

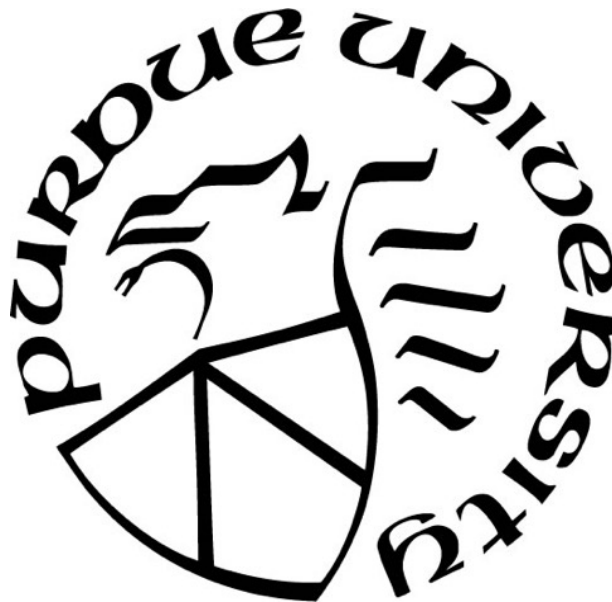
**RESTORATION OF MARITIME FORESTS: EVALUATING LIMITING
FACTORS OF *QUERCUS VIRGINIANA* (LIVE OAK) REGENERATION**

by
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A Thesis

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*Dedicated to my family who inspire me and
encourage my curiosity and love of science and nature.*

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ABSTRACT

Author: Thyroff, Emily C. MS

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Title: Restoration of Maritime Forests: Evaluating Limiting Factors of *Quercus virginiana* (Live Oak) Regeneration

Committee Chair: Douglass Jacobs

Maritime forests are a critical interface between ocean and terrestrial ecosystems, providing important ecosystem services and functions. Along the U.S. southern Atlantic coast, maritime forests are dominated by *Quercus virginiana*. Maritime forests and *Q. virginiana* have been heavily impacted by conversion to agriculture, residential development, and pine stands. Southern pine beetle outbreaks have led to salvage and thinning silvicultural treatments of pine stands which offer an opportunity to restore more complex maritime forests. This research project is comprised of two experiments which allowed me to study the performance of planted *Q. virginiana* seedlings in response to (1) animal browse, (2) competing vegetation, and (3) varying overstory pine canopies. For both experiments, one-year-old bareroot seedlings were planted as split-plot experimental designs. The first experiment evaluated control of deer browse (fenced and not fenced whole plots) and competing vegetation (0, 1, and 2-yr vegetation control subplots) as independent variables. Overall seedling survival was 60% after two years. There was a significant interaction between deer browse and competing vegetation for seedling height, diameter, crown width, and lateral branches. Seedlings were larger for all response parameters when fenced with vegetation control. Vegetation control significantly improved seedling performance only in fenced plots, indicating a shift in pressure from herbivory to competition when deer were excluded. Foliar nitrogen (N) was significantly greater in fenced plots than non-fenced plots and in 2-yr vegetation control subplots than non-weeded subplots. The second experiment evaluated varying pine overstories (clearcut, heavy thin, light thin, and no thin whole plots) and competing vegetation control (0 and 2-yr vegetation control subplots). Overall seedling survival was 78% after one growing season, with clearcut plots at the greatest survival (83%) and no thin at the lowest (72%). Seedling growth and foliar nitrogen were significantly greater in clearcut plots followed by the heavy

thin, light thin, and no thin plots. Vegetation control consistently promoted seedling height, but was only beneficial to diameter and crown width in clearcut/heavy thin plots. *Q. virginiana* seedlings demonstrated plasticity in their ability to acclimate to the varying microclimates created by silvicultural treatments, as demonstrated by light response curves, stomatal density, and specific leaf area. These results highlight the importance of fencing to remove deer browse, introducing light in the understory, and further improving seedling performance by removing competing vegetation.

CHAPTER 1. INTRODUCTION

1.1 Maritime Forests and the Importance of *Quercus virginiana*

Coastal ecosystems are dynamic and depend on connectivity for overall function and disturbance resiliency (Stanturf et al. 2007; Sheaves 2009; Buelow et al. 2017). Around the world, coastal ecosystems are valued as biodiverse hotspots and for disturbance resiliency (Ribeiro et al. 2009; Chen et al. 2017; Habel et al. 2017). Coastal ecosystems including maritime forests, however, are heavily impacted by humans (Weinstein et al. 2007; Ribeiro et al. 2009; Habel et al. 2017). Maritime forests are coastal woody ecosystems that develop on barrier islands and adjacent mainland. Diverse flora, fauna, and human development depend on the maritime forest ecosystems. In these ecoregions, dominant forest species must withstand harsh coastal stressors such as strong winds, saltwater spray, flooding, nutrient-poor soils, wildfires, and low freshwater availability (Naumann et al. 2009; Kurtz et al. 2013; Bissett et al. 2016; Chen et al. 2017). Additionally, the maritime forest communities are defined by latitude, island geography, dune system stability, and disturbance history (Bellis 1995; Evans and Keen 2013). Given the coastal context and complexity, maritime forests interface with the ocean, marshes, riparian areas, and estuaries (Figure 1.1).

In the United States, maritime forests of the southern Atlantic coast (North Carolina to Florida) are identified as regions of physiographical significance (Albers and Alber 2003) and serve critical functions such as stabilizing soil, recharging groundwater, and providing wildlife habitat for endangered or threatened species (Bellis 1995; Jones et al. 2013; Kurtz et al. 2013). Stabilizing sandy coastal soils minimizes erosion and maximizes disturbance resiliency (Bellis 1995; Kurtz et al. 2013). Recharging freshwater resources is critical since it is limited along the coast (Jones et al. 2013). Lastly, wildlife species that rely on maritime forest ecosystems for habitat include the wood stork (endangered), piping plover (threatened), red cockaded woodpecker (threatened), painted bunting (concerned), and northern yellow bat (concerned) (Figure 1.2). Additionally, some species preferentially

utilize Spanish moss (*Tillandsia usneoides*) for habitat, which is more abundant in old growth, maritime forests (USDA NRCS National Plant Data Center, 2003).

Southern maritime forests are dominated by *Quercus virginiana* (live oak) (Figure 1.3), a semi-evergreen, keystone tree species. It is resilient to many abiotic stressors of the maritime ecoregion, including saltwater spray, hurricanes, and forest fires (Bourdeau and Oosting 1959; Bratton 1993; Conner et al. 2005). Spanish moss is an integral part of maritime forest structure and *Q. virginiana* is a symbiont of Spanish moss. In addition to wildlife habitat, varying abundance of Spanish moss modifies throughfall and stemfall patterns, which changes soil composition (Rosier et al. 2015) (Figure 1.4). Availability of nutrients and water content in the soil influences microbe activity and plant distribution, which in turn affects the functional diversity of the forests (Smith and McGrath 2011; Rosier et al. 2015).

As a keystone species of maritime forests, *Q. virginiana*, provides habitat for wildlife via shelter including nests, foraging for food, generating shade and cooler temperatures, and protection from predators and/or storms (Bellis 1995; Kurtz et al. 2013). *Q. virginiana* reduces coastal erosion through its extensive root system, semi-evergreen crowns that protect the understory from strong winds, and freshwater recharge to minimize water runoff (Bourdeau and Oosting 1959; Bellis 1995; Jones et al. 2013). Lastly, it improves ecosystem stability via resistance to coastal abiotic stressors (Conner et al. 2005; Kurtz et al. 2013). Thus, conservation and restoration of maritime forests, and specifically considering *Q. virginiana*, is important for provisioning, regulating, and cultural ecosystem services as well as maintaining maritime forest ecosystem functioning.

1.2 Threats to Maritime Forests and *Q. virginiana*

Barrier islands of the southern Atlantic coast have a long history of human land use and transformation, having been used as foraging grounds, crop plantation fields, pine stands, and for residential development. Maritime forests on barrier islands are ideal for land use and transformation because they occur on more stable areas of the dynamic island sand dunes and coastline (Bellis 1995; Jones et al. 2013). Various land uses have been

implemented for as long as 4,000 years and the forests continue to be heavily impacted throughout its range (Bratton and Miller 1994; Fox et al. 2007).

Due to coastal geography, disturbances, and abiotic stressors, Maritime forests are naturally small, isolated, and fragmented with limited regeneration (Lopazanski et al. 1988); human development amplifies this natural fragmentation (Evans and Keen 2013). For example, expanding paved road systems affect water drainage on islands, which in turn affects the ability of *Q. virginiana* to survive natural disturbances and thrive as part of maritime forests (Conner et al. 2005). As maritime forests become more fragmented, the forests are able to support less biological diversity, which affects the overall maritime forest ecosystem functionality (Albers and Alber 2003). Results from a vegetation survey of barrier islands demonstrated plant diversity on undeveloped barrier islands increases with increasing area (Albers and Alber 2003). Minimizing the effects of fragmentation, therefore, also contributes to maintaining stable and resilient maritime forests (Lopazanski et al. 1988; Evans and Keen 2013).

Many maritime forests were fragmented and cleared for agriculture and later abandoned; the land was then often converted to *Pinus taeda* (loblolly pine) and *Pinus elliottii* (slash pine) stands. Similarly, in other regions of the world (e.g., Mediterranean, Scandinavia, South America), pine stands were established for afforestation, soil stabilization, and economic reasons (Fox et al. 2007; Brockerhoff et al. 2008; Löf et al. 2014; Alday et al. 2017). In the southeast U.S., *P. taeda* is a valuable commercial tree planted for financial return and to minimize erosion (Fox et al. 2007; Brockerhoff et al. 2008). Pines, however, do not perform well with hurricanes or saltwater spray and are at greater risk to disease and southern pine beetle (*Dendroctonus frontalis*) outbreaks (Conner et al. 2005; Nowak et al. 2015; Asaro et al. 2017) (Figure 1.5). Southern pine beetles are one of the most economically destructive native forest pests due to the exponential nature of outbreaks (Watson et al. 2013; Asaro et al. 2017). When there is an active outbreak, salvage and sanitation cuttings are used to harvest the remaining value and prevent the spread (Belanger et al. 1993). Thinning and intensive management can further minimize the potential of future outbreaks (Belanger et al. 1993; Watson et al. 2013; Asaro et al. 2017).

Other threats facing maritime forests and its regeneration include deer browse, non-native species, sea level rise, and climate change. Collectively, these threats have led to severe maritime forest habitat loss and degradation, leading to its current imperiled state (Jones et al. 2013; NatureServe Explorer, 2014). Although the original total area of maritime forests in this region is unknown, inventories estimate about 38,000 ha of undeveloped maritime forests remained in North Carolina to Florida with about 25,000 ha (65%) in Georgia (Mathews et al. 1980; Lopazanski et al. 1988). Conservation efforts help maintain the remaining maritime forests. Restoration efforts, however, are required in areas where natural regeneration is failing or where the forest type has been converted. Although *Q. virginiana* is a dominant, charismatic species in this region, little is known about its biology and ecophysiology, especially in a maritime forest regeneration and restoration context. This lack of knowledge prevents forest and conservation managers from confidently implementing silvicultural techniques that will lead to successful maritime forest restoration.

1.3 Limiting Environmental Factors

Landscape changes and reduction of predators have led to high populations of white-tailed deer (*Odocoileus virginianus*) in most forest regions of the eastern United States (Russell et al. 2001). Increased deer populations have major negative effects on forest regeneration and especially oak regeneration (Abrams and Mostoller 1995; McEwan et al. 2011; Taggart and Long 2015). Increased herbivory can negatively affect forest stand development by reducing recruitment and shifting regeneration composition towards unpalatable species (Russell et al. 2001; Owings et al. 2017). When underplanting nutrient rich, nursery-grown seedlings, the newly planted trees are more susceptible to browse (Burney and Jacobs 2011; Woolery and Jacobs 2014; Owings et al. 2017). On barrier islands, the negative effects of herbivory are enhanced because of inherent coastal abiotic stressors (Taggart and Long 2015). Understanding and quantifying the effects of browse on *Q. virginiana* will elucidate potential benefits of reducing browse on maritime forest regeneration.

Competition between planted seedlings and other regenerating vegetation limits the availability of critical environmental resources such as soil nutrients, water, and light (Wagner and Zasada 1991). Reduced resources from competition impairs basic plant physiological processes which restricts the ability of seedlings to establish, perform, and survive (Salifu et al. 2009; Grossnickle 2012). In clearcuts or heavy overstory removal treatments, oaks are especially sensitive because oak seedlings can be quickly suppressed by competition that thrive with increased light (Dey et al. 2008). Therefore, it is often necessary to reduce competition within clearcuts and heavy overstory removal treatments. Competing vegetation can be removed chemically or mechanically with various methods. Additionally the timing, frequency, target species, and forest type need to be consider as this changes the effectiveness of competition removal (Wagner and Zasada 1991). Therefore, the method, intensity, and duration of competing vegetation removal should be studied specifically for maritime forests and *Q. virginiana*.

Lastly, seedling shade tolerance and light availability contributes to seedling growth in forests with respect to growth and development (Canham et al. 1990; Pacala et al. 1996; Soto et al. 2017). Ecophysiology, is the study of plant function and interrelatedness to the environment, such as light. Limited light can reduce photosynthesis and carbon assimilation, whereas excess light can be damaging and lead to photoinhibition (Long et al. 1994; Gómez-Aparicio et al. 2006). Species-specific light requirements and response to varying light levels is critical to defining a species' regeneration niche and predicting the effect of forest management (Gómez-Aparicio et al. 2006; Brown et al. 2014; Soto et al. 2015). Yet shade tolerance dynamics are not fully understood in *Q. virginiana*. Forest management includes silvicultural techniques that manipulate light availability and therefore species abundance (Dey et al. 2008; Kern et al. 2017). For example in closed canopy pine stands with low light levels reaching the understory, thinning the pine trees can introduce light and aid in the conversion of monoculture stands to more diverse native forests species (Parker et al. 2001). Understanding light requirements and the ecophysiology of *Q. virginiana* is important to create specific, maritime forest restoration management prescriptions.

Thus, key factors that limit early establishment success of newly planted seedlings include animal browse, competition from other vegetation, and light availability (Stange and Shea 1998; Tripler et al. 2002; Jacobs et al. 2004; Oliet and Jacobs 2012; Soto et al. 2017). The effects of resource availability and interactions between light, water, nutrients, and browse are complex, however, and highly variable depending on species and ecosystems (Canham et al. 1990; Soto et al. 2017). Additionally, successful maritime forest restoration requires ecological and physiological knowledge of the dominant species, *Q. virginiana*. There is a need to understand browse, competition, and light with respect to *Q. virginiana* regeneration, consider silvicultural techniques to address these factors, and develop efficient methods to plant seedlings for successful and cost-effective maritime forest restoration. Effective restoration and management of maritime forests will help maintain biodiversity and maritime forest ecosystem function.

1.4 Justification and Objectives

There is significant local interest in restoring southern maritime forests and *Q. virginiana* regeneration due to their associated ecological services and functions. However, conditions for optimum maritime forest regeneration are not well understood. Management practices such as protection from animal browse, competition removal, and overstory manipulation need to be developed to successfully and efficiently restore maritime forest. Within the historic maritime forest range, there are extensive areas of pine stands experiencing, or at risk of, southern pine beetle outbreaks. These pine stands have potential to be converted and restored back to maritime forests to promote resilient coastal ecosystems.

Although the ecophysiology of *Q. virginiana* is not well understood, oaks are generally intermediate in shade tolerance (Dey et al. 2008, 2012; Kern et al. 2017). Therefore, natural *Q. virginiana* regeneration is likely to be most effective through colonization in gaps after moderate overstory canopy disturbance. Clearcutting or other large-scale disturbance will likely promote regeneration of shade intolerant pioneer species such as pine and less of the desirable *Q. virginiana*. Clearcuts, however, are required to reduce the spread of southern pine beetle outbreaks. Additionally, lack of natural regeneration and establishment of *Q. virginiana* in the understory is an identified problem within the maritime forest range. Thus,

artificial regeneration by planting nursery-grown seedlings will be beneficial to achieve successful oak establishment.

This research project studies the performance of planted *Q. virginiana* seedlings in response to (1) animal browse, (2) competing vegetation, and (3) varying overstory pine canopies. These research objectives will provide critical baseline ecophysiology and silvicultural knowledge of *Q. virginiana* to promote successful maritime forest restoration (Figure 1.6). Two experiments were carried out at Cannon's Point Preserve on St. Simon's Island, Georgia. In the first experiment (Chapter 2), I evaluated the relative influence of fencing to eliminate animal browse and vegetation control to remove competing vegetation on *Q. virginiana* seedling performance in clearcut pine stands. In the second experiment (Chapter 3), I evaluated *Q. virginiana* seedling performance and ecophysiology in response to varying overstory canopy density of pine stands and vegetation control to remove competing vegetation. In Chapter 4, I synthesize the key conclusions from these two experiment chapters and suggest priorities for future research.



Figure 1.1 Aerial photo of maritime forest meeting marsh on St. Simon's Island, Georgia (photo credit: Owen Burney).



