Responses of northern red oak seedlings to lime and deer exclosure fencing in Pennsylvania

Robert P. Long, Patrick H. Brose, and Stephen B. Horsley

Abstract: In Pennsylvania, two hypotheses compete to explain the chronic oak (*Quercus* spp.) regeneration problem: excessive deer browsing and soil cation depletion. We tested these hypotheses by evaluating the effect of forest liming and deer exclosure fencing on northern red oak (*Quercus rubra* L.) seedling growth and nutrition in five oak shelterwood stands in Pennsylvania over 6 years. In each stand, four planting plots were located inside a 2.4 m high woven wire fence and another four were established outside the fence. About 225 northern red oak acorns were planted in each plot in spring 2004. Dolomitic limestone was applied to randomly selected plots at rates of 0, 4.5, 9.0, and 13.5 $Mg{\cdot}ha^{-1}$ during May 2004. There were no statistically significant ($P \leq 0.05$) growth responses to lime applications. The only significant growth responses resulted from the fence versus no-fence treatment. A significant ($P < 0.003$) fence × year interaction for seedling height and root collar diameter indicates differential impacts of deer browsing. By 2009, seedlings inside fences averaged 32 cm tall, while seedlings outside the fences averaged 17 cm. Similarly, root collar diameter averaged 6.6 mm outside the fences and 9.1 mm inside fences.

Résumé : En Pennsylvanie, deux hypothèses s'affrontent pour expliquer le problème chronique de régénération du chêne (*Quercus* spp.) : le broutement excessif du chevreuil et l'épuisement des cations du sol. Nous avons testé ces hypothèses en évaluant l'effet après six ans du chaulage en forêt et de l'utilisation de clôtures pour exclure le chevreuil sur la nutrition et la croissance de semis de chêne rouge (*Quercus rubra* L.) dans cinq peuplements soumis à une coupe progressive en Pennsylvanie. Dans chaque peuplement, quatre parcelles de plantation étaient situées à l'intérieur d'une clôture grillagée de 2,4 m de haut et quatre autres étaient établies à l'extérieur de la clôture. Environ 225 glands de chêne rouge ont été plantés dans chaque parcelle au printemps 2004. De la chaux dolomitique a été appliquée dans des parcelles choisies au hasard à des taux de 0, 4,5, 9,0 et 13,5 $Mg{\cdot}ha^{-1}$ durant le mois de mai 2004. Les applications de chaux n'ont eu aucun effet significatif ($P \leq 0{,}05$) sur la croissance. La seule réaction significative de la croissance était associée au traitement d'exclusion. Une interaction significative ($P < 0{,}003$) entre le traitement d'exclusion et l'année dans le cas du diamètre au collet et de la hauteur des semis indique que l'impact du broutement des chevreuils varie. En 2009, les semis avaient une hauteur moyenne de 32 cm à l'intérieur des exclos tandis qu'ils n'avaient en moyenne que 17 cm à l'extérieur. De même, le diamètre au collet était en moyenne de 6,6 mm à l'extérieur des exclos et de 9,1 mm à l'intérieur.

[Traduit par la Rédaction]

Introduction

Regenerating oak (*Quercus* spp.) forests has been a persistent problem in Pennsylvania and other parts of the central hardwood region of eastern North America (Moser et al. 2006; McWilliams et al. 2007). In Pennsylvania, consumption and destruction of acorns by disease, insects, weather and wildlife, interfering vegetation, unsustainable harvesting practices, and excessive browsing by white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) on established oak seedlings cause or contribute to oak regeneration failures (Galford et al. 1991; Nyland 1992; Lorimer 1993; Brose 2011*a*).

The impact of deer browsing on the regeneration of Pennsylvania's forest is controversial with two polarized groups: a group that wants to reduce deer populations because of their detrimental impact on regeneration and a group that wants to maintain or increase deer populations for recreational hunting opportunities (Diefenback et al. 1997; Latham et al. 2005; Frye 2006). Ample scientific evidence links excessive deer browsing to damaged and degraded plant communities and altered or impeded forest regeneration processes in northern Pennsylvania (Hough 1965; deCalesta 1994; Horsley et al. 2003). Consequently, new hunting regulations have been implemented in Pennsylvania since 2000 to reduce the size of the deer herd to habitat-based targets (Frye 2006). The variable impacts of these new hunting regulations on forest regeneration across the landscape have prompted those opposed to reducing the deer population to suggest an alternative hypothesis to explain Pennsylvania's chronic, widespread forest regeneration problems. Atmospheric deposition and associated nutrient depletion are posited as the primary causal factors that impede successful woody regeneration (Mulhollem 2002; Frye 2006).

Atmospheric deposition is the input of strong acid anions (SO_4, NO_3) via precipitation (Driscoll et al. 2001). It has

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been occurring throughout eastern North America, particularly in the mid-Atlantic and New England region, for decades and causes the loss of essential plant nutrients such as Ca and Mg from organic and mineral soil horizons (Likens et al. 1996; Markewitz et al. 1998; Bailey et al. 2005). Base cation depletion and increased soil acidity have been documented over three decades on the Calhoun Experimental Forest in South Carolina (Markewitz et al. 1998). Likewise, research conducted in forest stands on the unglaciated Allegheny Plateau in Warren County, Pennsylvania, showed that between 1967 and 1997, there were significant decreases in exchangeable Ca and Mg and an increase in Al and acidity to a depth of >120 cm in soil profiles (Bailey et al. 2005).

Forest liming has been proposed as a remedial measure to mitigate these effects (Demchik and Sharpe 1999*a*; Mulhollem 2002; Sharpe and Voorhees 2006), although it is unknown which species may benefit from such treatment. In northern Pennsylvania, a one-time application of 22.4 $Mg \cdot ha^{-1}$ of dolomitic limestone resulted in sustained increases in basal area increment of overstory sugar maple (*Acer saccharum* Marsh.) but had no effect on American beech (*Fagus grandifolia* Ehrh.) and had a negative effect on the growth of black cherry (*Prunus serotina* Ehrh.) over 23 years (Long et al. 1997, 2011). In that study, significant increases in sugar maple crown vigor were first detected 3 years after lime application; significant basal area growth increases were apparent after 8 years. Nutrient requirements of the oak species are not well established and seedling responses to lime application only have been studied for short periods of 1–3 years (Demchik and Sharpe 1999*a*, 1999*b*). For example, in a Connecticut study, canopy northern red oak (*Quercus rubra* L.) (NRO) had increased radial growth on high-Ca soils (Bigelow and Canham 2002). A manipulative study with $CaSO_4$ and $(NH_4)_2SO_4$ additions to sapling stems elicited only a response to Ca when NH_4 was added, suggesting a colimitation by these two factors (Bigelow and Canham 2007).

Other research has used lime additions alone or in combination with fertilizer or vegetation removal to assess impacts on planted NRO seedlings and natural regeneration (Demchik and Sharpe 1999*a*, 1999*b*; Schreffler and Sharpe 2003). At a 7-year-old clearcut with failed natural regeneration, 2-0 NRO seedlings were planted within deer exclosure fences. Lime, fertilizer, and vegetation control (removal of fern rhizome mats) treatments were evaluated in a complete factorial study design (Demchik and Sharpe 1999*b*). Only two treatment combinations resulted in positive growth response for the NRO seedlings: (*i*) dolomitic lime (6.6 $Mg \cdot ha^{-1}$) combined with vegetation control and (*ii*) lime combined with fertilizer (91 $kg \cdot ha^{-1}$ K and 96 $kg \cdot ha^{-1}$ P) and vegetation control (Demchik and Sharpe 1999*b*). Other studies (Demchik and Sharpe 1999*a*; Schreffler and Sharpe 2003) only used combinations of lime and fertilizer, thus prohibiting evaluation of lime-only or fertilizer-only additions. In these studies, responses to lime and (or) fertilizer additions, while statistically significant, are inconsequential to forest management objectives, usually averaging only 2–4 cm greater height growth over 3 years compared with control or vegetation control only treatments (Demchik and Sharpe 1999*a*; Schreffler and Sharpe 2003).

