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Herbivory and Competing Vegetation Interact as Site Limiting Factors in Maritime Forest Restoration

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Abstract: Herbivory and competition during the regeneration phase influence forest successional dynamics. We demonstrated the importance of using the Target Plant Concept to identify and overcome site limiting factors for subtropical maritime forest restoration associated with deer browsing and competition. *Quercus virginiana* Mill. (live oak) bareroot seedlings were planted into clearcuts along the US Southern Atlantic coast with different treatment combinations of herbivory control (fenced or non-fenced) against white-tailed deer (*Odocoileus virginianus* Zimm.) browsing and competing vegetation removal (none, one-year, or two-years). After three growing seasons, mean seedling survival was 61% with no significant treatment differences. Control of browse and vegetation interacted to facilitate growth of live oak; seedlings were significantly larger for all response parameters (diameter, height, crown width) when fenced and treated with vegetation control. Removal of vegetation improved seedling performance only in fenced plots, however, indicating a shift in pressure from herbivory to competition as the most limiting site factor when deer were excluded. After the second growing season, foliar nitrogen was greater in fenced plots than non-fenced plots and greater in two-year vegetation control subplots than non-vegetation control subplots. This result, however, was absent after the third growing season. Three years after clearcutting, there was no evidence of *Q. virginiana* natural regeneration in non-fenced plots. Even with artificial regeneration in non-fenced plots, *Q. virginiana* growth was slow, indicating that herbivory was a key limiting factor. Our findings illustrate the importance of accounting for site limiting factors and may aid in developing management prescriptions to promote semi-evergreen oak regeneration in ecosystems with high pressure from herbivory and competing vegetation.

Keywords: maritime forest; *Quercus virginiana*; herbivory; competing vegetation; forest regeneration; limiting site factors; target plant concept; ecological restoration

1. Introduction

Worldwide, forests are challenged by herbivore behavior, population sizes, and changes in herbivore pressure on forest systems [1]. Herbivory by cervids (i.e., elk, deer, etc.), smaller mammals, and feral grazing animals such as cattle and hogs is a common forest regeneration concern across ecosystems [2–8]. Landscape changes, reduction of predators, and habitat fragmentation have contributed to high densities of herbivores resulting in over-browsing [1,9]. Additionally, browsing preference has potential to change forest dynamics as recruitment composition shifts towards less desired species [4,10–12].

When excluding animal browsers from forest regeneration sites, non-desired competing vegetation is also protected. A resulting shift toward competing vegetation as a dominant limiting factor suggests that simultaneous control of browsing and vegetative competition may synergistically improve seedling performance [13–15]. While there have been many studies on the individual effects of herbivory and competition, few previous studies have examined the interactive effects, with those that have showing varied results [16–21]. Competition between planted seedlings and neighboring vegetation limits the availability of soil nutrients, water, and light, impairing basic plant physiological processes [22]. In turn, competition restricts the ability of seedlings to establish, grow, and survive [23,24]. In clearcuts, light is notably increased, releasing competing vegetation from the seed bank and understory, while also providing habitat for recruitment of early successional competition via seed dispersal. Pioneer vegetation may acclimate quickly and take advantage of increased light and other resources in clearcuts, suppressing regeneration [25–27]. Controlling competition is therefore often deemed necessary following clearcutting. Under specific circumstances, however, a trade-off exists whereby competition may be beneficial to seedlings by acting as a natural shelter to hide seedlings from browsing animals or reducing the negative effects of drought or flooding [2,26,28,29].

Identified as regions of physiographical significance, maritime forests along the US Southern Atlantic coast provide major functions and services such as stabilizing soil, recharging groundwater, and biodiversity [30–33]. Late successional species comprise maritime forests and are dominated by *Quercus virginiana* Mill. (live oak), a semi-evergreen oak resilient to many coastal stressors [34–37]. A fraction of the original estimated land area of maritime forests exists, creating interest to conserve remaining maritime forests and restore transformed areas [34,38]. Dense pine stands established in parts of the historic maritime forest range often perform poorly under coastal stressors [37] and are frequently attacked by southern pine beetle (*Dendroctonus frontalis* Zimm.). Clearcuts are commonly required in pine stands with pine beetle outbreaks [39,40] and clearcutting of these sites provides the opportunity to convert unproductive, abandoned pine stands back to maritime forest.

