Tree Physiology 25, 1495–1500

Forest regeneration composition and development in upland, mixed-oak forests†

SONGLIN FEI,[1] PETER J. GOULD,[1] KIM C. STEINER,[1, 2] JAMES C. FINLEY[1] and MARC E. McDILL[1]

[1] *School of Forest Resources, The Pennsylvania State University, 104 Ferguson Building, University Park, PA 16802-4302, USA*

[2] *Corresponding author (kcs@psu.edu)*

Received October 29, 2004; accepted March 14, 2005; published online September 1, 2005

Summary Advance regeneration in 52 mature mixed-oak stands was analyzed and described. Red maple (*Acer rubrum* L.) was the most abundant species in the study area. Among oak (*Quercus*) species, northern red oak (*Q. rubra* L.) was the most abundant within the Allegheny Plateau physiographic province, whereas chestnut oak (*Q. montana* L.) was the most abundant within the Ridge and Valley physiographic province. Sixteen stands, for which data are available through the fourth growing season following harvest, were used to describe stand development. Cumulative height, a composite measure of size and density, was used to describe early stand development. Black gum (*Nyssa sylvatica* Marsh.) and black birch (*Betula lenta* L.) had dramatic increases in stand density and cumulative height after overstory removal. Cumulative height of northern red oak and chestnut oak showed a faster positive response to overstory removal than red maple. Oak retained its dominance in cumulative height for at least 4 years after harvest. Red maple nevertheless remained the most abundant tree species after overstory removal. Our results suggest that the principal advantage of red maple regeneration is its ability to accumulate in large numbers prior to harvest.

Keywords: cumulative height, dominance, Pennsylvania.

Introduction

Oak regeneration is often limited, even where oak species are dominant components in the overstory before harvest (Crow 1988, Abrams 1992, Lorimer 1993). Forest managers who rely on natural regeneration to restock stands after overstory removal are often interested in controlling and manipulating the size, density and composition of both advance regeneration and regeneration occurring after overstory removal. Interest in methods of enhancing oak regeneration has created a need to better understand tree seedling development shortly before and after timber harvests.

Early stage stand development is characterized by rapidly changing tree growth and species composition. The environment, growth pattern and size of each plant change more dramatically during this stage than during any other period (Oliver and Larson 1996). Failure to obtain adequate and prompt regeneration of desired species can leave a stand unproductive for many years, making it expensive to reclaim through artificial means and severely limiting its value for a wide range of forest uses (Marquis and Twery 1993). However, monitoring and understanding early stage stand development is difficult because young forest stands are often highly complex and exhibit seemingly unpredictable responses to a multitude of factors.

Observations in upland mixed-oak stands in the central Appalachians indicate that red maple (*Acer rubrum* L.) is becoming increasingly dominant in stands that have historically been dominated by oak species, especially following harvest (Nowacki et al. 1990, Smith and Vankat 1991, Abrams 1998, McWilliams et al. 2004). The reasons for this phenomenon are unclear, but may involve recent changes in deer density and fire frequency, and the virtual disappearance of American chestnut as a significant component of many stands. We know even less about how to manage or reverse this change in species dominance because there is a lack of quantitative, descriptive information about the process in stands where red maple is becoming increasingly dominant. The purpose of this paper is to describe advance regeneration and its early development in upland mixed-oak stands in the central Appalachians, where a transition to dominance by red maple seems to be rapidly occurring.

Materials and methods

Study area

The study area is located in Pennsylvania (40°13′ to 41°46′ N, 77°12′ to 78°36′ W) and crosses the Allegheny Plateau and the Ridge and Valley physiographic provinces, which are separate ecoregions (Cuff et al. 1989). Soils in the study area are derived from sandstone, siltstone and shale, and are typically well-drained and support moderately productive forests. Stand elevations range from 250 m a.s.l. in the Ridge and Valley provinces to 700 m on the Allegheny Plateau. Precipitation, temperature and length of growing season vary with latitude

† *This paper was among those presented at the 18th North American Forest Biology Workshop, which was sponsored by the Society of American Foresters and the USDA Forest Service, and hosted by the Michigan Technological University, Houghton, MI, July 11–15, 2004.*

and topography. Mean annual precipitation ranges from 960 to 1070 mm and mean annual temperature ranges from 8 to 11 °C. The length of the growing season ranges from 120 to 140 days in the northwest, and 140 to 180 days in the southeast.