From 2004 to 2009, we conducted a study to evaluate these two competing hypotheses (deer browsing and (or) base cation nutrient depletion) of NRO regeneration failures. The primary objective of this research was to determine the effects of dolomitic limestone applied at rates of 0, 4.5, 9.0, and 13.5 $Mg \cdot ha^{-1}$ and (or) fencing to exclude deer browsing on the growth of NRO seedlings from field-planted acorns. Our hypotheses were (1) the addition of the lime would increase the growth of the oak seedlings relative to native soil conditions and (2) fencing to exclude deer would further increase seedling growth. A secondary objective was to document changes in soil and foliage chemistry in response to the fence and lime treatments.

Materials and methods

Study sites

Five study sites were selected in western and central Pennsylvania based on input from Pennsylvania Bureau of Forestry and Pennsylvania Game Commission personnel. Study sites were in NRO-dominated forests that had partial overstory removal cuts (shelterwood harvest) to increase light within the past 12 years and had been fenced with 2.44 m tall woven wire to exclude deer. Five sites, covering a range of conditions in western and central Pennsylvania, were established in Pennsylvania Bureau of Forestry district Nos. 4 (LM, Somerset County), 7 (LV, Centre County), 8 (CC, Jefferson County), and 12 (BF, Lycoming County) and Pennsylvania State Game Lands No. 24 (GL, Forest County). Site locations, physiographic regions, soils, and other characteristics are detailed in Table 1.

Study implementation

In April 2004, eight 12.5 m by 8.5 m plots were established at each site; four plots were located within the 2.44 m tall deer exclosure fence and four were located outside the fence but still within the shelterwood treatment. All plots were separated by a minimum 10 m buffer. Plot areas were cleared of debris including small stumps, slash, or downed trees and vegetation. Small trees and shrubs, primarily *Kalmia latifolia* L. and *Vaccinium* spp., were removed with a power brush cutter or chainsaw, while ferns and other vegetation were clipped. NRO acorns used for the plantings were collected from a single dominant tree located in Pennsylvania State Forest district No. 13 in Cameron County. Plots were raked clear of leaf litter and 225 acorns were planted within 7.6 m by 3.7 m measurement plot. Acorns were planted in holes made with a tree-planting bar and then covered with soil. Previously weathered (to remove the zinc coating) 6.35 mm mesh hardware cloth was placed over the planted area and held in place with sod staples to protect acorns from small mammals. Leaf litter was removed because the hardware cloth would compact it and prevent successful acorn germination. Because of poor acorn germination in some plots, supplemental acorns from the same source tree were planted in June 2004. All hardware cloth was removed by spring 2006.

In May 2004, each fenced and unfenced treatment plot at every site was randomly assigned to one of four liming rates (0, 4.5, 9.0, and 13.5 $Mg \cdot ha^{-1}$). These rates were derived based on published literature and our desire to include a broad range of rates in a dose–response design. Commercial

Table 1. Study site locations and characteristics.

Site (Pennsylvania Bureau of Forestry district No., county)	Physiographic section[a]	Soil series[b]	Elevation (m)	Year harvested/ year fence installed
LM (4, Somerset)	Allegheny mountain	Cookport very stony loam; Hazleton very stony sandy loam	726	2002/2003
LV (7, Centre)	Appalachian mountain	Laidig extremely stony loam	488	1992/2002
CC (8, Jefferson)	High plateau	Dekalb very stony loam	573	2002/2004
BF (12, Lycoming)	Deep valleys	Cookport very stony loam	622	2003/2004
GL (SGL 24, Forest)	High plateau	Cookport very stony silt loam	482	2001/2002

[a]Physiographic sections from W.D. Sevon. 2000. 4th ed. (http://www.dcnr.state.pa.us/topogeo/index.aspx).

[b]Cookport, Aquic Fragiudult; Hazleton, Typic Dystrochrept; Laidig, Typic Fragiudult; Dekalb, Typic Dystrochrept.

pelletized dolomitic limestone (Ca = 20%, Mg = 10%, and CaO equivalent = 54.4) was applied over the entire treatment plot using lawn spreaders. Plastic snow fences (1.2 m tall) were erected around the four plots inside the deer fences in late summer 2004 to further protect seedlings from deer that may have remained undetected inside the fence. With abundant available browse inside the 2.44 m tall fences, a small barrier will discourage deer browsing in most cases.

Seedling measurements

Each year, 50 NRO seedlings in each plot were randomly selected and total height from the ground line to the terminal bud was measured to the nearest 0.5 cm. Basal diameter at the ground line was measured using digital calipers to the nearest 0.1 mm and root collar diameter was similarly measured by gently removing soil and litter from around the seedling and positioning the caliper on the root collar. Root collar diameter and basal diameter were not measured in fall 2004 to prevent damage and disturbance to young seedlings.

Total biomass accumulation was assessed at the end of the study by a destructive sample of 10 randomly selected NRO seedlings in each plot. Seedlings were carefully excavated in fall 2009 to obtain as much of the root system as possible. Seedlings were air-dried in a greenhouse and total taproot and stem lengths were measured to the nearest 0.5 cm and basal and root collar diameters were measured to the nearest 0.1 mm. Seedlings were then oven-dried at 65 °C to a constant mass and total root and stem dry mass were determined to the nearest 0.01 g for each excavated seedling.

Other measurements

Pre-treatment soil samples were obtained in late April 2004 by digging two small pits to a depth of 50 cm in the buffer area of each plot where acorns were not planted. Mineral soils were sampled at depths of 0–5, 5–10, 10–15, 15–30, and 30–45 cm after removal of the surface organic layers. Although soil samples were not obtained by genetic horizon, A horizons were usually within the upper 10 cm and B and E horizons were at the deeper sampled depths from 10 to 45 cm. The soils from each pair of sample depths at each plot were composited giving a total of five samples per plot each year. Soils were similarly sampled in mid-May from 2005 through 2009. Pit locations were systematically arranged around the perimeter so that no area was sampled more than once.

Soil samples were air-dried and passed through a 2 mm sieve. Soil chemistry was determined at the USDA Forest Service Laboratory in Durham, New Hampshire. Soil pH was measured in 0.01 mol·L^{-1} $CaCl_2$ (Hendershot et al. 1993*a*). Exchangeable cations, Ca, Mg, P, K, Al, and Mn, were determined by inductively coupled plasma spectroscopy after extraction with 1.0 mol·L^{-1} NH_4OAc (Hendershot et al. 1993*b*).

