

INVASION OF CHINESE TALLOW (*Sapium sebiferum*): A TEST OF DISPERSAL
AND RECRUITMENT LIMITATION IN MULTIPLE HABITATS

By

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Abstract of Thesis Presented to the Graduate School
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Biotic invasions are a leading threat to native flora and fauna throughout the world. Invasive exotic plants are especially widespread, and many benefit from mutualistic relationships with native fauna that help disseminate their pollen and seeds. Chinese tallow (*Sapium sebiferum*) is an exotic species in the southeastern USA that is readily dispersed by birds, and invades a wide diversity of habitats. However, it is absent in north Florida from several forest habitats that have been invaded elsewhere in its non-native range. I investigated seed dispersal, postdispersal seed predation, germination, and seedling establishment to identify barriers to recruitment in mixed pine-hardwood and oak hammock forest at a north Florida site where *S. sebiferum* is absent. The same data were collected in adjacent shaded and open wet prairie habitats, where *S. sebiferum* is invading. Twenty-one bird species dispersed seeds away from parent trees, and birds often flew into forest habitats after foraging in *S. sebiferum* trees. These species were frequently detected on point counts within the forest habitats. Together,

these results suggest that dispersal limitation is not responsible for the failure of this species to invade the forest habitats at my site. Likewise, postdispersal seed predation cannot explain the failure of *S. sebiferum* to invade the forest habitats, because predation was significantly higher in the prairie habitats. Germination, however, was nearly absent in the forest, but readily occurred in the prairie; replication of the germination experiment in a shade-house produced the same results. Thus, germination is a barrier to establishment in mixed pine-hardwood and oak hammock forests, likely due to a thick litter layer on the forest floor.

CHAPTER 1
GERMINATION OF CHINESE TALLOW (*Sapium sebiferum*): THE EFFECTS OF
HABITAT AND DISPERSAL METHOD ON ESTABLISHMENT

Introduction

Biotic invasions have received considerable attention from ecologists working in both applied and theoretical contexts. From an applied perspective, invasive exotic species are second only to habitat loss and degradation as a threat to native species (Wilcove et al. 1998), and are estimated to cause as much as \$138 billion in annual damages within the United States alone (Pimentel et al. 2000). From a theoretical perspective, the impact of invasions tests our understanding of community assembly rules, rates of dispersal, and competition (Parker et al. 1999, Mack et al. 2000).

Plants represent one of the most abundant and well-studied groups of invasive exotics, partly due to the intentional introduction of many plant species for use as food and ornamentals (Reichard and White 2001, Mack and Erneberg 2002). Numerous studies have sought to identify the most important factors that promote or prevent plant invasions. These include native-species diversity (Elton 1958, Levine and D'Antonio 1999, Naeem et al. 2000, Kennedy et al. 2002), disturbance (Burke and Grime 1996, D'Antonio et al. 1999, Jesson et al. 2000), and a lack of natural herbivory (Keane and Crawley 2002). In addition, many studies have attempted to identify a unified suite of attributes that invaders possess. This approach has resulted in limited predictive power (Mack et al. 2000), because successful invasion may often depend more on the condition of the community being invaded than on particular traits of the invader (Myers 1983,

Ewel 1986). Even so, general knowledge of a species' invasive potential and community invasibility may still not give us the power to predict which plant species are most likely to invade particular communities (Crawley 1987, Williamson 1996, Lonsdale 1999).

When populations of invasive plants lie adjacent to communities that have not been invaded, either propagules are failing to arrive, or those that do arrive are limited by inappropriate biotic or abiotic environments. These mechanisms (termed dissemination and establishment limitation respectively) are not mutually exclusive, and both may simultaneously limit plant recruitment (Schupp et al. 2002). Successful identification of the stage/s that limit recruitment must therefore consider both dispersal and postdispersal processes, since the relative importance of any one stage may be reduced or enhanced by another (Jordano and Herrera 1995, Nathan and Muller-Landau 2000). This approach can be used to identify habitats that are at most risk of being invaded, and to identify stages in an exotic species' life cycle that are most susceptible to management and control.

I used this approach to ask why an invasive tree, Chinese tallow (*Sapium sebiferum* (L.) Roxb.), Euphorbiaceae (hereafter *Sapium*) is failing to establish in forest habitats that have been invaded elsewhere in its non-native range. In coastal South Carolina, *Sapium* has successfully invaded mixed pine-hardwood and other upland forest habitats (Renne 2001, Renne et al. 2001). In north central Florida, however, it is conspicuously absent from these habitats, even though it is widespread in many other habitats that are often adjacent to forests. An investigation of each stage in the recruitment process revealed that germination is the principal stage preventing establishment of *Sapium* in these habitats at a Florida field site (Samuels, unpublished), and litter and duff on the forest

floor may be responsible. Thus, it was important to ask what factors influence this process, and how they vary among habitats. Here I focus on germination and the related process of seedling establishment in both prairie (invaded) and forest (noninvaded) habitats to address the following questions: (1) how does seed treatment (acid-treated to simulate gut passage, and water-soaked to simulate water dispersal) affect germination patterns in prairie sites; (2) how does the presence of litter affect germination in forest and prairie habitats; (3) how does herbivory influence seedling establishment and survivorship in the prairie habitats; and (4) does litter vary from a South Carolina forest site where *Sapium* readily invades, to a Florida forest site where it is absent?

Methods

Study Species

Chinese tallow tree (*Sapium sebiferum*) is native to eastern Asia, where it has been cultivated for approximately 14 centuries to supply soaps, waxes, fuels, dyes, and protein meal (Scheld et al. 1984, Jones and McLeod 1989, Jubinsky and Anderson 1996, Bruce et al. 1997). It has been established in the United States for over 200 years, and has become an invasive species of concern through much of the southeast (Jubinsky and Anderson 1996, Bruce et al. 1997). It is especially invasive in the coastal prairies of Texas, where it has formed monospecific woodlands in areas that were formerly treeless (Bruce 1993, Bruce et al. 1995, Barrilleaux and Grace 2000).

In Florida, *Sapium* flowers from March to May. Flowers occur on a spike-like thyrses, and are insect pollinated (Nijjer et al. 2002). The fruits are three-lobed capsules that dehisce from September to November. The white aril that covers the seeds is the source of the name “tallow,” providing a rich source of food for birds. While many species of birds have been observed feeding at *Sapium* trees, their quality as seed

dispersers varies depending on seed-handling behavior (Renne et al. 2000, Conway et al. 2002a, Renne et al. 2002). There is also evidence that seeds are dispersed by water (Bruce et al. 1997), since the waxy aril aids in flotation. Large *Sapium* trees may produce nearly 100,000 seeds in a season (Renne et al. 2000), with a mean mass of $0.121 \text{ g} \pm 0.002 \text{ SE}$ ($N = 100$; without aril). Germination occurs in a wide variety of habitats (Renne et al. 2001), although *Sapium* seeds may require some soaking to achieve maximum germination success (Conway et al. 2000). Exposure to cold temperatures or fluctuating temperatures may increase germination success (Cameron et al. 2000, Nijjer et al. 2002). *Sapium* seedlings are tolerant of a wide range of environmental conditions, including moderate flooding (Jones and Sharitz 1990) and heavy shade (Jones and McLeod 1989). Seedlings appear to be moderately tolerant of soil salinity, which helps explain the species' success in environments prone to coastal flooding (Conner 1994). However, elevated soil salinity may result in deleterious effects (Barrilleaux and Grace 2000). Finally, despite the dominance of *Sapium* in many of the habitats where it has invaded, there is little evidence this success is due to allelopathic effects (Keay et al. 2000, Conway et al. 2002b).

Study Site

I worked at two sites separated by 2 km, both within Paynes Prairie Preserve State Park (Figure 1-1), an 8500 ha natural area in Alachua County, Florida (29° 36' N, 82° 20' W, 25 m). The mean air temperature ranges from 13°C in January to 27°C in August. Mean annual precipitation is 1370 mm, with the wettest months in June through September. The preserve contains many biological communities, with basin marsh representing the largest and most extensive (FDEP 2001). *Sapium* has successfully invaded some areas of basin marsh, but suffers high mortality in areas where flooding

persists for long periods of time (J. Weimer, pers. comm.). It is most abundant in the wet prairie community that lies between the basin marsh and adjacent forests that rim the prairie.

This study was conducted in four habitats within the preserve: two where *Sapium* is currently invading (shaded wet prairie and open wet prairie); and two adjacent habitats where it is absent, but has been found elsewhere in its non-native range (mixed pine-hardwood and oak hammock). The two invaded prairie habitats are similar in vegetative composition, but differ in structural complexity. Open wet prairie is dominated by a thick understory of sand blackberry (*Rubus cuneifolius*) and saltbush (*Baccharis halimifolia*), with a canopy that rarely exceeds 2 m. Scattered clumps of persimmon (*Diospyros virginiana*) and *Sapium* represent the only large trees. The shaded wet prairie also has a thick understory composed mostly of saltbush (*Baccharis halimifolia*), dog fennel (*Eupatorium capillifolium*), elderberry (*Sambucus canadensis*), and winged sumac (*Rhus copallina*); but has a tree canopy that ranges from 5-10 m. Dominant trees include persimmon (*Diospyros virginiana*), sweetgum (*Liquidambar styraciflus*), and *Sapium*. These two habitats freely grade into each other via a “soft edge,” and are best separated by canopy height. Dominant soils of the prairie habitats include Wauberg Sand (a poorly drained loamy siliceous soil) and Shenks Muck (a poorly drained clayey montmorillonitic soil; Thomas et al. 1985).

Study sites where *Sapium* is absent were mixed pine-hardwood and oak hammock. These habitats freely grade into each other, yet form an abrupt “hard edge” with the adjacent prairie habitats. Mixed pine-hardwood is dominated by loblolly pine (*Pinus taeda*), live oak (*Quercus virginiana*), and sweetgum (*Liquidambar styraciflus*), with

scattered water oaks (*Quercus nigra*) in the understory. The oak hammock is more diverse than the mixed pine-hardwood, but is dominated only by live oak (*Quercus virginiana*). Other common tree species include laurel oak (*Quercus laurifolia*), water oak (*Quercus nigra*), sugarberry (*Celtis laevigata*), southern magnolia (*Magnolia grandiflora*), and American holly (*Ilex opaca*). Yaupon holly (*Ilex vomitoria*) and *Vitis* sp. are common in the understory. Dominant soils of the two forest habitats include Myakka Sand and Newnan Sand, both somewhat poorly drained sandy siliceous soils (Thomas et al. 1985).

In 2003, the density of *Sapium* > 3 cm dbh was 465 plants/ha in the prairie habitats, versus 0 plants/ha in the forest habitats (15 points/habitat; point-quarter method, Brower et al. 1990). *Sapium* is present in the prairie habitats up to the edge of the forest habitats, including the narrow ecotone that divides prairie from forest.

Seed Collection and Treatment

In December 2002, I collected approximately 2500 *Sapium* seeds from 12 different trees, eight of which grew in open wet prairie and four in shaded wet prairie. I attempted to collect seeds from a diversity of positions on each tree, since maternal investment may vary with position, which can affect germination patterns (Baskin and Baskin 1998). Seeds were brought to the laboratory and treated the same day of collection in two ways, hereafter referred to as acid-treated and water-soaked seeds. These treatments reflect the two ways that *Sapium* seeds may be dispersed. Acid-treated seeds mimic those that are ingested by birds and may arrive in all four habitats via avian dispersal. In contrast, water-soaked seeds mimic those dropped by birds or that fall from trees in the prairie habitats, where flooding periodically occurs and water dispersal is possible. Therefore, use of water-soaked seeds is restricted to germination experiments in the prairie sites.

