

Reconstructing the competitive dynamics of mixed-oak neighborhoods

Eric K. Zenner, Daniel J. Heggenstaller, Patrick H. Brose, JeriLynn E. Peck, and Kim C. Steiner

Abstract: The disparity between the potential for latent oak dominance within a stand and their region-wide decline in importance value raises questions about the competitiveness of oaks in early stand dynamics. We reconstructed tree height growth dynamics in mixed-species neighborhoods to determine if currently dominant oaks were ever shorter than their competitors and at what age currently subordinate oaks fell behind. In 23–36 year old mixed-oak stands in two physiographic provinces of Pennsylvania, we identified dominant and subordinate northern red oaks (*Quercus rubra* L.) and chestnut oaks (*Quercus prinus* L.) competing with adjacent non-oaks (red maple (*Acer rubrum* L.), sweet birch (*Betula lenta* L.), and black cherry (*Prunus serotina* Ehrh.)) of equal crown class. In each stand, we randomly selected 20 tree neighborhoods and collected stem cross sections every metre from the base to the tip of each tree. In the Allegheny Plateau province, dominant northern red oaks never averaged more than 2 m shorter than their competitors, while by age 20, subordinate oaks were commonly more than 2 m behind. Dominant chestnut oaks in the Ridge and Valley province were never more than 1 m shorter than their competitors; subordinate oaks, however, were generally always at least a metre behind. In both regions, growth dynamics of currently subordinate trees were indistinguishable from those of currently dominant trees during their first decade. Because oaks that were considerably behind at age 15 were likely to be subordinate by age 30, the window of opportunity for release to prevent oaks from becoming permanently overtopped and unable to recover may thus be relatively early (age 10–20).

Résumé : L'écart entre le potentiel de dominance latente du chêne dans un peuplement et son déclin en importance à l'échelle régionale suscite des questions à propos de la compétitivité des chênes au début de la dynamique des peuplements. Nous avons reconstitué la dynamique de croissance en hauteur des arbres dans des milieux regroupant plusieurs espèces pour déterminer si les chênes présentement dominants ont déjà été plus petits que leurs compétiteurs et à quel âge les chênes présentement dominés ont perdu leur dominance. Dans des peuplements mélangés de chênes âgés de 23 à 36 ans et situés dans deux provinces physiographiques de la Pennsylvanie, nous avons identifié des chênes rouges (*Quercus rubra* L.) et des chênes châtaigniers (*Quercus prinus* L.) dominants et dominés en compétition avec des espèces adjacentes autres que des chênes (érable rouge (*Acer rubrum* L.), bouleau flexible (*Betula lenta* L.) et cerisier tardif (*Prunus serotina* Ehrh.)) dont la classe de cime était équivalente. Dans chaque peuplement, nous avons sélectionné aléatoirement 20 arbres voisins et récolté des disques de bois à chaque mètre le long du tronc à partir de la souche jusqu'au sommet de chaque arbre. Dans la province du plateau Allegheny, les chênes rouges dominants n'étaient jamais, en moyenne, plus de deux mètres plus courts que leurs compétiteurs alors qu'à l'âge de 20 ans les chênes dominés étaient généralement plus de deux mètres plus petits que leurs compétiteurs. Les chênes de montagne dominants de la province Ridge and Valley n'étaient jamais plus d'un mètre plus courts que leurs compétiteurs, mais les chênes dominés étaient généralement au moins un mètre plus petits que leurs compétiteurs. Dans les deux régions, on ne pouvait distinguer la dynamique de croissance des arbres présentement dominés de celle des arbres présentement dominants au cours des 10 premières années. Parce que les chênes qui étaient considérablement plus petits à 15 ans étaient généralement dominés à 30 ans, la fenêtre d'opportunité pour dégager les chênes avant qu'ils ne deviennent irrémédiablement dominés peut donc survenir assez tôt (à l'âge de 10 à 20 ans).

[Traduit par la Rédaction]

Introduction

The apparent oak (*Quercus* spp.) regeneration crisis, a “paradox of a species that is dominant on the landscape, yet

difficult to regenerate” at the stand level (Crow 1988), has frustrated foresters for decades. On the one hand, oaks were once widespread throughout eastern North America (Abrams

Received 27 April 2012. Accepted 20 July 2012. Published at www.nrcresearchpress.com/cjfr on 22 August 2012.

E.K. Zenner and D.J. Heggenstaller. Ecosystem Science and Management, The Pennsylvania State University, 305 Forest Resources Building, University Park, PA 16802, USA.

P.H. Brose. USDA Forest Service, Northern Research Station, Irvine, PA 16329, USA.

J.E. Peck. Ecosystem Science and Management, The Pennsylvania State University, 207 Forest Resources Building, University Park, PA 16802, USA.

K.C. Steiner. Ecosystem Science and Management, The Pennsylvania State University, 301 Forest Resources Building, University Park, PA 16802, USA.

Corresponding author: Eric K. Zenner (eric.zenner@psu.edu).

and Nowacki 1992) and have been able to successfully establish and compete in many contemporary mixed-species stands (Norland and Hix 1996). A number of studies have demonstrated that initially outgrown and overtopped northern red oaks (*Quercus rubra* L.) can eventually overtop their competitors and (or) ascend to dominant canopy positions (Oliver 1980; Hibbs 1983; Arthur et al. 1997), providing a sense of inevitability of northern red oak dominance despite decades of overtopping (Oliver 1978). This apparent capacity for “latent dominance” (sensu O’Hara 1986), in which oaks eventually emerge above their competitors to predominate in the canopy, has even permitted the use of initially faster-growing competitors as trainer trees whose narrow crowns are eventually overtopped by spreading oak crowns (e.g., Lockhart et al. 2006). Were this mechanism widespread, we would not be seeing a region-wide decline in the importance value of oaks (see Fei et al. 2011).