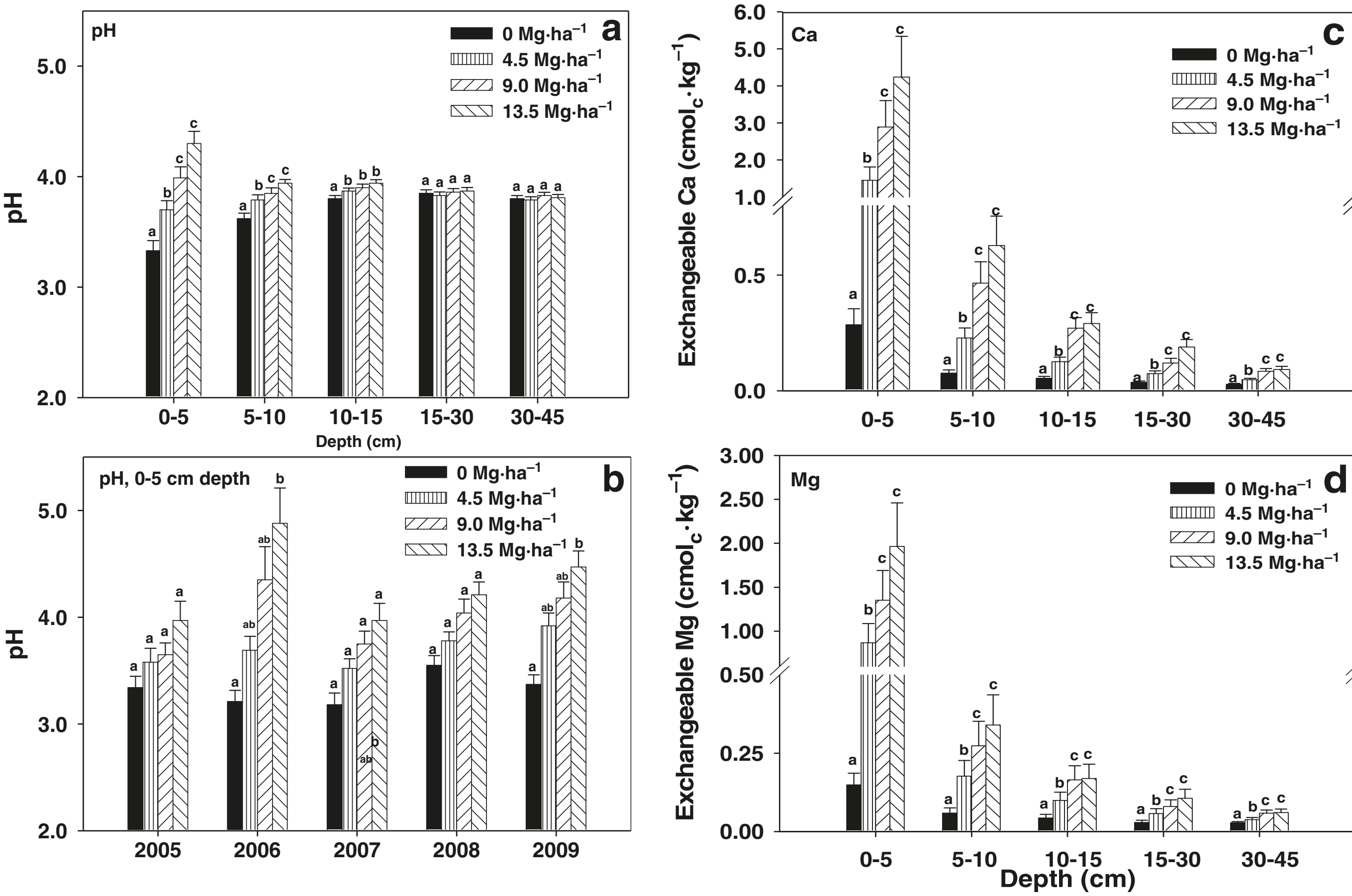
Foliage samples were obtained each year in mid-August from all plots containing at least 20–30 healthy NRO seedlings. Seedlings (20–30 per plot) were randomly selected and one normal-sized leaf was obtained per seedling. Leaves from each plot were composited as a single sample, oven-dried at 70 °C, and ground in a Tecator cyclotec mill. Samples from 2004 through 2007 were analyzed at the Forest Service Laboratory in Durham, New Hampshire. Samples were digested using a microwave-assisted acid digestion procedure (EPA method 3052, 1996) and analyzed for Ca, Mg, P, K, Mn, and Al by inductively coupled plasma spectroscopy. Total N was determined using a Perkin Elmer 2400 series 2 CHN analyzer. Because of a renovation at the Durham Laboratory, foliage samples from 2008 and 2009 were analyzed at the University of Maine Analytical Laboratory. Samples were dry ashed at 550 °C and taken up in HCl for analysis by inductively couple plasma spectroscopy (Chapman and Pratt 1961; Kalra and Maynard 1991). Total N was determined by dry combustion (EPA method 440). Based on a comparison with 2007 (Durham Laboratory) foliage samples that were rerun in 2008 (University of Maine Laboratory), differences in analytical methods caused only minor differences in the results (data not shown).

Percent open sky for each plot was estimated annually during midsummer by taking hemispheric photographs of the canopy trees from the plot center using a tripod-mounted 35 mm camera with a vertically oriented fisheye lens. Photographs were taken between 11 a.m. and 2 p.m. on uniformly overcast days (Rich et al. 1993; Canham et al. 1994; Robison and McCarthy 1999). The photographs were digitized and then analyzed using Hemiview software (Rich et al. 1999).

Statistical analyses

The analyses of annual growth, soil, and foliage chemistry variables used an analysis of covariance repeated-measures split-plot design. If covariates were nonsignificant, the model reduced to a repeated-measures split-plot design. Fencing (fence versus no fence) was the whole-plot treatment and four rates of lime (0, 4.5, 9.0, and 13.5 Mg·ha^{-1}) were the subplot treatments. Study sites (blocks) were considered random effects along with the block × fence interaction. Year,

Fig. 1. Lime treatment effects on (*a*) soil pH in the 0–5, 5–10, 10–15, 15–30, and 30–45 cm depths averaged across all years (2005–2009), (*b*) soil pH levels by year in the 0–5 cm depth, and (*c*) exchangeable Ca and (*d*) Mg concentrations at all five sampled depths averaged across all years. Bars with different letters are significantly different within a sample depth ($P \leq 0.05$) using the Tukey adjustment for multiple comparisons.



lime, and fence treatments (and their interactions) were treated as fixed effects. Statistical analyses were conducted with SAS version 9.2 using linear mixed models (PROC MIXED) and generalized linear mixed models (PROC GLIMMIX) (SAS Institute Inc. 2008). The Kenward–Rogers denominator degrees of freedom method was used in all analyses.

Soil and foliage chemistry data were evaluated using PROC GLIMMIX. For soils, the pre-treatment samples from spring 2004 provided baseline data that allowed the evaluation of a covariate to account for a potential source of variability. The different sampled soil depths (0–5, 5–10, 10–15, 15–30, and 30–45 cm) were analyzed separately. Models were evaluated using Gaussian, lognormal, and gamma distributions. For soils analyses, exchangeable cations were best described by the lognormal distribution to appropriately fit the data. Foliar nutrient data were similarly analyzed; however, no pre-treatment covariate was available. Different covariance structures were also tested in these repeated-measures models, and the autoregressive order 1 covariance structure, AR(1), or the autoregressive order 1 with heterogeneous variances, ARH(1), usually fit the data best based on comparisons of the corrected Akaike information criterion (AIC_c) and residual plots. Where a lime × year or fence × year interaction was significant ($P \leq 0.05$), least squares means were used to evaluate specific pairwise comparisons (Littell et al. 2006; SAS Institute Inc. 2008).

