EFFECTS OF DEER EXCLOSURES ON OAK REGENERATION IN CLOSED-CANOPY STANDS

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Abstract.—Studies of the effects of high deer densities on forest regeneration have shown altered species composition and reduced diversity in stands regenerating after harvest. The effects of browsing in fully stocked, undisturbed stands are less well known but important, as establishment of seedlings of oaks and other species prior to disturbance is very important for self-replacement. The purpose of this study was to quantify the effects of deer exclusion on existing cohorts of advanced oak seedlings in closed-canopy, mixed-oak stands in Pennsylvania. Permanent plots in six stands were established and measured in 2003, and half of each stand was subsequently fenced. The stands were remeasured in 2006 to quantify changes in the size and number of tree seedlings after two growing seasons as a result of protection from deer. Three additional stands were measured and fenced without controls for periods of 6 to 8 years. In general, fencing enhanced seedling abundance in stands that had good mast crops or reduced seedling mortality in stands that did not. Fencing also was associated with improvements in seedling height. None of the stands fenced for only 2 years exhibited marked improvements in the quality of advance oak regeneration. Two stands that were fenced for 6 to 7 years, both of which had relatively open understories, exhibited significant and rather substantial increases in oak seedling density, frequency of occurrence, and height. A third stand, which was fenced for 8 years and had heavy mountain-laurel cover, exhibited a significant but very small increase in oak seedling height but no lasting increases in seedling density or frequency of occurrence. The results show that preharvest fencing designed to enhance the level of oak advance regeneration may require several years to be effective and may need to be combined with stand thinning or other forms of vegetation control.

INTRODUCTION

High densities of white-tailed deer (*Odocoileus virginianus* Zimm.) can have profound influences on forest stands. Browsing can influence the ability of forests to regenerate after a disturbance such as harvesting because large populations of deer reduce the occurrence and density of seedlings of some species (Anderson and Loucks 1979). In Pennsylvania, high deer populations are known to influence regeneration in forest stands either through general regeneration failure (Marquis and others 1976, Marquis and Brenneman 1981) or reduced diversity of tree species following selective browsing (Bowersox and others 1995). In particular, Pennsylvania mixed-oak stands are inclined toward regenerating non-oak species, a shift that can be at least partially attributed to high deer densities (Gould and others 2005). Black birch (*Betula lenta* L.) and red maple (*Acer rubrum* L.) frequently replace oaks following harvests in central Pennsylvania (Fei and others 2005, Gould and others 2005, Abrams and Nowacki 1992). If high deer densities are present for a long time, vegetation composition can be shifted toward fewer species dominated by those not preferred by deer (Rossell and others 2005). The mixed-oak forests of Pennsylvania contain chestnut oak (*Quercus montana* Willd.), white oak (*Q. alba* L.), northern red oak (*Q. rubra* L.), black oak (*Q. velutina* Lam.), and scarlet oak (*Q. coccinea* Münchh.) as dominant overstory trees in different combinations and densities. Changes in understory vegetation composition, an overall reduction in species diversity, and a transition from forests dominated by oak species to red maple are possible long-term consequences of high deer densities in mixed-oak forests.

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Advance regeneration, regeneration present in advance of harvest or disturbance, is important for replacement of oak in forest stands (Abrams 1992, Larsen and Johnson 1998, Gould and others 2005, Sander 1972). Oak advance regeneration grows more quickly than newly germinated oaks because established seedlings have large, well developed root systems (Larsen and Johnson 1998). Quick growth aids in escaping competition, as advance oak regeneration or sprouts from advance regeneration are often able to compete successfully after heavy cutting (Lorimer 1984, Sander 1972). Deer herbivory and seed predation can reduce the abundance, survival, and height growth of advance oak regeneration, therefore limiting the ability of oak to be replaced successfully when harvest or disturbance occurs.

OBJECTIVES

Although fencing after harvest is commonly employed in areas with high deer densities, post-harvest fencing alone cannot compensate for inadequate advance regeneration, which is considered so important to oak regeneration success. By contrast, very little is known about the responsiveness of regeneration to preharvest fencing, i.e., protection from deer in closed-canopy stands (Rossell and others 2005, Griggs and others 2006). The purpose of this research was to quantify the effect of preharvest fencing on advance regeneration of oak. Aside from its obvious silvicultural implications, studying the effect of fencing in mature stands can provide further insight into the overall impact of high deer populations in mixed-oak forests.