Mid- to late-successional species, such as *Quercus* spp., show limited natural regeneration recruitment after disturbances, and artificial regeneration of these species is often necessary on clearcut sites [25,41]. Furthermore, browsing by white-tailed deer (*Odocoileus virginianus* Zimm.) may prevent regeneration of *Q. virginiana* and other maritime forest species [42]; or as another study posits, *Q. virginiana* recruitment and survival may be inherently low in this ecosystem and deer over-browsing may not be the most limiting factor [43]. However, there are few studies of impacts of deer browse on maritime forests [43]. While browse control techniques can be used (e.g., fencing and tree shelters), these are often logistically and economically prohibitive due to installation and maintenance costs [25,28,44].

The Target Plant Concept provides a conceptual framework for forest restoration to increase the likelihood of outplanting success [45]. A component of the concept is to identify and overcome important limiting site factors using site preparation [46]. The ecological principle of limiting factors states that limiting factors are not only cumulative, but also sequential; if the most limiting factor is not accounted for then it is not beneficial to address other limiting factors [47]. Herbivory and competing vegetation are two key factors that commonly limit forest regeneration [48–51], yet understanding how these two limiting factors interact to influence forest regeneration success is lacking, especially for maritime forest restoration. While maritime species are tolerant to coastal stressors, the negative effect of herbivory and competition may be enhanced for plant communities on barrier islands because of the inherent abiotic stressors [43].

Although *Q. virginiana* is a dominant charismatic species in the region, little is known about its regeneration. Thus, we evaluated the relative influence of fencing to reduce herbivory and vegetation control to reduce competing vegetation on planted *Q. virginiana* seedling performance in clearcut pine stands. Specifically, we hypothesized that (i) *Q. virginiana* survival and growth would be greatest in fenced plots with two years of vegetation control because both deer browse control and competing vegetation control would benefit seedling performance; (ii) an interaction would occur between fencing and vegetation control whereby competition would be a stronger driver of seedling performance in fenced plots; (iii) another interaction would occur, in which non-fenced seedlings without vegetation control would perform better than with vegetation control as the competing vegetation would act as a barrier to browsing deer.

2. Materials and Methods

2.1. Experimental Site

The 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 with approximately 50 ha dominated by abandoned pine plantations (mostly *P. taeda* with some *P. elliotti* Englem.). Tree rings and cores indicated that the pine stands were approximately 50 years old. In 2014–2015, areas of natural and planted pines affected by southern pine beetles were clearcut to salvage timber and reduce the future threat of pest outbreaks. The experiment consisted of four blocks, two located in a clearcut on the north end of the property and two located approximately 1.9 km south in another clearcut.

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 [52]. Composite soil samples were collected from each of the four blocks to evaluate physical and chemical characteristics using Mehlich III extraction (Brookside Laboratories, New Brennan, OH, USA) (Table 1).

Table 1. Mean ± SE of initial soil parameters using Mehlich III extraction averaged across the four blocks.

Chemical Characteristic	
Organic Matter (%)	4.35 ± 0.20
pH	5.5 ± 0.7
CEC (ME 100 g^{-1})	7.56 ± 3.52
Estimated nitrogen (kg ha^{-1})	104.8 ± 2.1
NO_3 (ppm)	13.7 ± 1.4
NH_4 (ppm)	8.1 ± 2.6
Phosphorous (ppm)	223 ± 4
Potassium (ppm)	24 ± 3
Magnesium (ppm)	63 ± 4
Calcium (ppm)	1367 ± 678

This region receives an average annual precipitation of 114 cm. The study period 2016–2018 had lower annual precipitation at 97.4 cm. Average annual temperature is 20.0 °C with slightly higher temperatures (20.4 °C) in 2016–2018 [53,54]. Hurricanes Matthew (October 2016; nine months into study) and Irma (September 2017; 22 months into study) resulted in increased precipitation, saltwater inundation, salt spray, and strong winds.