Data collection and analysis

Field measurements were performed on 52 mixed-oak stands (> 50% of basal area in oak species) on a total area of 966 ha during 1996–2003. Seventeen stands are located on the Allegheny Plateau and 35 stands are in the Ridge and Valley provinces. Depending on stand size, 15 to 30 permanent circular plots with an 8.02-m radius (0.05 acre, 202.3 m^2) were installed in a square grid to represent the whole stand. Four permanent subplots with a 1.13-m radius (0.001 acre, 4.047 m^2) were established within each main plot in a systematic arrangement. In total, 5732 subplots were established in the study area. All 52 stands were measured about 1 year before harvest, and 16 stands were remeasured 1 and 4 years after overstory removal. Tree regeneration was recorded by height and by species on each subplot. All stands included in this study had or were scheduled for overstory removal (shelterwood or clear-cut) after the first assessment.

Mean density, cumulative height (CumHt) and occurrence frequency of advance regeneration were calculated for each species within each stand and across all stands. Cumulative height is defined as the total height of all the individuals of a species or species group per unit area. Cumulative height is analogous to other forest measurements, such as basal area, that incorporate both size and density into a single value. Mean stand CumHt was calculated as:

$$\overline{\text{CumHt}} = \left(\sum_{i=0}^{k} \frac{\sum_{j=0}^{n} h_{ij}}{s} \right) \frac{1}{k} \quad (\text{m m}^{-2}) \qquad (1)$$

where h_{ij} is the height of jth seedling in ith subplot, n is number of seedlings in subplot i, k is the number of sample subplots, and S is the size of the subplot in m^2. Analysis of variance (ANOVA) was carried out to examine the difference in advance regeneration abundance between the two physiographical provinces based on mean stand CumHt. Mean stand CumHt of northern red oak (*Q. rubra* L.) and chestnut oak (*Q. montana* L.) were also mapped based on coordinates of stand centroids to illustrate the regional distributions of these species.

Sixteen stands for which data are available through the fourth growing season following harvest were used to describe stand development. Regeneration development of the three most abundant oak species (northern red oak, chestnut oak and white oak (*Q. alba* L.)) and non-oak species (red maple, black gum (*Nyssa sylvatica* Marsh.) and black birch (*Betula lenta* L.)) after harvest was summarized by density and size classes and by CumHt. Mean stand CumHt was used to describe the regeneration development of red maple and oak species. Linear regression equations were fit for CumHt of advance regeneration 1 year before harvest and 1 and 4 years after harvest. Because only three of the 16 stands are located on the Allegheny Plateau province, no attempt was made to examine the difference in regeneration development between the two physiographical provinces.

The percentage of subplots dominated by oak regeneration was calculated for each measurement period based on two criteria (CumHt and maximum height). Cumulative height dominance was calculated as the percentage of subplots where oak CumHt was greater than or equal to non-oak CumHt. Maximum height dominance was calculated as the percentage of subplots where the tallest stem of oak regeneration was taller than or equal to the tallest stem of any other tree species.

Results

Advance regeneration composition and distribution

A total of 49 species or species groups were identified in the sampled subplots. Mean density, CumHt and occurrence frequency for the 15 most frequently encountered advance regeneration species are listed in Table 1. Advance regeneration was heavily dominated by red maple, which had markedly higher mean density, CumHt and occurrence frequency than other species in the advance regeneration cohort. Northern red oak and chestnut oak were the second and third most abundant regeneration in the study area, respectively. Northern red oak had a higher density and occurrence frequency than chestnut oak, but slightly less mean CumHt (i.e., chestnut oak seedlings were, on average, taller than northern red oak seedlings). White oak and black oak were the third and fourth most abundant oak species and ranked fifth and eighth, respectively,

Table 1. Mean density, cumulative height and occurrence frequency of the 15 most frequent advance tree regeneration species in 52 mixed-oak stands in the central Appalachians.