Figure 1.2 Red-cockaded woodpecker, painted bunting, and wood stork (The Cornell Lab of Ornithology, 2018)

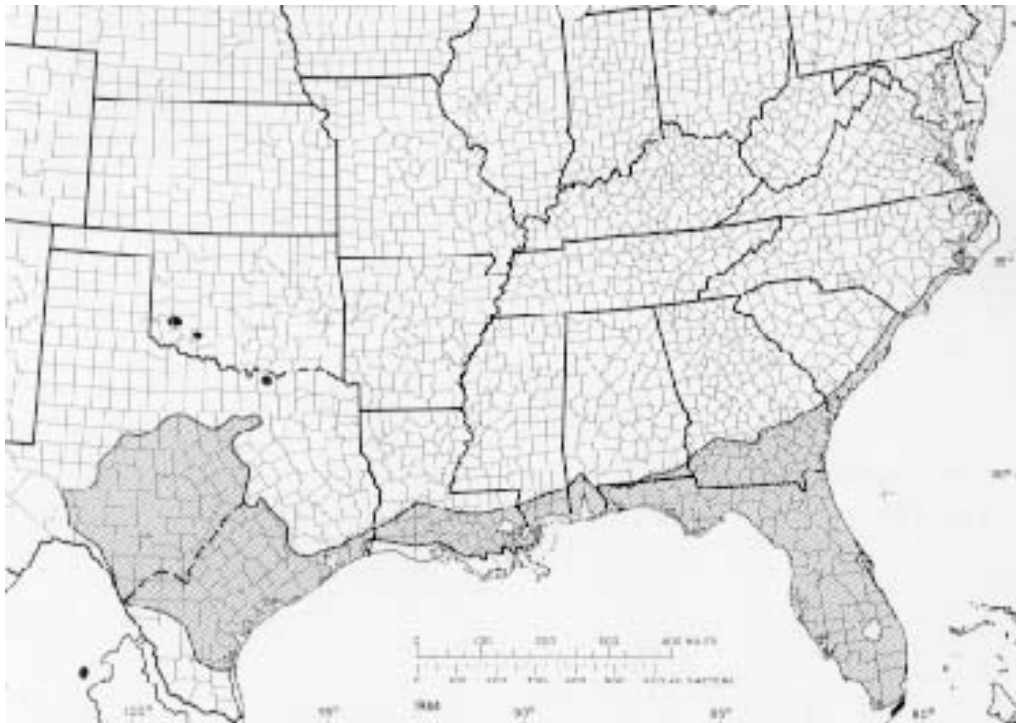


Figure 1.3 Distribution map of *Q. virginiana*. The dark grey illustrates *Q. virginiana* range (Harms, 1990)



Figure 1.4 (Left) *Quercus virginiana* with Spanish moss and (right) close up photo of Spanish moss (photo credit: Emily Thyroff).



Figure 1.5 (Left) *Pinus taeda* stand on St. Simon's Island. (Right) *P. taeda* with *Dendroctonus frontalis* damage (photo credit: Emily Thyroff; UGA Forestry Images).



Figure 1.6 (Left) *Quercus virginiana* seedling in front of mature *Q. virginiana* in a maritime forest. (Right) Sign denoting field site (photo credit: Owen Burney; Emily Thyroff).

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CHAPTER 2. DEER BROWSE AND COMPETITION INTERACT TO AFFECT PERFORMANCE OF PLANTED *QUERCUS VIRGINIANA* SEEDLINGS

2.1 Abstract

Maritime forests along the U.S. southern Atlantic coast, which are dominated by *Quercus virginiana* (live oak), have been heavily impacted by conversion to agriculture, residential development, and pine stands. Clearcut salvage of abandoned pine stands due to southern pine beetle outbreaks offers an opportunity to restore maritime forests. We evaluated the influence of white-tailed deer (*Odocoileus virginianus*) browse and competing vegetation on regeneration success of *Q. virginiana* planted into salvage clearcuts on a barrier island in coastal Georgia. One-year-old bareroot seedlings were planted as a split-plot experimental design with control of deer browse (fenced and not fenced whole plots) and competing vegetation (0, 1, and 2-yr vegetation control subplots) as independent variables. Seedling survival was 60% after two years and did not differ among treatments. There was an interaction between deer browse and competing vegetation for seedling height, diameter, crown width, and lateral branches. Seedlings were larger for all response parameters when fenced and with vegetation control. Vegetation control improved seedling performance only in fenced plots, indicating a shift in pressure from herbivory to competition when deer were excluded. Foliar nitrogen (N) was greater in fenced plots than non-fenced plots and in 2-yr vegetation control subplots than non-vegetation control subplots. These results highlight the importance of fencing to remove deer browse pressure and that seedling performance in fenced plots is further augmented with vegetation control. These findings will aid in developing prescriptions to promote *Q. virginiana* regeneration and maritime forest restoration along the southern Atlantic coast.

2.2 Introduction

Globally, coastal ecosystems are valued as biodiverse hotspots and for disturbance resiliency (Ribeiro et al. 2009; Chen et al. 2017; Habel et al. 2017). Coastal ecosystems are dynamic and depend on connectivity for overall function and services (Sheaves 2009;

Buelow et al. 2017). Of coastal ecosystems, maritime forests are a critical interface between the oceans and terrestrial ecosystems. In the United States, maritime forests of the southern Atlantic coast (North Carolina to Florida) are comprised of late successional coastal species on barrier islands and adjacent mainland (Lopazanski et al. 1988; Bellis 1995). Geography, disturbances, and coastal abiotic stressors are defining characteristics of maritime forests. Stressors influential on forest community structure include saltwater spray, flooding, saltwater inundation, and nutrient-poor soils (Naumann et al. 2009; Kurtz et al. 2013; Bissett et al. 2016; Chen et al. 2017). As a result, maritime forests are naturally small, isolated, and fragmented with limited regeneration (Lopazanski et al. 1988). Identified as regions of physiographical significance, maritime forests are dynamic habitats providing unique ecosystem functions and services (Albers and Alber 2003). Major functions and services include stabilizing soil, recharging groundwater, and flora and fauna biodiversity (Bellis 1995; Jones et al. 2013; Kurtz et al. 2013).

Coastal ecosystems including maritime forests have been heavily impacted globally by humans (Weinstein et al. 2007; Ribeiro et al. 2009; Habel et al. 2017). Along barrier islands of the southern Atlantic coast there is a long history of human land transformation (Bratton and Miller 1994; Fox et al. 2007), especially the more stable land of barrier islands where maritime forests develop (Bellis 1995; Jones et al. 2013). Conservation efforts help maintain the remaining maritime forests. Restoration efforts, however, are required in areas where natural regeneration is failing or where the forest type has been converted. For example, maritime forests were frequently cleared for agricultural fields and later abandoned due to low productivity and economic shifts. Abandoned agricultural land was often converted to stands of *Pinus taeda* (loblolly pine), a valuable, commercial tree in the southeast planted in timber stands for financial return and to minimize erosion (Fox et al. 2007; Brockerhoff et al. 2008). Pines, however, are prone to hurricane damage and do not perform well with saltwater spray and inundation, which are defining characteristics of barrier islands (Conner et al. 2005). Additionally, when pines are stressed in poorly managed, dense monocultures, the stands are at greater risk of disease and southern pine beetle (*Dendroctonus frontalis*) outbreaks (Nowak et al. 2015; Asaro et al. 2017). Due to the exponential and destructive nature of outbreaks, infected sites are typically clearcut to

mitigate the outbreak and to salvage residual timber value (Belanger et al. 1993; Watson et al. 2013; Asaro et al. 2017). Clearcuts provide the opportunity to convert unproductive, abandoned, and/or at end of rotation pine stands back to maritime forest. Restoration of maritime forest will reduce fragmentation, increase diversity, and enhance important ecosystem services required to maintain robust coastal ecosystems (Lopazanski et al. 1988; Albers and Alber 2003; Evans and Keen 2013; Kern et al. 2017).

Maritime forests of the southern Atlantic coast (North Carolina to Florida) are dominated by *Quercus virginiana* (live oak). *Q. virginiana* is a semi-evergreen, keystone maritime forest species, resilient to many coastal stressors (Bourdeau and Oosting 1959; Bratton 1993; Conner et al. 2005). *Q. virginiana* can dominant the forest canopy with wide-spreading horizontal branches, creating a unique sprawling structure. However, natural regeneration and recruitment of *Q. virginiana*, especially on barrier islands, is often limited (Taggart and Long 2015). Thus, clearcutting of pine stands after southern pine beetle outbreaks offers an opportunity to artificially regenerate *Q. virginiana* seedlings via planting to accelerate maritime forest restoration. Although *Q. virginiana* is a dominant charismatic species in the region, little is known about its regeneration, especially in a maritime forest restoration context. This lack of knowledge prevents forest and conservation managers from confidently implementing silvicultural treatments that may lead to successful maritime forest restoration.

Clearcuts used to mitigate southern pine beetle outbreaks, can create harsh environments for regeneration. When all trees are removed in a clearcut, site conditions change drastically such as light, temperature, and soil moisture. Two key factors that limit early seedling establishment success are animal browse and competition from other vegetation (Stange and Shea 1998; Tripler et al. 2002; Jacobs et al. 2004, 2015b; Oliet and Jacobs 2012). Animal browse has become an increasing concern as landscape changes and reduction of predators have led to a high density of white-tailed deer (*Odocoileus virginianus*) (Russell et al. 2001). Increased deer populations lead to more herbivory, and therefore greater strain on plant communities. Negative effects are especially prominent for oak regeneration as deer prefer palatable oak seedlings (Waller and Alverson 1997;

Wakeland and Swihart 2009; Borkowski et al. 2017). Browsing preference has potential to change forest dynamics as recruitment composition shifts towards less desired species (Abrams and Mostoller 1995; Rossell et al. 2005; McEwan et al. 2011; Taggart and Long 2015). The negative effect of animal browse is enhanced for plant communities on barrier islands because of the ecosystem's inherent abiotic stressors (Taggart and Long 2015). While browse control techniques can be used (e.g., fencing and tree shelters), these can be logistically prohibitive due to maintenance and management costs (Dey et al. 2008; Borkowski et al. 2017). It is important, therefore, to understand and quantify how animal browse affects *Q. virginiana* and determine which methods efficiently minimize negative effects.

Competition between planted seedlings and neighboring vegetation limits the availability of critical environmental resources (Wagner and Zasada 1991) such as soil nutrients, water, and light, which can impair basic plant physiological processes. This in turn restricts the ability of seedlings to establish, grow, and survive (Salifu et al. 2009; Grossnickle 2012). In clearcuts, light is notably increased, which releases competing vegetation from the understory and seed bank. Species are particularly competitive if able to acclimate quickly and take advantage of the increased light and other resources on the clearcut site, often times quickly suppressing oak seedlings (Paquette et al. 2006; Dey et al. 2008; Gardiner et al. 2010). Controlling competition is therefore often deemed necessary in clearcut treatments. Under specific circumstances, however, competition may be beneficial to seedlings by acting as a natural shelter and hiding seedlings from browsing animals or reducing the negative effects of drought or flooding (Gardiner et al. 2010; Borkowski et al. 2017; Oliver et al. 2018). The timing, frequency, target species, and forest type of competition removal is important to consider as each component changes the effectiveness of the removal method (Wagner and Zasada 1991).

We sought to determine how *Q. virginiana* seedlings planted in clearcut pine stands respond to animal browse and competition pressures. Thus, we experimentally evaluated the relative influence of fencing to eliminate deer browse and vegetation control to remove competing vegetation on *Q. virginiana* seedling performance. These results should aid in

development of silvicultural techniques to promote maritime forest restoration with *Q. virginiana*. Specifically, we hypothesized i) *Q. virginiana* seedlings would survive and perform best in fenced plots compared to non-fenced plots because deer browse would be a strong driver of seedling performance; ii) vegetation control for two years would increase seedling performance due to reduced competition compared to zero and one-year of vegetation control; iii) an interaction would occur between fencing and vegetation control such that in fenced plots without deer browse, competition would be a greater driver of seedling performance therefore vegetation control would be more beneficial in fenced than non-fenced plots; iv) a second interaction would occur, non-fenced seedlings in non-vegetation control subplots would perform better than vegetation control subplots as the competing vegetation would act as a barrier to browsing deer.

2.3 Methods

2.3.1 Experimental Site

This experiment was conducted on the north end of St. Simon's Island, Georgia at Cannon's Point Preserve (N 31°15'29" W 81°20'45"), which is a 246-ha wilderness tract managed by the St. Simons Land Trust. Cannon's Point Preserve has some of the last intact maritime forest on St. Simons Island. Many areas on the preserve, however, are dominated by abandoned pine stands. In 2014-15, areas of natural and planted pines were clearcut to salvage timber from an outbreak of southern pine beetles and reduce the future threat. Two clearcut sites were included in the study (Figure 2.1); the northern site was an old agriculture field formerly limed with oyster shells and the southern site was previously an open field or maritime forest. The abandoned pine stands were mostly *P. taeda* (loblolly pine) with some *P. elliotti* (slash pine). Examination of tree rings and cores indicated that the pine stands were approximately 50 years old at time of salvage.

Soils at Cannon's Point Preserve are a mixture of fine sandy soils dominated by Mandarin fine sand and Cainhoy fine sand, with 0-5% slopes. Pottsburg sand and Rutledge fine sand are also present (NRCS United States Soil Survey 2017). Soil samples (two randomly located samples from each of four replicates, where were composited by replicate) were

taken at a depth of 10 – 25 cm to evaluate physical and chemical characteristics using the Mehlich III extraction (Brookside Laboratories). The sites had soil differences creating variability across blocks, especially seen with the calcium standard error (Table 2.1).

The Georgia coastal region receives an average annual precipitation of 114 cm. 2015-2017 received lower annual precipitation at 97.4 cm. Average annual temperature is 20.0 °C with 2015-2017 receiving slightly higher temperatures at 20.4 °C (U.S. Climate Data 2017; Sapelo Island National Estuarine Research Reserve, 2017). Hurricanes Matthew (October 2016) and Irma (September 2017) resulted in increased precipitation, salt water inundation, salt spray, and strong winds during the study period.

Spotlight and browse surveys conducted by St. Simon's Land Trust were used to estimate Cannon's Point Preserve deer population, which was characterized as overpopulated. In 2014 there were estimated 121 deer at the preserve, averaging approximately 1 deer every 2 ha. In 2016 there were estimated 152 deer at the preserve, averaging approximately 1 deer every 1.6 ha.

2.3.2 Plant Material

One-year-old bareroot *Q. virginiana* seedlings were planted in January 2016. The seedlings were obtained from ArborGen Georgia (Louisiana seed source). From baseline morphology analysis ($n = 25$), mean seedling height was 47 cm (± 1.43), diameter was 5 mm (± 0.22), and root to shoot dry mass (g) ratio of 1.23 (± 0.82). The seedlings were sorted prior to planting to increase homogeneity among the seedlings and randomly assigned to plot treatments.

2.3.3 Experimental Design and Treatments

This study was a blocked, split-plot design using a factorial combination of animal browse control (two levels; fence and no fence) and competing vegetation control (three levels; zero, one, or two-years of vegetation control). The whole-plot factor was fencing and the sub-plot factor was vegetation control. There were four blocks, each with two plots. Each plot, 24 x 16 m, was randomly assigned fence (2.5 m height) or no fence and contains the

three vegetation control treatments randomly assigned (Figure 2.2). For vegetation control, competing vegetation was left unmanaged or manually removed for one or two years. Four months after planting (April 2016) the one and two-year vegetation control treatments were treated once with herbicide (glyphosate) 480 g/L with backpack sprayers. Subsequent vegetation control was done mechanically throughout the growing season 3 to 4 times with brush saws and hand clippers.

Seedlings were hand planted via planting bars at 2 m spacing. To maintain planting density and interspecific seedling competition a perimeter of buffer seedlings was planted 2 m from the research seedlings. There was a 50-m minimum buffer from the edge of the plots to the clearcut area to minimize the influence of adjacent pine canopies. Each treatment has a sample size of 20, therefore an overall sample size of 480 seedlings.

2.3.4 Measurements

At the time of planting (December 2015), ground line diameter and height to last live bud were measured with calipers and a meter stick. After each growing season (December 2016, November 2017), diameter and height were re-measured in addition to survival, health status, foliar nitrogen (N), and browse assessments. Survival was binary; a status of “alive” included seedlings with live leaves. Health status noted dieback, chlorosis, and/or insect damage. At the end of the second growing season (November 2017), foliar N was determined by randomly sampling five seedlings per treatment replicate. Three leaves per seedling were composited, dried, weighed, pulverized, and analyzed with an ECS 4010 CHNSO Analyzer (Costech, Valencia, California).

After each growing season (December 2016, November 2017), browse assessments included average crown width, number of lateral branches, estimated percent browse, and type of browse evidence. Average crown width was calculated using the north/south crown width and the east/west crown width. Classification of browse evidence included clean, rough, terminal, or lateral. Classification of foliar and/or branch browse helps with determining the browsing animal. Clean and rough browse classification refers to how the leaves or branch was browsed off of the seedling. Terminal and lateral browse

classification refers to where on the seedling the browse occurred. Clean, lateral browse is typically from rabbits; rough, terminal browse is typically from deer.

At the peak of vegetation cover on site (August/September) each year, six seedlings from each treatment were randomly selected for a 1-m² plot vegetation survey to assess percent competing vegetation cover within each plot (Appendix A2). In addition to the vegetation surveys, natural regeneration of tree species was tallied in June 2018 to assess which species naturally regenerated in the non-vegetation control subplots. For natural regeneration, all tree species were counted in non-vegetation control subplots of fenced and non-fenced plots.

2.3.5 Statistical Analysis

Only 2017 data was analyzed given that two growing seasons were needed for all three vegetation control treatments to be implemented; see appendix for 2016 data (Appendix A4, A5). Seedling performance (diameter, height, foliar N), browse assessment (crown width, lateral branches), and vegetation survey (competition cover and height) dependent variables were analyzed separately with general linear mixed models, with block as a random factor. A two-way analysis of variance (ANOVA) and type III sum of squares was used for each model. Natural regeneration was analyzed using a one-way ANOVA and type III sum of squares. Residuals from all response variables were tested to ensure normality and homogeneity of variance based on ANOVA assumptions. When significant treatment effects were detected ($p \leq 0.05$), Tukey's HSD test was used to test for pairwise comparisons ($\alpha = 0.05$). Logistic regression model was used to analyze survival. All data was analyzed with R software (R Version 3.2.4, R Core Team, 2017).

