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Regenerating White Pine (*Pinus strobus*) in the South: Seedling Position is More Important than Herbivory Protection

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ABSTRACT Seedling survival and growth in eastern white pines (*Pinus strobus* L.) might be limited by white-tailed deer (*Odocoileus virginianus*) browsing. However, most studies have occurred in areas central to the white pine range, making other factors such as seedling microenvironment unimportant. If microenvironment becomes a concern near the edge of the white pine range, then factors such as seedling placement in relation to forest openings could be important, especially given that deer herbivory tends to be most intense near forest edges. We evaluated the relative importance of deer browse and seedling position in openings on seedling survival and growth in central North Carolina at the southern edge of the white pine range. Further, we determined if bud caps and caging improved survival and growth. Seedlings $\leq$ 10 m from the edge survived at a greater proportion than those $>$ 10 m from the edge (83% and 73%, respectively). Initial height was the most important predictor of survival ($R^2 = 0.55$; $p < 0.01$). When controlling for initial seedling height, the location of the seedling ($p < 0.01$) within the opening was the only significant predictor of survival, despite the increase of browse near the edges of openings on unprotected seedlings. Caging and bud caps decreased seedling browse by 80% but had no effect on subsequent seedling survival ($p = 0.28$). A smaller proportion of seedlings with bud caps survived—an effect exacerbated by being internal to the opening. Our data indicate seedling microenvironment is an important consideration at the periphery of the white pine range.

Key words: Browse, bud caps, regeneration, temperature, white-tailed deer.

INTRODUCTION The eastern white pine (*Pinus strobus* L.) is a temperature-sensitive species that can be affected by climatic shifts (Jacobson and Dieffenbacher-Krall 1995), and the current southern edge of its range is expected to contract northward (Iverson and Prasad 1998). This range contraction is likely given the thermoneutral zone of the plant and the projected increases in temperature in the eastern USA. Because ambient temperatures are near the thermal maximum of the species, positioning seedlings in cooler microenvironments may be an important consideration.

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In the northeastern USA, in the center of the white pine range, silvicultural methods to improve seedling establishment, survival, and growth rate include partial harvest of the overstory strata (Ostry et al. 2010, Kern et al. 2012). Also, seedlings planted in open areas with full sun might survive better than those planted in partial to full shade (Ward and Mervosh 2008, Kern et al. 2012). However, these planting techniques might not be as applicable on the southern edge of the white pine range where seedling survival can be limited by ambient temperatures (Wendel and Smith 1990, Keenan and Kimmins 1993).

White pine regeneration is negatively affected by browsing of overabundant white-tailed deer (*Odocoileus virginianus* Zimmerman; hereafter deer) populations (Kittredge and Ashton 1995, Kern et al. 2012). Because white pines are of substantial importance to forest biodiversity and are aesthetically and commercially valuable (Wendel and Smith 1990), several methods have been employed to improve seedling survival and prevent overbrowsing. For example, Ward and Mervosh (2008) reported seedlings protected by mesh tubes (i.e., tree shelters) and bud caps (i.e., structure used to protect terminal buds from herbivory) had increased survival and growth rates. Protecting seedlings from browse with the aid of tree shelters is the most common method to mitigate deer damage (Ward et al. 2000), but bud caps can be used successfully, alone or in tandem with tree shelters, to protect seedlings from deer browse (Ward and Mervosh 2008).

We evaluated the influence of seedling placement in forest openings and type of browse protection method (i.e., deer exclusion and bud caps) on white pine seedling survival and growth in an isolated North Carolina population representing the lowest-elevation population in the southern edge of the range. Our objectives were to determine the relative importance of browse pressure and seedling placement within openings to white pine seedling survival and growth. Because our study area was at the southern extent of the white pine range and ambient temperatures were near the thermal maximum tolerance of the species, we hypothesized that seedling position in openings would be an important factor affecting seedling survival and growth in addition to herbivory.