Species	Density (stems ha^{-1})	Cumulative height ($m\ m^{-2}$)	Frequency (%)
Acer rubrum	60,885	0.699	93.0
Quercus rubra	8,154	0.110	45.7
Quercus montana	6,128	0.129	28.9
Amelanchier spp.	2,125	0.034	23.3
Quercus velutina Lam.	964	0.019	14.8
Quercus alba	1,730	0.036	12.6
Acer pensylvanicum L.	1,038	0.038	12.3
Betula lenta	1,186	0.032	11.8
Sassafras albidum (Nutt.) Nees	766	0.013	11.0
Nyssa sylvatica	618	0.010	10.0
Prunus serotina J. F. Ehrh.	692	0.010	9.7
Carya glabra (Mill.) Sweet	198	0.003	5.0
Quercus coccinea Muenchh.	222	0.007	4.1
Liriodendron tulipifera L.	272	0.002	3.8
Pinus strobus L.	148	0.012	3.5

among all species in density. Overall, only 11 species occurred on more than 5% of subplots, and only three species (red maple, northern red oak and chestnut oak) occurred on > 25% of all subplots. About half of the advance regeneration species had mean densities of less than 10 stems ha^{-1}. Advance regeneration was diverse but dominated by a few species.

Regional differences in advance regeneration abundance were observed between the two physiographic provinces in the study area. Red maple was more abundant on the Allegheny Plateau than in the Ridge and Valley, although the difference was not significant ($P = 0.07$). The three most abundant oak species, red oak, chestnut oak and white oak, showed significant differences in advance regeneration abundance between the two physiographic provinces ($P < 0.05$). Regional distribution maps of northern red oak and chestnut oak are plotted in Figure 1. Red oak was more abundant on the Allegheny Plateau, and chestnut oak was more abundant in the Ridge and Valley. White oak had a similar distribution to chestnut oak.

Regeneration development

Regeneration development of the three most abundant oak and non-oak species after harvest is summarized in Figure 2 by density and size class. Black gum and black birch densities increased rapidly, and were five to 10 times greater 4 years after harvest than before harvest. These species also experienced rapid height growth. About 12% of stems of black gum and black birch had developed into the largest size class (> 1.5 m) (313 and 470 stems ha^{-1}, respectively) 4 years after harvest, despite having few large stems (4 and 42 stems ha^{-1}, respectively) before harvest.

Red maple and northern red oak experienced a reduction in density in the first year after harvest, followed by a moderate recovery (Figure 2). Red maple densities declined by about one third, then recovered to about 80% of pre-harvest density (44,354 stems ha^{-1}). Northern red oak densities declined by 20% and recovered to values somewhat higher than before harvest. Both red maple and northern red oak had < 0.5% of

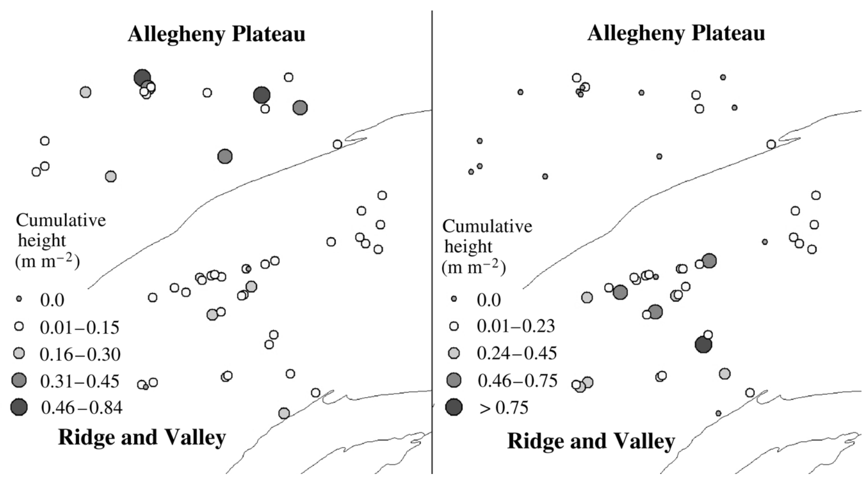

Figure 1. Distribution of mean cumulative heights of northern red oak (left) and chestnut oak (right) advance regeneration in 52 mixed-oak stands in the Allegheny Plateau and Ridge and Valley physiographical provinces.