On the other hand, recent decades have seen a reduction in the predominance of oak throughout the eastern mixed-hardwood forests as the mature second-growth oak-dominated stands originating in the late 19th and early 20th centuries have been harvested and regenerated (Fei et al. 2011). The young regenerated stands have much lower abundances of oaks than their predecessor stands (Gould et al. 2005) such that the abundance of these commercially and ecologically important species is declining across the landscape. Young stands throughout the region have been repeatedly observed to have lower oak abundances or importance values, while these same metrics have risen for competitor species such as red maple (*Acer rubrum* L.) and sweet birch (*Betula lenta* L.) (Moser et al. 2006). Further, a number of studies of early mixed-species stratification have found that oak is often outcompeted by species such as yellow-poplar (*Liriodendron tulipifera* L.) and black cherry (*Prunus serotina* Ehrh.) (Lorimer 1983; Loftis 1992), particularly on moist, productive sites (Gould et al. 2005). Oak can even be outcompeted on dry, nutrient-poor sites by sweet birch and red maple (Della-Bianca 1983; Loftis 1990; Liptzin and Ashton 1999). Even when advance regeneration is ample, oaks can be simply outgrown by their competitors (Cook et al. 1998; Loftis 1992), becoming permanently overtopped (Della-Bianca 1983; Palik and Pregitzer 1993).

The disparity between the potential for latent dominance within a stand and the actual abundance of oak on the landscape would seem to indicate that the ability of oak to attain a dominant canopy position is tenuous, which is supported by silvicultural studies indicating that oak regeneration depends heavily on site, initial species composition, and the availability of advance regeneration and seed (Crow 1988; Larsen and Johnson 1998; Liptzin and Ashton 1999). Nonetheless, these studies have also demonstrated that the probability of oak dominance can be successfully increased through careful management, such as application of the shelterwood system (Loftis 1990; Brose 2011) and crop tree management (Ward 2009). Because of the expense of the intensive management that may be necessary to ensure oak dominance on many sites, it is critical that any treatments be applied at an optimal level of intensity and timed for maximum effect (Larsen and Johnson 1998). Two issues are critical to optimizing management: determining whether or not release is necessary and identifying the optimal temporal

window for assessing the need for release (Trimble 1974; Miller 2000; Ward 2009).

These issues can be evaluated in several ways. One is to watch the development of stands over time and directly observe which trees ascend into the upper canopy using continuous plot monitoring (Bakker et al. 1996), which is costly and time consuming given the approximately 50 year time period that may be required to evaluate early stand dynamics in oak. Another is to characterize the species composition of trees in different canopy layers of stands at different points in time (e.g., Hibbs 1983) or along chronosequences of stands that capture different stages of stand development (e.g., Oliver 1978, 1981), which tracks succession and stand dynamics but not intertree competitive dynamics. A third option is to retrospectively reconstruct individual tree growth dynamics (e.g., Oliver 1978; Tift and Fajvan 1999). We chose to reconstruct growth dynamics in mixed-species neighborhoods in stands that are stratified by site, subject to similar stand-initiating disturbance, and composed of overlapping species of primary competitors. Although reconstruction limits the conclusions that can be drawn from this study to the competitiveness of extant oak in mixed-species neighborhoods, this approach has the advantage of directly indicating if and when a given tree became irreversibly suppressed, from which we can infer opportunities for release. Our specific objectives were to (1) ascertain if currently dominant focal oaks were ever shorter than their neighbors, and if so, at which age they equaled or surpassed them and (2) determine at what age currently subordinate oaks began to fall behind their competitors.

