Length * Breadth	-0.7250	0.3987	0.0690
2003	South Bradley Beach	Length	-0.5742	1.7804	0.7471
2003	South Bradley Beach	Breadth	-0.0060	2.5120	0.9981
2003	South Bradley Beach	Length * Breadth	0.0640	0.3339	0.8480
2003	South End Beach	Length	-2.0017	0.6166	0.0012
2003	South End Beach	Breadth	-2.6315	0.8785	0.0027
2003	South End Beach	Length * Breadth	0.3080	0.1037	0.0030
2003	Wassaw	Length	2.6772	2.2098	0.2257
2003	Wassaw	Breadth	4.2864	3.1308	0.1710
2003	Wassaw	Length * Breadth	-0.5274	0.3952	0.1821

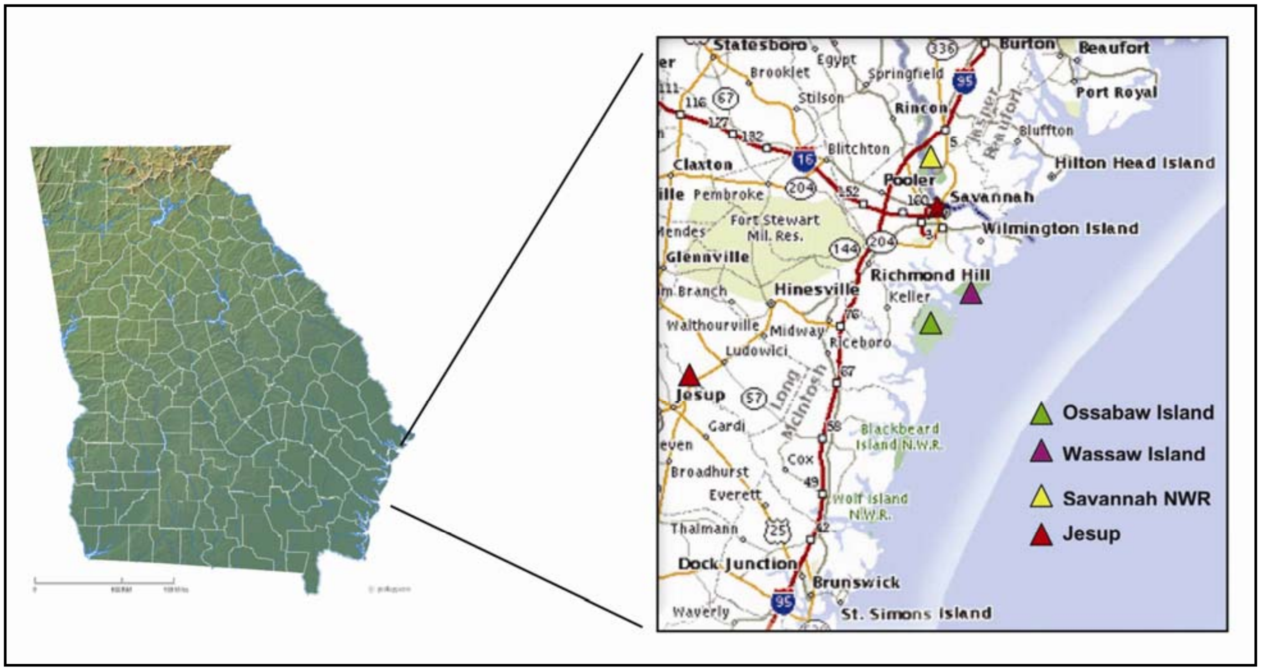

Figure 3.1. Locations of study sites in southern coastal Georgia. Ossabaw Island contained 13 populations, whereas Wassaw Island, Savannah NWR, and Jesup each contained a single population, for a total of n=16 populations.

Figure 3.2. Field technicians assist in the challenging task of collecting *S. sebiferum* seeds from designated parent trees using a 14’ pole pruner.