STUDY AREAS

For this study we measured nine mixed-oak stands, 36 to 71 acres in size, located in the Ridge and Valley and Appalachian Plateau provinces of Pennsylvania. All are on state lands managed by the Department of Conservation and Natural Resources (Pennsylvania Bureau of Forestry). The stands occur in an area covering approximately the central one-half of the state from north to south and the central one-fourth from west to east. Elevations range from 950 ft MSL in the Ridge and Valley province to a high of 2000 ft MSL on the Appalachian Plateau. Soils include loams from the Laidig, Dekalb, Ungers, and Wharton series. In all stands, oak makes up the plurality of basal area (39 to 60 percent), which ranges from 106 to 136 ft^2ac^{-1}. All are fully stocked to overstocked (Gingrich 1967). The principal oak species is chestnut oak in 6 stands, northern red oak in 3 stands, and black oak and white oak in one each. Understories are dominated by mountain-laurel (*Kalmia latifolia* L.), huckleberry (*Gaylussacia* spp. Kunth), striped maple (*Acer pensylvanicum* L.), hayscented fern (*Dennstaedtia punctilobula* (Michx.) T. Moore), or combinations of these species. Regionally, mean annual precipitation is 38 to 40 inches and length of the frost-free growing season is 130 to 170 days, but both vary with elevation and topography (Cuff and others 1989).

Six stands (stands 1-6) were measured initially in summer 2003 and half of each stand was subsequently fenced with 8-ft, woven wire fencing to exclude deer. These "divided stands" were measured again in 2006 after approximately two growing seasons and one to three autumns (depending on stand) following fence installation.

In three additional stands, the entire stand was operationally fenced with 8-ft woven wire shortly after measurement and unfenced comparisons were not available. In these stands, fencing treatment effects cannot be isolated because of the lack of controls, but these stands are significant because they were fenced much longer than the six described previously. Bell Furnace I was measured and fenced in the summer of 1997 and remeasured in 1998 and 2004 (after which the stand was harvested). Bell Furnace II was measured in 1998, fenced the following winter, and remeasured in 2004. Finally, Horsepath was measured in 1997, fenced the following winter, and remeasured in 1999, 2005, and 2006. We observed little or no browsing within the fenced portions of any of the nine stands and believe that the fences were generally effective in their intended purpose.

METHODS

Measurements of overstory and understory site and vegetation parameters were taken on permanent plots arranged systematically in a square grid with the area of the stand determining the number of plots, which range from 15 to 40 per site. Each plot consists of a 1/20 acre (26.4-ft radius) overstory plot and four understory milacre (3.72-ft radius) subplots arranged 16.5 ft away from plot center on the cardinal directions. The 1/20 acre plot was measured for overstory and site conditions, and trees with diameter at breast height (d.b.h.) greater than 2 inches were tallied by species. Measurements of vegetation cover and regeneration counts were taken on milacre subplots. Percentage low cover was visually estimated as percentage of projected vegetation cover, by species or species group, in increments of 5 percent for vegetation ≤5 ft in height, and overhead canopy cover was estimated using a convex-spherical densiometer. Tree regeneration data were tallied by counts of tree species in height groups (0 to 2 inches, >2 to 6 inches, >6 inches to 1 ft, >1 to 2 ft, >2 to 3 ft, >3 to 4 ft, >4 to 5 ft, and >5 ft). The dominant oak (largest healthy oak seedling) on each subplot was identified by species, and its height and basal diameter were recorded.

All statistical analyses were conducted using SAS/STAT System Release 9.0 (SAS Institute Inc. 2004). A generalized linear model with a logistic regression form and binomial distribution (SAS PROC GENMOD) was used to examine the effect of fencing or time under fence on changes in oak occurrence frequency for the divided stands. Changes in oak occurrence frequency at Horsepath and Bell Furnace I and II were analyzed using the chi-square test (SAS PROC FREQ). Three additional response variables, changes in mean oak density, height, and height of the dominant seedling on a plot, were evaluated using analysis of variance (SAS PROC GLM) for the divided stands. Residuals of these variables were tested for normality using the Shapiro-Wilk test and for homogeneity of variance using the Levene test. Stand 4 had a large mast crop in fall 2005 and was alone among the divided stands in experiencing a large influx of new oak seedlings during the period of study. Stand 4 was therefore omitted from the combined ANOVAs because including it would have clouded interpretation of the results. The Wilcoxon rank-sum test (SAS PROC NPAR1WAY) was used to analyze the Bell Furnace I and II and Horsepath stands because their data did not meet the normality assumption.