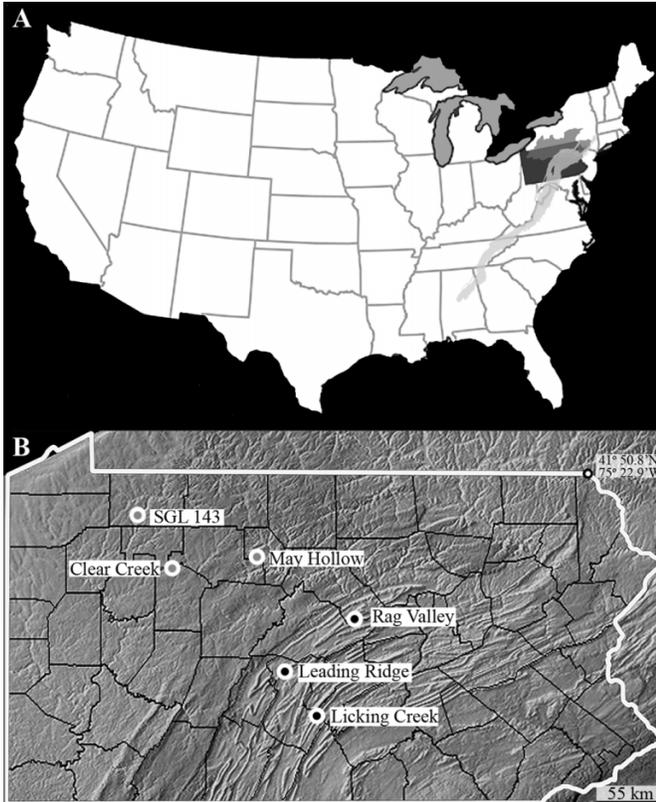
Methods

Study areas

Because management guidelines often evaluate regeneration success at canopy closure or in the third decade (Brose et al. 2008; Steiner et al. 2008), we sought unmanaged even-aged mixed-oak forest stands on adequately comparable sites that were less than 40 years of age. Three 23–36 year old sites each were identified within the two primary provinces of the Appalachian Mountains of Pennsylvania (Fig. 1; Table 1). The Allegheny Plateau (AP) stands in northern Pennsylvania were located on soils formed in sandstone, siltstone, and shale residuum or colluvium (Kopas 1993); site indices ranged from 23 to 25 m. Nearby mean annual temperature was 6.2 °C with a mean annual precipitation of 108 cm (Kopas 1993). The Ridge and Valley (RV) stands in central Pennsylvania were located on stony ridges underlain by sandstone and shale (Merkel 1978); site indices ranged from 21 to 23 m. Nearby mean annual temperature was 10.3 °C with a mean annual precipitation of 96.5 cm (Merkel 1978).

On the cooler, moister sites of the AP stands, the predominant oak (and our focal species) was northern red oak, which competed most directly with red maple, sweet birch, and black cherry; additional species in these stands included yellow-poplar, white ash (*Fraxinus americana* L.), and American beech (*Fagus grandifolia* Ehrh.). On the warmer, drier sites of the RV stands, the predominant and focal species of chestnut oak (*Quercus prinus* L.) competed primarily with red maple and sweet birch; other species present included black oak (*Quercus velutina* Lam.), white oak (*Quercus alba*

Fig. 1. (A) Sites were located in the two primary physiological provinces of the Appalachian Mountains in Pennsylvania (filled state), the Allegheny Plateau (AP) (dark grey overlay), and the Ridge and Valley (RV) (light grey overlay). (B) The focal oak species of the three stands in the AP (grey dots) was northern red oak (*Quercus rubra*), while the focal oak species in the three stands in the RV (black dots) was chestnut oak (*Quercus prinus*).



L.), and scarlet oak (*Quercus coccinea* Münchh.), black gum (*Nyssa sylvatica* Marsh.), and white pine (*Pinus strobus* L.). All stands were clearcut between 1970 and 1984 and had received no silvicultural treatments since the overstory removal and were dominated by non-oak species. Nomenclature follows the USDA Plants Database (www.plants.usda.gov/java/).

Neighborhood selection

Each stand was systematically surveyed to locate all potential focal oaks, defined as those judged to not be obviously of sprout origin (i.e., straight, single stemmed, no scars or knots near the base), surrounded by non-oak competitors, and directly competing (crown touching) with at least two non-oak competitors (combinations of sweet birch, red maple, and black cherry). From this list, a stratified random sample of 20 neighborhoods per stand was taken: 10 neighborhoods each were centered on focal oaks that were either (1) “dominant,” with formidable competitors (a dominant or codominant oak with any combination of two dominant and (or) codominant competitors), or (2) “subordinate,” with at least one less formidable competitor (an intermediate or suppressed oak with two non-oak competitors, at least one of which was also subordinate). Dominant trees had the largest

crowns in a neighborhood, while subordinate trees had narrower crowns receiving little or no direct sunlight from the sides. Because the assignment of crown class was based on crown size and not height, some subordinate trees had heights comparable with those of dominant trees; most, however, had notably smaller diameters. Supplementary material Table S1 demonstrates size disparities between dominant and subordinate trees.¹ Due to logistical difficulties, the actual number of neighborhoods per stand available for the analyses ranged from 16 to 20, totaling 283 trees (Table 2).

Sampling

Within each tree neighborhood, the focal oak and its two most direct non-oak competitors were chosen for sampling. The boles of each tree were marked at 0 cm (as close to the soil surface as possible), 30 cm, 60 cm, 1.4 m (breast height), and 2 m. The three trees were then felled and marks were made at every metre thereafter along the primary stem. Cross sections (~2–4 cm thick) were cut at each of the marked points, which were air dried for several months and then sanded using a belt sander with progressively finer sandpaper to facilitate ring detection; some samples had to be sanded by hand with finishing film down to 9 µm before they could be read. True rings were then counted under a stereo dissecting microscope, tallying rings from the bark inward on two transects at 90° offsets. Additional transects were counted and averaged (Stokes and Smiley 1968) if irregularities were observed.

Calculations

Initial tree height and subsequent increment was referenced to the year of the clearcut (“age 0”) to permit comparison of data across stands cut in different years. Trees originating before the year of the clearcut thus have a positive height at age 0. To determine the height of each tree at intermediate ages, we used the cross sections to estimate successive age differences and divided the change in height between these ages by the number of years passed and added this average height increment to the recorded heights as needed. Height disparities between focal oaks and their direct competitors were calculated at the neighborhood level at 5 year age intervals (0, 5, 10, 15, 20, 25, and 30 years). These values were then averaged across neighborhoods to the stand level for analysis.

Analyses

Height trajectories were visually compared among species using plots of tree height against age, by oak crown class, at the stand level. The statistical significance of height disparities among species and between crown classes was determined using mixed model repeated measures analysis (Littell et al. 2006) in SAS version 9.1 to account for the random effect of stand and the autocorrelation of time. Separate best (sensu Burnham and Anderson 2002, based on the Akaike information criterion) multiple linear mixed regression models were developed for each province (because province was confounded with oak and competitor species), testing height disparities between focal oaks and their neighbors at 5 year age intervals (from 5 to 30 years) among crown classes and species combinations. In both cases, best models included

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/x2012-119>.