Approximately 1600 (66%) of the collected seeds were acid-treated. These seeds were initially soaked in water for five hours to loosen the waxy aril that covers the seed, followed by 20 minutes of soaking in pH 2.0 HCL. This approximates the hydrogen ion concentration in the gizzard of a bird, where the lowest pH is expected (Sturkie 1976). The aril was then removed by agitating seeds between two layers of aluminum screening, applying enough pressure to ensure removal of the aril, but not enough to damage the seed coat. Acid-treated seeds were returned to the field and stored under cages (to prevent predation) in each of the four respective habitats until the germination experiment was initiated. This ensured that seeds were subjected to conditions of natural cold-stratification. No seeds germinated during storage.

The remaining 33% of the seeds were water-soaked with the aril intact in an eight-gallon bucket for one month between December and January. The bucket was kept outside in the shade during the entire soaking period to ensure that seeds would be subjected to natural temperature fluctuations, and water was changed once after two weeks of soaking. Most of the seeds floated when initially placed in the water, but gradually began to sink when the aril became saturated.

Field Germination Experiment

I conducted field germination experiments to evaluate the combined effects of habitat and seed treatment on germination. In January 2003, I selected 48 sites, 12 in each of the four habitats (open wet prairie, shaded wet prairie, oak hammock, and mixed pine-hardwood). Sites were located at 30 m intervals along two transects in oak hammock and open wet prairie, and three transects in mixed pine-hardwood and shaded wet prairie. I used existing trails to access sites, but placed seeds at least 30 m from the

nearest trail. Vegetation structure prevented me from placing transects in random locations.

Acid-treated seeds were removed from field storage cages and at each site, 16 seeds were placed on the ground in four groups of four, each group placed one meter from a center point in each of the four cardinal directions ($n = 192$ seeds/habitat). Four is a typical number of seeds in a bird defecation (I. Renne, pers. comm.). Seeds were placed on the surface of the soil (or leaf litter when present) to mimic the state of a recently dispersed seed. To prevent the loss of seeds from mammalian seed predators, I initially covered each group of four seeds with a cage (8x8x6 cm) made from 0.25 inch (23 gauge) galvanized wire mesh.

After one month, water-soaked seeds were removed from the bucket and immediately placed in the field to evaluate germination. Water-soaked seeds were placed at the same sites as the acid-treated seeds in the shaded and open wet prairie habitats. Acid-treated and water-soaked seeds were placed side by side under separate cages. Seeds were checked once per week starting in January 2003, and ending when germination had ceased (i.e., when the cumulative percent germination curve had reached a plateau). Germination was defined as a split seed coat and/or emergence of the radicle.

Shade-house Germination Experiment

Both the acid-treated and water-soaked experiments were replicated in a shade-house to provide greater consistency with respect to watering regime and light environment. The shade-house had a 240 X 120 cm base with 60 cm between the germination platform and the top. The top was covered with 62-70% shade-cloth to prevent direct exposure to the sun and to better simulate the shaded environment where most seedlings naturally occur. In addition, clear plastic was placed over the shade-cloth

to prevent natural precipitation from reaching the seeds. The shade house was located on the roof of Carr Hall, University of Florida (29° 38.626' N, 82° 20.694' W).

In December 2002, soil was collected from the upper 10 cm of the soil surface in each of the four habitats. In addition, litter and duff were collected from the two forest habitats. In the laboratory, soil from each habitat was thoroughly mixed, and randomly allocated to 100 mL cell packs with perforated bases. For the two forest habitat treatments, small amounts of litter and duff were applied to the surface of the soil in an attempt to simulate the presence of this vegetative material on the forest floor. Most experimental sites in the prairie were characterized by exposed soil and only a thin layer of leaf litter. Thus, no attempt was made to recreate the presence of litter on prairie soils in the shade-house. I placed four seeds/cell on the surface of the soil ($n = 144$ seeds/habitat-soil type), and cut holes in the potting trays onto which cell packs were placed to allow drainage. Cells were watered to saturation every 5 days from December through March, and every 4 days from April until May 20, 2003 when additional germination was no longer detected and the experiment was terminated. Potting trays were randomly shifted each time they were watered to control for placement effects. Seeds were checked for signs of germination every four days, and germinated seeds were marked with color-coded toothpicks to identify the date of germination.

Seedling Establishment

The fate of germinated seeds was followed to evaluate the effect of habitat on seedling establishment. In the field germination experiment, wire cages were removed only when a *Sapium* seedling was about to touch the top of the cage (6 cm tall). The position of the established seedling was then marked, and the remaining seeds were moved and re-caged approximately 0.25 m from the original site so their fate could be

monitored for the remainder of the germination experiment. This process was repeated for all seeds that germinated and established. After the germination experiment was terminated in May 2003, the heights of surviving seedlings were measured every 10 days, and the relative degree of herbivory (minor, moderate, heavy) was noted to explore habitat specific differences in the cause and extent of seedling mortality. All remaining seedlings were pulled from the ground and destroyed at the end of August 2003.

In the shade-house, established seedlings were pulled when they reached 10 cm height. Seedlings were dried overnight at 60°C and above ground dry mass weighed to 0.001 g. I did not measure below-ground biomass because the roots of some seedlings broke during extraction. This experiment was terminated on May 20, 2003, at which time seedlings were showing signs of physical stress. Seedlings that had not reached 10 cm by this date were not used in subsequent analyses.

Effects of Forest Litter

Because litter and duff on the forest floor appeared to affect germination success, I compared this attribute at Paynes Prairie to the Hobcaw Forest in South Carolina where *Sapinum* has invaded forest habitats. The 3077 ha Hobcaw Forest (33° 20'N, 79° 15' W) is located on the outer coastal plain in Georgetown County, South Carolina. Mean annual precipitation is 1315 mm, and mean air temperature ranges from 9°C in January to 27°C in August. The Hobcaw Forest contains a variety of habitats that are similar to those found at Paynes Prairie, although it lacks the large basin marsh. In contrast to Paynes Prairie, however, *Sapinum* has successfully invaded mixed pine-hardwood, loblolly pine forest, and other oak dominated forests at the Hobcaw site.

In August 2003, I randomly placed ten 30 m transects in mixed pine-hardwood forest at the Hobcaw field site. This procedure was repeated in September 2003 in mixed

pine-hardwood at Paynes Prairie. I did not assess litter in oak hammocks, since a comparable forest type was not adequately represented at the Hobcaw site. Litter depth was measured at 3 m intervals along each transect by inserting a thin wooden rod through the litter until it stopped at the soil surface. At the mid-point of each transect, I placed a 0.25 m² quadrat on the ground, and collected all of the litter within the square. Litter was dried at 60°C and weighed to 0.01 g.

Statistical Analyses

Because very few seeds germinated in the oak hammock and mixed pine-hardwood habitats, germination results did not meet parametric assumptions of normality and equal variance. Therefore, germination success for both the field and shade house experiments was compared among treatments with a Kruskal-Wallis test, where the response variable was the proportion of seeds that germinated per site (field) or per cell (shade-house). I used the Nemenyi test, a Tukey-type multiple comparison procedure, to detect significant differences among treatments (Zar 1999). Germination rate, the cumulative number of seeds that germinated over time, was compared among treatments for the shade-house experiment with a 2-sample Kolmogorov-Smirnov test. Germination rate was not determined in the field since some seeds could not be located until the experiment was terminated, and for them, it was impossible to determine when the seed coat had split. The mass of dried seedlings from the shade-house was compared using 1-way ANOVA. For the comparison of litter depth and mass between Paynes Prairie and the Hobcaw Forest, I used a one-sided t-test. This was based on the *a priori* expectation that litter depth at Paynes Prairie was greater, because germination occurred on Paynes Prairie forest soils in the absence of litter (Samuels, unpublished). Thus, I was testing the prediction that less litter was present at the Hobcaw Forest site. All analyses were

calculated using SPSS 10.0 (SPSS Inc., Chicago, IL) and Minitab 12.0 (Minitab Inc., State College, PA), and means are reported \pm SE, with $\alpha = 0.05$.

Results

Field Germination

Seeds placed in the field in December began to germinate at the end of February 2003, and germination peaked in March. Germination success in the field varied widely among the four habitats and between the two seed treatments (Figure 1-2A). Within each prairie habitat, germination success of water soaked seeds was significantly higher than acid treated seeds ($H = 53.79$, $df = 5$, $P < 0.001$), but water soaked treatments did not differ significantly between the two prairie habitats. Only one seed germinated in mixed pine-hardwood (MPH), while no seeds germinated in oak hammock (OH). Mean germination success for acid treated seeds was higher in shaded wet prairie (SWP) than open wet prairie (OWP), $\bar{x} = 0.19 \pm 0.04$ versus 0.10 ± 0.05 respectively, but OWP did not differ significantly from OH, MPH, or SWP (Figure 1-2A).

Shade-house Germination

As with the field experiment, seeds began to germinate in the shade-house in late February 2003, peaking in March. The pattern of germination success was very similar to that observed in the field (Figure 1-2B). The mean proportion of acid treated seeds that germinated on OWP soil was comparable to that for SWP ($\bar{x} = 0.14 \pm 0.03$ and 0.18 ± 0.04 , respectively). Acid-treated seeds in OH and MPH showed significantly lower germination than did acid-treated seeds in OWP and SWP, which in turn had lower germination than the water soaked seeds placed on the two prairie soils ($H = 94.15$, $df = 5$, $P < 0.001$). Two seeds germinated in OH, and only one in MPH.

On the prairie substrates, germination rate was primarily affected by seed treatment, but water-soaked seeds were also affected by soil substrate. Water-soaked seeds showed a burst of germination in late February, approximately 65 days after sowing (Figure 1-3). However, the rate of germination for water-soaked seeds in SWP was still significantly higher than that for water-soaked seeds in OWP ($Z = 1.945$, $n = 118$, $P = 0.001$). The difference in germination rate between acid-treated seeds for the two prairie soils was not significantly different ($Z = 1.237$, $n = 46$, $P = 0.094$).

Seedling Establishment

Of those seeds that successfully germinated ($n = 213$ in field, 168 in shade-house), a significantly larger proportion established in the shade-house than in the field ($H = 11.26$, $df = 3$, $P = 0.01$; Figure 1-4). A total of 25 seedlings (11.7%) initially established in the field (7 in OWP and 18 in SWP) compared to 69 seedlings (41.1%) in the shade-house (29 in OWP, 38 in SWP, 1 in OH, and 1 in MPH). Of the 213 seeds that germinated in the field, 53% were predated by fire ants (*Solenopsis invicta*), while most of the remaining seeds that germinated but did not establish appeared to die from desiccation. Of those that established as seedlings in the field, 15 were still alive by the end of May 2003. Mean seedling height was 12.2 ± 1.3 cm, and most showed some signs of herbivory. By the end of August only five were still alive. The fate of most of the seedlings was either attributed to herbivory (60%), or unknown causes (40%). Seedling death was attributed to herbivory when heavy leaf damage was noted on one visit, and the bare, leaf-less stem of the seedling was found on a subsequent visit. In the shade-house, seedlings reached 10 cm (and were pulled) in as little as 20 days. Only four seedlings died between the date of first establishment and termination of the experiment. The cause of death was unknown, although herbivory was absent within the shade-house.

Mean above ground dried mass of 10 cm seedlings ($\bar{x} = 0.086 \pm 0.004$ g) did not differ among the two prairie soils for either acid-treated or water-soaked seeds ($F_{3,40} = 1.25$, $P = 0.304$).

Effects of Forest Litter

Litter at both sites (Hobcaw Forest and Paynes Prairie) was dominated by pine needles. As expected, there was a significant correlation between litter depth and mass ($F_{1,18} = 23.99$, $r^2 = 0.57$, $P < 0.001$; linear regression). Mean litter depth at the Hobcaw Forest was significantly less than Paynes Prairie (2.17 ± 0.30 cm versus 3.17 ± 0.40 cm; $t = -2.10$, $df = 18$, $P = 0.03$).