RESULTS

Oak Occurrence Frequency

In the divided stands (excluding stand 4) there was an overall decrease in oak occurrence frequency between 2004 and 2006, and the difference was less for fenced than for unfenced areas (1.5 versus 7.2 percent) (Table 1). However, fencing was not a significant effect ($p = 0.076$) and neither was period of time fenced ($p = 0.873$). Although no notable seed crops were observed except in stand 4, it can be assumed that some acorns were produced each year and, because of this, slight increases in seedling abundance could occur. Only one stand (stand 6) experienced an increase in oak seedling frequency, an accumulation that occurred only in the protected part of the stand (a change from 26.8 to 39.4 percent). All of the unfenced areas of the divided stands experienced a decrease in occurrence frequency of oak seedlings. Stand 4, which had a large seed crop in 2005, showed similar increases in fenced and unfenced areas when measured in 2006.

Table 1.—Characteristics of oak advance regeneration in six mature, mixed-oak stands in which half the stand was protected for deer fencing for 2 years and half left unprotected

Stand	Treatment	# of plots	Frequency (%)		Seedling density (thousands/acre)		Mean dominant height (ft)		Mean height (ft)	
			2003	2006	2003	2006	2003	2006	2003	2006
1	Unfenced	80	88.8	76.3	4.67	2.95	0.61	0.49	0.44	0.42
	Fenced	80	86.3	80.0	6.50	3.88	0.60	0.59	0.45	0.48
2	Unfenced	76	72.4	68.4	4.93	3.87	0.80	0.97	0.59	0.70
	Fenced	79	86.1	86.1	8.33	6.63	0.65	0.93	0.52	0.69
3	Unfenced	72	36.1	29.2	2.65	1.26	0.40	0.43	0.37	0.39
	Fenced	80	26.3	25.0	0.73	0.64	0.34	0.38	0.32	0.35
5	Unfenced	60	90.0	81.7	25.77	13.85	0.60	0.59	0.37	0.38
	Fenced	60	85.0	70.0	8.00	4.40	0.39	0.44	0.32	0.35
6	Unfenced	71	39.4	29.6	0.74	0.71	0.32	0.32	0.32	0.32
	Fenced	71	26.8	39.4	0.84	0.87	0.32	0.34	0.32	0.33
Total	Unfenced	359	63.9	56.7	7.04	4.71	0.60	0.64	0.44	0.47
	Fenced	370	60.2	58.7	4.17	3.22	0.55	0.66	0.42	0.49
4	Unfenced	76	40.8	67.1	1.80	4.53	0.39	0.44	0.37	0.35
	Fenced	80	48.8	76.3	3.56	5.60	0.36	0.43	0.34	0.37

Horsepath initially gained in oak occurrence frequency after the fencing treatment, but then decreased significantly to below pretreatment levels ($p < 0.05$) (Table 2). In contrast, the Bell Furnace stands showed increases in oak occurrence frequency through the entire fencing period, with a significant increase in oak occurrence frequency for both fenced stands by 2004 ($p < 0.05$) (Table 3).

Oak Seedling Density

Although seedling density decreased during the study in both unfenced and fenced portions of the divided stand study areas (except stand 4), the protected areas lost fewer seedlings than unfenced areas (Table 1). By 2006 the unfenced areas had lost an average of 2,330 seedlings per acre compared to 950 for fenced areas ($p = 0.018$). Increases in seedling density as a result of the seed crop in stand 4 were similar between fenced and unfenced areas ($p > 0.05$).

The Horsepath stand experienced a significant ($p < 0.001$) increase of 2,680 seedlings per acre after 1 year of fencing, undoubtedly because of a good seed crop in fall 1998, but seedling density then declined to below the initial level by the time of the 2005 and 2006 measurements (Table 2). Both Bell Furnace stands exhibited rather substantial and significant ($p < 0.02$) increases in oak seedling density after the 1998 measurements, and the increases were sustained until the final measurements in 2004 (Table 3).

Mean Height of Dominant Oak Seedings

The mean height of the dominant oak seedling on milacre plots appeared to be marginally enhanced by fencing for two growing seasons in divided-stand study areas (Table 1), but the effect (if real) was not significant ($p = 0.142$). Results were similar for stand 4.