Analyses of the seedling growth variables, height, basal diameter, and root collar diameter were conducted using the same methods described for soils; however, the percent open sky also was evaluated as a potential covariate in these models. Open sky was not a significant ($P \leq 0.05$) covariate in any of the models and was therefore dropped from the models. Biomass measurements derived from the destructive harvest at the end of the study were evaluated with PROC GLIMMIX but without the repeated-measures component of the model. In most cases, lognormal or gamma distributions were the best fit for these data.

Results

Soil and foliar nutrient responses

Lime treatment altered the soil environment considerably, particularly in the upper 5 cm of mineral soil, while fencing had no detectable effect on soil nutrients. Pre-treatment pH of the upper 5 cm of mineral soils ranged from 2.7 at CC to 3.8 at GL. Post-treatment soil pH in 2005, 1 year after treatment application, ranged from 3.3 to 4.0 in the upper 5 cm of soil (Fig. 1*a*) and reflected decreased acidity with pH increasing in a pattern similar to Ca and Mg in the 0–5 cm layer. Soil

Table 2. Fixed effects *F* statistics and associated probability levels for repeated-measures analyses exchangeable Ca and Mg and pH in the 0–5, 5–10, 10–15, 15–30, and 30–45 cm depths of the mineral soil from 2005 through 2009.

	F (*P*)	*F* (*P*)	*F* (*P*)	*F* (*P*)	*F* (*P*)
Source	Ca, 0–5 cm	Ca, 5–10 cm	Ca, 10–15 cm	Ca, 15–30 cm	Ca, 30–45 cm
Fence	0.89 (0.386)	2.20 (0.147)	1.00 (0.363)	0.10 (0.770)	0.47 (0.498)
Lime	**104.86 (<0.001)**	**100.63 (<0.001)**	**68.82 (<0.001)**	**46.37 (<0.001)**	**24.05 (<0.001)**
Fence × lime	0.21 (0.885)	0.06 (0.980)	0.12 (0.947)	0.49 (0.692)	0.19 (0.899)
Year	**11.24 (<0.001)**	**4.89 (0.002)**	2.13 (0.089)	1.27 (0.284)	1.08 (0.401)
Covariate	**7.82 (0.008)**	**5.91 (0.022)**	**8.00 (0.010)**	**4.97 (0.030)**	**16.73 (<0.001)**
Source	Mg, 0–5 cm	Mg, 5–10 cm	Mg 10–15 cm	Mg 15–30 cm	Mg 30–45 cm
Fence	3.70 (0.061)	3.64 (0.064)	2.53 (0.118)	0.23 (0.639)	<0.01 (0.959)
Lime	**71.71 (<0.001)**	**70.56 (<0.001)**	**57.70 (<0.0010)**	**18.03 (<0.001)**	**26.75 (<0.001)**
Fence × lime	0.56 (0.642)	0.55 (0.788)	0.14 (0.938)	0.35 (0.788)	0.13 (0.939)
Year	**6.27 (<0.001)**	**5.58 (<0.001)**	**3.43 (0.011)**	0.83 (0.573)	1.78 (0.162)
Covariate	ns	ns	ns	**29.78 (<0.001)**	**25.79 (<0.001)**
Source	pH, 0–5 cm	pH, 5–10 cm	pH, 10–15 cm	pH, 15–30 cm	pH, 30–45 cm
Fence	2.35 (0.135)	0.91 (0.393)	0.42 (0.552)	0.70 (0.451)	2.46 (0.187)
Lime	**33.87 (<0.001)**	**18.52 (0.001)**	**7.80 (0.001)**	1.79 (0.161)	1.55 (0.216)
Fence × lime	0.97 (0.428)	2.05 (0.146)	0.27 (0.845)	0.82 (0.487)	0.71 (0.549)
Year	**11.04 (<0.001)**	**18.55 (<0.001)**	**21.89 (<0.001)**	**29.84 (<0.001)**	**33.94 (<0.001)**
Covariate	**12.06 (0.002)**	**10.83 (0.003)**	**16.27 (<0.001)**	**41.68 (<0.001)**	**62.51 (<0.001)**

Note: Boldface type highlights the effects significant at the $P \leq 0.05$ level. Fence × year, lime × year, and fence × lime × year interactions are not shown because all were nonsignificant ($P > 0.05$). "ns" denotes that the initial Mg level in 2004 was not a significant covariate ($F > 0.43$, $P > 0.514$) and therefore was not used in these models. The lime × year interaction was significant ($F = 2.37$, $P = 0.024$) for the pH model evaluating responses in the 0–5 cm depth; this interaction was nonsignificant at the remaining depths.

pH, when averaged across all sample times, increased in the 0–5, 5–10, and 10–15 cm layers in response to the lime treatments, but there were no significant lime treatment effects detected in the 15–30 and 30–45 cm sample depths (Table 2). For the 0–5, 5–10, and 10–15 cm depths, lime treatment effects averaged over all years were significant ($P < 0.001$) with pH significantly higher in the lime-treated plots compared with the control plots (Table 2). Soil pH was 3.6 at the 5–10 cm depth in the control plots and increased to 3.9 in the highest lime treatment when averaged across all years. At the 10–15 cm depth, control plot pH was 3.8 and increased to 4.0 in the highest lime treatment plots when averaged across all years.

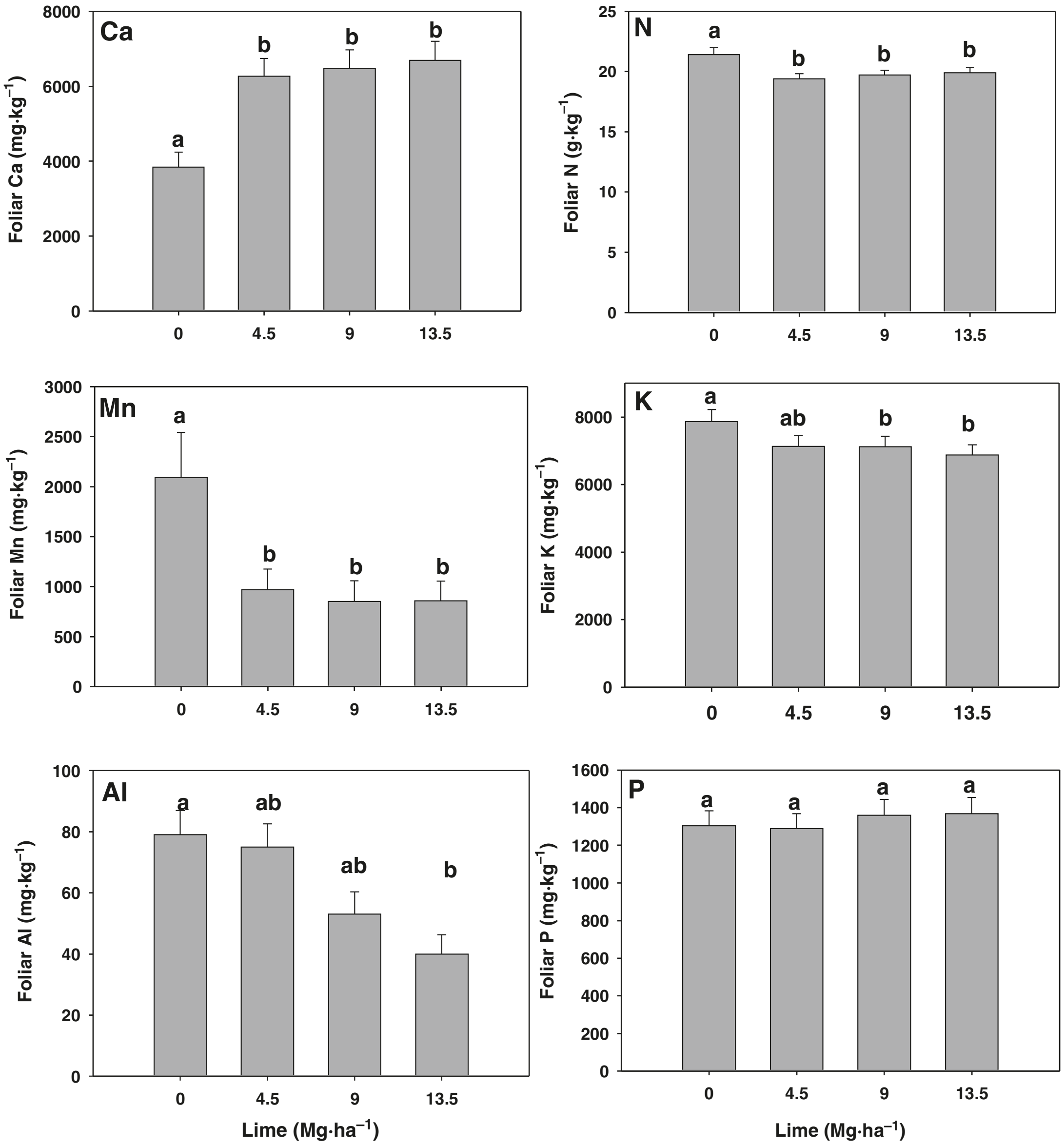
One notable difference in soil acidity was a significant ($F = 2.37$, $P = 0.024$) interaction of lime treatment and year at the 0–5 cm depth (Fig. 1*b*). In the 0–5 cm layer, soil pH was not affected by liming during 2005, the first year after application. In 2006, lime significantly increased the pH, but there were no significant differences among the three lime treatments and only the 13.5 Mg·ha^{-1} treatment was significantly greater than the control; this pattern was repeated in 2009. The interaction of lime treatment and year shows temporal variability in the upper soil.