2.2. Experimental Design and Treatments

A randomized complete block design with four blocks and a split-plot structure was used. The whole plot factor consisted of two browse control levels (fenced at 2.5 m height or non-fenced). The subplot factor consisted of three levels of vegetation control (none, one-year, or two-years of vegetation removal). A total of 20 seedlings were planted within each subplot. All treatment combinations were replicated by four blocks resulting in 480 total seedlings.

When establishing 24 × 16 m research plots, a 50 m minimum buffer from the edge of the plots to the edge of the clearcut area was maintained to minimize the influence of adjacent pine canopies. Initial vegetation control was accomplished three months after outplanting using a backpack sprayer with an application of herbicide at a mixed rate of 2.3 liters per hectare (41% active ingredient of glyphosate; Clearout® 41 Plus, reg. no. 28322, Chemical Products Technologies LLC, Cartersville, GA, USA). Subsequent vegetation control was done throughout the growing seasons (either one-year or two-years) using mechanical methods (i.e., brush saws and hand clippers).

2.3. Plant Material

One-year-old *Q. virginiana* bareroot seedlings were planted in January 2016. Seedlings were obtained from ArborGen Bellville Nursery (Claxton, GA, USA) with a Louisiana seed source. From baseline morphology analysis ($n = 25$), mean seedling diameter was 5 mm ± 0.22, mean seedling height was 47 cm ± 1.43, and root to shoot dry mass (g) ratio was 1.23 ± 0.82. Seedlings were sorted prior to planting and randomly assigned to plot treatments. Seedlings were hand planted with 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.

2.4. Measurements

At the time of planting (January 2016), measurements were taken on ground line diameter and height to last live bud. At the end of each growing season (December 2016, November 2017, November 2018), survival, diameter, height, crown width, and browse assessments were recorded. Survival was recorded as a binary response; "alive" included seedlings with any number of green leaves. At the end of the second and third growing season (November 2017 and 2018), foliar nitrogen (N) was determined by randomly sampling five seedlings per subplot. Three leaves per seedling were collected and composited, dried at 60 °C for 72 h, weighed, pulverized in vials with stainless steel balls, and analyzed with an ECS 4010 CHNSO analyzer (Costech, Valencia, CA, USA).

Browse assessments estimated percent browse and type of browse by qualitatively categorizing seedlings that appeared to be browsed such as missing terminal and lateral buds, broken branches, and torn leaves. Key characteristics for type of browse included clean, rough, terminal, or lateral browse. Clean, lateral browse was classified as rabbit browse and rough, terminal browse was classified as deer browse [55].

At the peak of vegetation cover on site during the second growing season (August 2017), six seedlings from each treatment were randomly selected for a 1 m^2 plot vegetation survey to assess percent competing vegetation cover, mean height of competition, and top competing species within each plot. In addition to the vegetation surveys, natural tree regeneration 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.

2.5. Statistical Analyses

All data was analyzed with R software version 3.5.3 [56] using the lme4 package [57] for general linear models, linear regressions, and logistic regression, the nlme [58] package for repeated measures models, and the multcomp package [59] for pairwise comparisons. A logistic regression model was used to analyze survival. Diameter, height, crown width, and foliar N were analyzed with repeated measures general linear mixed models with fencing, vegetation control, and time as fixed factors; block and individual tree as random factors. The vegetation survey was analyzed with a general linear mixed model, with fencing and vegetation control as fixed factors and block as a random factor. Natural regeneration was also analyzed with a general linear mixed model, but only with fencing as the fixed factor and block as a random factor. Residuals from all response variables were tested to ensure normality and homogeneity of variance. Crown width did not meet assumptions and this data was square root transformed. For all analyses, when significant treatment effects were detected ($p \leq 0.05$), Tukey's HSD test was used to test for pairwise comparisons ($\alpha = 0.05$).