Table 2.—Characteristics of oak advance regeneration in the Horsepath stand, fenced to exclude deer beginning in winter 1998 (99 sample plots)

	1997[1]	1999[1]	2005[1]	2006[1]
Density (thousand/acre)[2]	1.77[a](0.283)	4.45[b] (0.763)	1.93[a] (0.404)	1.06[a](0.219)
Mean dominant height (ft)[2]	0.41[a](0.030)	0.41[a] (0.020)	0.49[b] (0.034)	0.54[b](0.047)
Mean height (ft)[2]	0.36[a](0.036)	0.36[ab](0.032)	0.47[ab](0.039)	0.54[b](0.047)
Frequency[2]	55.0[ac]	66.7[a]	52.0[bc]	40.4[b]

[1]Standard errors are shown in parentheses.
[2]Means within a row that are not followed by the same letter differ significantly at $p < 0.05$.

Table 3.—Characteristics of oak advance regeneration in the two Bell Furnace stands, fenced to exclude deer beginning in summer 1997 and winter 1999, respectively

	1997[1]	1998[1]	2004[1]
	---------------------Bell Furnace I (116 plots)---------------------		
Density (thousand/acre)[2]	4.89[a](0.715)	5.22[a](0.762)	10.64[b](1.373)
Mean dominant height (ft)[2]	0.68[a](0.048)	0.67[a](0.042)	0.89[b](0.064)
Mean height (ft)[2]	0.42[a](0.020)	0.40[a](0.018)	0.61[b](0.028)
Frequency[2]	71.7[a]	70.8[a]	84.2[b]
	---------------------Bell Furnace II (80 plots)---------------------		
Density (thousand/acre)[2]	-	3.94a(0.763)	7.85[b](1.130)
Mean dominant height (ft)[2]	-	0.62a(0.049)	0.90[a](0.116)
Mean height (ft)[2]	-	0.40a(0.020)	0.85[b](0.044)
Frequency[2]	-	61.4a	77.5[b]

[1]Standard errors are shown in parentheses.
[2]Means within a row that are not followed by the same letter differ significantly at $p < 0.05$.

The mean height of dominant oak seedlings increased from 0.41 to 0.54 ft ($p = 0.01$) during the 9-year duration of observations at Horsepath (Table 2), from 0.68 to 0.89 ft ($p = 0.01$) over 7 years at Bell Furnace I (Table 3), and from 0.62 to 0.90 ft ($p = 0.12$) over 6 years at Bell Furnace II (Table 3).

Mean Oak Seedling Height

The mean height of all measured oak seedlings increased slightly between 2003 and 2006 in most divided stand study areas (Table 1). The increase was larger in fenced plots, but not significantly so ($p = 0.350$).

The mean height of seedlings at Horsepath increased from 0.36 to 0.54 ft between 1997 and 2006 ($p < 0.01$). Similar growth was observed at Bell Furnace I (from 0.42 to 0.61 ft, $p < 0.001$) and Bell Furnace II (from 0.40 to 0.85 ft, $p < 0.001$).

Effect of Covariates

Analyses of the effects of covariates on response variables in divided stands (excluding stand 4) revealed no significant effects of overhead canopy cover on oak seedling abundance or size. However, high levels of low cover (≤5 ft) were associated with greater reductions over the 3-year duration of the study in seedling density ($p = 0.028$) and smaller increases in mean oak seedling height ($p = 0.002$) and dominant seedling height ($p < 0.001$).

DISCUSSION

Estimates of deer densities for the areas encompassing our study stands ranged from 12 to 23 per square mile in 2004 and 2005 (Pennsylvania Game Commission 2006). Current deer densities, although generally lower than in recent decades, are greater than those thought to be present before European settlement (Seton 1909, McCabe and McCabe 1984) and are much greater than densities during the early 1900s when deer were nearly extirpated from Pennsylvania (Redding 1995, deCalesta 1997). Deer density, although a helpful tool to land managers, oversimplifies the complex relationship between habitat and deer. Not only are deer densities greater than those believed to be "natural", but the habitat for advance regeneration of oak (and for deer) has changed with the widespread emergence of a substantial mid-story population of red maple, thought to be attributable to active control of wildfires during the past century (Lorimer 1984, Abrams 1998). Red maple is less preferred as browse than oak, and closed-canopy, mixed-oak forest as represented by most of the stands in this study may provide less browse than what occurred historically, especially following decades of overbrowsing. Furthermore, vegetation growing in low light conditions may be particularly sensitive to the effects of herbivory (Maschinski and Whitham 1989, Baraza and others 2004).