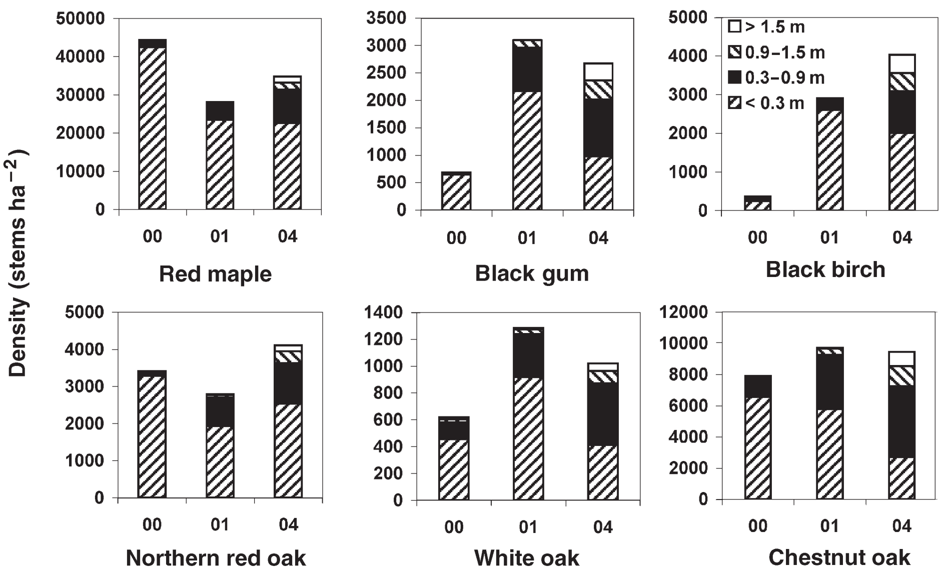

Figure 2. Change in regeneration density from before harvest (00) to 1 year after harvest (01) and 4 years after harvest (04) by height classes for red maple, black gum, black birch, northern red oak, white oak and chestnut oak for 16 mixed-oak stands.

stems in the largest height class (> 1.5 m) (213 and 16 stems ha^{-1}, respectively), but reached about 4% (1667 and 155 stems ha^{-1}, respectively) 4 years after harvest.

White oak and chestnut oak densities increased 1 year after harvest, but declined 4 years after harvest; however, densities of both species were higher 4 years after, than before, harvest. The percentage of chestnut oak in the largest size class increased from 0.5% (44 stems ha^{-1}) before harvest to about 10% (913 stems ha^{-1}) 4 years after harvest. The percentage of white oak in the largest size class remained nearly the same (around 4%), but the density increased from 17 to 56 stems ha^{-1}.

Mean CumHt development of the three most abundant oak and non-oak species is presented in Table 2. Mean CumHt for advance regeneration differs slightly from the values presented in Table 1 because of differences in sample size. All six species showed a monotonic increase in mean CumHt over time. Mean CumHts of black gum and black birch increased dramatically, reaching 12 to 20 times their pre-harvest values 4 years after harvest. Although there was little change in mean CumHt of red maple between 1 year before and 1 year after harvest, mean CumHt of red maple more than doubled between the first and fourth growing seasons after harvest, and was 2.6 times greater 4 years after harvest than before.

There were large increases in mean CumHt of northern red oak and chestnut oak at both 1 and 4 years after harvest. In northern red oak, mean CumHt was 1.6 times the pre-harvest value 1 year after harvest and 3.6 times 4 years after harvest. Mean CumHt of chestnut oak responded more rapidly to overstory removal than that of northern red oak, increasing to 1.9 times the pre-harvest value 1 year after harvest and 3.8 times 4 years after harvest. Mean CumHt for white oak increased over time, but the increase was not significant.