3. Results

3.1. Seedling Performance

Initial diameter and height of planted seedlings were similar across all treatments with a mean height of 48 ± 0.9 cm and a mean diameter of 3.8 ± 0.1 mm. Overall survival after three growing seasons was 61% ± 3.2% with no treatment differences ($X^2_{2,473} = 0.65$, $p = 0.721$). The interaction of fencing, vegetation control, and time was significant for mean diameter ($F_{2,886}$ = 26.88, $p < 0.001$), mean height ($F_{2,874}$ = 3.08, p = 0.006), and mean crown width ($F_{4,570}$ = 6.89, $p < 0.001$). The effect of vegetation control was different between the fencing treatments and the effects varied over time. Overall diameter, height, and crown width were greater in fenced plots; furthermore, only in fenced plots did vegetation control further increase seedling diameter, height, and crown width (Figure 1). For foliar N, only main effects after the second growing season were significant, showing increased foliar N in fenced plots ($F_{2,114}$ = 5.61, p = 0.020) and in subplots with vegetation control for two years compared to subplots with no vegetation control ($F_{2,283}$ = 6.39, p = 0.002) (Figure 2); after the third growing season, foliar N differences were absent.

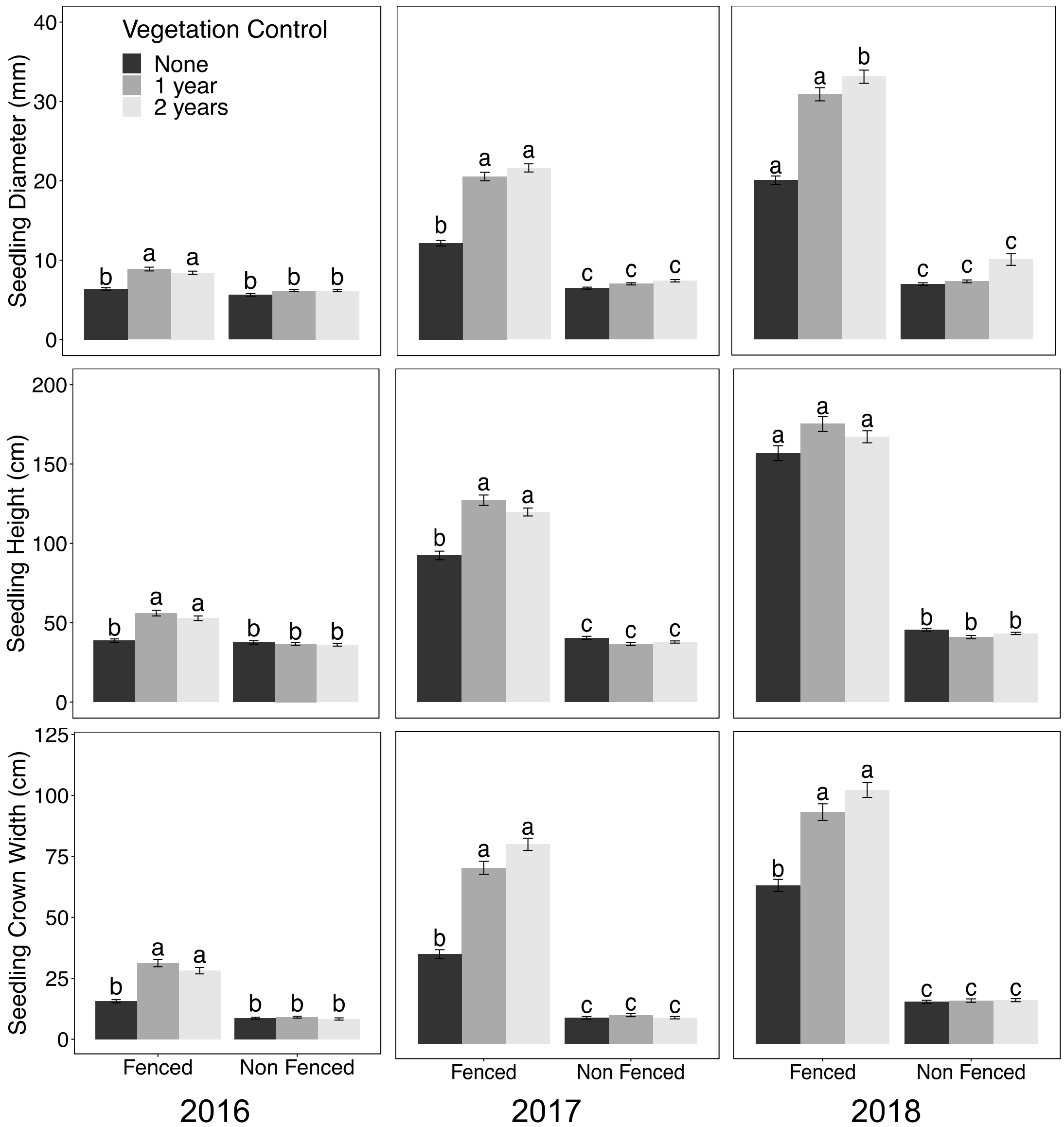

Figure 1. Mean ± SE diameter, height, and crown width growth of *Q. virginiana* seedlings after each of the three growing seasons. Seedlings were planted in fenced or non-fenced plots and competing vegetation was not removed or removed for one year or two years. In 2016, both vegetation control treatments (one year and two years) were the same. In 2017, vegetation control was done solely for the two-year treatment. Different letters indicate significant differences among the interaction of fencing and vegetation control treatments (α = 0.05).

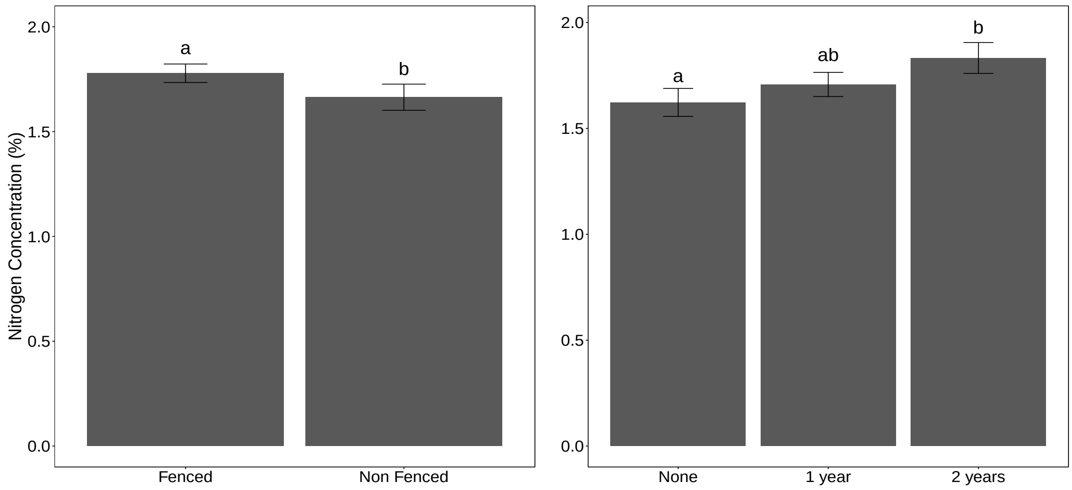

Figure 2. Mean ± SE foliar nitrogen (N) concentration (%) of *Q. virginiana* seedlings in 2017 after two growing seasons. Seedlings were planted in fenced or non-fenced plots and competing vegetation was not removed (None) or removed for one year or two years. Different letters indicate significant differences for each main effect, fencing and vegetation control ($\alpha = 0.05$).