Not surprisingly, protection from deer did not invariably enhance the abundance of oak regeneration in our study stands, since seedling abundance can increase appreciably only in the infrequent event of a good mast crop (Sharp and Sprague 1967, Auchmoody and others 1993, Sork and others 1993). Only one of the six divided stands (stand 4) had a significant mast crop during their 2 years of study, and fenced and unfenced areas in that stand both had similar increases in seedling density and frequency of occurrence on sample plots when measured the following July. The other divided stands, on average, sustained decreases in both density and frequency, but fencing against deer predation significantly reduced the net loss of seedlings per acre.

Both Bell Furnace stands, which were fenced for 6 to 7 years, experienced substantial and sustained increases in oak seedling density and frequency over the course of the study. The lack of controls for those stands makes it impossible to know whether fencing was responsible for their increases in advance regeneration. Nonetheless, that seems likely to be the case because their final densities were quite high for typical (unfenced) stands in this region of Pennsylvania (Steiner and Finley, unpublished data). In contrast, the Horsepath stand, which was fenced for 8 years, experienced large initial increases in both density and frequency of oak seedlings but subsequently declined in both measures of abundance to levels less than those present in 1997. The difference in outcome at Bell Furnace I and II vs. Horsepath is probably attributable to their very different understory conditions. Both of the Bell Furnace stands, although fully stocked in the overstory, contain sparse levels of understory and mid-canopy vegetation, while Horsepath has a dense understory of mountain-laurel and other tall shrubs. The presence of low shade under a full forest canopy can significantly reduce oak seedling growth and survival even in the absence of deer browsing (Miller and others 2004). This conclusion – that low shade at Horsepath prevented advance regeneration from responding to protection from deer – is bolstered by our finding that the level of low shade (≤5 ft) was significantly associated with reduction in oak seedling density and an inhibition of growth.

We observed significant increases in seedling height as a result of fencing in the divided stands or subsequent to fencing in the Bell Furnace I and II and Horsepath stands. However, the increase in mean seedling height was less than about 5 inches even in those stands that were fenced for 6 to 8 years, and it was quite negligible in those that were fenced for only about 2 years. As mentioned, low vegetation cover was significantly and negatively related to height growth, and it is probable that competition for light, water, and nutrients in these fully stocked stands was generally inhibitory to seedling growth even where deer browsing was not a factor.

Both Bell Furnace stands accumulated several thousand additional oak seedlings per acre while protected from deer, and the seedlings grew significantly in height. Based on current guidelines for regenerating oak in this region (Steiner and others 2008), both stands accumulated sufficient advance regeneration of oak to regenerate to a predominance of oak following harvest, and in fact they were harvested in 2005 and 2006.

In contrast, oak advance regeneration did not accumulate at Horsepath in spite of 8 years of protection from deer, although seedlings did become slightly larger. If Horsepath were harvested in its current state it would regenerate primarily to red maple with minor components of chestnut oak, northern red oak, white oak, and eastern white pine (*Pinus strobus* L.). Our experience with this stand makes it clear that protection from browsing, even if continued for many years, does not in itself ensure the establishment of a healthy cohort of advance regeneration.

Protecting advance regeneration from deer for 2 years had a significant effect on oak seedling density, but overall effects on the strength of the cohort of oak advance regeneration were negligible. Protection for longer periods may be effective in building a strong cohort of advance regeneration (Bell Furnace I and II), but even long-term protection will not guarantee this outcome in the presence of high levels of low shade (Horsepath). Although our study did not directly address the influence of shade and other manifestations of competition on oak seedling growth, it is apparent that protection from deer may have to be combined with some form of stand thinning or other competition control in order to be fully effective, especially where substantial levels of low shade are present. The growth and survival of small oak seedlings in the forest understory can be greatly enhanced by partial removal of shade, perhaps combined with fire (Loftis 1983, Loftis 1990, Brose and others 1999, Miller and others 2004). Mid-canopy and understory shade in our stands arises almost entirely from species that are generally avoided by deer, and their predominance is likely a result of decades of high deer populations. Overcoming the ecological legacy of decades of overbrowsing may require more than simply protecting new oak regeneration from deer.

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