METHODS

Study Area

Our study was conducted at White Pines Nature Preserve in the central Piedmont region of North Carolina. The 111-ha tract is genetically isolated and represents the lowest-elevation population in the southern part of the white pine range; the population is thought to be remnant from the expanded range of white pine during the last ice age (Wendel and Smith 1990, Jacobson and Dieffenbacher-Krall 1995). The property is comprised primarily of mature mixed pine/hardwood forest, bisected by multiple creeks and drainages, and is located about 120 km east of the nearest naturally occurring white pine population. With the majority of the North Carolina Piedmont providing intolerable climatic conditions (high temperature) for white pine, the isolated population might be genetically more adapted to warmer climates (Balmer and Williston 1983). Deer damage to white pine regeneration on the preserve was a concern because of observed understory herbivory damage (W. Tysinger, Triangle Land Conservancy, pers. comm., October 22, 2012). The estimated deer density was 12–17 deer/km^2 (North Carolina Wildlife Resources Commission 2014), which is double the density expected to cause significant browse damage to regenerating white pine seedlings (Ward and Mervosh 2008).

Experimental Design and Data Collection

During fall 2011, seeds from white pine cones were collected on site and planted in 4 L containers. In summer 2012, we randomly established seven forest openings ranging 0.1–0.2 ha with a timber harvest on the area. We selected this range in forest gap size because of previous recommendations for successful regeneration of white pine in the central part of its range (Hibbs 1982). During the dormant season, from December 2012 through February 2013, we planted 848 $\sim$2-yr-old white pine seedlings in the openings at 3 m $\times$ 3 m spacing. After planting, we randomly assigned bud caps and cages to seedlings stratified by spatial arrangement in the openings. Combinations of mechanical and chemical weed control were applied monthly through the growing season to minimize the effects of interspecies competition on white pine seedling survival and growth. We characterized seedlings $\leq$ 10 m of the opening boundary as "edge" and seedlings $>$ 10 m from the boundary as "middle." We stratified seedlings by position to forest edge because deer herbivory is often more intense nearer to forest edges (Alverson et al. 1988), and temperatures generally are cooler there than in the center of openings because of increased shade (Keenan and Kimmins 1993). Within days after planting, we deployed browse protection treatments on 89% of seedlings, with 33% receiving laminated bud caps and 56% receiving 1.2 m $\times$ 12 m deer exclusion cages. The primary purpose of this study was to maximize survival of seedlings, and thus browse protection was implemented on the most seedlings in anticipation of herbivory causing poor survival. Bud caps were recommended to protect buds from browse damage (Ward et al. 2000, Ward and Mervosh 2008), whereas exclusion cages were used to exclude deer from plants within a small area (Lashley et al. 2011, 2015).

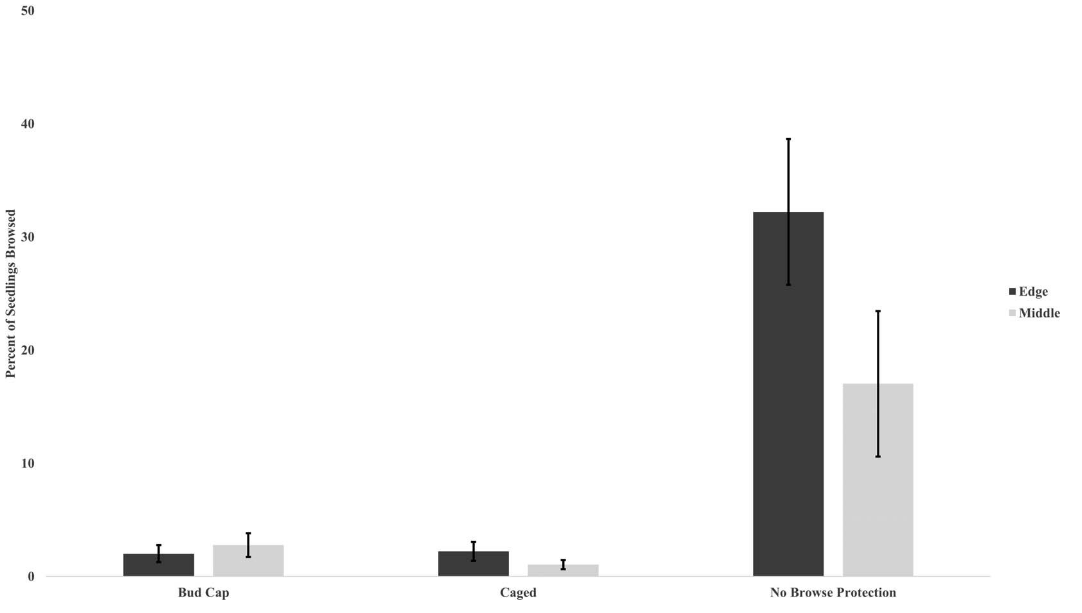

Figure 1. Percent of white pine seedlings with terminal bud browse (mean, SE) in relation to the position of the seedling in the opening and browse protection treatment, White Pines Nature Preserve, North Carolina in 2013.