Table 2. Mean cumulative height (CumHt) before harvest and 1 and 4 years after harvest of red maple (*Acer rubrum*), black gum (*Nyssa sylvatica*), black birch (*Betula lenta*), northern red oak (*Quercus rubra*), white oak (*Quercus alba*) and chestnut oak (*Quercus montana*) for 16 mixed-oak stands. Asterisks indicate mean CumHt within the same row not sharing same letters are significantly different at $P < 0.05$ (repeated measures ANOVA was applied using stands as the subjects, mean separation was further carried out if assessment time was a significant factor).

Species	Mean cumulative height (m m^{-2})		
	Before	1 Year after	4 Years after
Acer rubrum	0.573 a*	0.629 a	1.496 b
Nyssa sylvatica	0.021 a	0.049 ab	0.251 b
Betula lenta	0.010 a	0.093 ab	0.201 b
Quercus rubra	0.051 a	0.086 ab	0.185 b
Quercus alba	0.021 a	0.039 a	0.056 a
Quercus montana	0.187 a	0.355 ab	0.710 b

Regressions of CumHts of oak and red maple over time are plotted in Figure 3. The relationship between advance regeneration and regeneration 1 year after harvest was weaker than the relationship between regeneration 1 and 4 years after harvest. For red maple and oak, the coefficients of determination (r^2) for regressions of CumHts at 1 year before harvest versus

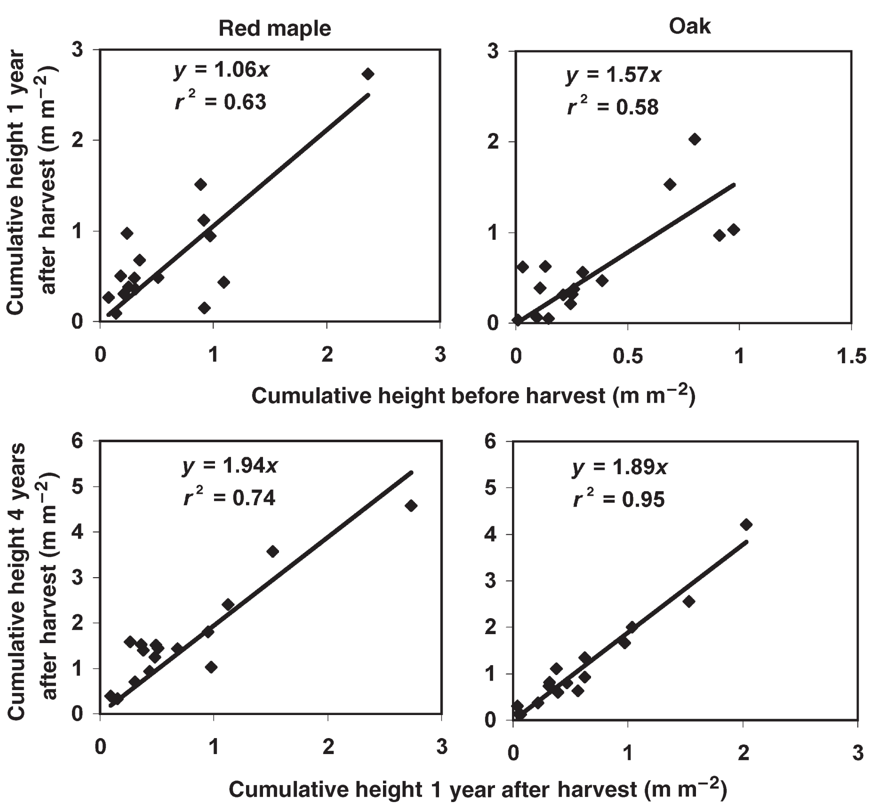

Figure 3. Regressions of cumulative height before harvest and 1 year after harvest (top), and between 1 and 4 years after harvest (bottom) for red maple (left column) and oak species (right column).

1 year after harvest were 0.63 and 0.58, respectively. However, r^2 values were 0.74 and 0.95 for red maple and oak, respectively, for regressions of CumHts at 1 year versus 4 years after harvest. Only small variations between stands were observed for regressions between 1 and 4 years after harvest.