2.4 Results

2.4.1 Seedling Survival and Growth

Initial height and diameter of planted seedlings were similar across all treatments with a mean height of 47 cm (± 0.9) and a mean diameter of 4.6 mm (± 0.1) (Appendix A3). Survival in 2017 after two growing seasons was 60 % (± 5) with no difference among treatments. There was an interaction of fencing and vegetation control for *Q. virginiana*

seedling height ($F_{2,283} = 9.21$, $p < 0.001$) and diameter ($F_{2,283} = 17.67$, $p < 0.001$). While seedling height and diameter were greater in fenced plots than non-fenced plots, vegetation control only increased height and diameter in fenced plots (Figure 2.3). Within the fenced plots, height and diameter were greater in vegetation control subplots (one and two-years of removal) compared to non-vegetation control (zero-year of removal) subplots. Mean fenced/vegetation control seedling height was 123 cm (± 6.2) and diameter 21 mm (± 1.1) compared to fenced/non-vegetation control seedling height of 92 cm (± 6.0) and diameter 12 mm (± 0.8). Non-fenced seedling height and diameter did not vary significantly between the vegetation control treatments with an average height of 38 cm (± 4.5) and diameter of 7 mm (± 0.3).

2.4.2 Foliar N

Q. virginiana seedling foliar N concentration (%) did not show a significant interaction of fencing and vegetation control; however, both main effects were significant (Figure 2.4). Foliar N in fenced plots was 1.80 % (± 0.04) compared to 1.66 % (± 0.06) in non-fenced plots was greater in fenced plots than non-fenced plots ($F_{2,114} = 5.61$, $p = 0.020$). Foliar N was greater with two-years of vegetation control compared to non-vegetation control subplots ($F_{2,283} = 6.39$, $p = 0.002$). Mean foliar N in two-year vegetation control subplots was 1.85 % (± 0.73) compared to 1.64 % (± 0.07) foliar N in non-vegetation control subplots.

2.4.3 Browse Assessments

Browse evidence of non-fenced seedlings increased to 97% and fenced seedling browse at < 1 % by the end of this study. Browse evidence in fenced plots were only clean and lateral, whereas browse evidence in non-fenced plots were a combination of clean, rough, terminal, and lateral (Appendix A6).

There was an interaction of fencing and vegetation control for *Q. virginiana* crown width ($F_{2,283} = 28.79$, $p < 0.001$) and number of lateral branches ($F_{2,283} = 9.95$, $p < 0.001$). Seedling crown width and lateral branches were greater in fenced plots than non-fenced plots (Figure 2.5). Within the fenced plots, crown width and lateral branches were greater in vegetation

control subplots (one and two-years) compared to non-vegetation control (zero-year) subplots. Mean fenced/vegetation control seedling crown width was 76 cm (± 4.4) cm with 6 (± 0.5) lateral branches compared to fenced/non-vegetation control seedling crown width of 36 cm (± 3.1) with 4 (± 0.5) lateral branches. Non-fenced seedling crown width and number of later branches did not vary between the vegetation control treatments, with an average crown width of 11 cm (± 1.0) with 1 (± 0.2) lateral branch.

2.4.4 Vegetation Surveys and Natural Regeneration

Competing vegetation percent cover and average height did not show a significant interaction of fencing and vegetation control; however, the vegetation control main effect was significant (Figure 2.6). Percent vegetation cover ($F_{2,66}=29.52$, $p<0.001$) and mean vegetation height ($F_{2,66}=21.43$, $p<0.001$) were greater in the non-vegetation control compared to the two-years of vegetation control subplots. One year of vegetation control had less percent vegetation cover than non-vegetation control but not significantly different average vegetation height.

For natural tree species regeneration, the only species present were *Persea borbonia* (PEBO, red bay), *Pinus taeda* (PITA, loblolly pine), *Quercus hemisphaerica* (QUHE, laurel oak), and *Quercus virginiana* (QUVI, live oak). There was more natural regeneration of tree species in fenced plots compared to not fenced plots ($F_{1,28}=13.73$, $p=0.001$) (Figure 2.7). Natural regeneration of *Q. virginiana* only occurred in fenced plots.

2.5 Discussion

2.5.1 Restoration Benefits of Fencing and Weeding

Seedling establishment during the first few years after planting is critical to the performance of forest regeneration (Jacobs et al. 2004, 2015a; Paquette et al. 2006; Grossnickle 2012). Our results indicate the importance of reducing animal browse and competing vegetation in promoting restoration of *Q. virginiana*. Although there were no significant effects of the treatments on survival, many non-fenced seedlings were in poor condition with just a few leaves and are not likely to survive long term. In support of our hypotheses, seedlings in fenced plots were approximately 2.5 times greater in height and

diameter and over 5 times greater in crown width than seedlings in non-fenced plots. The differences between *Q. virginiana* seedling height, diameter, crown width, and lateral branches with respect to fenced and non-fenced plots illustrate the high pressure from deer browse (Appendix A6). This positive seedling response to fencing contradicts findings of Taggart and Long (2015) that deer were not over browsing the understory vegetation, including *Q. virginiana* seedlings, on Bald Head Island, NC.

Although vegetation control in absence of browsing improved seedling development in fenced plots, herbivory was a greater driver of *Q. virginiana* performance than competition without fencing. Other studies have found deer have substantial negative effects on native hardwood seedling performance, and therefore regeneration success (Stange and Shea 1998; Russell et al. 2001; Russell et al. 2005). A mechanism by which deer decrease seedling performance is reduction of photosynthetic tissue through browse of terminal and lateral branches. When seedlings lose photosynthetic tissues, they rely on stored nutrients to regrow leaves therefore depleting nutrients for other development (Close et al. 2004; Woolery and Jacobs 2014). This in turn reduces seedling height, crown width, and ability to allocate resources to continual growth and development (e.g., diameter and foliar N). Height and diameter of regenerating seedlings is greater in areas with lower deer densities (Ward et al. 2000; Russell et al. 2001; Horsley et al. 2003; Shelton et al. 2014; Owings et al. 2017; Maltoni et al. 2019). Additionally, when deer browse has been sustained for an extensive period, the seed bank may be depleted of desired species such that natural regeneration is low even when browsing is reduced via exclosures or deer population (Côté et al. 2004).

Further supporting our hypotheses, fenced seedlings within vegetation control subplots were approximately 1.5 times greater in height and diameter and 2 times greater in crown width than seedlings in non-vegetation control subplots. Vegetation control to reduce competition has positive effects on native hardwood seedling performance and therefore regeneration and restoration (Davis et al. 1999; Wagner et al. 2006; Gardiner et al. 2010). However, vegetation control only improved seedling performance in fenced plots (Figures 2.3 and 2.5), due to the strong effect of animal browse. The interaction of fencing and

vegetation control illustrates the shift of pressures on seedling performance. In fenced plots, herbivory was absent (of both planted trees and competing vegetation); therefore, competition became a significant driver of *Q. virginiana* performance. A mechanism by which competition reduces growth is by reducing light, nutrients, and soil moisture available to seedlings (Kern et al. 2012). In non-fenced plots, however, herbivory was present to the extent that vegetation control to reduce competition did not improve seedling performance. We did not find support for the second predicted interaction that in non-fenced plots, seedlings may perform better in treatments without vegetation control as the competition may act as a barrier to deer browse (Borkowski et al., 2017; Maltoni et al., 2019). This result is likely due to high deer populations, on an isolated barrier island with limited food resources, resulting in high levels of herbivory where most vegetation was browsed (Close et al. 2004; Côté et al. 2004).

The rough, terminal and/or lateral browse common across the non-fenced plots was characterized as deer (*Odocoileus virginianus*). When comparing deer browse in fenced and non-fenced plots it is common for non-fenced plots to have significantly greater deer browse (Owings et al. 2017; Burney and Jacobs 2018). The 1% browse evidence in fenced plots were clean and lateral, which was attributed to rabbits. Both eastern cottontail (*Sylvilagus floridanus*) and marsh rabbit (*Sylvilagus palustris*) are present on St. Simon's Island. Therefore, fencing did exclude deer, but did not completely exclude rabbits.

After two growing seasons, there were no differences between one or two-years of vegetation control for seedling performance. While development of competing vegetation percent cover and height occur quickly, changes in plant performance may take longer to manifest. Treatment differences between one and two-years of vegetation control may come with time as there were trends of greater performance in two years of vegetation control compared to one year. Vegetation control for two years, however, resulted in greater foliar N than non-vegetation control subplots. Greater foliar N in fenced and vegetation control plots illustrated the importance of management at clearcut restoration sites. As an essential macronutrient, N is commonly the most limiting element for plants and greater foliar N is commonly correlated with overall increased seedling performance

(Uscola et al. 2015; Soto et al. 2017) because it is critical to performance processes such as the construction of amino acids, nucleic acids, and hormones (Lambers et al., 2008). Additionally, N is fundamental in chlorophyll and therefore required for photosynthesis (Holste et al. 2011; Lambers et al., 2008).

2.5.2 Management Implications and Conclusions

Our research provides evidence that restoration of maritime forests is possible when clearcuts are necessary (i.e. due to pine beetle outbreaks). Clearcuts often create harsh, competitive environments that can be difficult to reestablish, especially for hardwoods (Dey et al. 2008). Planting seedlings offers a first regeneration step in restoring degraded maritime forests or abandoned pine stands/agricultural land. In our study, natural tree species regeneration was greater in fenced plots but the regenerating species were dominated by *P. taeda* and *Q. hemisphaerica* rather than the target species *Q. virginiana*. Thus, artificial regeneration was needed to encourage *Q. virginiana* regeneration. Further, our results compliment other studies that cite additional tools such as deer and competition control being necessary when underplanting oaks (Kern et al. 2012; Löf et al. 2012). We found planting success of *Q. virginiana* in clearcuts with fencing to remove animal browse and further success within fenced plots with vegetation control to reduce vegetation competition.

Tree regeneration and recruitment is a critical mechanism for future resilient forests, as trees, especially oaks, are foundational species that support many other ecosystem components (Gardiner et al. 2010; Reyer et al. 2015). Maintaining successful regeneration and restoration of native forests is naturally complex and has become increasingly difficult. Global climate change adds an additional layer of complexity and increases the need to have resilient forest ecosystems with adaptive capacity (Jacobs et al. 2015b). Further, natural climate solutions such as reforestation and restoration contribute to mitigating climate change through carbon sequestration (Griscom et al. 2017).

Maritime forests are valuable coastal ecosystems due to the various services and functions the forests provide. The ability to restore and encourage healthy and robust maritime forests

can increase coastal resiliency, which is especially important in the era of climate change. An improved understanding on limiting factors to *Q. virginiana* regeneration will allow land managers to make informed decisions on maritime forest restoration to ensure the future of this important forest ecosystem. Understanding the benefit of artificially regenerating *Q. virginiana*, fencing to remove deer browse, and vegetation control to reduce competition will aid in development of management prescriptions that promote *Q. virginiana* regeneration and maritime forest restoration. Further, these conclusions may have implications for other semi-evergreen species in regions with strong herbivory and competing vegetation.

2.6 References

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Figure 2.1 Cannon's Point Preserve (managed by the St. Simons Land Trust) on the north end of St. Simons Island, Georgia. Yellow rectangles mark the two clearcut experimental site locations.

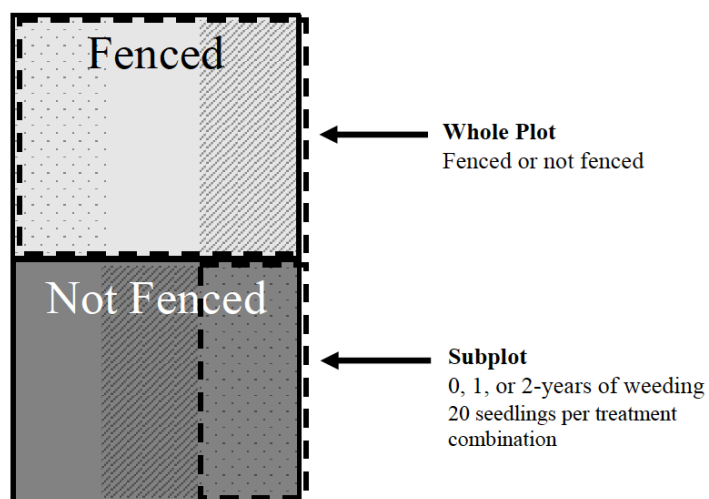


Figure 2.2 Experimental design layout for a replication (block). Two browse treatments (fenced and not fenced) and three levels of vegetation control (zero, one, and two-years of control). Twenty seedlings per treatment.

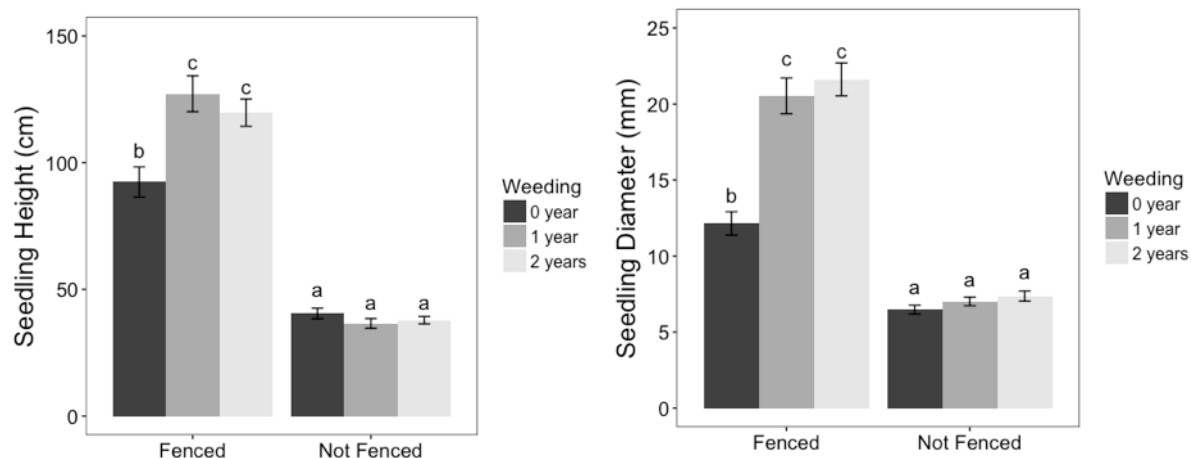


Figure 2.3 Mean (\pm SE) height (cm) and diameter (mm) of *Q. virginiana* seedlings after two growing seasons planted in fenced or non-fenced plots. Seedlings had competing vegetation removed for zero, one, or two-years. Different letters indicate significant differences among treatments ($\alpha = 0.05$).

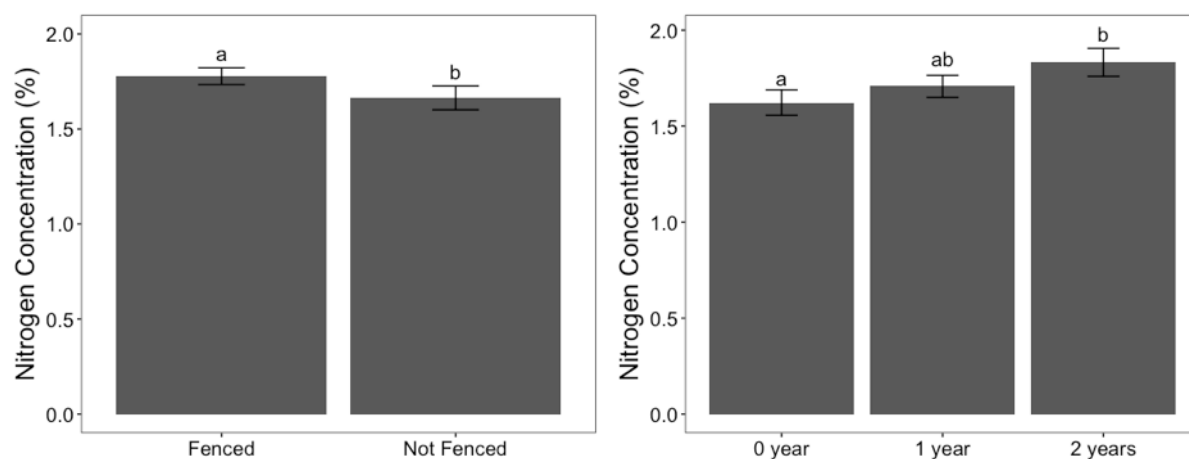


Figure 2.4 Mean (\pm SE) foliar N concentration (%) of *Q. virginiana* seedlings after two growing seasons planted in fenced or non-fenced plots. Seedlings had competing vegetation removed for zero, one, or two-years. Different letters indicate significant differences among treatments ($\alpha = 0.05$).