Table 1. Site information for the three sites in each of the provinces of the Allegheny Plateau (AP) and the Ridge and Valley (RV).

Province	Site	Elevation (m)	Location	Soil series	Aspect	Year harvested
AP	Clear Creek	550	41°20'43"N, 79°01'57"W	Cookport very stony loam	Level	1972
AP	May Hollow	490	41°26'37"N, 78°11'55"W	Harleton channery silt loam	Level-S	1974
AP	State Gamelands (SGL) 143	550	41°50'13"N, 79°24'27"W	Hanover silt loam	Level	1984
RV	Licking Creek	410	40°24'14"N, 77°44'17"W	Laidig extremely stony loam	Level-NW	1969
RV	Leading Ridge	350	40°38'36"N, 78°00'20"W	Hazleton-Dekalb channery sandy loam	Level-SE	1976
RV	Rag Valley	470	41°02'24"N, 77°26'13"W	Hazleton channery sandy loam	SE	1972

Table 2. Mean (\pm standard error) height (m) of dominant (D) and subordinate (S) trees at the time of sampling by province, focal oak crown class (CC), and site (total number of trees of each species and crown class indicated).

Province	CC	Site	D-oak ($n = 55$)	S-oak ($n = 50$)	D-RM ($n = 56$)	D-SB ($n = 56$)	D-BC ($n = 24$)	S-RM ($n = 20$)	S-SB ($n = 19$)	S-BC ($n = 3$)
AP	D	Clear Creek	20.1 (0.6)		18.5 (0.6)	19.2 (1.1)	22.5 (0.5)			
AP	D	May Hollow	17.4 (0.3)		17.0 (0.0)	17.2 (0.4)	17.5 (1.0)			
AP	D	SGL 143	15.3 (0.6)		15.3 (0.5)	15.4 (0.6)	17.0 (0.6)			
AP	S	Clear Creek		17.1 (1.2)	16.0 (2.1)	17.0 (na)	22.7 (1.2)	18.7 (1.5)	19.3 (0.9)	17.0 (1.0)
AP	S	May Hollow		14.8 (0.9)	15.0 (na)	16.7 (0.2)	19.1 (0.3)	15.2 (0.4)	17.4 (0.3)	
AP	S	SGL 143		15.3 (0.8)	16.3 (0.5)	16.0 (na)	15.0 (2.0)	13.5 (0.5)	13.8 (0.9)	18.0 (na)
RV	D	Licking Creek	20.4 (0.4)		19.0 (0.6)	19.1 (0.6)				
RV	D	Leading Ridge	17.9 (0.7)		17.5 (0.4)	16.6 (0.3)				
RV	D	Rag Valley	18.6 (0.4)		18.8 (0.8)	18.8 (0.4)				
RV	S	Licking Creek		16.6 (1.0)	18.9 (0.6)	16.3 (0.7)		18.4 (1.5)	16.4 (1.4)	
RV	S	Leading Ridge		16.2 (0.5)	16.2 (0.3)	16.3 (0.8)		17.3 (0.5)	15.0 (0.6)	
RV	S	Rag Valley		17.9 (0.9)	18.3 (0.6)	20.0 (0.3)		17.8 (1.9)		

Note: RM, red maple (*Acer rubrum*); SB, sweet birch (*Betula lenta*); BC, black cherry (*Prunus serotina*). AP, Allegheny Plateau; RV, Ridge and Valley. na indicates too few replicates to calculate a standard error.

age ($P < 0.02$) and the three-way interaction among crown class, age, and species of neighbor ($P < 0.04$); in the RV, the crown class of the focal oak was also retained in the model ($P < 0.001$).

Results

Allegheny Plateau

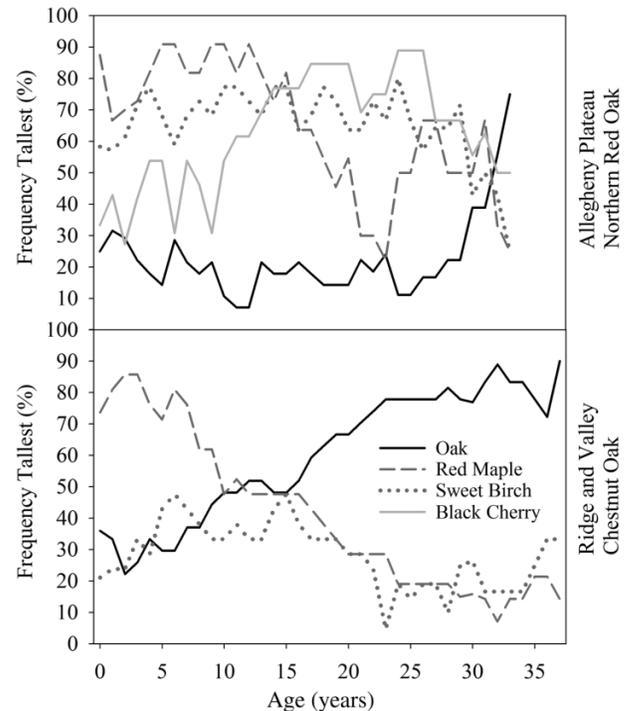
In neighborhoods around currently dominant northern red oaks in the AP stands, red maple and sweet birch (when present) were initially taller than the focal oak 60%–90% of the time (Fig. 2). After age 15, increasingly fewer red maples remained taller than northern red oaks, while sweet birch remained taller than northern red oak in the majority of neighborhoods in which it occurred until age 32. By age 15, black cherry was typically taller than its dominant northern red oak neighbors and remained so until age 32. Only after age 30 did the dominant northern red oaks start to commonly become the tallest trees in their neighborhoods.