Figure 4 shows the percentage of plots dominated by oak species for each measurement period, based on CumHt and maximum height. Oak dominance assessed as maximum height was much more frequent than dominance based on CumHt in each measurement period. Percentage of subplots with oak CumHt greater than or equal to non-oak CumHt showed a slight increase 1 year after overstory removal, and then fell to its previous value 3 years later. The percentage of subplots where oak maximum height was greater than or equal to that of non-oak species decreased monotonically with time from 54 to 39%.

Discussion

Advance regeneration abundance of red maple and oak species differed between the two physiographic provinces comprising the study area. Red maple and northern red oak are more abundant on the Allegheny Plateau, whereas chestnut oak and white oak are more abundant in the Ridge and Valley. These differences reflect differences between the physiographic provinces in general topography, geomorphic process, surficial geology, and soil and local climate, which can affect the composition, abundance and distribution of vegetation (Cleland 1993).

Our findings indicate that oak regeneration experiences two kinds of forest tree competitors. The first is typified by red maple. Red maple regeneration, on average, is not large, but has a significantly greater density than that of oak species, both before and after overstory removal. Red maple currently occupies space that would otherwise be occupied by oak. The presence of abundant red maple regeneration and sparse oak regeneration in the central Appalachians raises concerns about the success of oak regeneration in future stands in the region (Lorimer 1984). It has been widely observed that red maple has increased in dominance and has become almost ubiquitous across sites in forests of eastern North America (Lorimer 1984, Abrams 1992, 1998). Red maple is a "super-generalist," having characteristics of both early and late successional species, and can thrive in most edaphic conditions because it has a low minimum requirement for nutrients and light (Abrams 1998). The second kind of competitor to oak regeneration is the fast-growing "invader" species, such as black gum and black birch. Although regeneration of both species is small and occurs at low density before harvest, it can increase dramatically in both size and density after harvest. Black birch, in particular, shows increasing dominance in young stands in the central Appalachians (McWilliams et al. 2004).

Although future stand composition is strongly a function of seedling size (Sander et al. 1984), seedling density cannot be ignored, and even small seedlings may contribute to future composition. Our results indicate that small oak seedlings (< 0.3 m) can grow into larger size classes (> 1.5 m) 4 years after overstory removal. Most of the large oak seedlings present 4 years after overstory removal had developed from the small advance regeneration. In similar stands, Ward and Stephens (1999) found that advance regeneration oak ranging from < 0.3 to 1.5 m in height can reach a dominant crown position 12 years after harvest.

Cumulative height, a composite measure of seedling size and density, provided a basis for reasonably deterministic models describing early stand development, especially for oak species after overstory removal. The CumHt data revealed two findings of particular interest. First, the two most abundant oak species (northern red oak and chestnut oak) exhibited a faster CumHt response to overstory removal than red maple. Second, the percentage of subplots dominated by oak, based on the CumHt criterion, has changed only slightly over time, indicating that oak regeneration has neither lost nor gained in overall dominance, even though the largest oak seedlings are usually not growing as fast as the largest seedlings of non-oak species.

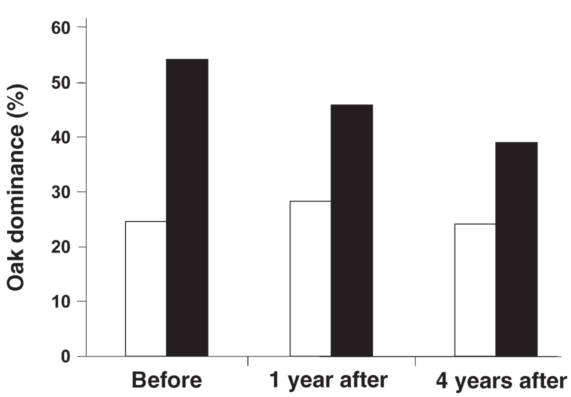

Figure 4. Percentage of plots dominated by oak species, before and 1 and 4 years after harvest, based on cumulative height (open bars) and maximum seedling height (filled bars).