Discussion

The high germination success of water-soaked seeds cannot explain the significant difference among acid-treated seeds sown in the prairie versus forest habitats. In both the field and the shade-house, there was virtually no germination for the oak hammock or mixed-pine hardwood sites, suggesting that germination is the leading barrier to establishment in these habitats where *Sapium* is currently absent. Lack of germination alone cannot explain the failure of *Sapium* to invade the forest habitats because of the independence among stages in the recruitment process, and the outcome of one process obscuring or enhancing the effects of another (Jordano and Herrera 1995). However, in a parallel study at the same time and site (Samuels, unpublished) I quantified both dispersal and seed-predation and the results indicate that germination is the process most responsible for preventing initial establishment in oak hammock and mixed pine-hardwood.

Germination Experiments

The great similarity between field and shade-house results demonstrates both the success of the shade-house in mimicking field conditions, and the important effects of litter and seed treatment on germination when watering regime and light conditions were held constant. Seeds were placed on the surface in all treatments to mimic the state of seeds that had recently been dispersed by a bird or (in the case of water-soaked seeds) had recently arrived via water dispersal. The 15% germination success of acid-treated seeds in the two prairie habitats (field and shade-house) was comparable to the 20% observed by Renne et al. (2001) for bird-defecated seeds placed on the surface of vermiculite in a greenhouse environment. Several studies have evaluated germination only for buried *Sapium* seeds, and often without any attempt to mimic avian gut passage. Burial of untreated *Sapium* seeds resulted in germination success of $52.4 \pm 5.9\%$ (Cameron et al. 2000), but seeds in this study were stored for six years prior to sowing. Less than 20% germination success was observed by Bruce (1993) in grassland and *Sapium* woodland for seeds that were untreated and placed on the soil surface. However, the combined effect of avian gut passage and seed burial may increase germination success to as much as 80% (Renne et al. 2001), with acid-treated seeds showing similar emergence patterns to defecated seeds.

While germination success might have been improved through seed burial, burial is not likely immediately following bird dispersal. In the prairie habitats, however, water may provide an alternative means of dispersal after heavy rains, and germination success of water-soaked seeds greatly exceeded that of acid-treated seeds both in the field and the shade-house. Conway et al. (2000) soaked *Sapium* seeds in water (for 6, 20, 48, and 72 hours) and found germination success to be much lower than water-soaked seeds in my

study. Most of their results (which combined the effect of soaking duration with chilling) showed a mean germination success of only 3.33%. The great difference with the present study is likely due to soaking duration (30 days verses 3 days maximum), and the germination environment used by Conway et al. (2000), which involved petri dishes as the germination substrate that were then placed in a germination chamber.

Water dispersal for *Sapium* is mentioned in the literature (Bruce et al. 1997), but has not been rigorously examined. Hydrochory may be the optimal mode of dispersal in seasonally flooded habitats, while ornithochory still ensures that *Sapium* seeds can arrive in habitats where water dispersal is not possible. The maintenance of such different dispersal mechanisms likely diversifies the range of dispersal distances (Williamson and Costa 2000). Thus, water appears to play a key role in the maintenance and spread of *Sapium* in the prairie habitats, while the absence of flooding in the forest reduces the chance of *Sapium* establishment. For seeds that do arrive in the forest, however, germination appears to be the leading barrier to recruitment.

The much higher germination success in prairie than forest habitats may be due to a thick layer of litter, which is dominated by leaves in oak hammock, and by pine needles in mixed pine-hardwood. Most of the seeds, which were placed on the surface of the litter, remained within or on top of a layer of vegetation that quickly dried after rainfall. Thus, seeds were rarely in a moist microenvironment long enough to promote imbibition. This conclusion is further supported by the observation that the only seed that germinated in the forest (mixed pine-hardwood) was located in a spot where water pooled after a heavy rain, and the seed became trapped among wet leaves. Furthermore, the only shade-house seeds that germinated for the two forest habitat treatments had dropped

below the layer of litter and duff applied to their cells, and were thus in contact with moist soil. Burial of seeds in moist forest soil probably would have increased germination success. An alternative explanation is that the forest habitats buffer against temperature fluctuations, since germination success of *Sapium* may increase with fluctuating temperatures (Nijjer et al. 2002). However, this mechanism seems unlikely since temperature fluctuations were consistent among treatments in the shade-house. Furthermore, germination did take place in the shade-house on soil collected from both oak hammock and mixed pine-hardwood, when no litter/duff was applied (Samuels, unpublished).

Seedling Establishment

The relationship between seed germination and seedling establishment was far from 1:1, especially in the field. Given that only 11.7% of germinated seeds successfully established in the field, equating germination with establishment would be misleading. The lower field establishment than in the shade house (41.1%) is best explained by (1) the foraging activity of fire ants (*Solenopsis invicta*), and (2) periodic dry conditions, both of which were absent in the shade-house.

Bisected seed coats initially revealed foraging activity by *S. invicta*. In contrast, mammalian predators leave splintered and haphazardly broken seed coats (Samuels, unpublished). Furthermore, seeds in the field germination experiment were protected from mammalian predators by cages. I later encountered *S. invicta* swarming recently germinated seeds and consuming the endosperm entirely. This observation is consistent with the foraging activity of *S. invicta* in many agricultural systems of the southeast USA (Morrison et al. 1997), where ant activity can also result in reduced seedling vigor, damage to cotyledons, and an increase in malformed seedlings (Shatters and

Vander Meer 2000). Ready and Vinson (1995) found that small seeds are moved and damaged more often than large seeds by *S. invicta*, and that the seed coat may protect some seeds from attack. This is also consistent with my observation that ants were never seen associating with intact (ungerminated) seeds, which are too large for *S. invicta* to carry and too hard to penetrate.

During the field germination experiment (Jan-May), there was considerable variation in monthly precipitation; mean = 88.0 mm \pm 39.4. This resulted in days when some cages that protected seeds were subjected to moderate flooding, followed by shorter periods without rain when the ground was dry. Seeds placed on the soil surface are likely to be much more sensitive to such climatic fluctuations than buried seeds. Desiccation of germinated seeds appeared to be a common cause of mortality, second to ant predation. Overall, the placement of seeds on the surface is likely the main reason that establishment in the field was lower than that observed by Renne et al. (2001). In the shade-house (where I watered seeds every 4-5 days and ants were absent) it is less certain why establishment of germinated seeds was still < 50%.

Effects of Forest Litter

In seed introduction studies, recruitment following seed addition indicates the presence of a regeneration niche for that species, and may be a sign of dispersal limitation (i.e., seeds are failing to arrive at suitable microsites; Turnbull et al. 2000). The near absence of germination in the forest sites at Paynes Prairie combined with the observation that avian dispersers carried seeds to these sites (Samuels, unpublished) implicate postdispersal processes as the most likely barrier to establishment. At the Hobcaw Forest in South Carolina, mean litter depth was significantly less than at Paynes Prairie, and *Sapinum* readily established under a mixed pine-hardwood canopy. Seedlings of *Sapinum*

that had recently emerged from the litter were seen adjacent to transects at the Hobcaw site, as were larger saplings and adult plants. In contrast, no *Sapium* plants of any ages were encountered along transects in mixed pine-hardwood at Paynes Prairie.

The effects of litter on germination and establishment have received considerable attention, and the response is often mixed and species specific (Molofsky and Augspurger 1992, Facelli 1994, Hastwell and Facelli 2000, McAlpine and Drake 2003). Inhibition of germination and/or establishment by litter may be indirect through alteration of habitat for seed predators, or changes in exposure to solar radiation. Allelopathic effects due to litter leachates are also possible (Barritt and Facelli 2001). Deep litter may also result in seedling desiccation if seeds germinate without contact with soil (Fowler 1988). It is unknown which, if any, of these factors may play a role in preventing *Sapium* from establishing in oak hammock and mixed pine-hardwood at Paynes Prairie; establishment in these forest habitats was never evaluated because germination was negligible. In general, however, litter has a stronger overall effect on seed germination than seedling establishment, and litter-reducing disturbances may facilitate germination in some systems (Xiong and Nilsson 1999). One such disturbance that differs between Paynes Prairie and the Hobcaw Forest is fire.

Fire has been suppressed at the forest sites at Paynes Prairie for many years, in part due to a residential area that borders the park. In contrast, prescribed fire is regularly used at the Hobcaw Forest. This recurring disturbance reduces litter and duff every three to five years, which may open windows of opportunity for *Sapium* seeds to germinate. Fire may have direct effects through stimulation of germination via heating of the soil surface where seeds are present (Tyler 1995). Alternatively, indirect effects of fire may

induce germination by removing litter, and manual removal of litter has successfully imitated this disturbance in some studies (Lambert and Menges 1996, McConnell and Menges 2002). If fire were restored to the forest habitats of Paynes Prairie State Park, *Sapium* might be able to expand its distribution there.

In summary, my results show that seeds of *S. sebiferum* fail to germinate in oak hammock and mixed pine-hardwood at a north Florida field site. At the same time, *Sapium* may benefit from both bird-dispersal and water-dispersal in wet prairie habitats, where flooding occurs. The geographic extent of *Sapium* invasion in the southeast USA remains to be seen. In north Florida, however, postdispersal processes rather than dispersal limitation currently prevent *Sapium* from establishing in some forest habitats. Large-scale disturbances that can reduce litter may create windows of opportunity for *Sapium* to invade if other microsite conditions are suitable for establishment.

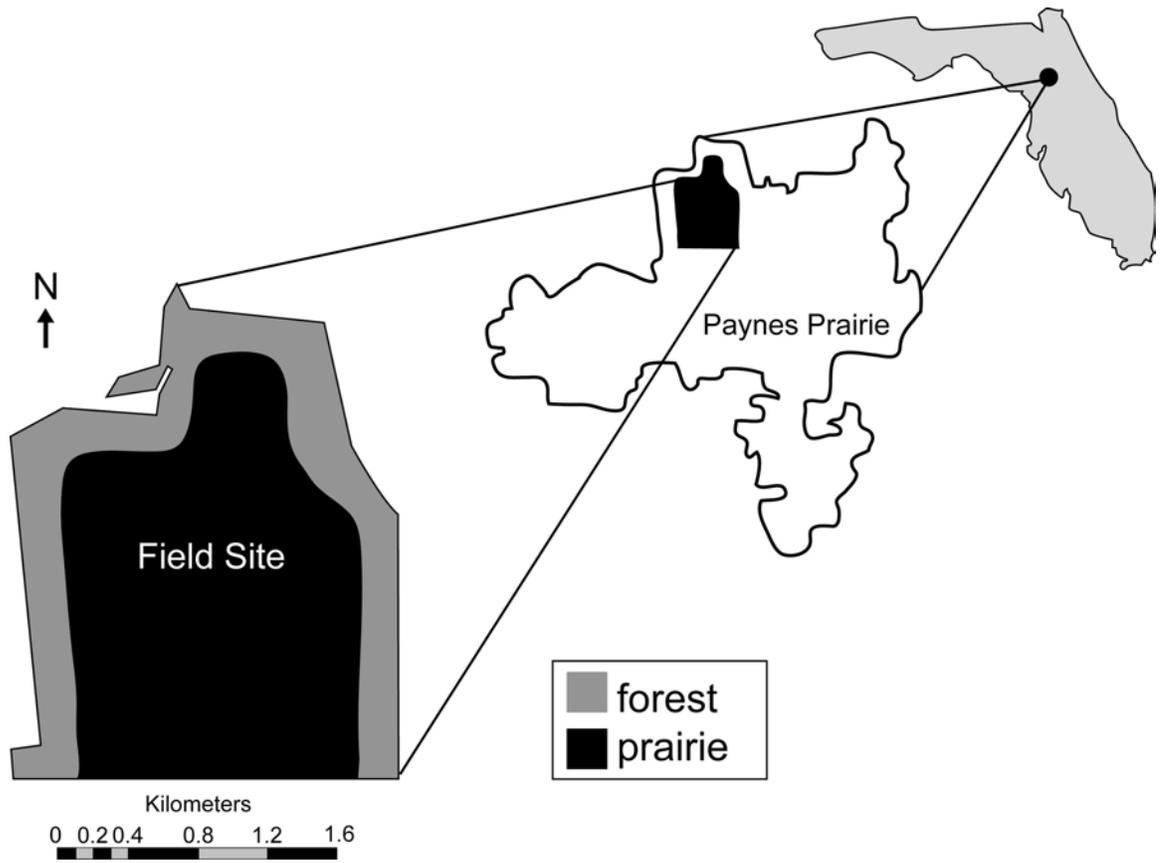


Figure 1-1. Map of the research field site at Paynes Prairie Preserve State Park, Alachua County, Florida.