We used bud caps and cages in a similar ratio for edge and middle seedlings.

During March and April 2013, we examined seedlings for evidence of deer herbivory (Lashley et al. 2014) and measured initial seedling height to the nearest millimeter because seedling survival and vigor is related to initial seedling size (Ward et al. 2000). In September 2013, we tallied survival and measured seedling height, evidence of herbivory, and whether the terminal bud was browsed. Ideally, long-term data on recruitment would be collected to compare seedling recruitment, but first-year survival rate is obviously necessary for future recruitment and is positively correlated with long-term survival rate in white pine seedlings in many cases (Kern et al. 2012). Thus, we believe first-year survival provides useful information about future recruitment success.

Data Analysis

We used nominal logistic regression in JMP 10.0 (SAS Corporation, Cary, North Carolina) to determine the relative importance of deer exclusion method, seedling placement, and a binary terminal bud browse variable (seedling terminal bud was browsed or not) on seedling survival. We used browse on the terminal bud as our indication of herbivory damage because that location on the seedling is most sensitive to browsing and the terminal bud is the primary area protected by bud caps (Ward et al. 2000, Ward and Mervosh 2008). We coded seedling survival as a binary response variable with 1 corresponding to surviving seedlings. Deer exclusion method and seedling placement were categorical predictor variables, along with an interaction term. We controlled for initial seedling height to avoid biases in survival due to initial seedling size (Ward et al. 2000). We used standard least squares regression to determine the relative importance of deer exclusion method, seedling placement, and terminal bud browse on seedling growth. We coded seedling growth as a continuous response variable. Deer exclusion method and seedling placement were categorical predictor variables, and terminal bud browse was a binary predictor variable. We controlled for initial seedling height to avoid biases in seedling growth due to initial seedling size (Ward et al. 2000).

RESULTS

Of the 848 seedlings planted, 79% of seedlings survived the first growing season and 4% included terminal bud browse (Figure 1), although 24% of the seedlings showed evidence of browse. Unprotected seedlings had the terminal bud browsed on over 30% of the

Table 1. Variable predictive power of eastern white pine seedling survival at White Pines Nature Preserve, North Carolina in 2013. Nparm indicates the number of parameters associated with the effect, DF indicates the degrees of freedom for the effect test, and L-R ChiSquare indicates the likelihood-ratio chi-square statistic.

	Nparm	DF	L-R ChiSquare	Prob>ChiSq
Preseason seedling height	1	1	15.96	<0.001
Seedling location	2	2	10.83	0.004
Browse treatment	2	2	2.57	0.277
Terminal bud browsed	1	1	0.11	0.741

seedlings in the edge and 18% of the seedlings in the middle. Edge seedlings ($n = 457$) survived at a greater proportion than middle ($n = 391$; 83%, and 73%, respectively). Initial seedling height was positively correlated with seedling survival and its most important predictor ($p < 0.001$) (Table 1). Surviving seedlings had an average initial height of 40.8 cm ($\pm$0.4 cm) and seedlings that died had an average height of 36.9 cm ($\pm$0.7cm). When controlling for initial seedling height, the location of the seedling within the opening was the only significant predictor ($p = 0.004$) of survival (Table 1), despite the increase of browse near the edges of openings on unprotected seedlings. Caging and bud caps decreased seedling browse substantially (Figure 1) but had no effect ($p = 0.28$) on subsequent seedling survival; however, compared to caged seedlings, a smaller proportion of seedlings with bud caps survived (Table 1, Figure 2) especially middle seedlings with bud caps. Terminal bud browse had no effect ($p = 0.74$) on subsequent seedling survival (Table 1). Initial seedling height was the most important predictor ($R^2 = 0.55$; $p < 0.001$) of growth (Table 2). When controlling for initial seedling height, the location of the seedling within the opening ($p = 0.031$) and browsing on the terminal bud affected growth ($p = 0.004$) (Table 2, Figure 3). However, browse protection treatment did not affect growth ($p = 0.41$, Table 2).