This pattern can also be seen in the height trajectories, which show that in all but one stand, the average height of dominant black cherry was greater than that of all other species by age 15 and remained so throughout the monitoring period (Fig. 3). In contrast, the average height of dominant red maple often began greater than that of its dominant competitors, but was no longer so by age 15. By the end of the monitoring period, only black cherry appeared to remain taller than dominant northern red oaks. Subordinate northern red oaks followed a similar developmental pattern to their dominant counterparts for roughly the first decade of stand development, but by age 10, the height disparity with dominant neighbors was much greater in two of the three stands.

On average, both dominant and suppressed northern red oaks were statistically significantly shorter than their direct competitors throughout much of the monitoring period, particularly before age 25–30 for dominant oaks (Fig. 4). On average, dominant northern red oaks were never significantly taller than their neighbors, but rather significantly shorter than their dominant red maple competitors at ages 5 and 10 (by 1.2 and 1.9 m, respectively, SE 0.6, $P < 0.05$) and marginally significantly shorter at age 15 ($P = 0.06$). They were also marginally significantly shorter than dominant sweet birch at ages 10 and 15 ($P < 0.09$) and significantly shorter than dominant black cherry at age 20 (by 1.7 m, SE 0.6, $P = 0.006$). However, dominant northern red oaks were never more than 2 m shorter than their direct competitors.

On average, subordinate northern red oaks were marginally significantly shorter than their subordinate red maple neighbors by age 15 ($P = 0.08$) and significantly shorter at ages 20–30 (by 1.5–1.9 m, SE 0.6–0.7, $P < 0.05$). Subordinate northern red oaks were significantly shorter than dominant sweet birch from ages 10 to 30 (increasing over time from 1.3 to 5 m, SE 0.6–0.7, $P < 0.05$), dominant black cherry from ages 15 to 30 (by 2.2–3.0 m, SE 0.6–0.7, $P < 0.01$), and subordinate black cherry at ages 25 and 30 (by 2.7–2.9 m, SE 0.9–1.0, $P < 0.01$). By age 20, subordinate oaks were commonly more than 2 m shorter than neighboring dominant sweet birch and black cherry. After about age 25, dominant northern red oaks tended to decrease their height deficiency over time, while the deficiency continued to grow for subordinate oaks (Fig. 5).

Fig. 2. Proportion of the time that currently dominant oaks (black solid line) were the tallest trees in a neighborhood and the proportion of time that each competitor species was taller than its focal oak (when that species was present in the neighborhood) by years since the clearcut (age) for the Allegheny Plateau and Ridge and Valley provinces.



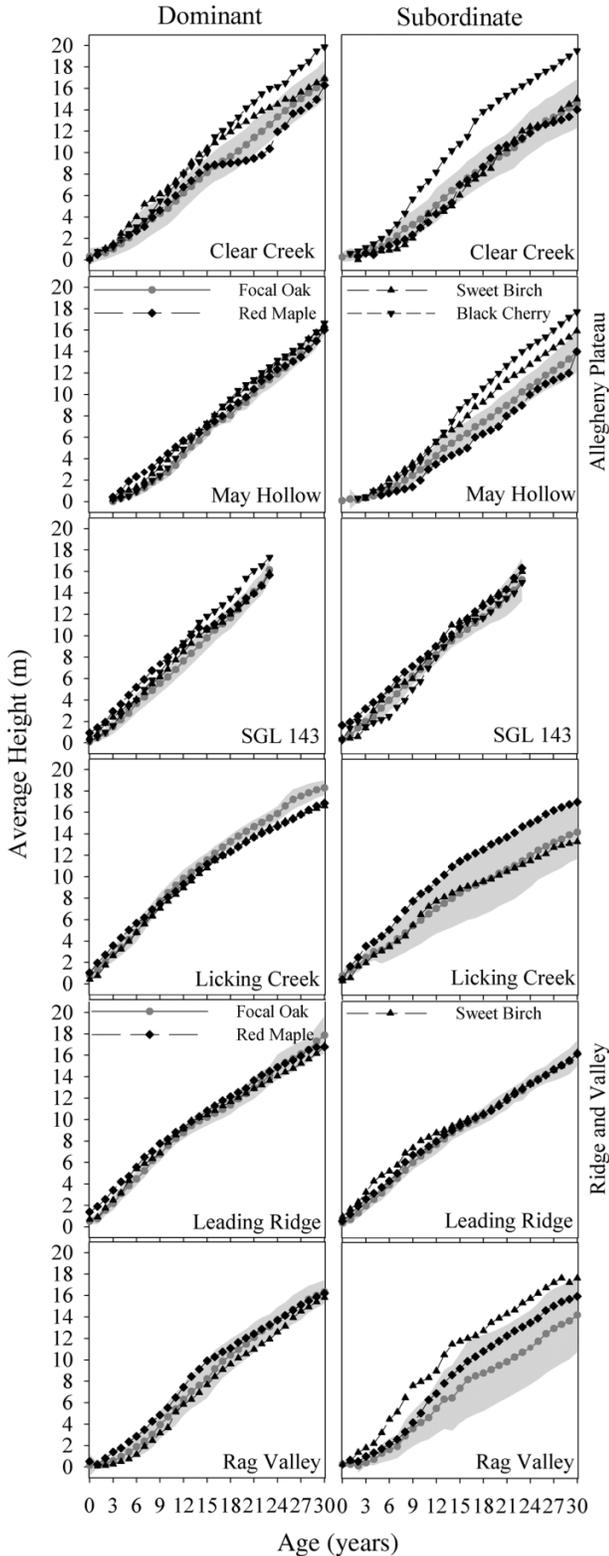
At age 10, dominant red maples had a 1.8 m (SE 0.9) greater height advantage over subordinate focal oaks than over dominant focal oaks ($P = 0.04$). At age 20, dominant sweet birch had a 1.7 m (SE 0.9) greater height advantage over subordinate focal oaks than over dominant focal oaks ($P = 0.04$), which had increased to 3.2 m (SE 0.9) by age 25 and 5.1 m (SE 1.0) by age 30 ($P < 0.001$). At age 25, dominant black cherry had a 2.1 m (SE 0.9) greater height advantage over subordinate focal oaks than over dominant focal oaks ($P = 0.03$); this advantage remained marginally significant at age 30.