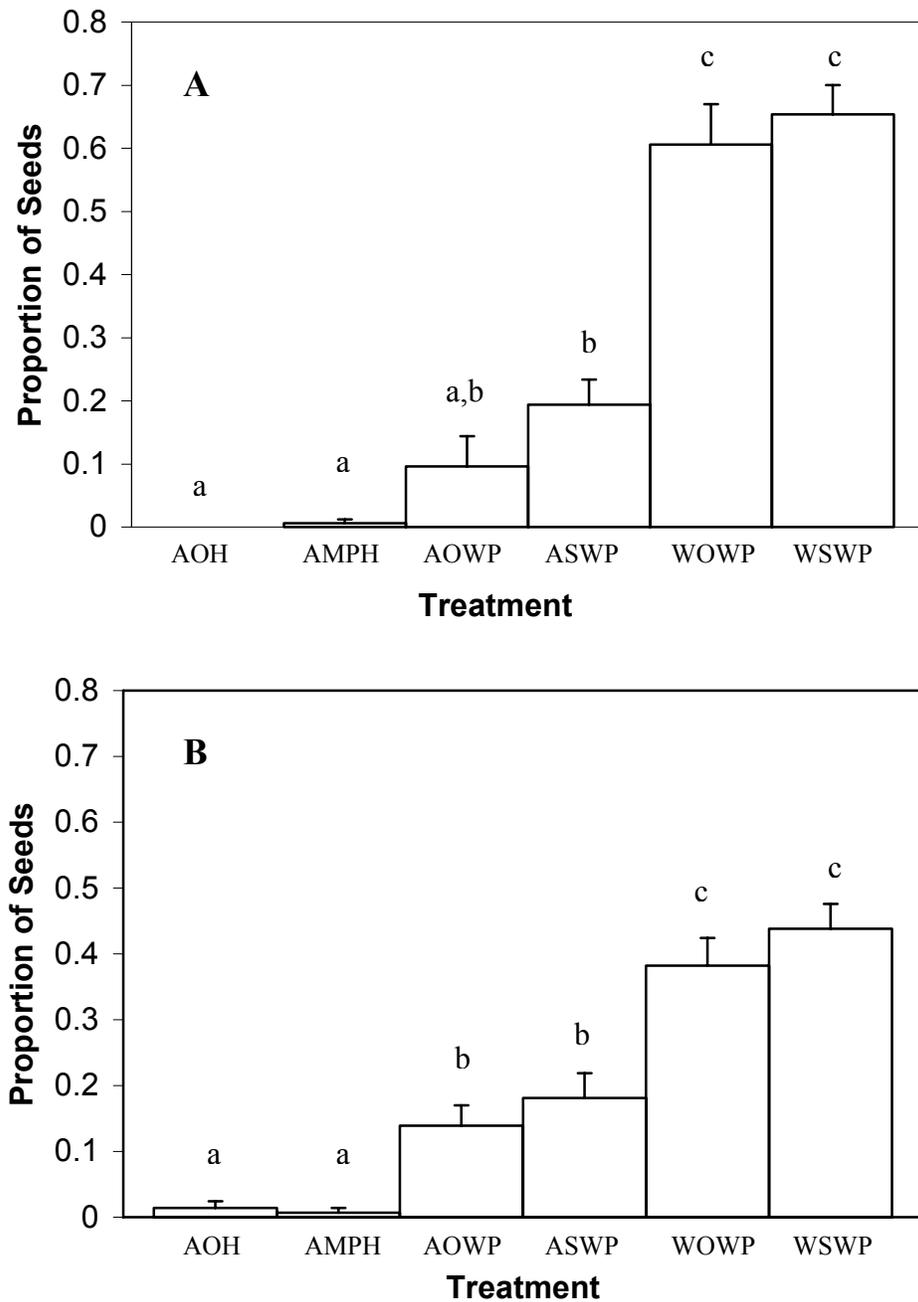


Figure 1-2. Mean proportion (+ 1 SE) of seeds that germinated. A) In the field. B) In the shade-house. Acid-treated seeds were placed in oak hammock (AOH), mixed pine-hardwood (AMPH), open wet prairie (AOWP) and shaded wet prairie (ASWP). Seeds soaked in water for one month were only placed in open wet prairie (WOWP) and shaded wet prairie (WSWP). Treatments with the same letters above error bars are not significantly different at $\alpha = 0.05$.

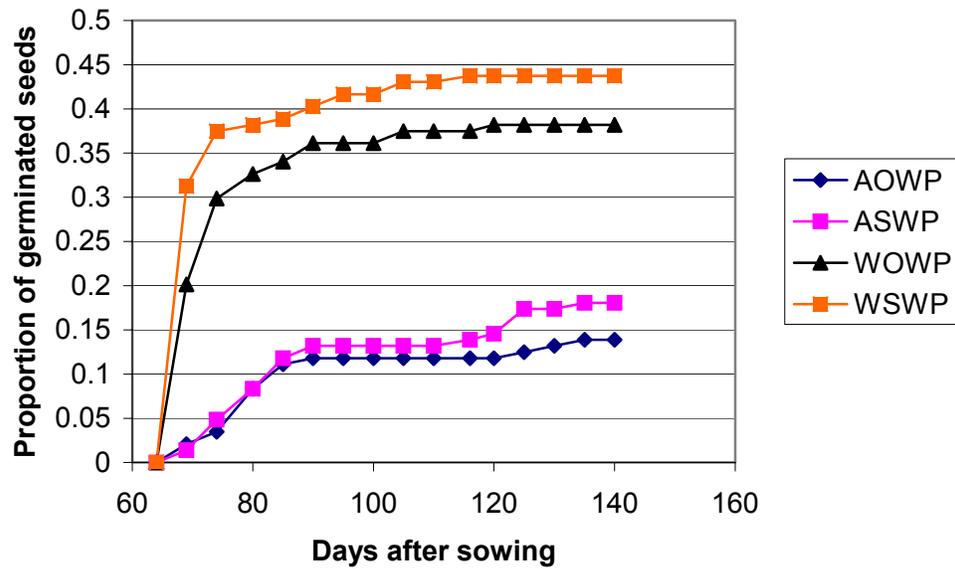


Figure 1-3. Germination rate in the shade-house represented as the cumulative proportion of seeds germinating over time. Both acid-treated seeds (AOWP and ASWP) and seeds soaked in water for one month (WOWP and WSWP) were placed on soil taken from the two respective prairie habitats. Germination on the forest habitat soils was insufficient to calculate rate. All germination curves are significantly different from each other except for AOWP and ASWP ($Z = 1.24$, $N = 46$, $p = 0.094$; two-sample Kolmogorov-Smirnov test).

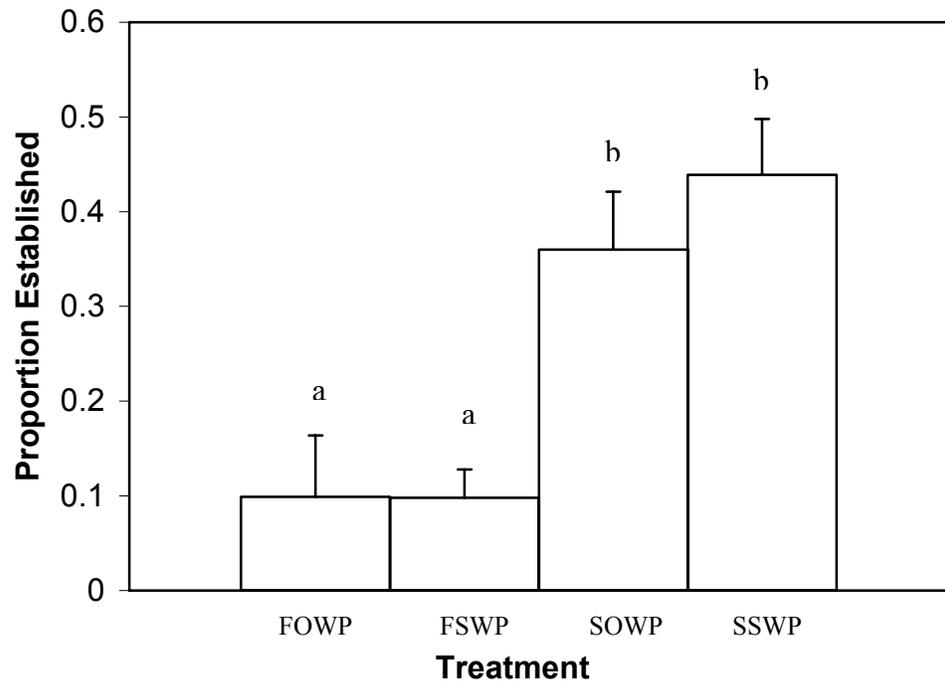


Figure 1-4. Mean proportion (+ 1 SE) of germinated seeds that established in the field (FOWP and FSWP) and shade-house (SOWP and SSWP). Data are pooled for acid-treated and water-soaked seeds within each habitat X location combination. Treatments with the same letters above error bars are not significantly different.

CHAPTER 2
IDENTIFYING BARRIERS TO RECRUITMENT FOR CHINESE TALLOW (*Sapium
sebiferum*) IN TWO FOREST HABITATS

Introduction

Understanding the effects of biotic invasions has become a priority for both scientists and policy makers. Although we still lack a common framework for quantifying and comparing the impact of different invaders (Parker et al. 1999), invasive species as a whole are second only to habitat loss and degradation as a threat to native organisms in the United States (Wilcove et al. 1998). Unfortunately, human practices of cultivation and husbandry have increased the chances that many nonindigenous populations will become established (Mack et al. 2000), and exotic species continue to be introduced throughout the world.

Invasive plants are perhaps the most conspicuous taxon of nonindigenous organisms. The high diversity of invasive plant species in many regions is partly due to the intentional introduction of plants for utilitarian and aesthetic purposes (Mack 2001), and partly due to the relative ease with which non-native plants develop mutualisms in their new range (Richardson et al. 2000). Exotic plants with fleshy fruits or those that offer some form of nutritious reward for seed removal may be easily utilized by frugivorous animals. Birds in particular have been quick to take advantage of exotic plants that offer such rewards, with numerous examples of plant invasions assisted by avian frugivory (Buchanan 1989, White and Stiles 1992, Sallabanks 1993, Figueiredo 1997, Lockhart et al. 1999, Renne et al. 2000, Reichard et al. 2001). If germination fails

to occur without gut passage of seeds, successful invasion may be highly dependent upon avian frugivores (Panetta and McKee 1997).

Assuming that a given exotic plant species can find mutualistic partners for pollination, seed dispersal, or mycorrhizal relationships, many other factors may still determine whether that species can invade. These factors include native plant diversity (Naeem et al. 2000), disturbance (D'Antonio et al. 1999), the number of times a species is introduced (Williamson and Fitter 1996), and the environmental conditions of the community being invaded (Ewel 1986). Studies of exotic plant invasions have often focused on the spread and impact of these species, and some studies have emphasized the processes that facilitate invasion from the species level to the community level. However, little attempt has been made to understand why particularly invasive plants do not establish in seemingly appropriate habitats where dispersal of seeds may be high.