Seedling diameter and crown width in fenced plots increased by approximately 400% with two-year vegetation control, 300% with one-year vegetation control, and 200% with no vegetation control.

After the third growing season, in fenced plots seedling height increased by 100% regardless of vegetation control, despite greater height growth the first two growing seasons in subplots with one-year and two-year vegetation control compared to subplots with no vegetation control. In non-fenced plots, regardless of vegetation control, seedlings had marginal height growth, but the diameter and crown width increased by 100% regardless of the vegetation control.

After the third growing season, 98% of non-fenced and <1% of fenced seedlings were browsed. Browse in fenced plots was only clean and lateral, which was attributed to rabbits (*Sylvilagus floridanus* and *S. palustris*), whereas browse evidence in non-fenced plots was a combination of clean, rough, terminal, and lateral. Relative height growth rate was negative after three growing seasons in non-fenced plots due to browse and dieback.

3.2. Vegetation Surveys and Natural Regeneration

Only the vegetation control main effect was significant for both percent cover and mean height (Figure 3). 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 in subplots with no vegetation control compared to those with two-year vegetation control. One-year vegetation control had a lower percent of competing vegetation cover than the no vegetation control treatment, but no significant differences in average vegetation height. Top competing species included: *Eupatorium capillifolium* Lam., *Paspalum notatum* Flueggé, *Cyperus* spp. L., and *Rubus trivialis* Michx.

For natural tree species regeneration, the only species present were *Persea borbonia* (L.) Spreng. (PEBO, red bay), *P. taeda* (PITA, loblolly pine), *Q. hemisphaerica* W.Bartram ex. Willd. (QUHE, laurel oak), and *Q. virginiana* (QUVI, live oak). There was more natural regeneration of tree species in fenced plots with no evidence of *Q. virginiana* natural regeneration in non-fenced plots ($F_{1,28} = 13.73$, $p = 0.001$) (Figure 4).

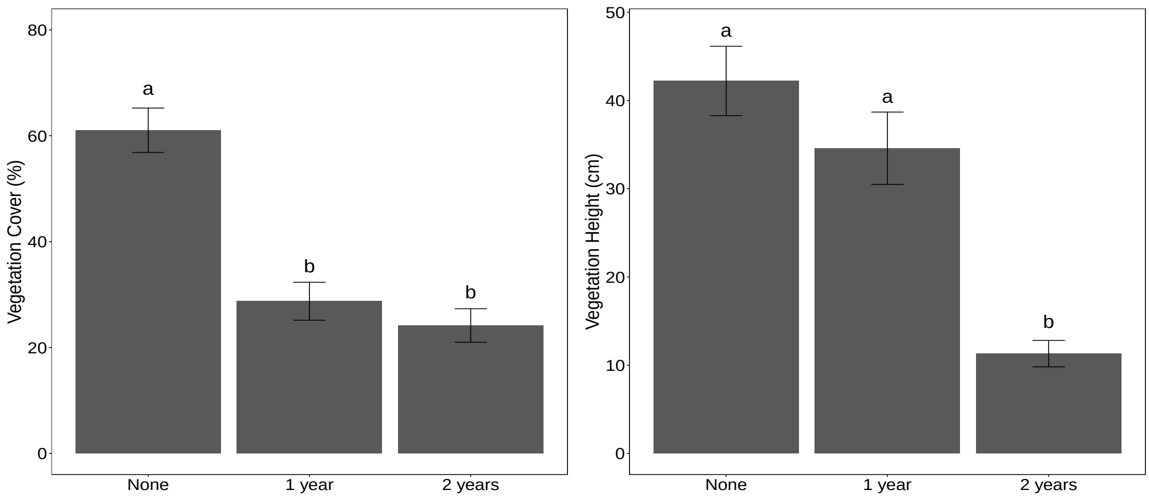

Figure 3. Mean ± SE cover (%) and height (cm) of competing vegetation in a 1-m^2 survey around *Q. virginiana* seedlings. Seedlings were planted in fenced or non-fenced plots and competing vegetation was not removed or removed for one year or two years. Different letters indicate significant differences for each main effect, fencing and vegetation control (α = 0.05).