Ridge and Valley

In neighborhoods around currently dominant chestnut oaks in the RV stands, red maples were initially taller than their chestnut oak neighbors in the majority of neighborhoods in which they were present until about age 10, but notably less so thereafter (Fig. 2). Sweet birch was never taller than chestnut oak in more than half of the neighborhoods in which it occurred. By age 20, chestnut oak was usually the tallest tree in its neighborhood. The early height advantage of red maple in the dominant neighborhoods had subsided by age 10, and chestnut oak gradually gained in relative height over time — even surpassing its competitors in height by age 20 in one stand (Fig. 3). In contrast, subordinate chestnut oaks tended to remain notably shorter than their dominant red maple or sweet birch competitors throughout the 30 year monitoring period in two of the three stands.

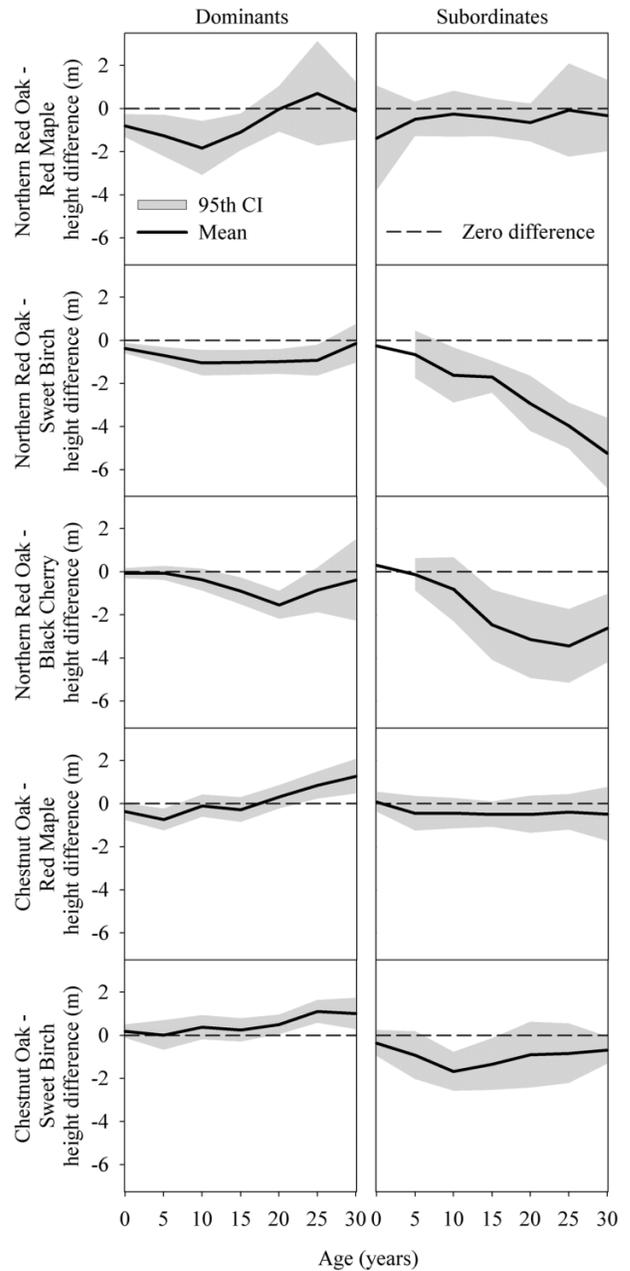
On average, dominant chestnut oaks were always taller

Fig. 3. Mean heights of focal oaks (95th CI, shaded grey) and dominant competing species by crown class and stand in the Allegheny Plateau (northern red oak (*Quercus rubra*)) and Ridge and Valley (chestnut oak (*Quercus prinus*)) provinces.



than their dominant sweet birch neighbors and surpassed their dominant red maple neighbors in height by age 20 (Fig. 4). Dominant chestnut oaks were never significantly