Exchangeable Ca in the upper 5 cm was least in the unlimed control plots, 0.3 cmol$_c$·kg^{-1}, and significantly more in the three limed treatments, peaking at 4.2 cmol$_c$·kg^{-1} in the 13.5 Mg·ha^{-1} treatment when averaged from 2005 to 2009 (Table 2; Fig. 1*c*). Only the 9.0 and 13.5 Mg·ha^{-1} treatment means were not significantly different from each other. Much lower exchangeable Ca values were evident in all of the remaining sampled depths, but statistically significant differences between treatments were detected as deep as 30–45 cm (Fig. 1*c*). Calcium in control plots had the lowest value followed by the 4.5 Mg·ha^{-1} lime-treated plots and then the highest two lime treatment rates (9.0 and 13.5 Mg·ha^{-1}), which were not significantly different from each other. Similar to Ca, exchangeable Mg in the upper 5 cm of mineral soil followed the same pattern with the highest lime application rate producing Mg levels of 2.0 cmol$_c$·kg^{-1}, while control soils had only 0.1 cmol$_c$·kg^{-1} Mg when averaged from 2005 through 2009 (Fig. 1*d*). As with Ca, exchangeable Mg decreased substantially in all of the remaining sampled depths, but significant treatment effects were detected in these deeper soils.

Exchangeable K and P also were measured but showed no significant differences compared with controls for both lime and fence treatments (data not shown). Exchangeable K in the upper 5 cm averaged 0.176 cmol$_c$·kg^{-1}, decreasing to 0.095 cmol$_c$·kg^{-1} in the 30–45 cm layer. Likewise, exchangeable P did not show any significant response to lime or fence treatments; however, there was a trend of decreasing P with increasing lime application rate for the 0–5 cm layer. Exchangeable P ranged from 0.058 cmol$_c$·kg^{-1} in the control plots to 0.048 cmol$_c$·kg^{-1} in the plots treated with 13.5 Mg·ha^{-1} of dolomitic limestone, but these changes were not statistically significant.

NRO foliar nutrients were also altered by lime treatments but were not affected by the fence treatment (Fig. 2; Table 3). Seedling foliar nutrient concentrations usually did not follow the dose–response pattern seen in the soils. Foliar Ca averaged about 3800 mg·kg^{-1} in seedlings from control plots, while lime-treated seedlings all had Ca concentrations exceeding 6000 mg·kg^{-1}; however, none of these lime treatment means were significantly different from each other. Lime

Fig. 2. Lime treatment effects on northern red oak (*Quercus rubra*) foliar concentrations of Ca, K, P, Mn, Al, and N when averaged across all years. Bars with different letters are significantly different ($P \leq 0.05$) using the Tukey adjustment for multiple comparisons.



treatments significantly reduced foliar Mn levels in NRO seedlings. Foliage from control plots averaged about 2100 mg·kg^{-1} Mn, while foliage from lime-treated plots averaged about 900 mg·kg^{-1} Mn. Foliar Al was only marginally reduced by liming ($P = 0.060$) and was only significantly different for the highest lime treatment where Al was 40 mg·kg^{-1} compared with 79 mg·kg^{-1} in foliage from control plots. Foliar N was significantly less in lime treatments, but none of the lime treatments produced a differential effect. Foliar N was about 19.7 g·kg^{-1} in foliage from lime-treated plots compared with foliar N of 21.4 g·kg^{-1} in foliage from control plots. Foliar K concentrations decreased significantly in NRO foliage, but only in the two highest lime treatments. Potassium concentrations decreased from 7868 mg·kg^{-1} in the control plots to 6880 mg·kg^{-1} in the 13.5 Mg·ha^{-1} treatment plots. Foliar P concentrations were not significantly affected by lime treatments and averaged about 1330 mg·kg^{-1} across all treatments.

Foliar Mg showed the most complex response by having a significant lime treatment × year interaction (Table 3; Fig. 3). In August 2004, the first growing season following treatment application, NRO seedling foliage did not have significantly elevated Mg, with concentrations ranging from 1313 mg·kg^{-1} in unlimed controls to 1977 mg·kg^{-1} in the highest lime treatment. However, significantly elevated Mg concentrations were detected in all treatments each year from 2005 to 2009 (Fig. 3). There were no significant differences in foliar Mg among the different lime treatments as concentrations ranged from about 2500 mg·kg^{-1} to about 3300 mg·kg^{-1} over all years in the lime-treated plots.

Growth responses

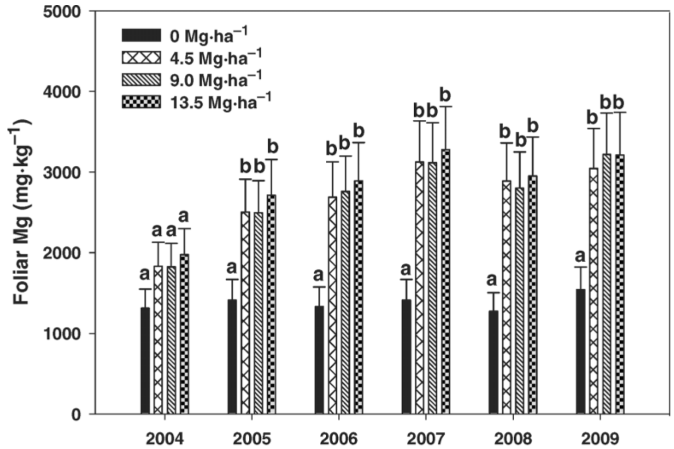
There were no statistically significant NRO height, basal diameter, or root collar diameter growth responses to any of the lime treatments (Table 4). Variable browsing pressure, both at the different sites and in different years, produced a

Table 3. Fixed effects *F* statistics and associated probability levels for repeated-measures analyses of foliar concentrations (mg·kg^{-1}) of Ca, Mg, N, P, K, Mn, and Al from 2004 through 2009.