The spread of such species to these sites may be limited by one or more stages in the recruitment process. Barriers to recruitment may occur if there is a source limitation (i.e., seed output is low), if there is dispersal limitation (i.e., seeds fail to arrive at potential recruitment sites), or if there is establishment limitation (i.e., postdispersal mortality of seeds or seedlings is disproportionately high; Schupp et al. 2002). All of these barriers may simultaneously limit recruitment and the establishment of new populations. Although recruitment cannot occur without seed arrival, seed arrival is no guarantee of recruitment; postdispersal processes must also be considered to understand the impact of dispersal agents on recruitment (Nathan and Muller-Landau 2000). By viewing dispersal as just one event in a sequence, the effect of this stage may be contrasted with subsequent interactions that follow, thus gauging the relative importance

of dispersal in driving recruitment dynamics (Rey and Alcántara 2000). Such an integrated approach is especially important, given that the vulnerability of any particular habitat to invasion may vary from stage to stage in the plant's life cycle (Schupp and Fuentes 1995). This independence of processes operating at different stages, or uncoupling of different stages, can offset or obscure the effects of previous stages (Jordano and Herrera 1995). The most complete picture of the recruitment process is therefore provided by studies that explicitly link patterns of seed dispersal to demographic consequences at all sequential stages (Schupp and Fuentes 1995).

I used this approach to study the invasion dynamics of the exotic tree Chinese tallow (*Sapium sebiferum* (L.) Roxb.), Euphorbiaceae (hereafter *Sapium*). In coastal South Carolina, this species regularly invades mixed pine-hardwood forests and oak dominated forests (Renne et al. 2000, Renne et al. 2001), yet it is conspicuously absent from these habitats in north central Florida despite the floristic similarities between the regions. I investigated both dispersal and postdispersal processes at a north Florida site to ask (1) which bird species are most effective with respect to quantity of *Sapium* seed dispersed, and are seeds being dispersed into adjacent forest habitats where *Sapium* is absent; and (2) how does postdispersal seed-predation, germination, and seedling establishment vary among two prairie habitats where *Sapium* is present, and two forest habitats where it is absent? Finally, I link together both dispersal and postdispersal processes as the product of process-specific transition probabilities to identify the stage(s) acting as a barrier to recruitment in oak hammock and mixed pine-hardwood forests.

Methods

Study Species and Site

Chinese tallow (*Sapium sebiferum*) was intentionally introduced to the United States for cultivation over 200 years ago because of its many uses. In China (where it has been cultivated for 14 centuries) the aril is made into waxes, fuels and soaps, while the leaves are used for dyes (Scheld et al. 1984, Jones and McLeod 1989, Jubinsky and Anderson 1996, Bruce et al. 1997). *Sapium* has become a particularly invasive species in the southeast USA, especially on the gulf coast of Texas where it has invaded coastal prairie and created monoculture woodland where previously no forest was present (Bruce 1993, Bruce et al. 1995, Barrilleaux and Grace 2000).

Flowering takes place from March to May in Florida, where this study was conducted. Inflorescences are in the form of spike-like thyrses, which mature into a 2-3 seeded capsule that dehisce from September through December. The white arillate seeds are dispersed by a variety of bird species, although there is much variation in the quality of avian dispersal agents due to seed handling behavior (Renne et al. 2000, Conway et al. 2002a, Renne et al. 2002). It has also been suggested that seeds are dispersed by water (Bruce et al. 1997), since the waxy aril aids in flotation. Germination may occur in a variety of habitats (Renne et al. 2001), although cold stratification (Cameron et al. 2000), fluctuating temperatures (Nijjer et al. 2002), and moisture (Conway et al. 2000) are abiotic factors that increase germination success. Emerging seedlings are also tolerant of a wide variety of conditions including moderate flooding (Jones and Sharitz 1990), heavy shade (Jones and McLeod 1989), and moderate soil salinity (Conner 1994). Despite the invasiveness of this species, there is currently little evidence of allelopathic inhibition of other plant species (Keay et al. 2000, Conway et al. 2002b).

This study was conducted in Paynes Prairie Preserve State Park, Alachua County, Florida. See Chapter 1 for a more detailed description of the park and field sites. Research took place in four habitats: two prairie habitats where *Sapium* is present (shaded wet prairie and open wet prairie); and two forest habitats where it is absent (oak hammock and mixed pine-hardwood), but where it occurs elsewhere in its non-native range. The two prairie habitats freely grade into each other, and are best separated by structural diversity; the shaded wet prairie having more trees. Similarly, oak hammock and mixed pine-hardwood freely grade into one another, the latter being distinct through the presence of pines. However, the prairie habitats form an abrupt edge with the forest habitats.

Avian Seed Dispersal

In order to determine if seeds were being dispersed to the forest habitats, I evaluated the relative effectiveness of avian frugivores with respect to the quantity of seeds they disperse, which is a function of the number of visits made by a disperser and the number of seeds dispersed per visit (Schupp 1993, Jordano and Schupp 2000). Six *Sapium* trees that were comparable in size were selected for observation: three in open wet prairie and three in shaded wet prairie. Two trees in open wet prairie and one in shaded wet prairie were located close to the forest edge (≤ 10 m), while two trees in shaded wet prairie and one in open wet prairie were located far from the edge (≥ 100 m). Only data from close trees (#1-3) were used to calculate transition probabilities of dispersal (see below) as it was often difficult to determine where birds flew after foraging in trees far from the edge. However, data from close trees was compared with those from far trees (#4-5) to verify that visitation rates to close trees were representative of the population as a whole.

An observer with binoculars was stationed ~ 15 m from a tree, starting 15 minutes after sunrise and continuing for 1-3 hours on a given day. Bird activity declined considerably by midmorning, so foraging observations did not extend beyond three hours. Trees were observed for a total of 106.5 h ($\bar{x} = 17.8 \pm 1.6$ SD h/tree) between 6 October 2002 and 25 February 2003. For each bird that visited, the species, duration of visit, number of seeds carried, number of seeds ingested, number of seeds dropped, and direction of postforaging movement were recorded. In addition, it was noted if birds pecked at seeds, or scraped off the aril without removing seeds from the tree. Foraging observations were terminated when trees had been depleted of seeds.

Point Counts

To determine which bird species that disperse *Sapium* seeds in the prairie are also present in the forest, I used fixed-radius point counts to assess the relative abundance of seed-dispersing bird species in the two habitats where *Sapium* is absent (i.e., oak hammock and mixed pine-hardwood). I used standard bird monitoring protocols (Ralph et al. 1993, Ralph et al. 1995) to establish 24 fixed-radius point count stations (50 m radius), 12 in oak hammock and 12 in mixed pine-hardwood. Points were located approximately 250 m apart, and at least 50 m from the edge of any adjacent habitat type. The number of points in the mixed pine-hardwood habitats was subsequently reduced to 11 after one station was found to be too close to the prairie-forest edge. A count period of 5 min was used, during which all birds seen and/or heard were recorded. In subsequent analyses, I did not include flyovers or species that were never seen ingesting or carrying *Sapium* seeds at prairie trees.

I revisited each point seven times during the season when *Sapium* trees contained seeds (October-February). For each point count station, I then calculated the mean

number of individuals detected per point per visit for each species. Counts started 15 minutes after sunrise and continued for two hours or less. Points were visited in random order, and counts were not conducted during inclement weather.

Seed-predation Experiment

To determine if higher seed-predation might account for the failure of *Sapium* to establish in forest habitats, I followed the fate of experimentally placed seeds in the field over 55 days. In each of the four habitats, twelve sites were systematically spaced 30 m apart along two transects in oak hammock and open wet prairie, and three transects in mixed pine-hardwood and shaded wet prairie. I used existing trails to access sites, but placed seeds at least 30 m from the nearest trail. Vegetation structure prevented me from placing transects in random locations. In October 2002, approximately 1000 seeds were collected from eight trees at the site. At 1.0 m distances from the center point of a site in each of the four cardinal directions, four seeds were placed together on the ground (12 sites X 16 seeds/site = 192 seeds/habitat). Placing seeds on the surface simulates the state of recently dispersed seeds, and four *Sapium* seeds are a typical number found together in a bird defecation (I. Renne, pers. comm.). Prior to placement in the field, seeds were treated with 2.0 pH HCL to simulate avian gut passage; see Chapter 1 for more complete seed treatment methods. Forceps were used to place seeds on the ground (taking special care not to touch seeds with the hands) since human scent can bias seed removal data (Duncan et al. 2002, Wenny 2002). Each group of four seeds was surrounded by three toothpicks inserted half way into the ground to facilitate relocation. I visited experimental sites every three days, and recorded the number of seeds remaining. Prior to the experiment, I used a Trailmaster® 550 motion/IR triggered camera to identify seed predators in the study area.

Seed Germination and Establishment

The same experimental design used in the seed predation experiment was used here to determine if low germination or lack of seedling establishment might explain the failure of *Sapium* to establish in forest habitats. See Chapter 1 for a more complete discussion of the methods and results of this experiment.

Seeds were collected from 12 trees at the Paynes Prairie field sites in December, 2002, and treated in two ways prior to placement in the field. I acid-treated 768 seeds (192/habitat), and soaked 384 seeds with the aril intact in water for one month to simulate the effects of water dispersal (i.e., immersion in water) on germination. Acid-treated seeds were stored under cages in the field to ensure that seeds were subjected to natural environmental conditions.

The sites where seeds were placed in the seed predation experiment were moved 3 m in a random direction to avoid disturbed ground. In late January, acid-treated seeds were reallocated to each of these new experimental sites in all four habitats, and covered with a cage (8x8x6 cm) made from 0.25 inch (23 gauge) galvanized wire mesh, to prevent predation. Seeds were placed on the surface to simulate the condition of a recently dispersed seed. At this time, water-soaked seeds were sown under separate cages adjacent to acid-treated seeds in the two prairie habitats (192 seeds/habitat). Water-soaked seeds were only sown in the prairie habitats, since water dispersal would not be expected in the forest habitats at this site where flooding does not occur.

Seeds were monitored weekly for signs of germination (split seed coat and/or emergence of the radicle). The cage was removed only when an established seedling was near the top of a cage. Germination was monitored through May 2003, when cages and

remaining seeds were removed from the field. The survivorship of established seedlings was monitored until August 2003, at which time all seedlings were destroyed.

Linking the Stages

I calculated transition probabilities (TPs) for each stage, from seed removal through seedling establishment (Rey and Alcántara 2000, Traveset et al. 2003). The first two TPs are based on observational data from foraging observations collected at adult *Sapium* trees in the prairie habitats, while the remaining three TPs come from the experimental tests conducted in all four habitats. Each TP is the ratio of the number of individuals that survived a given stage to the number of individuals that entered that stage.

TP₁ is the probability that a seed is bird-dispersed, and is calculated as 1-probability of a seed being dropped. Seeds that were removed from branches and dropped below the parent tree were assumed no longer available for avian dispersal. The probability of being dropped is the ratio of the number of seeds dropped: total number of seeds removed by birds. This makes the assumption that all seeds not dropped are dispersed by birds. Renne et al. (2000) estimated that approximately 10% of seeds are dislodged from branches and fall to the ground without being handled by birds. To estimate this metric for my study trees, I bagged six branches and observed a comparable abscission rate to that of Renne et al. (2000). I also observed bill marks on nearly all seeds found on the ground, evidence of removal by birds. Therefore, I assumed seeds not dropped were dispersed because all study trees were depleted of seeds by late February, when foraging observations were terminated.

TP₂ is the probability a seed will be dispersed to a particular habitat, as estimated from postforaging movement. Seeds may be dispersed away from parent trees if they are carried or ingested. Because the next perch was not always seen and because seed arrival

could not be confirmed, I simplified postforaging habitats into prairie and forest, and I assumed that birds stayed in these habitats long enough to defecate or regurgitate seeds. Thus, the proportion of seeds dispersed to forest sites is the ratio of the number of seeds ingested + carried in bill to the forest: total number ingested + carried in bill. Likewise, the proportion of seeds dispersed to prairie sites is the ratio of the number of seeds ingested + carried in bill to sites within the prairie: total number ingested + carried in bill. This TP was only calculated for trees close to the forest edge (see above).