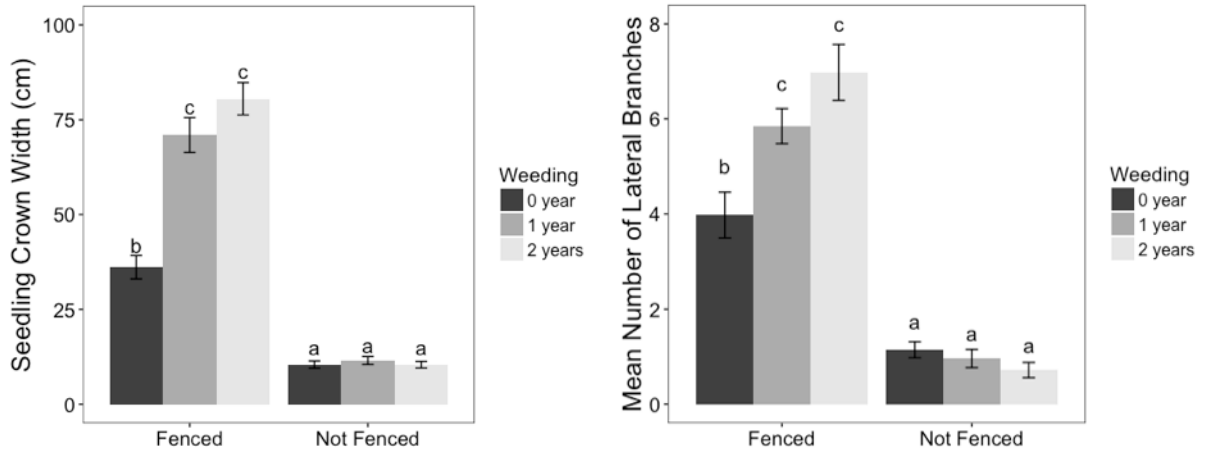


Figure 2.5 Mean (\pm SE) crown width (cm) and number of lateral branches of *Q. virginiana* seedling after two growing seasons planted in fenced or non-fenced plots. Seedlings had competing vegetation removed for zero, one, or two-years. Different letters indicate significant differences among treatments ($\alpha = 0.05$).

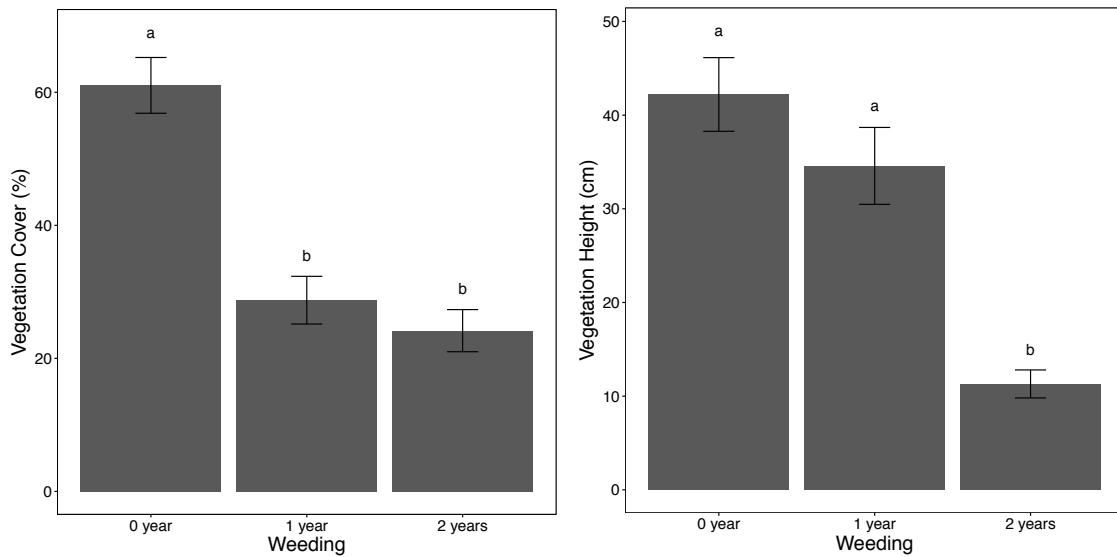


Figure 2.6 Mean (\pm SE) vegetation cover (%) and vegetation height (cm) of competing vegetation in a 1 m² survey around *Q. virginiana* seedlings. Different letters indicate significant differences among treatments ($\alpha = 0.05$).

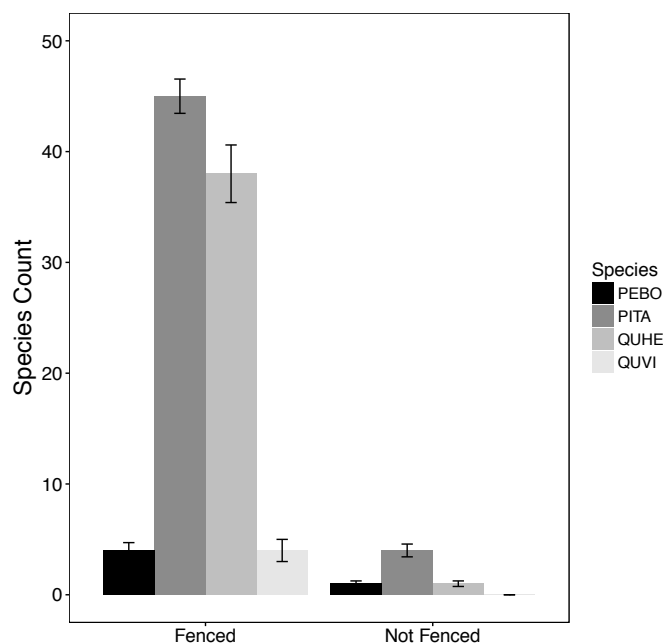


Figure 2.7 Number of natural regenerating individuals in non-weeded subplots within fenced and non-fenced plots. PEBO = *Persea borbonia* (red bay). PITA = *Pinus taeda* (loblolly pine). QUHE = *Quercus hemisphaerica* (laurel oak). QUVI = *Quercus virginiana* (live oak).

Table 2.1 Analysis of soils at the southern and northern sites using the Mehlich III extraction, sample size of 4.

Chemical characteristic	
Organic Matter (%)	4.3 (\pm 0.2)
pH	5.5 (\pm 0.7)
CEC (ME/100 g)	7.6 (\pm 3.5)
Estimated Nitrogen (kg/ha)	104.8 (\pm 2.1)
NO3 (ppm)	13.7 (\pm 1.4)
NH4 (ppm)	8.1 (\pm 2.6)
Phosphorous (ppm)	223.0 (\pm 4.4)
Potassium (ppm)	23.8 (\pm 3.4)
Magnesium (ppm)	63.25 (\pm 3.5)
Calcium (ppm)	1366.8 (\pm 677.5)

CHAPTER 3. PERFORMANCE AND ECOPHYSIOLOGY OF PLANTED *QUERCUS VIRGINIANA* SEEDLINGS IN RESPONSE TO VARYING PINE STAND OVERSTORY AND COMPETING VEGETATION

3.1 Abstract

Maritime forests are a critical interface between ocean and terrestrial ecosystems, providing important ecosystem functions and services. Along the U.S. southern Atlantic coast, maritime forests were often cleared for agricultural land, abandoned, and then converted to pine stands. Pine beetle outbreaks have led to salvage and thinning silvicultural treatments that offer an opportunity to restore more complex maritime forests, dominated by the keystone species, *Quercus virginiana* (live oak). While *Quercus* spp. are generally intermediate in shade tolerance, there is wide variation among species in shade tolerance and plasticity. Further, knowledge specific to *Q. virginiana* is lacking. We evaluated the influence of understory light and competing vegetation in determining regeneration success and ecophysiology of *Q. virginiana*. One-year-old bareroot seedlings were planted on St. Simon's Island, Georgia, as a split-plot experimental design with independent variables of pine overstory (clearcut, heavy thin, light thin, and no thin whole plots) and vegetation control (0 and 2-yr competition removal subplots). Overall seedling survival was 78% after one growing season, with clearcut plots having the greatest survival (83%) and no thin having the lowest (72%). Seedling growth and foliar nitrogen were greater in clearcut plots followed by the heavy thin, light thin, and no thin plots. Vegetation control consistently promoted seedling height, but was only beneficial to diameter and crown width in clearcut/heavy thin plots. *Q. virginiana* seedlings demonstrated high plasticity in their ability to acclimate to varying microclimates in silvicultural treatments, as demonstrated by light response curves, stomatal density, and specific leaf area. Our results highlight the importance of reducing pine stand overstory to allow sufficient light and controlling competing vegetation to increase understory resources for planted seedlings.

3.2 Introduction

Coastal ecosystems are dynamic, biodiverse hotspots, dependent on connectivity for overall function and services including disturbance resiliency (Ribeiro et al. 2009; Sheaves 2009; Buelow et al. 2017; Chen et al. 2017; Habel et al. 2017). Maritime forests form a critical interface between the oceans and terrestrial ecosystems, providing soil stabilization, groundwater recharge, and wildlife habitat (Bellis 1995; Jones et al. 2013; Kurtz et al. 2013). In the United States, maritime forests of the southern Atlantic coast (North Carolina to Florida) occur on barrier islands and the adjacent mainland (Lopazanski et al. 1988; Bellis 1995). Regional disturbances and coastal stressors characterize maritime forests. Coastal stressors include saltwater spray, flooding, saltwater inundation, and nutrient-poor soils (Naumann et al. 2009; Kurtz et al. 2013). In southern maritime forests, *Quercus virginiana* (live oak) is a keystone maritime forest species resilient to many coastal stressors (Bourdeau and Oosting 1959; Bratton 1993; Conner et al. 2005). Within the range of *Q. virginiana*, there is a long history of human land transformation, particularly on the more stable land where maritime forests develop (Bratton and Miller 1994; Bellis 1995; Fox et al. 2007; Jones et al. 2013). Forests were often cleared for agriculture, subsequently abandoned, and then pine stands were established as an investment and to minimize erosion (Fox et al. 2007; Brockerhoff et al. 2008).

While pine stands are commercially valuable in the southeast, planted pines may perform poorly when exposed to coastal stressors inherent to the maritime forest range (Conner et al. 2005; Fox et al. 2007). Further, pine stands affect site characteristics through soil acidification, differing nutrient concentrations, increasing pine dominance in seed banks, and a thick duff layer of pine bark and needles that decompose slowly (Berg and McClaugherty 2003). Additionally, these pine stands sometimes receive little or no management due to changes in land ownership and parcellation. Abandoned monoculture pine stands are prone to disease and outbreaks of southern pine beetles (*Dendroctonus frontalis*) (Nowak et al. 2015; Asaro et al. 2017), which are an economically destructive forest pest due to the exponential nature of outbreaks that require management intervention (Watson et al. 2013; Asaro et al. 2017). Clearcuts are often prescribed to salvage residual timber value and reduce continual spread following an active beetle outbreak (Belanger et

al. 1993). Overstory thinning may be used to minimize future outbreaks in previously infected or at-risk stands (Belanger et al. 1993; Watson et al. 2013; Asaro et al. 2017). Clearcuts or thinning harvests used to address southern pine beetle outbreaks affect the microclimate, regeneration potential, and site ecology (Dey et al. 2008; Kern et al. 2017), and may provide opportunities for maritime forest restoration. Successful maritime forest restoration, including *Q. virginiana*, regeneration will enhance coastal resiliency and strengthen coastal ecosystem functions and services.

In the case of *Q. virginiana*, natural regeneration and recruitment is often limited, especially on barrier islands (Taggart and Long 2015). Overstory harvesting treatments may affect light, temperature, soil moisture, and soil compaction in complex feedback loops, which are dependent on species and ecosystem (Canham et al. 1990; Soto et al. 2017). If the management objective is to convert pine stands back to diverse hardwood maritime forests, then thinning and underplanting of desired species may facilitate the forest restoration processes (Parker et al. 2001; Löf et al. 2010). The ecophysiology of natural or planted regeneration of *Q. virginiana* is not well understood, and therefore it is difficult to apply prescriptions to promote regeneration of this species in beetle infected pine stands. *Quercus* spp. are generally intermediate in shade tolerance, suggesting that underplanting may provide a more effective means to restore these species (Dey et al. 2012). In clearcuts, oaks may be outcompeted by pioneer species, such as aggressive herbaceous species and pine regenerating from the harvested or adjacent stands (Dey et al. 2008, 2012; Kern et al. 2012). However, there is much variation in shade tolerance and plasticity across the *Quercus* genus (Gil-Pelegrin et al. 2017). It is unclear, therefore, if *Q. virginiana* will establish better in thinned pine overstories compared to clearcuts.

Two key factors limiting early establishment of newly planted seedlings are understory light and competition from other vegetation for light, water, and nutrients (Tripler et al. 2002; Grossnickle 2012; Oliet and Jacobs 2012; Jacobs et al. 2015; Soto et al. 2015). Controlling for understory light and competition can accelerate restoration (Wagner and Zasada 1991; Soto et al. 2017) by increasing availability of light, water, and nutrients. Species-specific light requirements and response to varying light levels define a species'

regeneration niche, which helps to predict the effect of silvicultural treatments (Gómez-Aparicio et al. 2006; Brown et al. 2014a; Soto et al. 2015). Fully stocked pine stands have low light levels and may not provide sufficient light to underplanted seedlings, resulting in low performance. Thinning the pine overstory may optimize light levels and increase underplanted seedling performance (Parker et al. 2001; Paquette et al. 2006) as the remaining pine overstory protects underplanted seedlings from exposure to elements, including excess light and competing vegetation (Paquette et al. 2006). Further, thinning improves stand health by increasing resources such as water and nutrients and reduces future potential southern pine beetle outbreaks (Löf et al., 1998; Nowak et al., 2015; Asaro et al., 2017).

Competing vegetation is also affected by forest stand dynamics. When light availability increases via clearcuts and heavy thinning, competing vegetation is released from the understory and/or seed bank. Species that can acclimate rapidly and take advantage of higher light are particularly competitive, often quickly suppressing oak seedlings (Paquette et al. 2006; Dey et al. 2008; Gardiner et al. 2010). Limited light, nutrients, and water resources from competition can negatively affect physiological processes, which inhibits seedling survival and growth (Salifu et al. 2009; Grossnickle 2012). Removal of competing vegetation, therefore, has potential to channel limited resources to underplanted seedlings. Competition removal, however, can be logistically prohibitive due to maintenance and management costs. Maintaining partial overstory may introduce enough light to optimize growth in the target species, while restricting release of faster growing competing vegetation (Elliott and Swank 1994; Brown et al. 2014b).

The principal goal of this research was to determine how *Q. virginiana* seedlings planted under varying densities of pine overstory and in combination with competition removal respond to environmental changes. In addition to monitoring growth and survival, studying the ecophysiology of target species will yield a better understanding of the interaction between environmental variables and tree physiology (Gauthier and Jacobs 2018). Overstory silvicultural treatments alter the environment of underplanted *Q. virginiana* seedlings, which may then acclimate through whole plant, leaf, and cellular adjustments

(Chaves et al. 2003; Valladares and Niinemets 2008; Brown et al. 2014b). To address these issues, we experimentally evaluated the relative influence of pine overstory density to manipulate light, and vegetation control to reduce competing vegetation on *Q. virginiana* seedling performance. Specifically, we hypothesized that i) *Q. virginiana* survival, growth, and leaf development (i.e., foliar N, SLA, and stomatal density) would peak in the thinned treatments when competition was controlled. Under this scenario, seedlings should show higher CO₂ assimilation and greater growth and development, while avoiding photoinhibition; ii) an interaction would occur between overstory and vegetation control treatments, whereby performance in response to overstory treatments would be dependent on competition control (Figure 3.1).

3.3 Methods

3.3.1 Experimental Site

This experiment was conducted on the north end of St. Simon's Island, Georgia at Cannon's Point Preserve (N 31°15'29" W 81°20'45"), which is a 246 ha wilderness tract managed by the St. Simons Land Trust. Cannon's Point Preserve has some of the last intact maritime forest on St. Simons Island. Many areas on the preserve, however, are dominated by abandoned pine stands. As part of the management plan for Cannon's Point Preserve, pine stands are designated for conversion to maritime forest. In 2016, areas of natural and planted pines affected by southern pine beetles were clearcut to salvage timber and reduce the southern pine beetle outbreak. To continue mitigating the threat of southern pine beetle outbreaks, additional pine stands were randomly selected for clearcut, heavy thin, light thin, or no thin overstory treatments (Figure 3.2). The abandoned pine stands are mostly *Pinus taeda* (loblolly pine) with some *P. elliotti* (slash pine). Examination of tree rings and cores estimate the pine stands at approximately 50 years old.

Soils at Cannon's Point Preserve are a mixture of fine sandy soils dominated by Mandarin fine sand and Cainhoy fine sand, zero to five percent slopes. Pottsburg sand and Rutledge fine sand are also present (NRCS United States Soil Survey 2017). At each plot, four soil samples were taken and composited to evaluate physical and chemical characteristics using

the Mehlich III extraction (Brookside Laboratories). Soil characteristics were similar with slight differences creating variability across blocks (Table 3.1).

The Georgia coastal region receives an average annual precipitation of 114 cm and average annual temperature of 20.0 °C (U.S. Climate Data 2017). Hurricane Irma (September 2017) resulted in increased precipitation, salt water inundation, salt spray, and strong winds.

3.3.2 Plant Material

Q. virginiana is a semi-evergreen hardwood species that defines the maritime forest range. One-year-old bareroot seedlings were planted in February 2017. Seedlings were obtained from Superior Trees in Lee, Florida (Louisiana seed source). From baseline morphology analysis ($n = 20$), mean seedling height was 54 cm (± 2.00), diameter was 5 mm (± 0.20), and root to shoot dry mass (g) ratio was 0.89 (± 0.76).

3.3.3 Experimental Design and Treatments

This study was a blocked, split-plot design. The whole plot factor was overstory removal (four levels; clearcut, heavy thin, light thin, no thin) and the subplot factor was competing vegetation control (two levels; weeded or non-weeded) (Figure 3.3; Appendix B1). There were four blocks each with four plots, totaling 16 plots. Overstory removal treatments of clearcut, heavy thin, light thin, and no thin were randomly applied to a 66 x 44 m area. Within the overstory treatment area, 26 x 14 m research plots were established and weeding subplot treatments randomly assigned. All plots were fenced (2.5 m height) to exclude white-tailed deer (*Odocoileus virginianus*). Deer are known to be overpopulated at Cannon's Point Preserve and heavily browse vegetation including *Q. virginiana* seedlings (Chapter 2). The four heavy thin fenced plots were expanded to 26 x 22 m to accommodate another experiment.