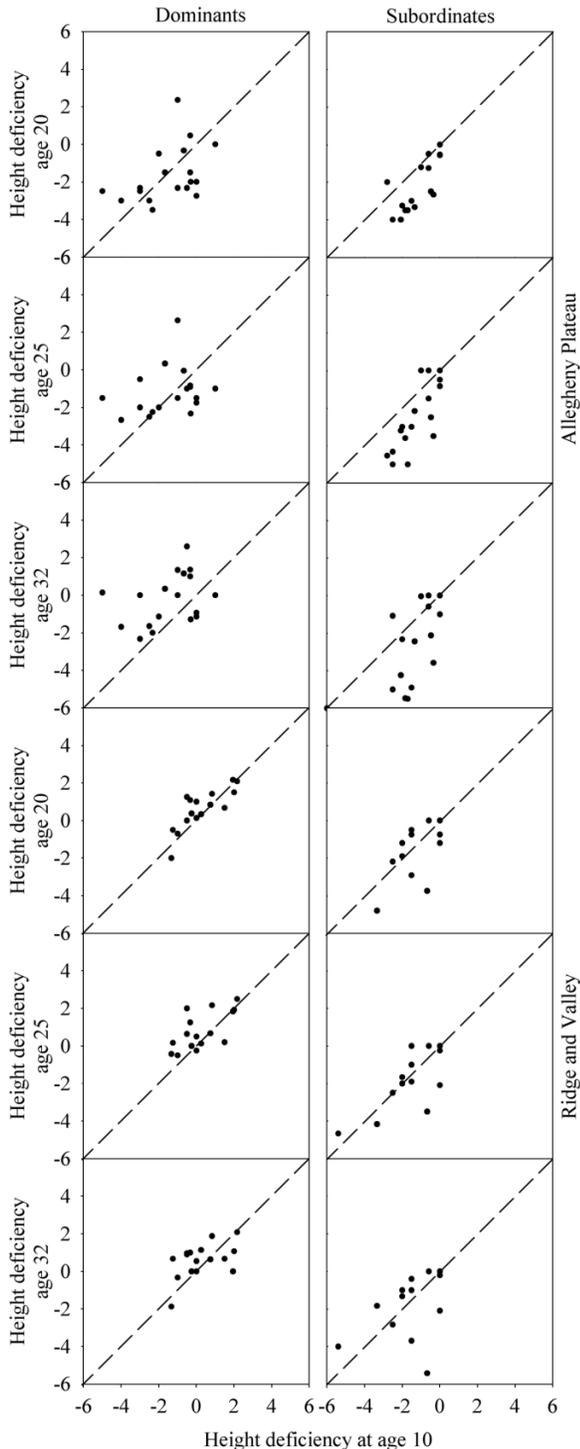
Fig. 4. Mean height difference (black line, 95th CI in grey) between dominant and subordinate focal oaks and each species of directly competing dominant neighbor in the Allegheny Plateau (northern red oak (*Quercus rubra*)) and the Ridge and Valley (chestnut oak (*Quercus prinus*)) provinces.



shorter than their most direct competitors but were taller than neighboring dominant red maple by age 25 (by 1.1 m, SE 0.5, $P = 0.02$) and both red maple and sweet birch by age 30 (by 1.3 and 1.0 m, respectively, SE 0.5, $P < 0.04$). Dominant chestnut oaks were never more than 0.75 m shorter than their direct competitors.

In contrast, the average height of subordinate chestnut oaks was nearly always less than that of their most directly competing dominant or subordinate neighbors (Fig. 5). Throughout the monitoring period, subordinate chestnut oaks were shorter than their dominant red maple neighbors (but non-

Fig. 5. Relationship between the height differences between dominant focal oaks and their tallest competing neighbor at different ages. Points at the [0,0] intersection would indicate oak trees that were the same height as their tallest competitor. The diagonal line represents the 1:1 relationship between height differences at different ages: more points above the line as you move down (with time) would indicate that some oaks improved their relative height position over time. Data are shown for trees in the two stands in each province for which all three time periods were available.



significantly, $P > 0.1$) and significantly shorter than their subordinate red maple neighbors (by 1.2–1.8 m, SE 0.5, $P < 0.02$). Subordinate chestnut oaks were also significantly shorter than their dominant sweet birch neighbors from ages 10 to 25 (by 1.2–1.7 m, SE 0.5, $P < 0.02$) and still marginally significantly shorter at age 30 ($P = 0.08$). By age 10, subordinate oaks were commonly more than 1.25 m shorter than both red maple and sweet birch neighbors. By age 25, the height deficiencies of dominant and subordinate chestnut oaks had stabilized (Fig. 5).

At age 25, dominant red maples had a 1.3 m (SE 0.7) greater height advantage over subordinate focal oaks than over dominant focal oaks ($P = 0.05$); this advantage had grown to 1.9 m (SE 0.7) by age 30 ($P = 0.007$). The height advantage of dominant sweet birch over subordinate focal oaks varied between 1.8 and 2.1 m greater than that over dominant focal oaks between ages 10 and 30 (SE 0.7, $P < 0.01$).

Discussion

The results of this study confirm that latent dominance is not an uncommon growth strategy for oaks that attain dominant canopy status by their third decade. Most of the currently dominant oaks in this study were shorter than their neighboring competitors throughout at least their first decade. These findings corroborate previous observations that oak is able to persist through early periods of slower relative height growth, enduring 1–1.5 m height deficits compared with neighboring competitors, and still achieve a dominant crown position (Oliver and Stephens 1977; Oliver 1980). In post-disturbance stands from New England to Kentucky, after 10–40 years, oaks have been found to approach or exceed the height or dominance class of fast-growing neighboring species that had initially overtopped them (Hibbs 1983; Arthur et al. 1997; Ward and Stephens 1999). Early absolute height dominance is therefore not required for successful ascension of oak into the canopy, which is consistent with the strategy of subsuming early height growth to root growth (Loftis 1990; Brose 2008).