TP₃ is the ratio of the number of seeds remaining (not predated): the total number of seeds placed at experimental sites (192 seeds/habitat). TP₄ is the ratio of the number of seeds that germinated: the total number of seeds placed at experimental sites (192 seeds/habitat). Finally, TP₅ is the ratio of the number of germinated seeds that successfully established: the total number of seeds that germinated in a given habitat. Because the calculation of transition probabilities is based on bird-dispersal, data from water soaked seeds were not used. The overall or cumulative probability of recruitment in a particular habitat is the product of the TPs for that habitat. The goal is to compare among habitats the probability that a seed will become an established seedling.

Statistical Analyses

Data frequently met neither assumptions of normality nor equal variance, and thus I relied primarily on nonparametric statistical tests. Because only close trees were used in the calculation of TP₂ (dispersal), I wanted to verify that avian foraging activity at close trees was comparable to that at far trees. Thus, differences between close and far trees with respect to the number of seeds dispersed, number of visits, and duration of visits by the ten most effective dispersers of *Sapium* were compared using a Mann-Whitney U-test. This test was also used to compare point count detections of these same ten

species in oak hammock and mixed pine-hardwood to look for differences between these habitats that might reflect differences in seed arrival. Equation 2-1 shows the Jaccard index of community similarity, which was used to compare disperser diversity of these two habitats,

$$C_j = \frac{j}{a + b - j} \quad (2-1)$$

where j is the number of species common to sites a and b , a is the number of species in site a and b is the number of species in site b (Nur et al. 1999).

The proportions of seeds that survived the seed predation experiment were compared among habitats using 1-way ANOVA of angular transformed data. Tukey's multiple comparison procedure was used to separate habitats when a significant habitat effect was found. To compare the proportion of seeds that germinated, I used a Kruskal-Wallis test, followed by the Nemenyi multiple comparison procedure to separate habitats (Zar 1999). Seedling establishment, however, only occurred in the two prairie habitats, which were compared using a Mann-Whitney U-test. The effect of seed treatment (acid vs. water) on the establishment of seedlings in paired field experiments where germination occurred (open and shaded wet prairie combined) was analyzed with a Wilcoxon signed-rank test. Because successful establishment was rare, I compared the overall probability of recruitment through germination rather than through establishment using a Kruskal-Wallis test, with habitat groups separated with the Nemenyi multiple comparison procedure. For statistical analyses I used SPSS 10.0 (SPSS Inc., Chicago, IL) and Minitab 12.0 (Minitab Inc., State College, PA). All means are reported \pm SD, with $\alpha = 0.05$.

Results

Avian Seed Dispersal

A list of 25 bird species that visited study trees and utilized *Sapium* seeds as a food source is given in Table 2-1, with the ten most effective dispersers of *Sapium* (based on the number of seeds ingested or carried) highlighted in bold. An additional eight species visited study trees, but had no interaction with *Sapium* seeds. Of the 33 species total that visited trees, 21 species (64%) were observed ingesting or carrying seeds. *Dumetella carolinensis* ingested or carried 333 seeds, more than any other species. However, *D. carolinensis* often dropped into thick vegetation below parent trees after foraging, and is therefore less likely to disperse seeds into adjacent forest habitats. Woodpeckers (Picidae), on the other hand, made up 40% of the most effective disperser species, and were frequently seen making long flights into the forest from prairie trees. In addition, woodpeckers consumed more seeds per visit than any other taxon of birds (Table 2-1). *Cardinalis cardinalis* was ranked as one of the top ten dispersers, primarily because it made more visits and spent more time in trees than any other species. While this species did carry and ingest seeds, most seeds removed by it were dropped below parent trees after the aril was scraped off. Of the seeds removed from branches by birds, 19.8% were dropped below parent trees, leaving 80.2% of the seed crop available for dispersal. Of these remaining seeds, 34% were carried to other sites within the prairie, while 66% were carried to the forest.

Several differences were evident between trees close to the forest edge (≤ 10 m), and those far from the edge (≥ 100 m). Among the ten most effective seed dispersers, significantly more seeds were ingested or carried from close trees ($\bar{x} = 64.8 \pm 46.2$) than from far trees ($\bar{x} = 39.1 \pm 68.8$; $U = 137.0$, $P = 0.017$). This difference can largely be

attributed to the woodpeckers, all of which were more common at close trees (Table 2-1). However, the number of visits/h and amount of time (minutes/h) spent in close versus far trees did not significantly differ when all ten species were considered together ($U = 117.0, P = 0.385$ and $U = 123.0, P = 0.186$ respectively).

Point Counts

A total of 17 frugivorous bird species that ingested or carried seeds at prairie trees were detected on point counts in oak hammock and mixed pine-hardwood (Table 2-2). This represents 81% of the frugivores that visited prairie trees and dispersed seeds. The Jaccard index of community similarity = C_j (which ranges from 0 to 1.0) was high (0.88), indicating that most of these frugivores occurred in both oak hammock and mixed pine-hardwood. In addition, all ten of the most effective dispersers of *Sapium* were detected in both oak hammock and mixed pine-hardwood (Table 2-2), and the mean number of individuals detected/point/visit did not significantly differ between these two habitats ($U = 117.5, P = 0.364$). *Melanerpes carolinus* was the most common of these ten species in both habitats, being detected at all point stations with an average of 1.06 birds/point/visit in oak hammock.

Seed-predation Experiment

Seed survival in the prairie habitats was distinctly different from the forest habitats (Figure 2-1). Seeds were rapidly consumed in the prairie habitats during the first ten days after placement, whereas seeds in the forest habitats were subjected to lower levels of predation. The proportion of seeds remaining at the end of the experiment (55 days) was significantly different among habitats ($F_{3,44} = 13.65, P < 0.001$), with 28% and 39% remaining in shaded and open wet prairie respectively, versus 85% and 79% remaining in mixed pine-hardwood and oak hammock. The two prairie habitats were significantly

different from the two forest habitats, but open wet prairie was not significantly different from shaded wet prairie, nor was oak hammock significantly different from mixed pine-hardwood. Most predation occurred soon after the experiment began, with little additional seed-predation in any of the four habitats after 20 days. Evidence of mammalian seed-predation (broken seed coats) was found at experimental sites where seeds had been placed.

Seed Germination and Establishment

Only one of 192 seeds germinated in mixed pine-hardwood, and seeds failed to germinate altogether in oak hammock. The highest level of germination success was observed for water-soaked seeds in shaded wet prairie (65.4%), followed closely by water-soaked seeds in open wet prairie (60.6%). This was significantly higher than acid-treated seeds in shaded wet prairie (19.4%) and open wet prairie (9.6%), ($H = 53.79$, $df = 5$, $P < 0.001$; Chapter 1). The relatively low germination success of acid-treated seeds in open wet prairie made this habitat statistically indistinguishable from oak hammock and mixed pine-hardwood, and from acid-treated seeds in shaded wet prairie (Figure 2-2).

Successful germination was no guarantee of successful establishment. Pooling the results for acid-treated and water-soaked seeds, only about 10% of seeds that germinated also established. The difference between shaded and open wet prairie was not significant, SWP = 0.098 ± 0.146 vs. OWP = 0.111 ± 0.269 ($U = 318.0$, $P = 0.335$). For sites in the two prairie habitats where both acid-treated and water-soaked seeds germinated, a slightly higher proportion of water-soaked seeds established (mean = 0.12 ± 0.16) than acid-treated seeds (mean = 0.09 ± 0.25). However, this difference was not significant ($T = -1.173$, $P = 0.241$). In both open and shaded wet prairie, newly

germinated seeds were frequently attacked by fire ants (*Solenopsis invicta*) soon after the seed coat had split, thus preventing seedling establishment. In addition, some seeds germinated in moist microsites that subsequently desiccated shortly after the seeds germinated. These seeds rarely survived long enough to become established seedlings.

Linking the Stages

Multiplying the process-specific transition probabilities (TPs) pooled across all 12 sites within each habitat resulted in an overall probability of recruitment through the seedling stage of 0.001 in both prairie habitats, and zero in the two forest habitats (Figure 2-3). With each site considered an independent replicate, there was a significant difference among habitats in the overall probability of becoming a germinated seed ($H = 11.26$, $df = 3$, $P = 0.01$). Pooled across all sites within each habitat, the overall probability of becoming a germinated seed was 0.010 and 0.015 in open and shaded wet prairie respectively, versus 0.003 and zero in mixed pine-hardwood and oak hammock. However, relatively low germination success in open wet prairie made this habitat statistically indistinguishable from oak hammock and mixed pine-hardwood. Only in shaded wet prairie was there a significantly higher probability of becoming a germinated seed.

Discussion

Establishment probability may be determined by dispersal or by postdispersal processes. In this study, dispersal limitation is unlikely to explain the absence of *Sapium* in oak hammock or mixed pine-hardwood. This conclusion is supported by the observation that 66% of seeds taken by birds at close trees were moved in the direction of the forest habitats, and all ten of the most effective dispersers of *Sapium* were detected on point counts in the two forest habitats. I am unable to confirm if the individuals detected

on point counts also foraged at *Sapium* trees in the adjacent prairie habitats. Seed traps were not used in the forest due to the infinite number of perch sites below which seed deposition might occur. However, the frequent movement of seeds into forest habitats combined with the abundance of these species in the forest strongly suggests that seed arrival is taking place. This underscores the importance of examining multiple stages in the recruitment process, and then linking these stages to determine which if any is responsible for limiting recruitment at a given site. At this site, I showed that germination is the stage most likely responsible for preventing recruitment in the forest habitats.

Avian Frugivory and Seed Dispersal

This is the first study to examine avian frugivore activity at *Sapium* in Florida, yet close parallels exist with respect to species richness and foraging behavior from sites in South Carolina, Louisiana, and Texas. In South Carolina, Renne et al. (2000, 2002) also found woodpeckers to be among the most common dispersers of *Sapium* seeds. However, they also found *Sturnus vulgaris*, *Corvus ossifragus*, and *Quiscalus major* to be potentially important dispersers, largely because they arrived in flocks that collectively consumed many seeds. In this study, not only did these species not visit *Sapium* trees, but flocks of birds were rarely observed. If flocks visited study trees outside of observation periods, one would expect large variation in removal rates from day to day. I marked eight branches on four trees, and instead observed a gradual loss of seeds over the winter (Samuels, unpublished). This confirms that flocks did not commonly visit study trees outside of observations, and that foraging data accurately represent frugivore activity at *Sapium* trees through the winter of 2002-03. It is unknown why flocks were

virtually absent at this site, but it may relate to the low density of *Sapium* trees due to past control efforts.

I observed *Cardinalis cardinalis* dropping more seeds below parent trees than any other species, an observation that agrees with Renne et al. (2000, 2002). Dropping of seeds usually was preceded by scraping, where the bill is used to scrape the aril off the seed without ingesting the seed. However, Conway et al. (2002a) never observed *C. cardinalis* scraping seeds at a site in Texas. Furthermore, they found *Icterus galbula* to be frequent consumers of *Sapium* seeds that never scraped seeds. In the present study, *I. galbula* never ingested seeds, but readily scraped them to consume the aril.

The 21 bird species observed ingesting or carrying *Sapium* seeds belong to eight families with a diversity of foraging strategies. This supports the view that generalized dispersal syndromes common to vertebrate-dispersed plants have aided the invasion process of exotic plants that possess these traits (Richardson et al. 2000). Introduced species may account for as much as one-third of the bird-dispersed flora in eastern North America (White and Stiles 1992), and the presence of fruits during winter when insect availability is low may further increase the use of these resources at least in the southeast USA (Skeate 1987, McCarty et al. 2002). Avian dispersal of exotic seeds then leads to the formation of satellite populations, although it remains unclear how land-use and landscape connectivity affect the movement of invasive species into natural areas (Reichard et al. 2001). Dispersers of *Sapium* at this site readily crossed abrupt habitat boundaries, insuring that seeds arrived in a wide diversity of microsites. Successful invasion of new locations at this site is most likely to depend on postdispersal processes.