Overstory treatments were installed by modifying the basal area of the original pine overstory. Target basal areas were clearcut at 0 m²/ha, heavy thin at 4-9 m²/ha, light thin at 18-23 m²/ha, and no thin at 27+ m²/ha. Logging operations to implement overstory treatments were completed in December 2016. Target basal areas were monitored by the

contracted forester and logger. Only pines were removed and when possible, naturally regenerated hardwoods in the pine stand were left standing. Additionally, all midstory trees, understory vegetation, and large slash were removed after the pine harvest to reduce possible confounding effects. For vegetation control, competing vegetation was weeded for zero or one-year. Weeding was done mechanically throughout the growing season 3 to 4 times with brush saws and hand clippers.

Seedlings were hand planted via planting bars at 2 m spacing. To maintain planting density and interspecific seedling competition, a perimeter of buffer trees was planted 2 m from the research seedlings. Each treatment combination has a sample size of 25, for an overall sample size of 800 seedlings.

3.3.4 Site Characteristics

Basal area, light, and soil compaction were collected in summer 2017 at each plot. All mature tree species in each fenced plot (and part of the surrounding overstory treated pine stand) were identified and diameter taken at breast height (DBH; 1.37 m) to the nearest cm. Basal area was calculated using the following formula:

$$BA = \frac{\pi \times \left(\frac{DBH}{2}\right)^2}{10,000}$$

Hemispherical photographs were taken at three points in the plot (left, center, and right along the center horizontal line) under homogeneous diffuse sky conditions. Photos were analyzed with CIMESOSX to determine percent canopy closure. Lastly, at each plot four penetrometer readings were averaged to assess soil compaction (kg/cm²).

Each plot had an Em50 digital data logger with two 5TM sensors (Meter Group, Pullman, Washington) located in the approximate subplot center to record soil moisture and soil temperature every 2 hr. Each data logger was installed at a depth of 25 cm. Four of the plots (all of block 1) had additional sensors installed; PAR sensors to monitor light and VP4 sensors to capture air temperature, relative humidity, and air pressure recorded every 2 hr. At the peak of vegetation cover on site (August/September), five seedlings from each

treatment (160 total) were randomly selected for a 1-m² plot vegetation survey to assess percent competing vegetation cover within each plot (Appendix B2).

3.3.5 Performance

At the time of planting (February 2017), ground line diameter and height to last live bud were measured with calipers and a meter stick. After the first growing season (November 2017), diameter and height were re-measured in addition to survival, health status, number of lateral branches, and foliar nitrogen (N). Survival was binary; a status of “alive” included seedlings with live leaves. Health status noted dieback, chlorosis, and/or insect damage. Number of lateral branches was a count measurement. Foliar N was calculated for five seedlings that were composited per treatment replicate. Three leaves per seedling were composited, dried, weighed, pulverized, and analyzed with an ECS 4010 CHNSO Analyzer (Costech, Valencia, California).

3.3.6 Leaf Anatomy and Physiology

Gas exchange, SLA, and stomatal density were measured during the growing season (June 2018). Leaf gas exchange measurements were taken with a portable LI-6400XT (LI-COR Biosciences, Lincoln, Nebraska) to create light response curves. Four *Q. virginiana* seedlings were randomly selected per plot, two from the vegetation control subplot and two from the non-vegetation control subplot. From the seedlings, a randomly selected, upper-canopy, fully expanded, recently mature leaf was measured between the hours 10:00 and 14:00. Light levels used to create light response curves were: 1600, 1400, 1200, 1000, 800, 600, 400, 300, 200, 100, 50, 0 ($\mu\text{mol CO}_2 \text{ m}^{-1} \text{ s}^{-1}$). Infrared gas analyzers of the LI-6400XT (IRGAs; reference and sample) were matched at the beginning and end of each seedlings light curve measurements. Relative humidity ($\sim 60\%$), vapor pressure deficit (< 3.0), and temperature (leaf and block) were monitored for consistency. The gas exchange data point was taken after sample gas values (H_2O and CO_2) and CO_2 assimilation stabilized at a low coefficient of variation. *Q. virginiana* leaves do not fully fill the 2 x 3 cm LI-6400XT leaf chamber, therefore, gas exchange measurements were adjusted for the actual leaf areas. Leaf areas were determined from a photo of the leaf in the chamber using ImageJ (National Institutes of Health, Bethesda, Maryland). Light response curves were created by plotting

CO₂ assimilation (A_N , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) against PAR. The curves were fitted to a non-rectangular hyperbola (SigmaPlot V11.0, Systat Software, San Jose, California). Methodology to calculate final parameters from the model followed Coombs, 1995. Final parameters were used to calculate light compensation ($\mu\text{mol CO}_2 \text{ m}^{-1} \text{ s}^{-1}$) and light saturation ($\mu\text{mol CO}_2 \text{ m}^{-1} \text{ s}^{-1}$) points.

SLA and stomatal density, which affect water-use efficiency, transpiration, temperature regulation, and CO₂ assimilation (Brown et al. 2014b; Ramírez-Valiente et al. 2017), were sampled for the same four randomly selected *Q. virginiana* seedlings per plot used for gas-exchange measurements. Three randomly selected, upper-canopy, fully expanded, recently mature leaves were used for each seedling. In the no thin overstory some seedlings did not have many leaves, therefore in those cases only two leaves were collected. SLA was calculated by dividing leaf area by leaf mass (cm^2/g). Collected leaves were scanned to measure leaf area (cm^2) using ImageJ. Leaves were dried at 60 °C then weighed for leaf mass (g).

Stomatal density (stomata/ mm^2) was calculated by dividing the average number of stomata by image area. Leaf impressions were taken on the abaxial (lower) side in the middle of each leaf, midway between the midrib and the leaf margin. Leaf impressions were made on microscope slides using superglue. Five leaf impression images (DCM 900 microscope CMOS Camera, Oplenic Optronics, Hangzhou, China) were taken of a $0.19 \times 0.14 \text{ mm}$ (0.0266 mm^2) area under $40\times$ magnification using a microscope (BH-2 microscope, Olympus, Tokyo, Japan) for stomatal counts. Stomatal counts were conducted using ImageJ and the cell counter plugin (Kurt De Vos, University of Sheffield). For unbiased counting, all whole stomata were counted within the impression image area and stomata partially within the image were only counted on the top and right sides.

3.3.7 Statistical Analysis

Site characteristics (basal area, canopy closure, dataloggers, and soil compaction) were analyzed separately with general linear mixed models, with overstory as the fixed factor and block as a random factor. A one-way analysis of variance (ANOVA) and type III sum

of squares was used for each model. Growth (diameter, height, crown width, lateral branches, foliar N), ecophysiology (light compensation/saturation points, SLA, stomatal density), and vegetation survey dependent variables were analyzed separately with general linear mixed models, with overstory and vegetation control as fixed factors and block as a random factor. A two-way ANOVA and type III sum of squares was used for each model. Residuals from all response variables were tested to ensure normality and homogeneity of variance. Variables were transformed as needed to meet statistical assumptions (i.e., crown width). When significant treatment effects were detected ($p \leq 0.05$), Tukey's HSD test was used to test for pairwise comparisons ($\alpha = 0.05$). A logistic regression model was used to analyze survival. All data was analyzed with R software (R Version 3.2.4, R Core Team, 2017).

3.4 Results

3.4.1 Site Characteristics

Basal area (m^2/ha), canopy closure (%), light (PAR), mean air temperature ($^{\circ}\text{C}$), and soil compaction (kg/cm^2) all followed a progression of light availability (Table 3.2). Clearcuts had the least basal area and canopy closure, resulting in greatest PAR. This pattern was consistent along the light progression with intermediate thinned plots and lastly no thin plots with greatest basal area and canopy closure, resulting in the lowest PAR.

Throughout the experiment, average soil moisture was consistently greater in vegetation control subplots than non-vegetation control subplots. Soil moisture was greatest in heavy thin plots, followed by clearcut, then light thin, and lastly no thin plots. Soil temperature was greater in clearcut plots, followed by heavy thin, light thin, and lastly no thin plots having the lowest soil temperature (Table 3.3). Throughout March 2017 to June 2018 soil moisture peaked in late summer/early autumn and fluctuated throughout the remainder of the year (Appendix B3).

3.4.2 Vegetation Surveys

The interaction of overstory and vegetation control was significant for percent vegetation cover ($F_{3,54} = 6.84$, $p = 0.001$) as the effect of vegetation control was different between the overstory treatments. While vegetation control decreased percent vegetation cover in clearcut, heavy thin, and light thin plots, it did not decrease percent vegetation cover in no thin plots (Figure 3.4). Within clearcut, heavy thin, and light thin plots, vegetation control decreased percent vegetation from 57% (± 5.7) to 19% (± 2.0), 36% (± 7.0) to 12% (± 2.5), and 31% (± 5.2) to 10% (± 2.5) (respectively). Within the no thin plots, percent vegetation cover was not different with an average cover of 10% (± 2.3).

3.4.3 Seedling Survival and Growth

Initial height and diameter of planted seedlings were similar across all treatments with an average height of 48 cm (± 0.9) and an average diameter of 3.8 mm (± 0.1) (Appendix B4). Overall survival was 78 % (± 5). The interaction of overstory and vegetation control was not significant, however the main effect of overstory was significant for survival ($X^2_{3,794} = 9.86$, $p = 0.020$) and dieback occurrence ($X^2_{3,794} = 22.29$, $p < 0.001$). Seedling survival and dieback followed a linear pattern with respect to light availability (Figure 3.5). Survival was greater in the clearcut plots at 83% (± 0.7) than no thin plots at 72 % (± 1.4) survival. Whereas, dieback occurrence was lowest in clearcut plots at 42 % (± 0.3) and greatest in no thin plots at 81 % (± 0.2).

The interaction of overstory and vegetation control was not significant for height or lateral branches, however the overstory main effect was significant (Figure 3.6). *Q. virginiana* seedling height ($F_{3,621} = 40.15$, $p < 0.001$) and number of lateral branches ($F_{2,283} = 9.95$, $p < 0.001$) were greater in clearcut plots than heavy thin, light thin, or no thin plots. Mean seedling height in clearcut plots was 48 cm (± 1.5) compared to 38 cm (± 1.3) in heavy thin, 34 cm (± 1.1) in light thin, and 30 cm (± 1.2) in no thin plots. Clearcut plots also had the most lateral branches at an average of 2.2 (± 0.1), followed by 1.3 (± 0.1) in heavy thin, 0.8 (± 0.1) in light thin, and 0.4 (± 0.1) in no thin plots. Additionally, the vegetation control main effect was significant where greater heights were observed in vegetation control subplots compared to non-vegetation control subplots ($F_{1,621} = 5.30$, $p = 0.022$). Seedling

height was 39 cm (± 1.0) in vegetation control subplots as compared to 36 cm (± 0.9) in non-vegetation control subplots.

Similarly, the interaction of overstory and vegetation control was not significant for foliar N, however both main effects were significant. *Q. virginiana* seedling foliar N was greater in clearcut plots than heavy thin, light thin, and no thin plots ($F_{3,217} = 2.91$, $p = 0.035$). Seedlings in clearcut plots had 1.87 % N (± 0.04) compared to 1.72 % N (± 0.04) in the other plots. Additionally, foliar N was greater in vegetation control subplots compared to non-vegetation control subplots ($F_{1,217} = 8.31$, $p = 0.004$). Vegetation control subplots had 1.82 % N (± 0.03) and non-vegetation control plots had 1.70 % N (± 0.03).

The interaction of overstory and vegetation control was significant for diameter ($F_{2,283} = 9.21$, $p < 0.001$) and crown width ($F_{3,618} = 4.60$, $p = 0.003$) as the effect of vegetation control was different between the treatment combinations. Clearcut plots had greater diameter and crown width compared to other overstory treatments. Whereas vegetation control only increased seedling diameter in clearcut plots and only increased crown width in clearcut and heavy thin plots (Figure 3.7). Seedling diameter in clearcut plots averaged 7 mm (± 0.27) as compared to 5 mm (± 0.16) in heavy thin, 4.5 mm (± 0.14) in light thin, and 4 mm (± 0.12) in no thin plots. Within clearcut plots, vegetation control increased the diameter average from 6 mm (± 0.23) to 7 mm (± 0.31). Crown width in clearcut plots was 23 cm (± 1.3) compared to 15 cm (± 0.7) in heavy thin, 13 cm (± 0.5) in light thin, and 12 cm (± 0.4) in no thin plots. Vegetation control increased crown width for clearcut and heavy thin plots moving the crown width average from 19 cm to 28 cm and 12 cm to 15 cm respectively.

3.4.4 Light Response Curves

Maximum CO₂ assimilation was greatest in clearcut plots, followed by heavy thin, light thin, and lastly no thin plots (Figure 3.8). The interaction of overstory and vegetation control was not significant for light compensation or saturation points, however the overstory main effect was significant for both (Figure 3.9). Light compensation point ($F_{3,57} = 8.10$, $p < 0.001$) and light saturation point ($F_{3,57} = 23.56$, $p < 0.001$) were greater in

clearcut plots than heavy thin, light thin, and no thin plots. Light compensation point in clearcut plots was reached at $53 \mu\text{mol m}^{-1} \text{s}^{-1}$ (± 5.7) compared to $38 \mu\text{mol m}^{-1} \text{s}^{-1}$ (± 4.6) in heavy thin, $30 \mu\text{mol m}^{-1} \text{s}^{-1}$ (± 5.6) in light thin, and $22 \mu\text{mol m}^{-1} \text{s}^{-1}$ (± 2.3) in no thin plots.

Light saturation point in clearcut plots was reached at $1449 \mu\text{mol m}^{-1} \text{s}^{-1}$ (± 93.8) compared to $1059 \mu\text{mol m}^{-1} \text{s}^{-1}$ (± 93.9) in heavy thin, $873 \mu\text{mol m}^{-1} \text{s}^{-1}$ (± 76.9) in light thin, and $603 \mu\text{mol m}^{-1} \text{s}^{-1}$ (± 44.2) in no thin plots. Additionally, light saturation point had a significant vegetation control main effect with greater light saturation point in vegetation control subplots compared to non-vegetation control subplots ($F_{1,57} = 5.56$, $p = 0.022$). Light saturation point in vegetation control subplots was $1080 \mu\text{mol m}^{-1} \text{s}^{-1}$ (± 86.5) as compared to $912 \mu\text{mol m}^{-1} \text{s}^{-1}$ (± 65.9) in non-vegetation control subplots.

3.4.5 Specific Leaf Area and Stomatal Density

The interaction of overstory and vegetation control was not significant for SLA or stomatal density, however both main effects were significant (Figure 3.10). For the overstory main effect, *Q. virginiana* seedling SLA was lower ($F_{3,57} = 12.60$, $p < 0.001$), while stomatal density was greater in clearcut plots ($F_{3,57} = 21.20$, $p < 0.001$). SLA in clearcut plots was $74.0 \text{ cm}^2/\text{g}$ (± 1.9), compared to $95.8 \text{ cm}^2/\text{g}$ (± 2.4) in heavy thin, $98.6 \text{ cm}^2/\text{g}$ (± 4.7) in light thin, and $112.0 \text{ cm}^2/\text{g}$ (± 6.4) in no thin plots. Stomatal density in clearcut plots was $89.3 \text{ stomata/mm}^2$ (± 3.1) compared to $80.64 \text{ stomata/mm}^2$ (± 3.8) in heavy thin, $71.33 \text{ stomata/mm}^2$ (± 2.6) in light thin, and $59.73 \text{ stomata/mm}^2$ (± 2.6) in no thin plots.

For the vegetation control treatment, SLA was lower in vegetation control subplots ($F_{1,57} = 6.28$, $p = 0.015$), while stomatal density was greater in vegetation control subplots ($F_{1,57} = 5.37$, $p = 0.024$). SLA in vegetation control subplots was $91.1 \text{ cm}^2/\text{g}$ (± 3.1) compared to $99.0 \text{ cm}^2/\text{g}$ (± 4.3) in non-vegetation control subplots. Stomatal density in vegetation control subplots was $78.45 \text{ stomata/mm}^2$ (± 3.3) compared to $72.06 \text{ stomata/mm}^2$ (± 2.4) in non-vegetation control subplots.

3.5 Discussion

3.5.1 Restoration Benefits of Overstory Thinning and Weeding

Site characteristics and vegetation survey data showed that the overstory and vegetation control treatments were successful in modifying site characteristics (Table 3.2, Table 3.3). When overstory trees are removed, soil moisture increases due to reduced transpiration (Paquette et al., 2006). Overstory removal also reduces precipitation interception, resulting in more water directly contacting the soil and so while clearcuts create intense post-logging environments (i.e., high light levels and increased air temperatures), soil moisture is generally higher. In the clearcut plots, soil moisture was lower than the heavy thin plots, likely due to soil moisture being limited by increased solar radiation and soil temperature, which resulted in greater evaporation (Pallardy 2008).

Competing vegetation strongly affects seedling growth via influencing water, nutrient, and light availability (Fleming et al. 2006). Consistent with this in our study, vegetation control increased soil moisture (Table 3.3). Vegetation control decreased percent vegetation cover in clearcut, heavy thin, and light thin plots, but had no effect in no thin plots as more competition was released with increasing light in the clearcut and thinned plots.