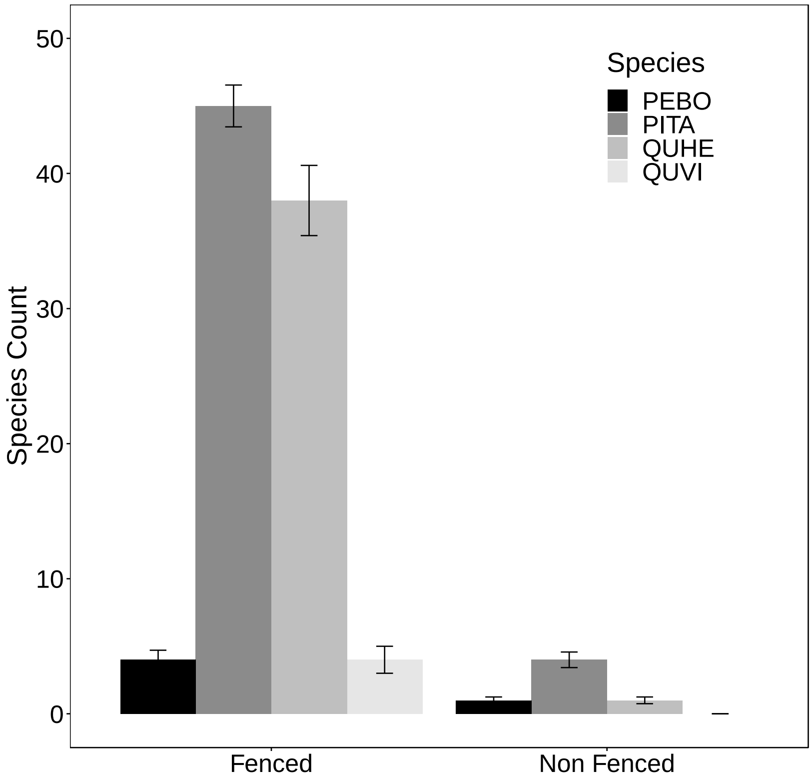

Figure 4. Total number of natural regenerating individuals of each tree species in non-weeded subplots within fenced and non-fenced plots in 2018 after three growing seasons. PEBO = *Persea borbonia* (red bay). PITA = *Pinus taeda* (loblolly pine). QUHE = *Quercus hemisphaerica* (laurel oak). QUVI = *Quercus virginiana* (live oak).

4. Discussion

Maritime forests of the southern Atlantic coast conform to the global trend of compositional shifts in forests due to factors including deer herbivory [1,4,9]. Our results indicate the importance of reducing animal browse and competing vegetation to promote regeneration of *Q. virginiana*. Few studies have tested simultaneous exclusion of animal browse and control of competing vegetation on performance of hardwood trees and fewer studies have reported significant interactions [13,14,16]. Although there were no significant effects of the treatments on survival, the health of non-fenced seedlings was poor and their long-term survival is unlikely as seedling establishment during the first few years after planting is critical to regeneration [24,27,51,60]. In support of our hypotheses, seedlings in fenced plots had greater diameters, were taller, and had larger crown widths than seedlings in non-fenced plots (Figure 1), illustrating the high pressure from deer browse for planted *Q. virginiana*. This positive seedling response to fencing in our study is consistent with regional results for *Q. virginiana* of Bratton et al. (1994); however, our conclusions differed from Taggart and Long (2015) that deer were not over browsing the maritime forest understory vegetation, including *Q. virginiana* seedlings, but that there were even greater limiting factors such as low light levels and squirrel acorn predation.