DISCUSSION Eastern white pine seedling survival increased nearer the edges of openings,

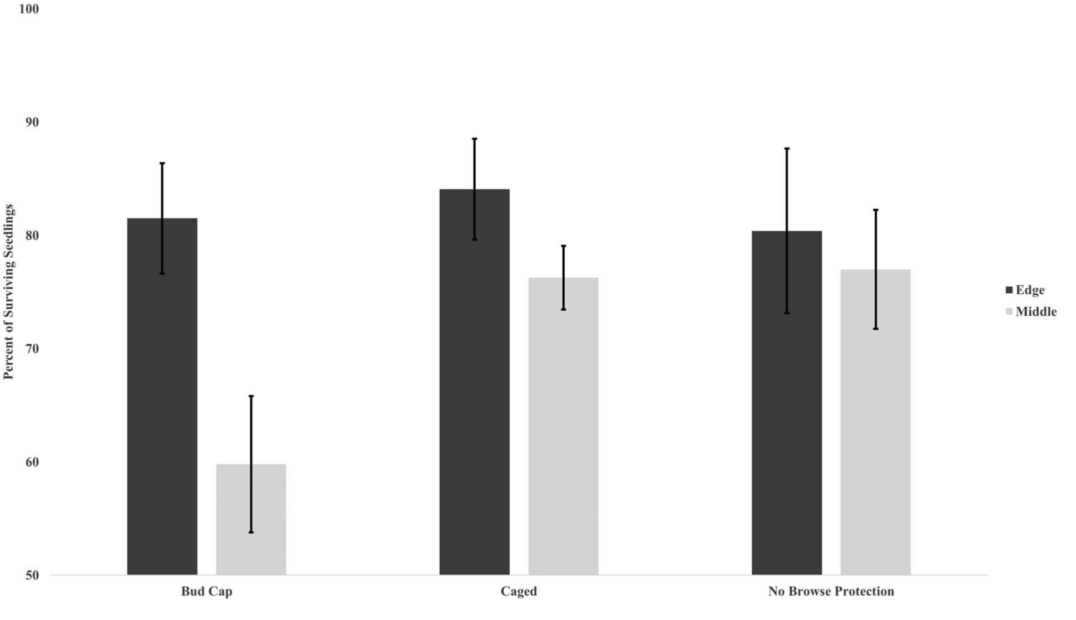

Figure 2. Percent of white pine seedlings surviving (mean, SE) in relation to the position of the seedling in the opening and browse protection treatment, White Pines Nature Preserve, North Carolina in 2013. Note that initial seedling height was the most important predictor of survival and is not accounted for in this graphic.

Table 2. Variable predictive power of eastern white pine seedling growth at White Pines Nature Preserve, North Carolina in 2013. Nparm indicates the number of parameters associated with the effect and DF indicates the degrees of freedom for the effect test.

	Nparm	DF	Sum of Squares	F Ratio	Prob>F
Preseason seedling height	1	1	875.46707	86.1463	<0.001
Seedling location	2	2	71.66759	3.5261	0.031
Browse treatment	2	2	18.17925	0.8944	0.409
Terminal bud browsed	1	1	83.13776	8.1808	0.004

likely because of a more appropriate microenvironment provided with shading from the adjacent forest canopy (Keenan and Kimmins 1993). Similarly, a lower proportion of seedlings with bud caps survived, especially when exposed to full sunlight, likely from increased ambient temperature near the buds. In fact, being positioned near the edge of the opening was most important to survival, as evidenced by the lack of effect of seedling protection method and a larger proportion of seedlings near the edge of the openings being browsed. Although we did not measure the microenvironment, temperature is well known to be greater in openings than forest edges or partial to full canopy conditions (Keenan and Kimmins 1993). Moreover, the white pine range has been predicted to retract northward as the climate warms (Iverson and Prasad 1998). Thus, because our study occurred at the periphery of the white pine range, in environmental conditions nearer the thermal maximum tolerance of white pines, microenvironmental conditions affected by forest structure such as temperature likely played the most critical role in survival (Ostry et al. 2010).