3.5.2 Seedling Growth and Ecophysiology

With increasing light, seedlings had greater survival, height, lateral branches, foliar N, and less dieback. Rather than seedling survival and growth peaking in the thinned treatments as hypothesized, survival and performance were consistently greatest in clearcut plots (i.e., survival, dieback occurrence, height, lateral branches, and foliar N). Seedlings in clearcut plots were able to utilize the high light levels, increase photosynthesis, which increased growth and development (Gómez-Aparicio et al. 2006; Soto et al. 2017). Supporting this result, *Q. virginiana* has been reported as a fast growing species, allocating resources to aboveground biomass development (Gil-Pelegrin et al. 2017). Additionally, in a dense overstory, soil moisture and nutrients are typically limited because of canopy tree dominance and competition (Cooper et al., 2014). Other studies have found that lack of sufficient light and soil moisture have significant negative effects on hardwood seedling performance (Dey et al., 2008; Bendevis et al., 2010). The differences between *Q.*

virginiana seedling performance with respect to overstory treatments illustrated the strong influence of microclimate on early seedling performance.

Diameter and crown width were also greatest in clearcut plots, though the significant interaction between overstory and vegetation control showed that vegetation control is beneficial in clearcut and heavy thin treatments while not the light thin or no thin treatments (Figure 3.8). Without thinning, light and soil moisture were greater limitations to *Q. virginiana* performance than understory competing vegetation. Semi-evergreen *Quercus spp.* have varying photosynthetic responses to different environments with a range of growth rates and shade tolerance (Gil-Pelegrin et al. 2017). With clearcuts or heavy thinning, understory vegetation competition became more important and a greater limitation (Ter-Mikaelian et al. 1999). In our study, vegetation control benefited seedling growth, particularly on sites with more light (i.e., clearcut and heavy thin). Vegetation control increased height in all overstory treatments whereas vegetation control only increased diameter and crown width in clearcut and heavy thin overstory treatments. Diameter and crown width responses to vegetation control illustrated a shift in pressure from light limited environments to resource limited environments. Overall, our results align with other studies supporting that vegetation control enhances seedling establishment and performance (Fleming et al. 2006). Further, foliar N concentrations, which is an essential macronutrient for seedlings establishment and performance (Abrams and Mostoller, 1995; Colombo, 2005; Soto et al., 2017), was significantly greater in leaves of seedlings in vegetation control subplots, indicating the greater accessibility of this limiting resource to seedlings (Kobe 2006; Uscola et al., 2015).

Leaf area increases with increasing height, crown width, and lateral branches, creating a positive feedback loop with increased photosynthetic tissues increasing seedling allocation of resources to growth and development. Our results support that *Q. virginiana* can acclimate to varying environments as maximum CO₂ assimilation was in clearcuts (Figure 3.13) aligns with the increased height, diameter, crown width, and lateral branches in clearcut plots. Light response curves can identify maximum CO₂ assimilation and risk of photoinhibition (Gómez-Aparicio et al. 2006). Acclimation and plasticity are particularly

beneficial for trees as an individual may experience several environmental changes (Gil-Pelegrin et al. 2017). With higher light compensation and saturation points, clearcut seedlings took longer to achieve positive CO₂ assimilation, but were able to utilize increased PAR by increasing photosynthesis. Similar to other oak studies, *Q. virginiana* seedlings responded to the other overstory treatments in a linear progression with respect to light availability (Gil-Pelegrin et al. 2017; Cooper et al., 2014). Seedlings in the no thin plots reached positive CO₂ assimilation quickest at the lowest PAR, however, no thin seedlings were not able to maximize photosynthesis with increasing PAR since saturation occurred at a lower PAR. Therefore, CO₂ assimilation was limited and lowest for seedlings in no thin plots.

Stomatal density and SLA, which are associated with seedling growth and development, responded in a linear progression with respect to light availability in overstory and vegetation control treatments. Leaf variation of *Quercus* spp. tends to be on the lower end of the leaf economic spectrum aligning with early to mid-successional classification (Wright et al. 2004; Niinemets and Valladares 2006; Gil-Pelegrin et al., 2017). Higher stomatal density increases gas exchange potential, which increases CO₂ assimilation (Wright et al., 2004). Along with increased gas exchange potential, however, comes increased risk of desiccation; therefore, a trade-off is necessary to maximize performance. For example, SLA decreased with increasing light and was lowest in clearcut plots, thereby lowering leaf temperatures and reducing the risk of transpiration and leaf desiccation.

Vegetation control, which reduced competition for resources (i.e., light, water), increased stomatal density and decreased SLA. Additionally, when analyzing stomatal density impressions, more trichomes occurred in clearcut plots followed by heavy thin plots. This may be due to trichomes affecting gas exchange by reducing water loss and heat exchange (Bickford et al., 2016).

3.5.3 Management Implications and Conclusions

Understanding effects of silvicultural treatments on availability of light, soil moisture, and nutrients is important to prescribe silvicultural techniques that promote regeneration and early growth. Trade-offs are well known in forest systems especially when viewing forests as complex adaptive systems (Paquette et al., 2006; Puettman et al., 2009). Our research provides encouraging evidence for successful restoration of maritime forests through artificial regeneration. In our study where the overstory densities were manipulated to manage for southern pine beetle outbreaks, clearcuts best facilitated the establishment and development success of *Q. virginiana* although interactions occurred with vegetation control. We also demonstrated that *Q. virginiana* is capable of acclimating to the varying silvicultural treatments, and *Q. virginiana* may be more light tolerant than other oaks as indicated by its performance in clearcut plots. In addition to being a keystone species, *Q. virginiana*'s ability to establish well in clearcuts makes its regeneration a promising first step in maritime forest restoration. After a clearcut or heavy thinning, *Q. virginiana* regeneration may close the canopy, allowing more favorable conditions for establishment of other maritime forest species that will diversify the site.

Although *Q. virginiana* responses did not follow the predicted trend of seedling performance peaking in the heavy/light thin overstory (but rather in clearcuts), thinning is among the most effective practices for preventing or mitigating southern pine beetle outbreaks. Thinning pine stands improves tree health and creates barriers to beetle population growth and spread (Nowak et al., 2015; Asaro et al., 2017). The gradual transition and conversion from pine stands back to maritime forests allows a greater maintenance of ecosystem complexity and overall ecosystem stability. While heavily infected stands require clearcuts, thinning of less infected or healthy stands helps to diversify age structure, which increases overall resiliency. Further, clearcuts may result in additional damage to adjacent forest stands by funneling winds. Underplanting *Q. virginiana* in both clearcut and thinned stands increases regeneration potential of a key maritime forest species while reducing management costs with the need of competing vegetation removal. Additionally, clearcuts had higher soil compaction levels, which may negatively affect plant growth.

Complexity is an inherent trait of forest ecosystems and should be highly valued when managing ecosystems (Puettmann et al. 2009). An adaptive management approach focusing on complexity and resilience of restoring forests may yield more robust ecosystems that can adapt to disturbance and change. Tree regeneration and recruitment is a critical mechanism for future resilient forests, as trees, especially oaks, are foundational species that support many other ecosystem components (Gardiner et al. 2010; Reyer et al. 2015). Rather than prescribing a single treatment (e.g., clearcut) that optimizes live oak development, an alternative may be to prescribe several treatments that result in cost-effective restoration while also creating resilient, diverse, and complex forest stand structures.

3.6 References

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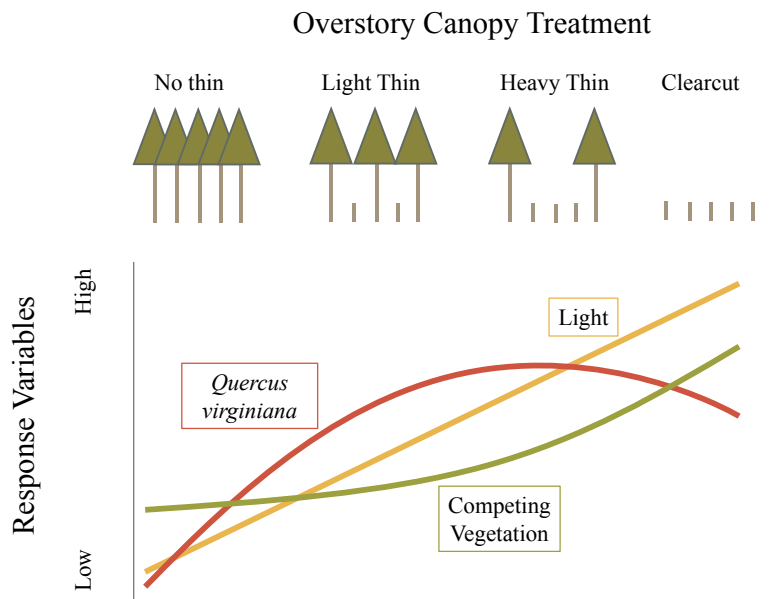


Figure 3.1 Predicted light availability, competing vegetation, and *Q. virginiana* performance with respect to the four different overstory manipulations (i.e., clearcut, heavy thin, light thin, no thin).



Figure 3.2 Cannon's Point Preserve (managed by the St. Simons Land Trust) on the north end of St. Simons Island, Georgia. 16 plots were established with varying overstory treatments. White rectangles represent clear cuts, light grey rectangles represent heavy thinning, dark grey rectangles represent light thinning, and black rectangles represent no overstory manipulation.

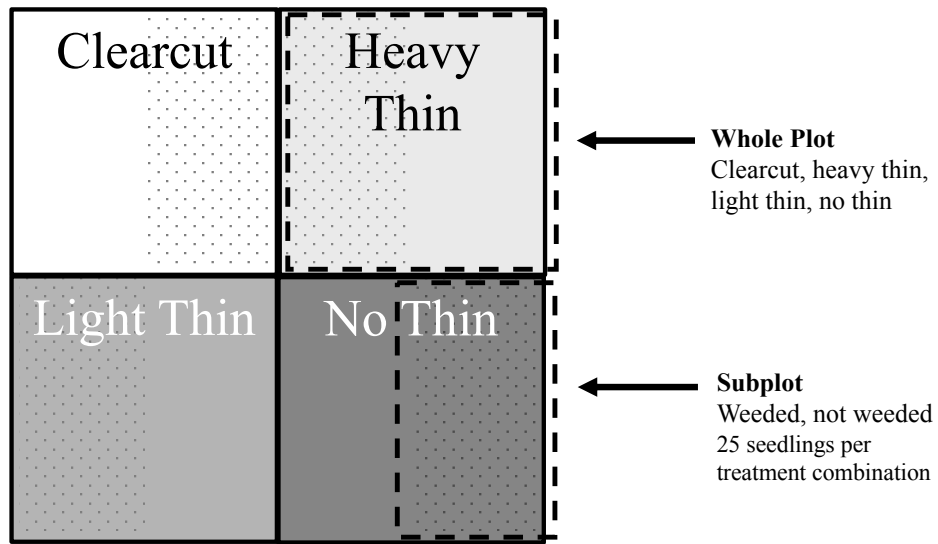


Figure 3.3 Experimental design layout for a single replication (block) showing treatments including: four overstory treatments (clearcut, heavy thin, light thin, no thin) and two levels of vegetation control (zero or one-year of weeding).

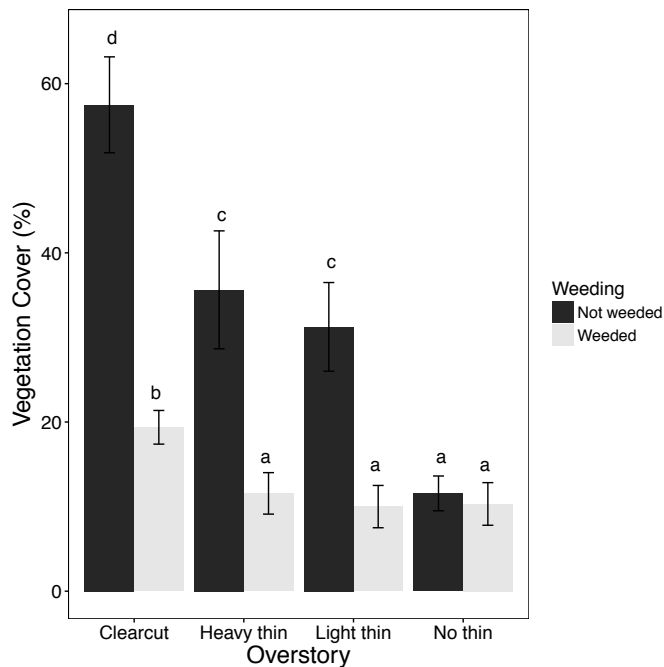


Figure 3.4 Mean (\pm SE) vegetation cover (%) of competing vegetation in a 1-m² survey around *Q. virginiana* seedlings planted in clearcut, heavy thin, light thin, no thin plots. Competing vegetation removed for zero or two-years. Different letters indicate significant differences among treatments ($\alpha = 0.05$).

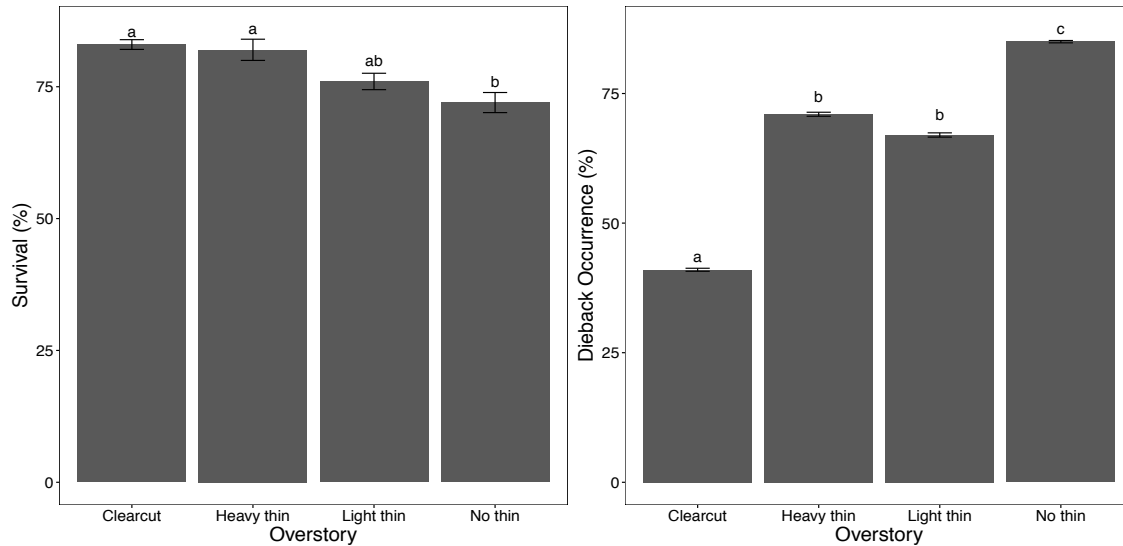


Figure 3.5 Mean (\pm SE) survival (%) and dieback occurrence (%) of *Q. virginiana* seedlings planted in clearcut, heavy thin, light thin, or no thin plots. Different letters indicate significant differences among treatments ($\alpha = 0.05$).

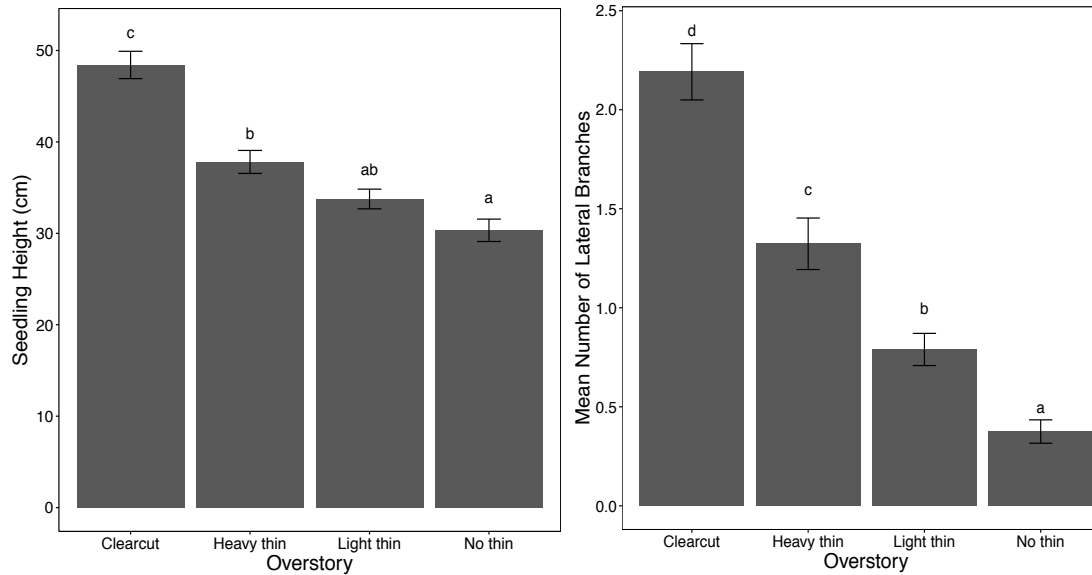


Figure 3.6 Mean (\pm SE) height (cm) and number of lateral branches of *Q. virginiana* seedlings planted in clearcut, heavy thin, light thin, or no thin plots. Different letters indicate significant differences among treatments ($\alpha = 0.05$).