	F (*P*)						
Source	Ca	Mg	N	P	K	Mn	Al
Fence	0.01 (0.936)	<0.01 (0.972)	2.03 (0.228)	0.35 (0.584)	2.60 (0.181)	2.37 (0.178)	1.33 (0.320)
Lime	**18.94 (<0.001)**	**21.17 (<0.001)**	**5.21 (0.010)**	1.94 (0.143)	**5.31 (0.005)**	**64.64 (<0.001)**	2.65 (0.060)
Fence × lime	0.20 (0.897)	0.08 (0.972)	1.69 (0.206)	0.93 (0.436)	0.29 (0.831)	1.96 (0.159)	0.71 (0.552)
Year	**10.09 (<0.001)**	**50.80 (<0.001)**	**12.19 (<0.001)**	**21.51 (<0.001)**	**10.47 (<0.001)**	**33.41 (<0.001)**	**12.44 (<0.001)**

Note: The models for Ca and Al were fit using the lognormal distribution and an AR(1) covariance structure; the models for Mg, N, P, K, and Mn were fit using the gamma distribution and an AR(1) covariance structure. None of the higher order interactions, fence × year, lime × year, fence × lime × year, were significant ($P \leq 0.05$) except for Mg, which had a significant ($F = 2.30$, $P = 0.008$) lime × year interaction. Boldface type highlights the effects significant at the $P \leq 0.05$ level.

Fig. 3. Lime treatment effects on northern red oak (*Quercus rubra*) foliar concentrations of Mg over each year from 2005 through 2009. Bars with different letters are significantly different ($P \leq 0.05$) using the Tukey adjustment for multiple comparisons.



significant fence × year interaction for all three growth variables, as greater growth occurred inside the fences compared with outside the fences (Fig. 4). Yearly pairwise comparisons showed marginally significant ($P \leq 0.10$) differences for fence versus no-fence comparisons in 2008 and 2009 for both mean root collar diameter and mean seedling height.

Observations during the study and subsequent seedling growth data revealed substantial differences among the sites in response to differential deer browsing pressure. NRO seedlings were shorter outside the fences than inside at four of the five sites (Fig. 5). This result was most pronounced at the LV site starting in 2005 and became evident at the BF, CC, and LM sites by 2006 or 2007. Conversely, mean height of NRO seedlings was greater outside the fence than inside at the GL site due to breach of the fence by deer in 2006. Despite the fencing breech, overall growth of seedlings at the GL block was significantly greater ($P = 0.004$ using best linear unbiased predictors) than in the other four blocks (Littell et al. 2006).

Destructively harvested seedlings sampled at the end of the study in fall 2009 were evaluated for eight components of biomass and size (Table 5). Lime treatment had no statistically significant effect on any of these components. In contrast, the fence treatment did have a statistically significant effect on six biomass and size components: basal diameter, root collar diameter, root length, root dry mass, stem dry mass, and total root plus stem dry mass. Stem height and root to stem dry mass ratio were not significantly affected by the fence treatment. Root collar diameter averaged 9.4 mm in fenced plots and only 5.7 mm in unfenced plots. Similarly, root length averaged 33 cm in fenced plots and only 22 cm in unfenced plots. Total root plus stem dry mass also showed a dramatic difference, as seedlings in fenced plots averaged about 19.8 g·seedling^{-1} compared with only 5.3 g·seedling^{-1} in unfenced plots. The biomass and size attribute results do not account for the number of seedlings eliminated by deer, for example, no adjustment was made to the data for the sparse number of seedlings at the LV block where two unfenced plots had only four and seven seedlings, respectively.

Table 4. Fixed effects *F* statistic and associated probability values for repeated-measures analyses of seedling height, root collar diameter, and basal diameter growth of northern red oak (*Quercus rubra*) seedlings.

	F (*P*)		
Source	Height[a]	Root collar diameter[b]	Basal diameter[c]
Fence	2.27 (0.202)	2.01 (0.214)	1.38 (0.295)
Lime	0.32 (0.812)	0.76 (0.530)	0.66 (0.587)
Fence × lime	0.25 (0.856)	1.16 (0.349)	0.54 (0.662)
Year	**28.67 (<0.001)**	**79.05 (<0.001)**	**8.17 (<0.001)**
Fence × year	**3.39 (0.009)**	**4.72 (0.002)**	**10.07 (<0.001)**
Lime × year	0.70 (0.782)	0.33 (0.981)	0.42 (0.923)
Fence × lime × year	0.56 (0.895)	0.65 (0.788)	1.00 (0.449)

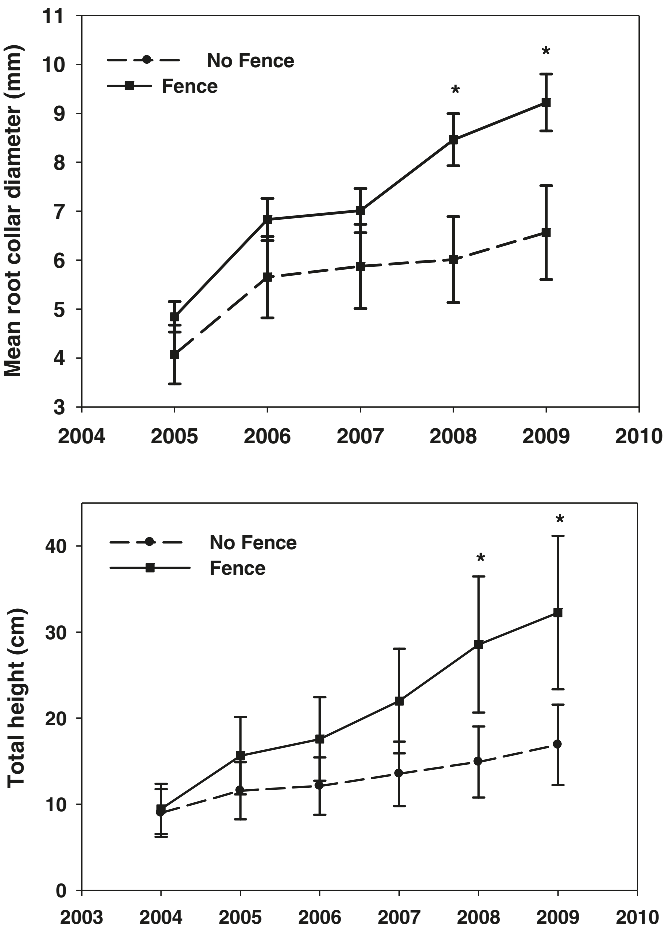
Note: Boldface type highlights the effects significant at the $P \leq 0.05$ level.

[a]The model was fit using the gamma distribution and the ARH(1) covariance structure for data from 2004 through 2009. The light covariate was not significant and was omitted from the model.

[b]The model was fit using the lognormal distribution and the AR(1) covariance structure for data from 2005 through 2009. The light covariate was nonsignificant and was omitted from the model.

[c]The model was fit using the gamma distribution and the AR(1) covariance structure with data from 2006 through 2009.

Fig. 4. Fence versus no-fence treatment effects on northern red oak (*Quercus rubra*) mean root collar diameter from 2005 through 2009 and mean total seedling height from 2004 through 2009. Years with as asterisk indicate a significant ($P \leq 0.10$) pairwise comparison between fence versus no fence for the indicated year.