Postdispersal Processes

Postdispersal seed-predation varied among habitats, but the survival of seeds was similar between the two prairie habitats, and likewise between the two forest habitats. The level of predation was significantly higher in the prairie habitats where *Sapium* presently occurs, thus postdispersal seed-predation cannot solely explain the failure of *Sapium* to establish in the forest habitats at this site. The lower level of seed loss in the forest habitats may be due to a lower species richness or abundance of seed predators. Through preliminary investigations, I obtained photos of marsh rabbit (*Sylvilagus palustris*), eastern cottontail (*Sylvilagus floridanus*), and rice rat (*Oryzomys palustris*) consuming *Sapium* seeds in the prairie habitats, but no photos were obtained of seed-predators in the forest. The open understory and tall tree canopy in the forest habitats may increase the risk of predation to mammalian seed-predators relative to the prairie habitats where cover is present near the ground. The extent of cover can alter the foraging behavior and habitat selection of potential seed-predators (Lima and Dill 1990, Bowers and Dooley 1993). Alternatively, the deep litter present in the forest habitats may have succeeded in sheltering seeds from potential predators. Thick litter has been shown to hinder the detection of seeds by rodents (Cintra 1997).

Mammals (especially rodents) are well known to be important seed-predators in temperate ecosystems (Mittelbach and Gross 1984, Hulme 1998, Hulme and Hunt 1999, Anderson and MacMahon 2001, Maron and Simms 2001), and there is no evidence that exotic species are less susceptible than native species to seed-predation (Blaney and Kotanen 2001). Seed burial reduces postdispersal predation, and it is likely some *Sapium* seeds would enter the seed bank following avian dispersal. Renne et al.(2001) found that *Sapium* seeds buried for one and two years did not differ in viability. Furthermore,

Cameron et al. (2000) suggest that seeds may be viable for up to seven years.

Extrapolation of surface seed-predation data to the dynamics of plant recruitment should therefore proceed with caution (Hulme 1994).

The nearly complete lack of germination in the two forest habitats suggests that germination is a strong barrier to recruitment, and is preventing establishment of *Sapium* in oak hammock and mixed pine-hardwood forests at Paynes Prairie. Placement of seeds on top of the litter layer, which was meant to simulate the state of recently dispersed seeds, may have inhibited germination by preventing contact with a moist soil substrate. Seeds that were suspended in litter were always dry when sites were checked for signs of germination, and litter appeared to dry out quickly after rains. It is thus not surprising that the only seed that germinated in mixed pine-hardwood forest was at a site where water had pooled after heavy rain, and conditions were appropriate for imbibition to occur. Soaking of *Sapium* seeds in water has been suggested as a process that initiates germination (Conway et al. 2000).

Alternatively, seeds may have failed to germinate in the forest habitats because of reduced variation in daily temperature fluctuations. Fluctuating temperatures have been shown to increase germination success of *Sapium* (Nijjer et al. 2002), and forest habitats may buffer microsites against large fluctuations. This hypothesis is unlikely, however, because seeds also failed to germinate in a shade-house that simulated the forest floor environment, and temperature fluctuations were consistent among treatments that included high levels of germination (Samuels, unpublished).

The presence of a thick litter layer in forest habitats at Paynes Prairie is partly a result of fire suppression near residential areas. Reduction of litter through fire or

through manual removal can alter microsites to create favorable conditions for germination (Carrington 1999, McConnell and Menges 2002), introducing the possibility that a fire in the forested habitats at the Paynes Prairie site might create suitable sites for *Sapium* establishment if seeds arrived. In contrast, Renne (2001) found *Sapium* invading mixed pine-hardwood and other forest habitats at a site in South Carolina where prescribed burns are common. In a field plot study, Renne (2001) observed over 40% emergence of sown seeds in mixed pine-hardwood. Plots had been cleared of litter and vegetation to standardize treatments, and seeds were sown 0.5 cm deep. Both of these factors likely contributed to the large differences in germination success between that study and the present study; burial likely increased the chance that seeds would be surrounded by moisture. In comparison, Siemann and Rogers (2003) added *Sapium* seeds to the surface of a mesic forest in Texas dominated by pines and oaks and observed low germination success (5-10%) and 100% seedling mortality. Thus, if seeds had germinated and established in oak hammock and mixed pine-hardwood forests in the present study, seedling mortality may still have prevented the recruitment of adult plants in these habitats.

Recruitment Limitation in Forest Habitats

The outcome of any one stage alone cannot be used to predict recruitment patterns because of independence among processes acting at different stages (uncoupling), and because patterns of uncoupling among stages are site-specific (spatial discordance; Jordano and Herrera 1995). Thus, uncoupling between consecutive stages within a site or spatial discordance in the probability of seed survival, germination, or establishment among sites can obscure the importance of any particular stage when considered in isolation (Herrera et al. 1994, Jordano and Herrera 1995, Houle 1998). However, the

relative importance of each stage in the recruitment process can be evaluated through an experimental framework where seed dispersal is monitored or manipulated through seed sowing experiments, and the fate of a cohort of propagules is followed through each stage (Schupp and Fuentes 1995, Nathan and Muller-Landau 2000, García 2001, Banack et al. 2002, Balcomb and Chapman 2003). Using this general framework, I was able to identify germination as the limiting stage, or the “Achilles heel” in the process of seedling recruitment in oak hammock and mixed pine-hardwood. Recruitment following seed introduction indicates the presence of a regeneration niche, and a lack of recruitment may indicate that suitable microsites were absent at the time of seed sowing (Turnbull et al. 2000). However, suitable microsites for seedling establishment still do not guarantee that plants will survive to become reproductive adults, which is required to satisfy the assumption that existing seed shadows ultimately translate into self-reproducing populations (Schupp and Fuentes 1995).

By calculating transition probabilities among stages, I was able to detect both uncoupling between successive stages within habitats, as well as spatial discordance of particular stages among habitats. High spatial discordance has been detected in other studies using similar research designs. Rey and Alcántara (2000) found that seedling survival was the most critical process during recruitment of *Olea europaea* (Oleaceae), with the most favorable places for seeds becoming the worst places for seedlings. Traveset et al. (2003) found both seedling survival and postdispersal seed-predation to be critical stages for *Rhamnus ludovici-salvatoris* (Rhamnaceae), with high spatial discordance among habitats. In both studies, water stress was identified as the principal reason seedlings failed to survive, with low precipitation also contributing to low

germination (Traveset et al. 2003). In the present study, spatial discordance occurred among habitats for the germination stage, imposing an abrupt contrast between forest and prairie habitats with respect to this stage. Because germination was virtually absent in the forest habitats, this stage obscured the relative importance of earlier stages in the recruitment process. It remains unknown whether seedlings could have established in oak hammock and mixed pine-hardwood had they germinated in these habitats.

Estimates of transition probabilities in this study are constrained by the short, one year, duration of the study. There has been growing interest in how the effects of variation in the physical environment interact with biology to produce patterns seen in nature (Chesson 2003). Seedling recruitment and survival vary considerably from year to year both within and among populations, and one year's results cannot be used as reliable long-term estimates of these parameters (Clark et al. 1999, Ibáñez and Schupp 2001). However, germination was such a formidable barrier to recruitment in the forest habitats that this parameter seems unlikely to increase substantially unless some form of litter-reducing disturbance is imposed. Annual fluctuations in temperature and precipitation are unlikely to create favorable regeneration niches in the forest habitats, although such variation could easily alter the extent of recruitment success in the prairie habitats.

Assessing recruitment limitation in the forest habitats relied upon the assumption that observational data of avian foraging behavior can be tied to experimental data of postdispersal processes. The overall probability of recruitment explicitly includes both forms of data as the product of all transition probabilities, where TP_1 and TP_2 are derived from observational data, while all remaining transition probabilities come from

experimental data (Figure 2-3). However, the probability of a seed being dispersed to forest vs. prairie habitats is based on observation only of the three trees close to the forest edge. This may explain why 66% of seeds were dispersed to forest habitats. *Sapium* trees near the edge were visited by many woodpeckers that likely came from and returned to the forest. However, the percent of seeds dispersed to prairie habitats (34%) is likely an underestimate, since most seeds dispersed away from trees more distant in the prairie are more likely to arrive within prairie habitats. In addition, seeds dropped below parent trees arrive in the prairie habitats, even if they are not dispersed. To evaluate the potential impact of this bias, I let TP_1 and $TP_2 = 1.0$, while all other TPs were held constant. This resulted in an overall probability of recruitment of 0.004 and 0.003 for shaded and open wet prairie respectively, compared to 0.001 for both prairie habitats when $TP_1 = 0.802$ and $TP_2 = 0.340$ (Figure 2-3). Thus, variance in these parameters does not have a large effect on the overall probability of becoming a seedling. Alternatively, TP_2 (dispersal) may be an overestimate for the forest habitats. However, the overall probability of recruitment goes to zero regardless of the probability of dispersal because germination was the limiting stage.

The long-term forecast for *Sapium* invasion at Paynes Prairie Preserve State Park and other natural areas in north Florida may depend on future management activities that create or remove appropriate microsites for establishment. For now, *Sapium* is absent from oak hammock, mixed pine-hardwood forest, and other upland mixed hardwood forests. Results from the present study suggest that postdispersal processes are limiting the current extent of invasion, but that seeds may be present to take advantage of regeneration niches if or when they become available. Control efforts continue at Paynes

Prairie within the prairie habitats themselves, although outright eradication appears remote due to the inaccessibility of some trees, rapid maturation of new recruits, and continued arrival of seeds via local waterways and birds. Paynes Prairie and other natural areas will continue to be at risk from seed input originating from ornamental trees still present in local residential areas. While efforts to increase awareness of this species have been somewhat successful (Putz et al. 1999), source trees are likely to be present for some time to come.

Table 2-1. Bird species seen visiting six *Sapium sebiferum* trees during 106.5 hours of observation between 6 October 2002 and 25 February 2003, Paynes Prairie Preserve State Park, Alachua County, FL.

Species	Status ^a	Ingested Seeds		Dropped Seeds		Carried Seeds		Visits/hr to Trees		Min/hr in Trees	
		Near	Far	Near	Far	Near	Far	Near	Far	Near	Far
<i>Melanerpes carolinus</i>	I,D,C	12	12	1	1	47	1	0.35	0.08	0.61	0.09
<i>Picoides pubescens</i>	I,D,C,S	10	11	1	0	14	12	0.50	0.44	0.81	0.45
<i>Colaptes auratus</i>	I,D,C	171	23	1	2	1	0	0.17	0.10	0.48	0.29
<i>Dryocopus pileatus</i>	I	91	0	0	0	0	0	0.09	0	0.19	0
<i>Sayornis phoebe</i>	I,D,C	54	23	1	1	4	0	0.62	0.38	0.86	0.59
<i>Myiarchus cinerascens</i> *	I	13	0	0	0	0	0	0.07	0	0.17	0
<i>Cyanocitta cristata</i>	I,D,C,S	1	3	2	0	1	2	0.37	0.19	0.28	0.22
<i>Regulus calendula</i>	P	0	0	0	0	0	0	0.15	0.06	0.15	0.05
<i>Catharus guttatus</i>	I,C	7	4	0	0	1	2	0.09	0.06	0.10	0.05
<i>Turdus migratorius</i>	I,D	33	12	1	0	0	0	0.24	0.04	0.75	0.12
<i>Dumetella carolinensis</i>	I,D,C	96	221	5	17	4	12	2.00	2.12	2.68	3.06
<i>Mimus polyglottos</i>	I,D	30	25	1	0	0	0	0.37	0.52	0.76	1.28
<i>Toxostoma rufum</i>	I	0	9	0	0	0	0	0	0.12	0	0.07
<i>Vireo griseus</i>	I,D,C	22	4	1	0	0	3	0.39	0.19	0.36	0.20
<i>Vireo solitarius</i>	I,D	4	1	1	0	0	0	0.11	0.02	0.13	0.02
<i>Vireo olivaceus</i>	I	0	1	0	0	0	0	0	0.02	0	0.02
<i>Vermivora celata</i>	P	0	0	0	0	0	0	0.13	0.04	0.10	0.04
<i>Dendroica pinus</i>	D,C,P	0	0	1	0	2	0	0.09	0.02	0.10	0.01
<i>Dendroica coronata</i>	D,C,S,P	0	0	0	3	1	2	1.49	1.83	2.94	4.43
<i>Cardinalis cardinalis</i>	I,D,C,S	36	24	115	107	23	8	2.77	1.37	4.07	2.13
<i>Passerina cyanea</i>	C	0	0	0	0	0	1	0.02	0.02	0.04	0.01
<i>Agelaius phoeniceus</i>	I	0	1	0	0	0	0	0	0.08	0	0.15
<i>Quiscalus quiscula</i>	I	1	0	0	0	0	0	0.15	0.02	0.15	0.04
<i>Icterus galbula</i>	D,S,P	0	0	0	5	0	0	0.17	0.13	0.21	0.23
<i>Carduelis tristis</i>	S	0	0	0	0	0	0	0.07	0	0.05	0
Total:		581	374	131	136	98	43	10.46	8.06	16.00	13.72

Species in bold are the ten most effective dispersers of *Sapium* at this site. For each species, the number of seeds ingested, dropped, and carried is given along with the amount of time spent in observation trees.