Deer browsing has substantial negative effects on native hardwood seedling performance, and therefore regeneration success [9,12,48]. When seedlings lose photosynthetic tissues via browse of terminal and lateral branches, they rely on stored nutrients to regrow leaves, therefore depleting nutrients for other development [61,62]. This, in turn, reduces seedling height, crown width, and ability to allocate resources to growth and development (e.g., diameter and foliar N). Several studies have found greater diameter and height of regenerating seedlings in areas with lower deer densities [2,9,16,63–65]. Despite extensive browse and lack of height/crown width growth in non-fenced plots, seedlings did have some diameter growth, which may signal an allocation of resources to survival and, potentially, belowground growth [25]. With a decrease in ungulate pressure, the seedlings may rebound by re-allocating belowground biomass to aboveground biomass. The limited time frame of this study did not capture this potential effect, however, as there can be long-term delays in recovery requiring other intervention strategies [66]. 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 control [67].

Further supporting our hypotheses, we observed an interaction with vegetation control having variable effects in the fenced vs. non-fenced plots. This aligns with results of Owings et al. (2017), which showed increased height of planted *Castanea dentata* (Marshall) Borkh. when deer and invasive honeysuckle were excluded, Miller et al. (2016) who predicted more co-dominant oaks in plots with deer and competing vegetation excluded, and Sweeney et al. (2002) who found increased riparian restoration success with tree shelters and reduced competition. However, Owings et al. (2017) did not find this interaction with *Q. rubra* L. seedlings and other studies have also not observed consistent interactions between excluding browsers and vegetation control/site preparation [17–20]. Although vegetation control in the absence of browsing improved seedling development in fenced plots, herbivory was a greater driver of *Q. virginiana* performance than competition in non-fenced plots. Vegetation control only improved seedling performance in fenced plots (Figure 1), due to the overwhelming effect of browse without deer exclusion. The interaction of fencing and vegetation control illustrates the shift of pressures on seedling performance: from browse-limited to resource-limited. Vegetation control to reduce competition has positive effects on native hardwood seedling performance and, therefore, regeneration and restoration [26,68,69]. In fenced plots, herbivory was absent (both for planted trees and competing vegetation); therefore, competition became a larger driver of *Q. virginiana* performance. A mechanism by which competition impairs growth is by reducing light, nutrients, and soil moisture available to seedlings [70]. The greater foliar N in vegetation control subplots after the second growing season illustrated the importance of this treatment to channel resources to planted seedlings in clearcuts. As an essential macronutrient, N is commonly the most limiting element for plants and greater foliar N is often correlated with overall increased seedling performance [71,72] because it is critical to performance processes such as the construction of amino acids, nucleic acids, hormones, chlorophyll, and rubisco [71,73]. The absence in foliar N difference after the third growing season (one year after vegetation control ceased) may, however, indicate that such benefits are transient.

We did not find support for the second predicted interaction that in non-fenced plots, seedlings may perform better in treatments without vegetation control because the competition may act as a barrier to deer browse [2,28]. 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 palatable vegetation was browsed [62,67], regardless of *Q. virginiana* seedlings being obscured by competing vegetation.

5. Conclusions

Our research provides evidence that restoration of maritime forests through artificial regeneration of a keystone species is possible following clearcutting (e.g., for pine beetle outbreaks). 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*. The high deer pressure in the non-fenced plots resulted in poor performance of planted seedlings and a lack of natural regeneration of *Q. virginiana*. Fencing, or possibly the use of other physical barrier methods (i.e., tree shelters), therefore, is essential for restoring degraded maritime forests or abandoned pine stands/agricultural land when heavy deer browse pressure is expected. Our results compliment other studies of underplanted oaks [70,74] that cite the effectiveness of additional silvicultural tools, such as removal of competing vegetation. In our study, artificial regeneration success of *Q. virginiana* in clearcuts was augmented with vegetation control to reduce competition if the primary limiting factor of deer browse was controlled. An improved understanding of limiting factors to *Q. virginiana* regeneration will allow land managers to make informed decisions to ensure the function of this important forest ecosystem and associated services [30,34,75]. Our results may also apply to other semi-evergreen species in regions with strong herbivory and competing vegetation.

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