Discussion

The long-term impact of atmospheric deposition inputs on unglaciated forested soils in Pennsylvania has been proposed as a major factor limiting oak regeneration success by those who discount the alternative hypothesis of excessive deer browsing (Mulhollem 2002; Frye 2006). Forest liming has been hypothesized as a means of mitigating atmospheric deposition and improving the growth of oak reproduction (Demchik and Sharpe 1999*a*, 1999*b*; Schreffler and Sharpe 2003). Our primary objective was to compare these two hypotheses and to test whether forest liming promoted NRO seedling growth more than excluding deer through fencing.

In this study, we found no support for the forest liming hypothesis. Soil chemical properties were quickly altered by lime application and NRO seedlings accumulated greater quantities of Ca and Mg in their foliage. However, there were no significant changes in seedling growth due to liming during the 6 years of annual measurements. Destructive harvests of seedlings in year 6 to evaluate biomass accumulation further confirm the findings of no response to lime applications. These results show that NRO seedling growth is not limited by putative deficiencies in Ca and Mg or by Al or Mn toxicity in acidified soils in western and central Pennsylvania. Unfortunately, the optimal nutrient regime for NRO seedling growth has not been established nor is the toxicity level for Al and Mn concentrations under field conditions well established.

These results are consistent with earlier liming research conducted in the eastern United States showing that despite changes in soil chemistry and uptake by overstory trees (i.e., black cherry, sugar maple, American beech, paper birch (*Betula papyrifera* Marsh.), and yellow birch (*Betula alleghaniensis* Britt.)), there was no significant growth response to lime application (Safford 1973; Leaf and Bickelhaupt 1975). However, in these earlier studies, only modest amounts of lime (1.1–4.4 $Mg{\cdot}ha^{-1}$) were applied and responses were measured for only 2–3 years. Both the amount of lime applied and the period of post-treatment evaluation were probably insufficient to observe a response, even if one was

Fig. 5. Fence versus no-fence treatment effects on northern red oak (*Quercus rubra*) mean seedling height growth in the five individual blocks comprising all of the study sites.

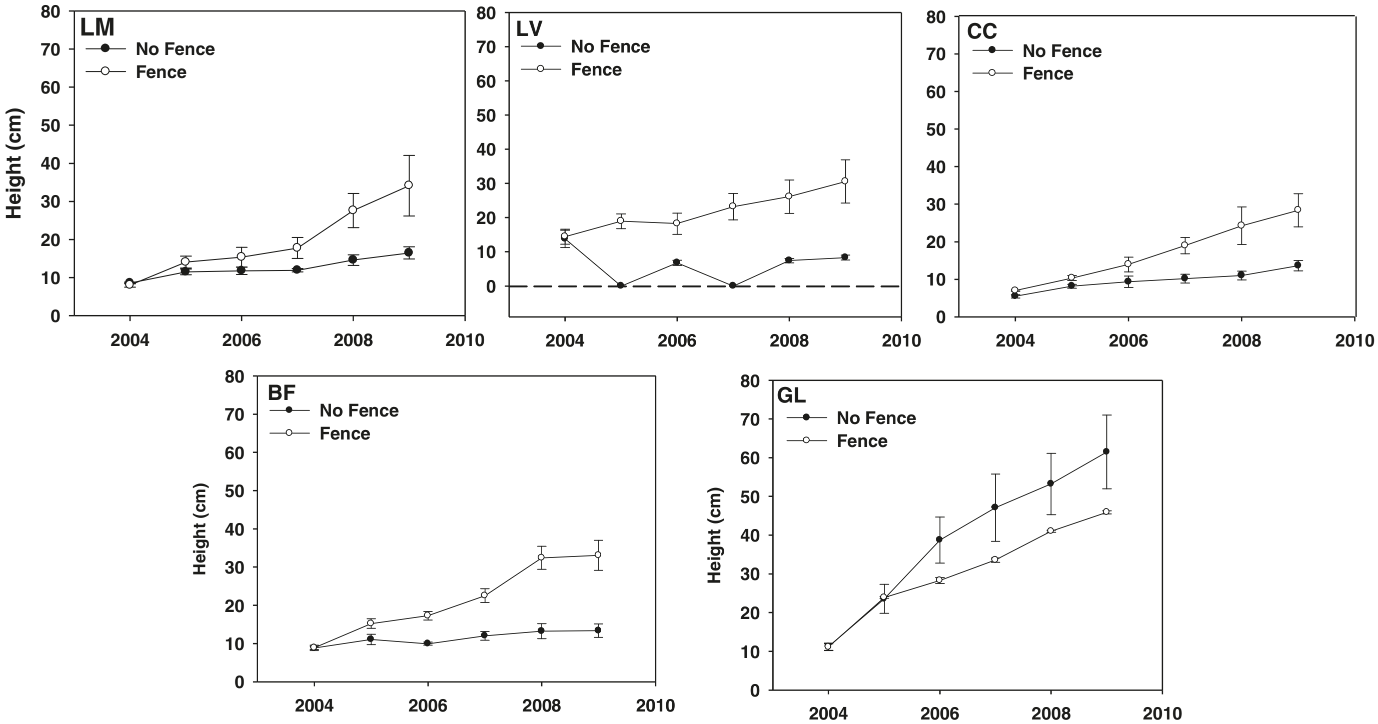


Table 5. Results of statistical analyses evaluating lime treatment and fencing effects (*F* statistics and associated probability values) on biomass components and related measurements from destructively harvested northern red oak (*Quercus rubra*) seedlings in 2009.

	F (*P*)		
Variable	Lime	Fence	Fence × lime
Basal diameter	0.92 (0.445)	**7.19 (0.043)**	0.42 (0.738)
Root collar diameter	0.61 (0.613)	**7.04 (0.049)**	0.24 (0.864)
Root length	0.96 (0.428)	**25.99 (0.007)**	1.76 (0.183)
Root dry mass	0.86 (0.476)	**7.90 (0.048)**	0.53 (0.665)
Stem height	0.50 (0.687)	4.71 (0.086)	0.93 (0.443)
Stem dry mass	0.39 (0.764)	**8.90 (0.041)**	0.28 (0.838)
Total root plus stem dry mass	0.75 (0.531)	**9.15 (0.039)**	0.49 (0.692)
Root to stem dry mass ratio	1.10 (0.367)	1.25 (0.309)	0.83 (0.488)

Note: All analyses are based on plot means from 10 destructively sampled seedlings in each of eight plots per block ($N = 40$); however, for the LV block, plot 2, only two seedlings remained and for LV, plot 4, only seven seedlings remained. Boldface type highlights the effects significant at the $P \leq 0.05$ level.

present. Research conducted in Potter County, Pennsylvania, with a single 22.4 Mg·ha^{-1} application of dolomitic limestone showed differential response for overstory species: sugar maple basal area growth increased, American beech had no response, and black cherry had a negative basal area growth response (Long et al. 2011). The current study is among the few to use a dose–response application and to observe potential seedling responses over 6 years, enough time to detect growth responses if present.

Oak seedlings develop an extensive taproot during early establishment. This period is crucial for seedling success and the development of a large root system allows seedlings to resprout after top kill from browsing, burning, or other aboveground disturbances. Depending on stand density, lighting conditions, and competing vegetation, taproot length was 20 to almost 60 cm in length after 5 years in acorn-origin plantings in Pennsylvania forests with differing silvicultural treatments (Brose 2011*b*). Our data show a similar pattern of root development for seedlings inside the fences, but liming had no significant effect on root development.