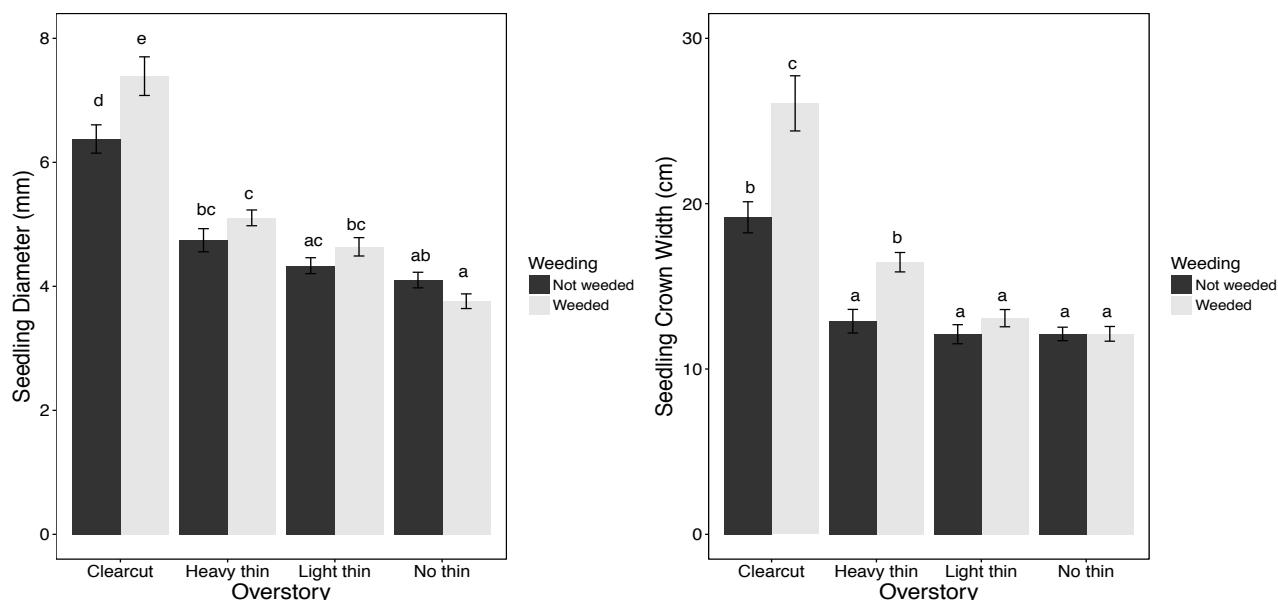


Figure 3.7 Mean (\pm SE) seedling diameter (mm) and crown width (cm) of *Q. virginiana* seedlings planted in clearcut, heavy thin, light thin, or no thin plots. Competing vegetation removed for zero or two-years. Different letters indicate significant differences among treatments ($\alpha = 0.05$).

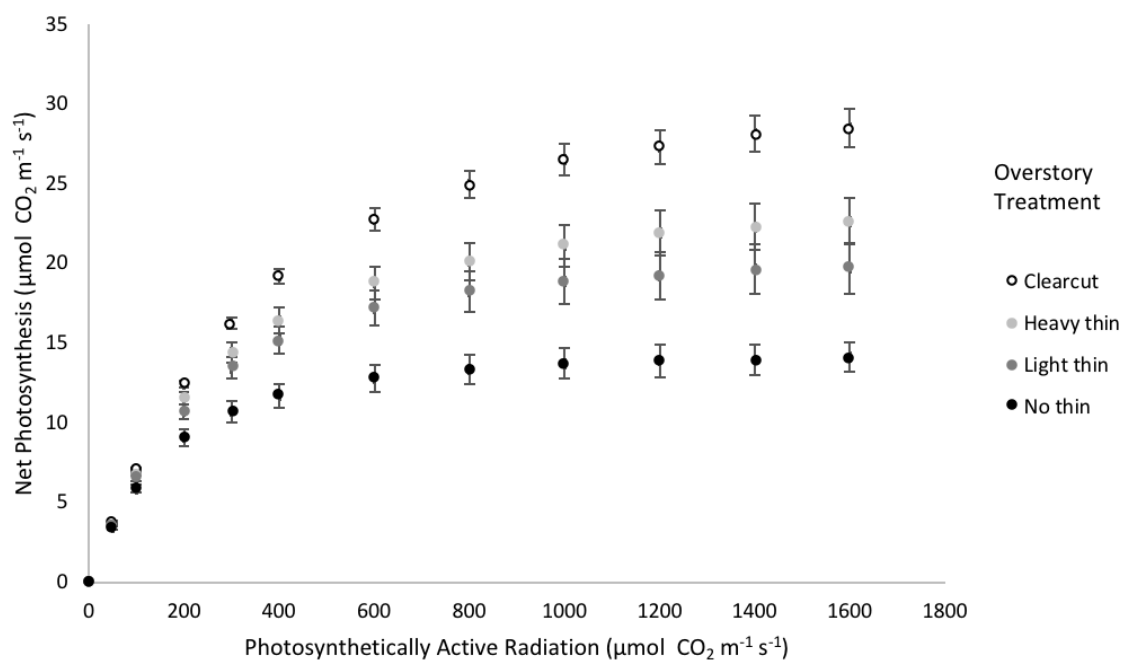


Figure 3.8 Mean (\pm SE) light response curves (net photosynthesis plotted by photosynthetically active radiation) of *Q. virginiana* seedlings planted either in clearcut, heavy thin, light thin, or no thin plots.

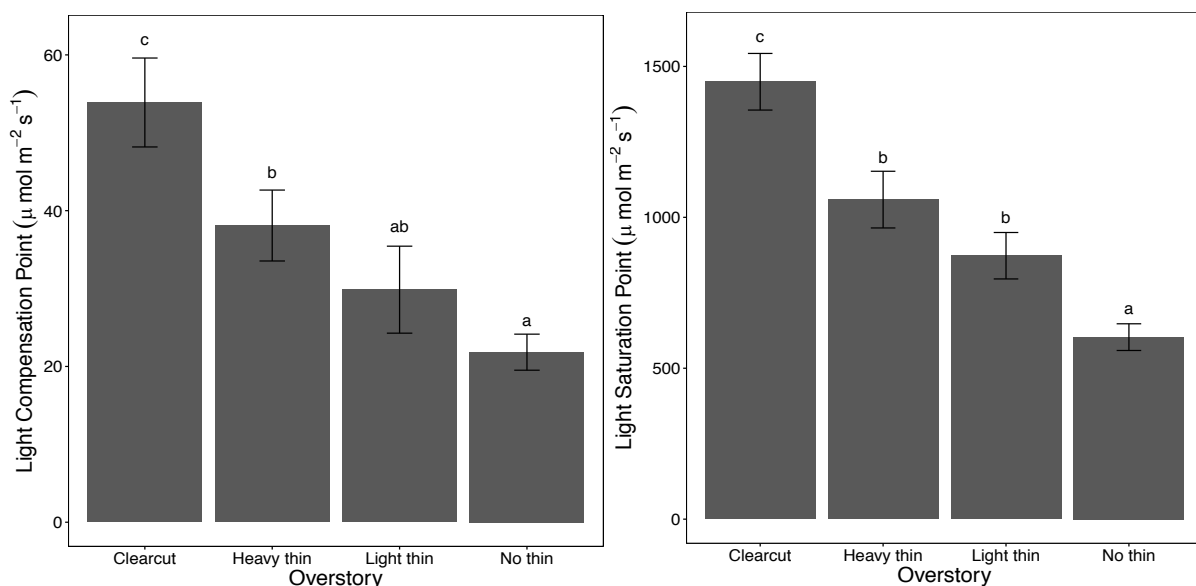


Figure 3.9 Mean (\pm SE) light compensation point ($\mu\text{mol m}^{-1} \text{s}^{-1}$) and light saturation point ($\mu\text{mol m}^{-1} \text{s}^{-1}$) of *Q. virginiana* seedlings planted either in clearcut, heavy thin, light thin, or no thin plots. Different letters indicate significant differences among treatments ($\alpha = 0.05$).

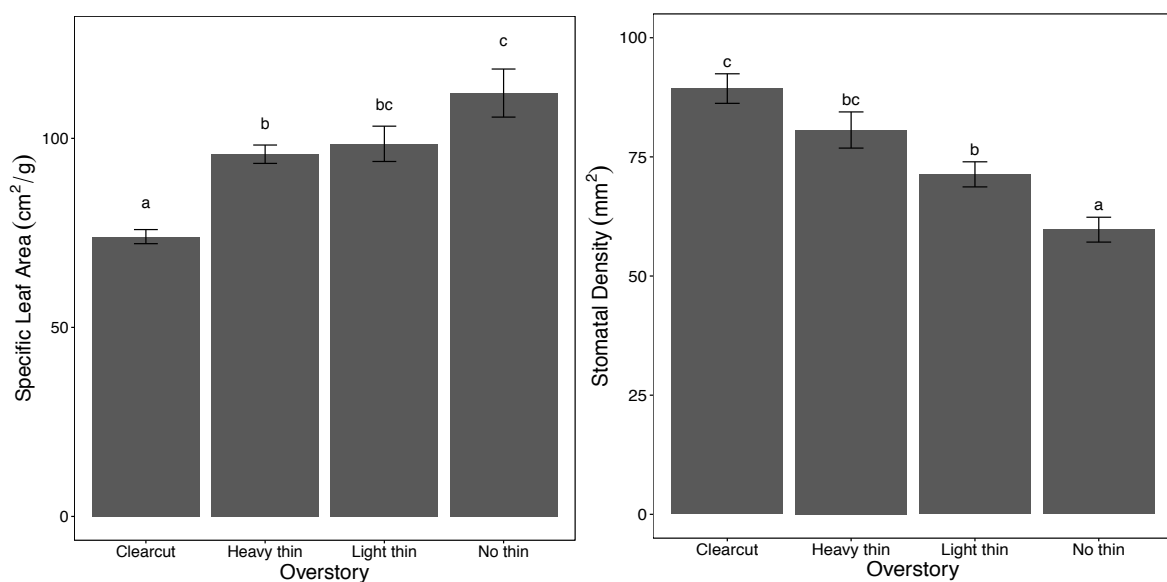


Figure 3.10 Mean (\pm SE) specific leaf area (cm^2/g) and stomatal density (stomata/ mm^2) of *Q. virginiana* seedlings planted in clearcut, heavy thin, light thin, or no thin plots. Different letters indicate significant differences among treatments ($\alpha = 0.05$).

Table 3.1 Analysis of soils using the Mehlich III extraction for all 16 plots averaged by block.

Chemical characteristic	
Organic Matter (%)	2.1 (\pm 0.3)
pH	4.6 (\pm 0.3)
CEC (ME/100 g)	2.2 (\pm 0.7)
Estimated Nitrogen (lb/A)	60.5 (\pm 5.1)
Soluble sulfur (ppm)	8.5 (\pm 1.0)
Phosphorous (ppm)	99.6 (\pm 24.5)
Potassium	17.3 (\pm 1.4)
Magnesium	35.8 (\pm 4.6)
Calcium	257.1 (\pm 93.3)
Sodium	35.7 (\pm 1.8)

Table 3.2 Target basal area from logging operation, basal area from stand inventory, canopy closure from hemispherical photos. Maximum PAR levels, mean air temperature from dataloggers. Soil compaction measured with a soil penetrometer. Different letters indicate significant differences among treatments ($\alpha = 0.05$).

	Basal Area (m ² /ha)	Canopy Closure (%)	PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Mean Air Temperature (°C)	Soil Compaction (kg/cm ²)
Clearcut	0 (\pm 0.0) a	0 (\pm 0.00) a	2115 (\pm 9.3) a	25.5 (\pm 0.07) a	25.6 (\pm 2.3) a
Heavy thin	16.9 (\pm 2.3) b	60 (\pm 0.05) b	1585 (\pm 4.4) b	22.4 (\pm 0.09) b	18.8 (\pm 2.0) b
Light thin	24.2 (\pm 1.5) b	67 (\pm 0.04) b	1450 (\pm 7.5) b	20.1 (\pm 0.11) c	13.1 (\pm 1.7) c
No thin	33.9 (\pm 3.5) c	78 (\pm 0.05) b	908 (\pm 2.5) c	20.7 (\pm 0.10) c	14.8 (\pm 1.3) c

Table 3.3 Mean soil moisture and soil temperature from dataloggers, averaged across all 16 plots.

	Clearcut		Heavy thin		Light thin		No thin	
	Weeded	Non-weeded	Weeded	Non-weeded	Weeded	Non-weeded	Weeded	Non-weeded
Soil moisture (%)	19 (\pm 0.01)	17 (\pm 0.02)	22 (\pm 0.04)	18 (\pm 0.03)	17 (\pm 0.03)	14 (\pm 0.02)	17 (\pm 0.01)	15 (\pm 0.01)
Soil temperature (°C)	23.5 (\pm 0.9)	24 (\pm 1.1)	22.0 (\pm 0.5)	22.1 (\pm 0.4)	21.4 (\pm 0.2)	21.5 (\pm 0.2)	21.0 (\pm 0.2)	21.8 (\pm 0.6)

CHAPTER 4. CONCLUSIONS

4.1 Study Objectives

The goal of this study was to evaluate limiting factors in maritime forest restoration. To address restoration challenges, we focused on the regeneration of the keystone species, *Q. virginiana*, on the U.S. southern Atlantic coast. Two field experiments were established on St. Simon's Island, Georgia at Cannon's Point Preserve, which has some of the last intact maritime forest on St. Simons Island. Many areas on the preserve, however, are dominated by abandoned pine stands. Southern pine beetle outbreaks generated immediate management action. Pine stands affected by outbreaks were clearcut in 2014, 2015, and 2017. Additionally, in 2017 pine stands were thinned to reduce the threat of future outbreaks. *Q. virginiana* seedlings were planted in split-plot experimental designs at clearcut and thinned stands. Independent variables recognized as potential key limiting factors to *Q. virginiana* establishment and therefore manipulated in the experiments were:

- Fencing - fenced plots or unfenced clearcut plots
- Overstory treatments - clearcut, heavy thin, light thin, or no thin pine stands
- Vegetation control - 0, 1, or 2, years of competing vegetation removal

It was important to determine if *Q. virginiana* would survive and perform when planted in clearcut pine stands as well as when underplanted in thinned or untreated pine stands. *Q. virginiana* was chosen for planting because of its ecological and restoration value. It is a dominant maritime forest species, integral in coastal ecosystem function and services. Performance of planted *Q. virginiana* was measured through several response variables:

- Survival and health status
- Performance - height, diameter, crown width, and lateral branches, and foliar nitrogen (N)
- Ecophysiology responses - net carbon assimilation, light compensation/saturation points, stomatal density, and specific leaf area (SLA)

In the first experiment, I evaluated the relative influence of fencing and competing vegetation removal on *Q. virginiana* seedling performance in clearcut pine stands. Fencing reduced the pressure of animal browse on planted seedlings. Competing vegetation removal increased resource availability. In the second experiment, I studied the relative influence of overstory pine canopy density and competing vegetation removal on *Q. virginiana* seedling growth and ecophysiology. Overstory treatments changed site microclimates by manipulating light availability as well as other abiotic factors such as air temperature, soil moisture/temperature, relative humidity, and soil compaction. Competing vegetation removal increased resource availability.

4.2 Synthesis of Experiments

4.2.1 Experiment 1: Deer Browse and Competition Interact to Affect Performance of Planted *Quercus virginiana* Seedlings

In December 2015, 480 1-year-old bareroot seedlings were planted in a blocked, split-plot experimental design. The whole plot factor was fencing (fence or no fence) and the subplot factor was competing vegetation removal (vegetation control for 0, 1, or 2-years). After two growing seasons, survival was $60\% \pm 5\%$ with no treatment differences. Greatest *Q. virginiana* performance was in fenced plots. There were significant statistical interactions between fencing and vegetation control for diameter, height, crown width, lateral branches. Vegetation control increased performance only when seedlings were fenced. Without fencing, vegetation control was not beneficial to seedling growth because of high browsing pressure. Additionally, foliar N concentrations were significantly greater in fenced plots and after 2 years of vegetation control compared to non-weeded subplots.

4.2.2 Experiment 2: Performance and Ecophysiology of Planted *Quercus virginiana* Seedlings in Response to Varying Pine Stand Overstory and Competing Vegetation

In February 2017, 800 1-year-old bareroot seedlings were planted in a blocked, split-plot experimental design. The whole plot factor was overstory treatment (clearcut, heavy thin, light thin, or no thin) and the subplot factor was competing vegetation removal (vegetation control for 0 or 2-years). After one growing season, survival was $78\% \pm 5\%$. There was a significant overstory treatment difference. Survival was greater in clearcut plots (83%) than

no thin plots (72%). Heavy and light thin plots were intermediate in survival. Site conditions were different after the logging operation. Clearcut plots had the greatest light availability, air temperature, soil temperature, and soil compaction. Heavy thin plots had the next greatest site conditions, followed by light thin plots, and lastly no thin plots. Greatest *Q. virginiana* growth (height, diameter, crown width, lateral branches, and foliar N) occurred in clearcut plots; lowest performance was in no thin plots. Vegetation control increased height, diameter, and foliar N across all overstory treatments. For diameter and crown width, however, there was significant statistical interaction whereby vegetation control was only beneficial for diameter and crown width in clearcuts and heavy thin plots. Similar to growth, maximum photosynthesis (net photosynthesis and light compensation/saturation points) occurred in clearcut plots followed by heavy thin, light thin, and no thin plots. Lastly, clearcut plots had greater stomatal density and lower SLA than no thin plots. Thinning treatments were intermediate for stomatal density and SLA.

4.3 Management Directions

In the first experiment, my research provided evidence that removing animal browse was critical to restoration of maritime forests. I found that planting success of the desired maritime forest keystone species, *Q. virginiana*, was possible in clearcuts when using fencing to reduce animal browse. Animal browse from deer was strong and seedlings planted in non-fenced plots had minimal growth and foliar N. Further, in fenced plots seedling performance was most successful with vegetation control to reduce competing vegetation. Vegetation control was expensive to implement, however to see a significant increase in foliar N, which is commonly a limited nutrient for seedling development, 2-years of vegetation control was required.

The second experiment provided evidence that introducing light in the understory is critical to restoration of maritime forests. Seedlings survived and performed best with a reduction of pine overstory. Further, vegetation control increased several performance variables especially in clearcut and heavy thin plots (i.e., diameter and crown width). Ecophysiology results indicate that *Q. virginiana* seedlings acclimated not only at a whole plant level, but

also leaf, and molecular level to varying environments created by different silvicultural treatments.