^a Frugivory status of birds at *Sapium sebiferum*, Paynes Prairie Preserve State Park, Alachua County, Florida. I = ingested seeds, D = dropped seeds after removing from branch, C = carried seeds away from tree, S = scraped aril off seeds, P = pecked at aril on seeds.

* Out of range species.

Table 2-2. Frugivorous bird species detected on point counts in oak hammock and mixed pine-hardwood habitats between 12 October 2002 and 5 March 2003, Paynes Prairie Preserve State Park, Alachua County, FL.

Species	Status ^a	Oak Hammock		Mixed Pine-Hardwood		% (Total) ^d
		Mean (SD) ^b	% (50-m) ^c	Mean (SD) ^b	% (50-m) ^c	
<i>Melanerpes carolinus</i>	I,C,D	1.06 (0.24)	100.0	0.75 (0.35)	100.0	100.0
<i>Picoides pubescens</i>	I,C,D,S	0.23 (0.21)	83.3	0.26 (0.12)	100.0	91.3
<i>Colaptes auratus</i>	I	0.05 (0.07)	33.3	0.14 (0.13)	63.6	47.8
<i>Dryocopus pileatus</i>	I	0.04 (0.09)	16.7	0.06 (0.13)	27.3	21.7
<i>Sayornis phoebe</i>	I,C	0.14 (0.16)	66.7	0.05 (0.10)	27.3	47.8
<i>Vireo olivaceus</i>	I	0	0	0.03 (0.09)	9.1	4.3
<i>Vireo griseus</i>	I	0.27 (0.27)	75.0	0.04 (0.07)	27.3	52.2
<i>Vireo solitarius</i>	I	0.01 (0.04)	8.3	0.08 (0.10)	45.5	26.1
<i>Cyanocitta cristata</i>	S,C	0.65 (0.30)	100	0.25 (0.31)	63.6	82.6
<i>Turdus migratorius</i>	I	0.08 (0.10)	50.0	0.38 (0.88)	63.6	56.5
<i>Catharus guttatus</i>	I,C	0.14 (0.19)	50.0	0.06 (0.10)	36.4	43.5
<i>Dumetella carolinensis</i>	I,C,D	0.29 (0.34)	66.7	0.03 (0.06)	18.2	43.5
<i>Mimus polyglottos</i>	I	0.17 (0.19)	50.0	0.03 (0.09)	9.1	30.4
<i>Toxostoma rufum</i>	I	0.11 (0.12)	58.3	0.03 (0.06)	18.2	39.1
<i>Dendroica pinus</i>	P,C	0.06 (0.06)	25.0	0.18 (0.36)	36.4	30.4
<i>Cardinalis cardinalis</i>	I,C,D,S	0.81 (0.64)	91.7	0.30 (0.24)	81.8	87.0
<i>Quiscalus quiscula</i>	I	0.69 (1.58)	33.3	0	0	17.4

Species in bold represent the ten most effective seed dispersers of *Sapium sebiferum* based on foraging observations in adjacent prairie habitats (Table 2-1).

^a Frugivory status as in Table 2-1.

^b Mean number of individuals detected per 50-m-radius point count per visit (n = 7 visits/point to 12 points in Oak Hammock, and 11 points in Mixed Pine-Hardwood).

^c The percentage of 50-m-radius point counts within which the species was detected.

^d The percentage of all forest point counts (OH + MPH) within which the species was detected.

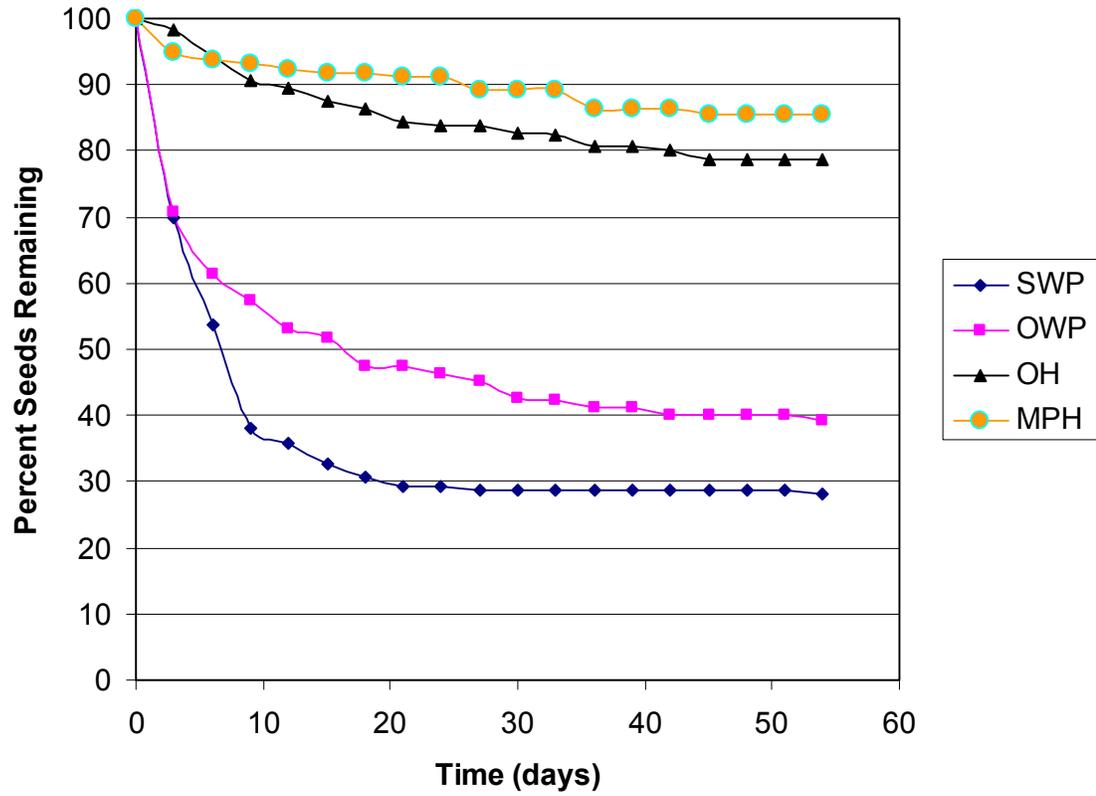


Figure 2-1. *Sapium* seed survivorship in shaded wet prairie (SWP), open wet prairie (OWP), oak hammock (OH), and mixed pine-hardwood (MPH) habitats at Paynes Prairie Preserve State Park, Alachua County, FL. Time 0 = 22 October, 2002.

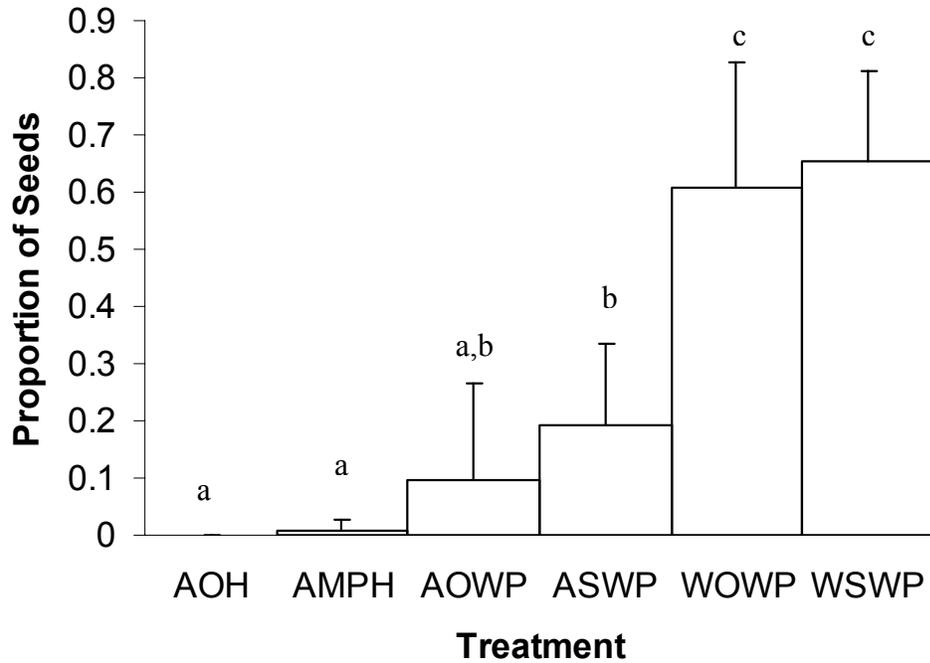


Figure 2-2. Mean proportion of *Sapium* seeds (\pm SD) that germinated. Treatment groups from left to right include acid treated seeds in oak hammock (AOH), mixed pine-hardwood (AMPH), open wet prairie (AOWP) and shaded wet prairie (ASWP). Water soaked treatments were applied to open wet prairie (WOWP), and shaded wet prairie (WSWP). Treatments with the same letters above error bars are not significantly different at $\alpha = 0.05$. Figure modified from Chapter 1.

	Habitat			
	<u>SWP</u>	<u>OWP</u>	<u>MPH</u>	<u>OH</u>
TP ₁	0.802	0.802	0.802	0.802
	↓	↓	↓	↓
TP ₂	0.340	0.340	0.660	0.660
	↓	↓	↓	↓
TP ₃	0.281	0.391	0.854	0.786
	↓	↓	↓	↓
TP ₄	0.194	0.096	0.006	0
	↓	↓	↓	↓
TP ₅	0.071	0.091	0	0
	↓	↓	↓	↓
OPR	0.001	0.001	0	0

Figure 2-3. Spatial dynamics of recruitment through seedling establishment for *Sapium sebiferum* in shaded wet prairie (SWP), open wet prairie (OWP), mixed pine-hardwood (MPH) and oak hammock (OH). The values in boxes represent overall process-specific transition probabilities (TPs), the product of which gives the overall probability of recruitment (OPR) for *S. sebiferum* in that habitat. TP₁ is the probability that a seed is bird dispersed, TP₂ is the probability of seed dispersal to each of the four habitats, TP₃ is the probability that a dispersed seed is not predated, TP₄ is the probability that a seed will germinate, and TP₅ is the probability that a germinated seed will establish. TP₁ and TP₂ were obtained through foraging observations at *S. sebiferum* trees; all other TPs obtained through experimental data pooled across all 12 sites in that habitat. Diagram based on Figure 2 in Rey and Alcántara (2000).

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BIOGRAPHICAL SKETCH

Ivan Samuels was born in San Francisco, California, where he developed an interest in birds and nature at the age of 12. He completed Bachelor of Arts degrees in biology and environmental studies at the University of California, Santa Cruz in 1998. After graduating, Ivan pursued numerous field-work opportunities, studying birds in both temperate and tropical locations, with an emphasis in conservation.