Conclusions

Advance regeneration in the study area is diverse but dominated by few species, mostly red maple, northern red oak and chestnut oak.

There are regional differences in oak regeneration abundance. Northern red oak is more abundant on the Allegheny Plateau, whereas chestnut oak and white oak are more abundant in the Ridge and Valley physiographical provinces.

Cumulative height, as a composite variable of size and density, summarizes post-harvest seedling development, especially for oak.

Small advanced oak regeneration contributes to new stand development, and oak species neither gain nor lose dominance in CumHt, at least during the first 4 years after harvest.

Black gum and black birch dramatically increase in both density and CumHt after harvest. Chestnut oak and northern red oak respond to overstory removal faster in CumHt than red maple.

The principal advantage of red maple regeneration is its ability to accumulate in larger numbers before harvest compared with the co-occurring oak species.

Acknowledgment

This study was funded by the Pennsylvania Department of Conservation and Natural Resources, Bureau of Forestry.

References

Abrams, M.D. 1992. Fire and the development of oak forests. BioScience 42:346–353.

Abrams, M.D. 1998. The red maple paradox. BioScience 45: 355–363.

Cleland, D.T., P.E. Avers, W.H. McNab et al. 1993. National hierarchical framework of ecological units. ECOMAP, USDA Forest Service, Washington, DC, 20 p.

Crow, T.R. 1988. Reproductive mode and mechanisms for self-replacement of northern red oak: a review. For. Sci. 34:19–40.

Cuff, D.J., W.J. Young, E.K. Muller, W. Zelinsky and R.F. Abler. 1989. The atlas of Pennsylvania. Temple University Press, Philadelphia, PA, 288 p.

Lorimer, C.G. 1984. Development of the red maple understory in northeastern oak forests. For. Sci. 30:3–22.

Lorimer, C.G. 1993. Causes of the oak regeneration problem. *In* Oak Regeneration: Serious Problems, Practical Recommendations. Eds. D.L. Loftis and C.E. McGee. USDA For. Serv. Gen. Tech. Rep. SE-84, Southeastern For. Expt. Sta., Asheville, NC, pp 14–39.

Marquis, D.A. and M.J. Twery. 1993. Decision-making for natural regeneration in the northern forest ecosystem. *In* Oak Regeneration: Serious Problems, Practical Recommendations. Eds. D.L. Loftis and C.E. McGee. USDA For. Serv. Gen. Tech. Rep. SE-84, Southeastern For. Expt. Sta., Asheville, NC, pp 156–171.

McWilliams, W.H., C.A. Alerich, D.A. Devlin, A.J. Lister, T.W. Lister, S.L. Sterner and J.A. Westfall. 2004. Annual inventory report for Pennsylvania's forests: results from the first three years. USDA Forest Service Resour. Bull. NE-159, Northeastern Res. Sta., Newtown Square, PA, 95 p.

Nowacki, G.J., M.D. Abrams and C.G. Lorimer. 1990. Composition, structure and historical development of northern red oak stands along an edaphic gradient in North-Central Wisconsin. For. Sci. 36: 276–292.

Oliver, C.D. and B.C. Larson. 1996. Forest stand dynamics. John Wiley and Sons, New York, 520 p.

Sander, I.L., P.S. Johnson and R. Rogers. 1984. Evaluating oak advance reproduction in the Missouri Ozarks. USDA Forest Service RP NC-251, North Central For. Expt. Sta., St. Paul, MN, 8 p.

Smith, L.L. and J.L. Vankat. 1991. Communities and tree seedling distribution in *Quercus rubra*- and *Prunus serotina*-dominated forest in southwestern Pennsylvania. Am. Midl. Nat. 126:294–307.

Ward, J.S. and G.R. Stephens. 1999. Influence of cutting method on 12-year-old hardwood regeneration in Connecticut. *In* Proc. Ninth Central Hardwood Forest Conference. Eds. W. Stringer and D.L. Loftis. USDA For. Serv. Gen. Tech. Rep. SRS-24, Southeastern For. Expt. Sta., Asheville, NC, pp 204–208.