At Cannon's Point Preserve, natural regeneration occurred more in fenced plots; however, the regenerating species were dominated by *P. taeda* and *Q. hemisphaerica*. To encourage *Q. virginiana* regeneration, artificial regeneration via planting seedlings provided a first regeneration step in restoring maritime forests. The second step was to reduce animal browse. Herbivory pressure may be different on other islands and the mainland range of maritime forest as other animals (e.g., rabbits, voles, armadillos, hogs) may be an equal or larger concern than deer. Therefore, it is important to understand local dynamics to determine best management practices. For example, tapered fencing to exclude smaller herbivores or shelters to minimize tree girdling could be important considerations. When underplanting seedlings in stands with an established, dense, overstory, the third step was to introduce light. Additionally, when working in an abandoned pine stand, the reduction in the pine overstory can increase pine stand health by reducing potential outbreaks of southern pine beetles and increase resource availability.

The interaction of fencing and vegetation control in the first experiment and the interaction of overstory and vegetation control in the second experiment helped to determine cost-effective options for management activities to restore maritime forests. Fencing and introducing sufficient light are critical to seedling establishment and performance. Vegetation control further enhances seedling performance, which may be especially beneficial during years with stressful environmental conditions (e.g., drought, flooding, winds).

4.4 Future Directions

This study followed the first experiment through two growing seasons and the second experiment through one growing season. It will be important to follow up with these experiments to assess how seedlings progress into the sapling and potentially adult cohorts. At that time, reevaluating success to determine if/how the planted *Q. virginiana* need to be thinned can be assessed. Additionally, it may be beneficial to diversify the plantings by

incorporating other important native maritime forest species such as red bay, *Persea borbonia*.

The important finding of fencing to reduce animal browse can be explored further. It is expensive for managers to fence both in terms of materials and time. Not only to implement, but also to maintain. For the first experiment we used metal fencing that tapers at the bottom to reduce deer browse as well as smaller animals. For the second experiment we used plastic fencing, which was less expensive and easier to manipulate in pine stands. Wooden or metal support posts are necessary and it can be difficult to get materials to remote field sites. For maintenance managers must continually check for breaches in the fences and fix them. However, protecting seedlings has been shown to have a large impact on seedling survival and growth for several species, which has potential to outweigh the added cost. To evaluate alternatives to fencing, we will establish a new study in November 2018 to examine three different tree shelters (plastic shelter with vents, mesh shelter, or no shelter) and fertilizer (yes or no). The shelters may be easier to implement and maintain than fencing and fertilizer application may help the seedlings reach free-to-grow status above browse line quicker.

There are several additional avenues for maritime forest restoration research including:

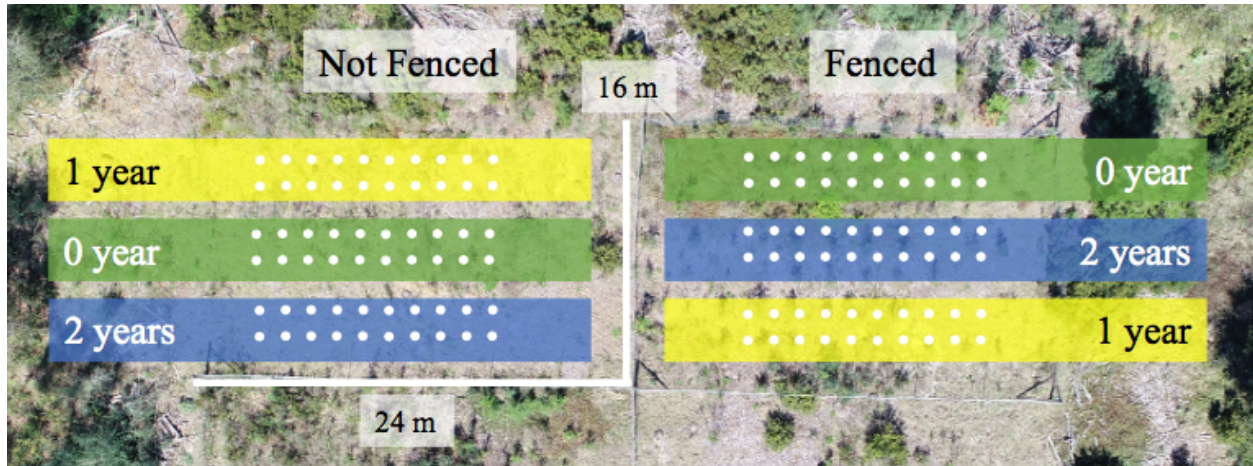
- Stocktypes - bareroot vs. container seedlings
- Identifying seed sources for local collection
- Seed collection methods, as *Q. virginiana* acorns are subject to weevil attack and precocious radical development
- Genetic diversity when identifying seed sources and tree improvement
- Different thinning methods such as geometric or gaps
- Nucleation plantings to create islands of regenerating maritime forests
- Effects of prescribed burning on regeneration and reducing fuel loads
- Stress tolerance such as salt-water and drought

In future experiments, destructive sampling may be beneficial to measure root-to-shoot ratio and total tree biomass. These measurements could provide a more detailed

comparison on resource allocation, plant moisture stress, and growth patterns. Finally, a formal cost analysis of the various management options would be helpful in making decisions to restore maritime forest. Comparing the costs of management treatments and potential effects on seedling growth would help land managers make informed decisions. In conclusion, we presented options to restoring maritime forests based on experimental results. As valuable coastal ecosystems, restoring healthy and robust maritime forests can increase coastal resiliency and maintain critical ecosystem functions and services.

APPENDIX A. EXPERIMENT 1

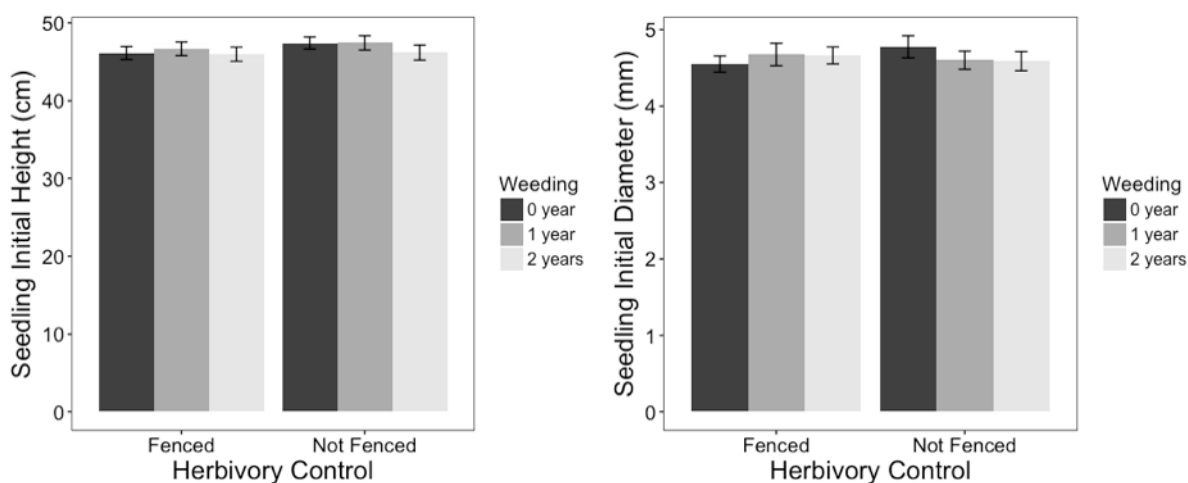
Appendix A1. Experimental design layout for a replication (block). Two browse treatments (fenced and not fenced) and three levels of vegetation control (zero, one, and two-years of control). Twenty seedlings per treatment. Aerial drone photograph, Owen Burney.



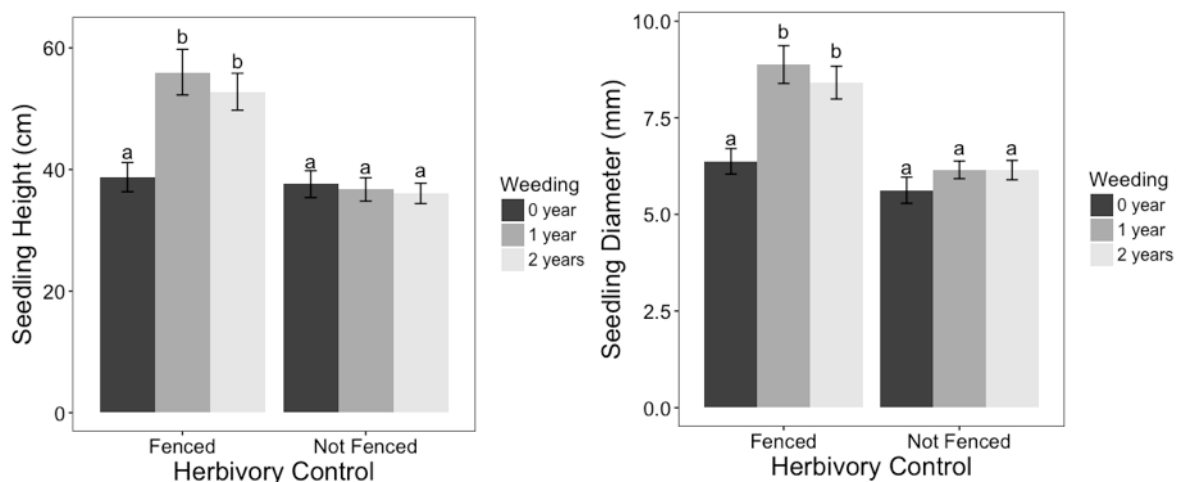
Appendix A2. 1-m² plot vegetation survey around a *Q. virginiana* seedling (noted with pin flag).



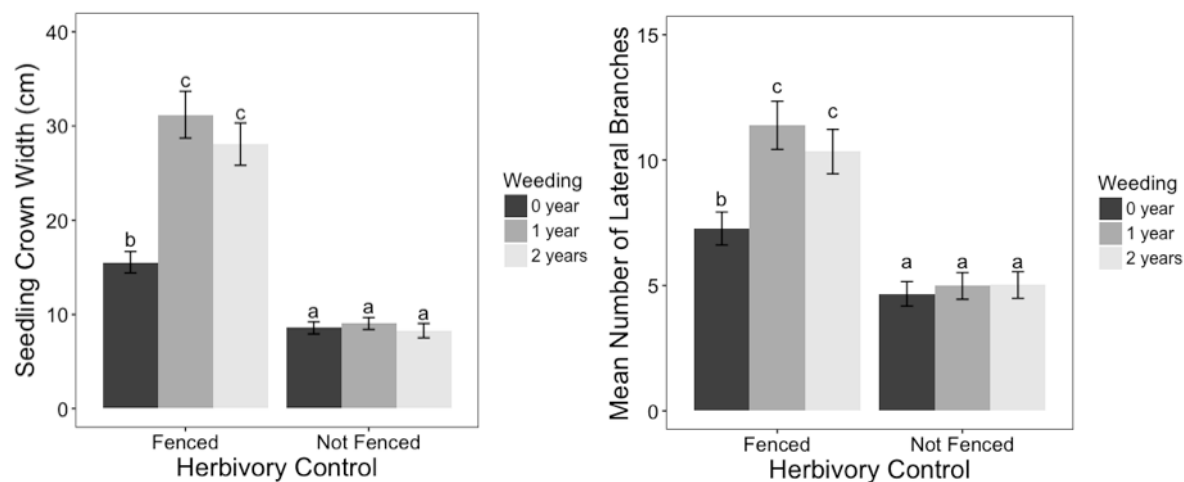
Appendix A3. Mean (\pm SE) initial height (cm) and initial diameter (mm) of *Q. virginiana* seedlings after planted in fenced or non-fenced plots. Competing vegetation removed for zero, one, or two-years.



Appendix A4. Mean (\pm SE) 2016 *Q. virginiana* seedling height (cm) and diameter (mm) planted in fenced or non-fenced plots. Competing vegetation removed for zero, one, or two-years.



Appendix A5. (Mean \pm SE) 2016 *Q. virginiana* seedling crown width (cm) and number of lateral branches planted in fenced or non-fenced plots. Competing vegetation removed for zero, one, or two-years.

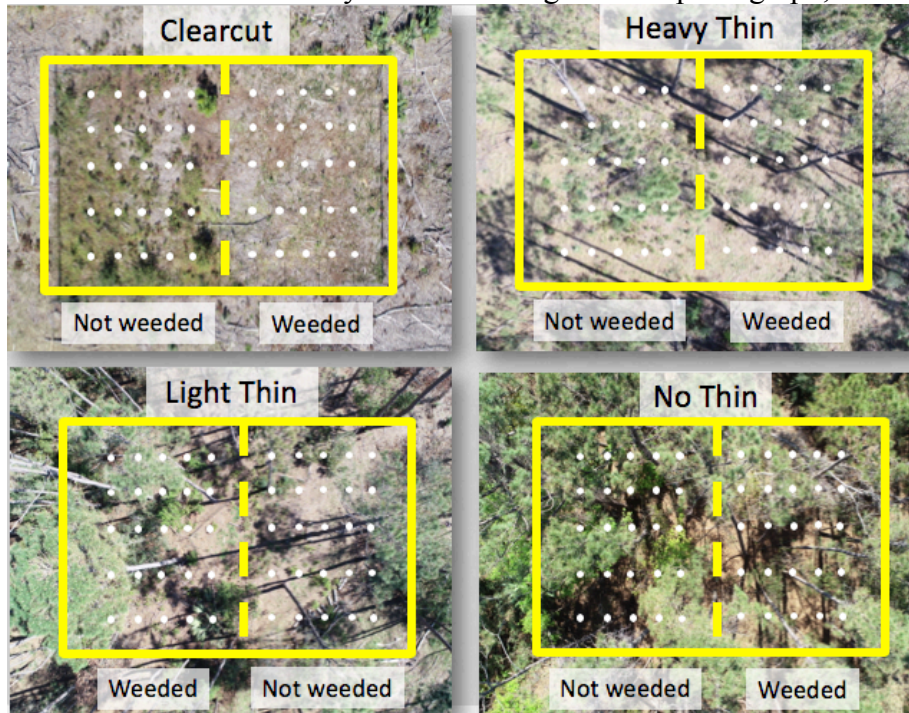


Appendix A7. Research seedlings after two growing seasons in November 2017. (Left) *Q. virginiana* seedling in fenced plot (right) and in non-fenced plot. Orange pin flags for scale.



APPENDIX B. EXPERIMENT 2

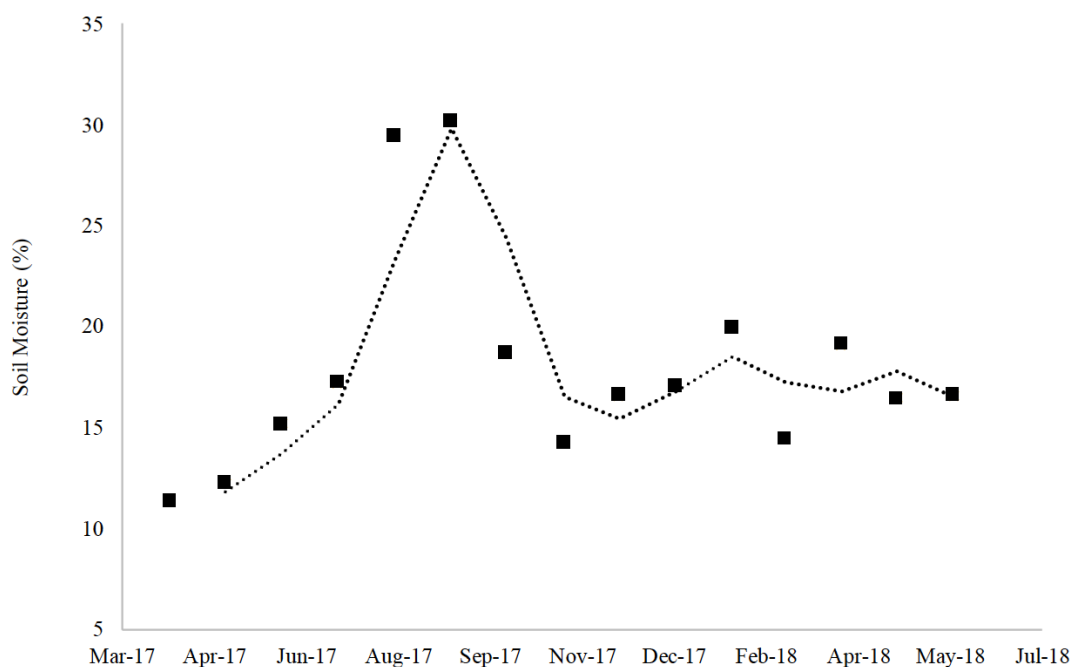
Appendix B1. Experimental design layout for a single replication (block). Four overstory treatments (clearcut, heavy thin, light thin, no thin) and two levels of vegetation control (zero or one-year of vegetation control). Twenty-five seedlings, represented by white circles, per treatment combination surrounded by buffer seedlings. Aerial photograph, Owen Burney.



Appendix B2. 1 m² plot vegetation survey around a *Q. virginiana* seedling (noted with pin flag).



Appendix B3. Average soil Moisture (%) from four clearcut plots from March 2017 to June 2018. Soil moisture was recorded every two hours. Dashed line is a moving average of the monthly soil moisture averages.



Appendix B4. Mean (\pm SE) initial height (cm) and initial diameter (mm) of *Q. virginiana* seedlings after planted in clearcut, heavy thin, light thin, no thin plots. Competing vegetation removed for zero or two-years.