Our study demonstrates that browse pressure might not be the most important consideration to regenerating white pine in the south. Moreover, Ward and Mervosh (2008) suggested planting white pine seedlings in full sun to increase seedling growth by releasing stems from deer browsing. Although they reported lower deer density and a smaller proportion of seedlings browsed than we report, Ward and Mervosh (2008) still determined that deer browse was the leading cause of seedling

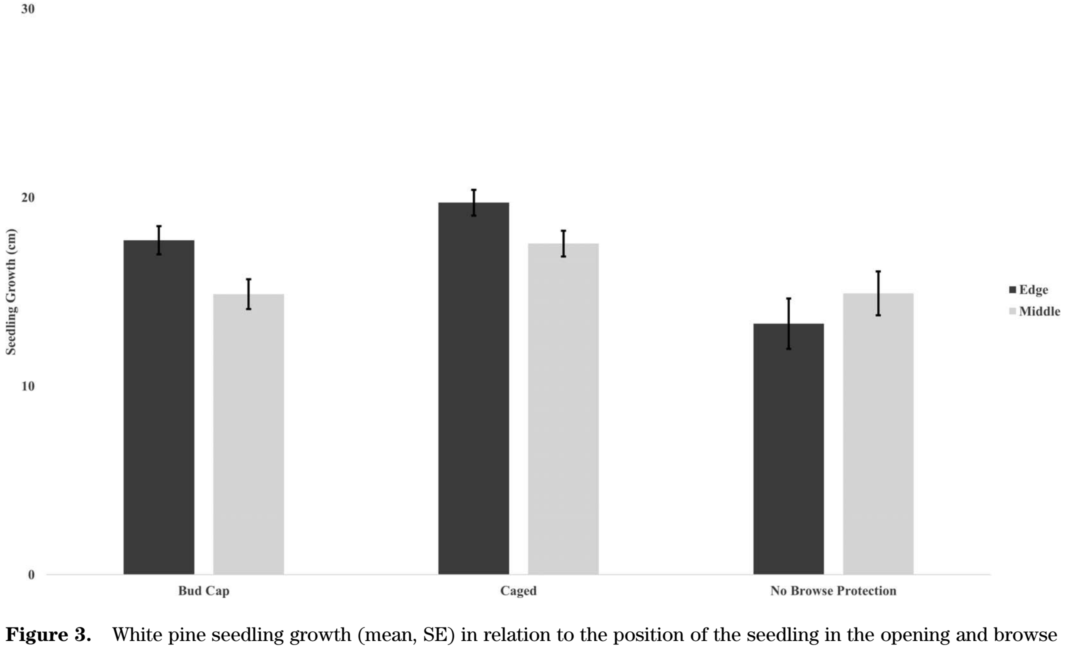

Figure 3. White pine seedling growth (mean, SE) in relation to the position of the seedling in the opening and browse protection treatment, White Pines Nature Preserve, North Carolina in 2013. Note that preseason seedling height was the most important factor affecting seedling growth.

mortality. In our study, seedling growth increased near the edge of openings, particularly when seedlings were not protected from deer browse, suggesting factors limiting white pine seedlings are site-specific, not only in their frequency but in their relative importance to survival and growth, and therefore, strategies to mitigate damaging agents should be site-specific (Ostry et al. 2010, Kern et al. 2012). Furthermore, although not a significant relationship, caging seedlings promoted survival and growth and substantially decreased browse on our site. Therefore, when herbivory is limiting, caging could be the recommended practice for protecting white pine seedlings over bud caps, which can increase temperature around buds (Oliet and Jacobs 2007).

Given the overwhelming scientific consensus that climate is changing (Cook et al. 2013), consideration of the genetic diversity contributions held within relict or disjunct populations near the edge of species' ranges is important in the conservation of plants (Hampe and Petit 2005). Further, rear-edges of range shifts are most likely to be negatively influenced by warming climates (Jacobson and Dieffenbacher-Krall 1995, Hampe and Petit 2005). Currently, southern and low-elevation white pine populations represent the rear-edge of the species' range and are most susceptible to reduced growth and survival under climate-warming scenarios. As such, future climate warming might make consideration of seedling microenvironment more important than other damaging agents across the range of white pine.

SUMMARY When restoring eastern white pine at the southern edge of its range, the relatively large seedlings with local genotypes should be planted to maximize survival and growth. Furthermore, abiotic conditions should be considered when planting near the edge of the range of a species. For increased seedling growth, efforts to minimize deer browsing are necessary, particularly for protecting terminal buds. However, if browse protection becomes necessary, we recommend exclusion cages or reducing herbivore density to improve planting success.

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