Large-scale dose–response studies provide a more reliable demonstration of treatment effects than small-scale studies. For example, research conducted near Laurel Mountain in southwestern Pennsylvania, an area that receives high levels of atmospheric deposition inputs, has shown equivocal effects of lime treatment on NRO seedling growth in two small-scale studies (Demchik and Sharpe 1999*b*; Schreffler and Sharpe 2003). In one study (Demchik and Sharpe 1999*b*), lime applied at a rate of 6.6 Mg·ha^{-1} inside a fence resulted in zero survival of planted seedlings after 27 months, while 42% of seedlings that received lime and mechanical vegetation control (removal of fern rhizome mat) survived. Despite enhanced survival for these seedlings, median height growth (36.5 cm) was less than for control trees (39 cm), also planted inside the protective fences. Short-term (≤3 years) studies on small plots may not provide a reliable test of lime effects and frequently have been confounded with concurrent fertilizer applications or other treatments.

In another southwestern Pennsylvania study, lime plus fertilizer had no significant effect on NRO median height growth; however, control of fern (sulfometuron methyl herbicide) significantly increased height growth of NRO seedlings by 2–4 cm (Schreffler and Sharpe 2003). The addition of lime plus fertilizer to herbicide-treated plots had no additional significant effect on NRO height growth, which is consistent with the results from our study using lime only.

Pennsylvania has had historically high deer densities ranging from 15 to 22 deer·km^{-2} in the twentieth century (Horsley et al. 2003). Beginning in 2000 and continuing through 2004, the Pennsylvania Game Commission altered hunting regulations to bring deer densities down to targets based on habitat conditions in wildlife management units. Deer impact, a measure of deer density and forage availability, changes considerably across Pennsylvania and was variable, but detectable, at all of our study sites. Our results show the unequivocal impact of deer browsing on NRO growth. In our study, fencing to exclude deer browsing was the only significant factor affecting seedling growth during the 6 years, although browsing effects were not consistent at each location or for each year. At the LV block in Centre County, deer virtually eliminated all of the NRO seedlings in two of four plots located outside the fence by 2005, while the BF (Lycoming County), CC (Jefferson County), and LM (Somerset County) blocks did not exhibit a reduction in the NRO seedling growth outside the fences until 2006 or 2007. The GL site (Forest County) had a unique growth response of NRO seedlings growing better outside the fence than inside the fence due to breach of the fence by deer. Also, this site had received an herbicide treatment in 2001 (H. Wurzbacher, personal communication) that likely accounts for the enhanced growth of NRO seedlings (both inside and outside the fence) at this site compared with the other sites.

Our secondary objective was to document the effects of liming on soil and foliar chemistry. Pre-treatment soils were highly acidic; pH ranged from 2.7 to 3.8 in the upper 5 cm and the lime application raised theses values to 3.3–4.0, depending on the location. The extreme acidity and small change may be due, in part, to the use of $CaCl_2$ instead of water to determine pH. Using $CaCl_2$ provides a more stable estimate of soil pH but tends to provide a lower estimate of acidity by about 0.6–0.8 pH unit compared with measurement in water (Kissel et al. 2004). Apparently, the amount of added limestone was insufficient to significantly alter the pH of the deeper mineral soil. In Potter County, PA, where pulverized dolomitic limestone was applied at a rate of 22.4 Mg·ha^{-1}, soil pH, measured in water instead of $CaCl_2$, increased from 3.8 in the 0–5 cm layer to about 5.3 one year after lime application (Long et al. 1997). However, as with the current study, an additional 2–4 years was required before pH was altered in the 5–10 and 10–15 cm depths. Although acidity changes in the current study were modest, lime application significantly changed Ca and Mg concentrations even at the 15–30 and 30–45 cm depths. Mean root length for limed seedlings was 33 cm in fenced plots and 22 cm outside the fences. Given the movement of the Ca and Mg in the soil profile and the observed concentrations in the foliage, the seedling roots were able to exploit the available nutrients. However, results from our study indicate that Ca and Mg are not limiting for NRO seedling growth.

NRO seedlings, germinated from acorns planted in spring 2004, showed increased foliar Ca and Mg as early as August 2004, although the increases were not statistically significant until 2005. By August 2005, foliar Mg was significantly greater in all three lime treatments, but there were no differences among the three rates of lime application. Based on foliar chemistry, NRO seedlings are apparently unable to take advantage of the extra Ca and Mg available in the 9.0 and 13.5 Mg·ha^{-1} treatments. The rapid response to the lime application is probably due to the seedling roots quickly exploiting the upper soil layers where the lime impacts were focused. Additionally, the lime became available rapidly because of the pelletized form of lime applied. In a pelletized form, limestone is pulverized to less than 100 mesh and then bound to a lignosulfonate and dried. Pellets break down rapidly when exposed to moisture and leave the finely pulverized limestone to solubilize more rapidly, increasing Ca and Mg concentrations in the soil and then in the NRO foliage.

Monitoring the Ca/Al molar ratio in soil solution, foliage, and fine roots has been proposed as a method to assess the risk from soil acidification (Cronan and Grigal 1995). Foliar Ca from seedlings in control plots averaged 3844 mg·kg^{-1} and foliar Al was 79 mg·kg^{-1}. Cronan and Grigal (1995) proposed a foliar Ca/Al molar ratio of ≤12.5 in deciduous foliage as presenting a 50% risk of impacts on tree growth. NRO foliage in our study had Ca/Al molar ratios that averaged 34 in control plots and increased to >70 in foliage from seedlings in plots treated with 13.5 Mg·ha^{-1} dolomitic limestone. Based on the guidelines from Cronan and Grigal (1995), NRO seedlings, even under native soil conditions, were not at risk from Al toxicity.

Manganese, although an essential nutrient, may be toxic at high concentrations and exchangeable Mn is more available at pH < 5.0 (Brady and Weil 1999; St. Clair and Lynch 2005). Manganese toxicity in highly acidic soils has been demonstrated with sugar maple (McQuattie and Schier 2000), but no empirical data have demonstrated this effect with NRO. Foliar Mn concentrations were significantly reduced from 2090 mg·kg^{-1} for control seedlings to about 850–970 mg·kg^{-1} in lime-treated seedlings. In a southwestern Pennsylvania study, foliar Mn from mature overstory NRO was higher, 1612 mg·kg^{-1}, on sites with high NRO mortality compared with 1202 mg·kg^{-1} on sites with low mortality (Demchik and Sharpe 2000). However, in our study, we observed no symptoms of Mn toxicity on unlimed seedlings. Limed seedlings with less than one-half the concentration of Mn in their foliage than in unlimed seedlings exhibited no increase in growth. We conclude that high foliar Mn in unlimed seedlings was not limiting to growth.

Conclusions

NRO seedling growth was not limited by soil nutrient status, despite long-term inputs of atmospheric deposition, but was negatively impacted by deer browsing. There was no growth response of NRO seedlings to any of the lime treatments over the 6 years and three applied rates of lime in this study. Fencing to prevent deer browsing was the only treatment that elicited a significant growth response by NRO seedlings. Although soil chemical properties were altered by lime application and NRO seedlings accumulated greater quantities of Ca and Mg in their foliage, there were no significant changes in seedling growth or biomass accumulation in response to these changes in soil chemistry. These results show that NRO seedling growth is not limited by putative deficiencies in Ca and Mg or by Al and (or) Mn toxicity in acidified soils.

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