The pattern and speed of latent dominance, however, varied by species and thus physiographic province, reinforcing the important constraints imposed by both site and species composition. This is perhaps best seen in the contrast between the AP and the RV sites with respect to the primary species of oak competitor: dominant chestnut oaks became the tallest members of their maple–birch neighborhoods earlier and more often in the RV than northern red oaks did in the AP in their maple–birch–cherry neighborhoods. Although the confounding of species and region precludes comparisons, these trends may nonetheless be useful for developing silvicultural prescriptions within each region. Regional and site differences affecting relative competitive dynamics in mixed stands may also explain the difference between the slow (and by no means inevitable) latent dominance of oak in the current study and the clear height dominance of northern red oak by age 10 years observed in Massachusetts (Oliver 1978). It is possible, for instance, that the greater relative tolerance of oaks for poorer sites (such as our RV sites) permits them to emerge as dominants sooner despite shading from competitors (C. Oliver, personal communication (2012)).

It is also possible that oaks destined to ascend into the canopy begin with the advantage of advanced root development (Loftis 1990; cf. Brose 2011). In an examination of root collar height among a subsample of our oaks, 88% had root systems that were on average 2–3 years older than the aboveground stems (Heggenstaller et al. 2012), indicating that most of our dominant and subordinate oaks were probably of seedling- or stump-sprout origin. The effect of this apparent advantage on competitive dynamics, however, is unclear, as fully half of the non-oaks in this study also had a measurable height at the time of the clearcut (i.e., were older than the clearcut) and were thus either surviving advance regeneration or post-clearcut sprouts. In this region, both oaks and their primary competitors of maple and black cherry are commonly older just below the root collar than just above it (Ward 1966). The tree neighborhoods explored in this study, therefore, were likely composed of typical mixtures of species of various origin and age.

Although our reconstructive approach limits our inferences to the competitiveness of oak in mixed-species neighborhoods and not to the success of oaks in general in stands or on the landscape, our findings are consistent with the first two stages of a three-stage successional model in which the first stage (<~15 years) is characterized by a dominance of pioneer species (here black cherry and sweet birch), the second stage (15–40 years) maintains partial dominance by red maple, birch, and cherry over oak, and the third stage (~40+ years and beyond the scope of the current study) is marked by the emergence into the dominant canopy layer of oak with continued codominance by the primary competitors (Hibbs 1983). This may be facilitated by the more spreading growth form of the oak crown compared with the narrower crowns of black cherry, red maple, and sweet birch (Lamson 1987) or through crown abrasion on tougher twigs of neighboring oak trees (Oliver 1978; Lockhart et al. 2006).

Equally important to the growth dynamics of current dominant oaks, our findings indicate that the growth dynamics of currently subordinate trees were indistinguishable from those of currently dominant trees during their first decade or more. However, although trees destined to become dominants were not clearly on that path until 20 years of age or more, our sampled currently subordinate trees had already fallen well behind their competitors by age 15 years in the AP and age 10 years in the RV. Once oaks fall behind into lower strata, they are less likely to ever advance into a higher crown class (Tift and Fajvan 1999; Dey et al. 2007; Drobyshev et al. 2007). In stands in which management objectives require oaks to reach a dominant canopy position, management interventions may thus be called for to increase the odds of success for individual oaks at risk of being permanently overtopped (Ward 2009).

Such interventions, however, are costly and not always effective. If the release comes too late, the suppressed oaks may be less likely to respond to release than their suppressed red maple or birch neighbors (Kobe et al. 1995; Caspersen and Kobe 2001). Although some oaks that have already fallen into an intermediate crown class by age 10–15 can display very high 10 year survival rates, with some individuals even upgrading dominance class (Miller 2000), nearly half of intermediates may die or regress to the suppressed crown class even following a full release (Ward 2009). If the release

comes too early (<10 years of age) or is too light, it may only be marginally effective as rapidly growing sprout clusters quickly fill in the openings created by release (Trimble 1974). However, if the release is too heavy, it could trigger increased branching and reduced clear stem length (Miller 2000).

Although our results indicate that it may not be possible to definitively identify a future dominant oak (based on height alone) until about age 20 years, it should be evident if an oak is at risk of a subordinate path as early as age 10, and by age 20 years, it will be too late for most subordinate oaks. In this study, many of these oaks were still in a competitive position at age 10 years. Across all stands, 38% of oaks that became subordinate by age 30 years showed no greater height discrepancy to their red maple neighbors at age 10 years than did currently dominant oaks, and 20% of currently subordinate oaks were no shorter than their sweet birch neighbors than were currently dominant oaks. Based on height alone, then, at least one in five currently subordinate oaks were just as competitive as currently dominant oaks at age 10 years.

These results indicate a roughly 10 year window of opportunity for oak release starting at approximately age 10 years. This corresponds well to work from Maryland and West Virginia that indicates that releases at ages in the 12 to 16 year range are more effective than earlier releases (Miller 2000). In that study, nearly all codominant trees that received full releases survived and maintained codominant canopy positions. Many oaks in our study that had regressed to a subordinate crown class by age 30 years were likely to be codominant between age 12 and 15 years, suggesting that a full release might have prevented their regression. Competition from sweet birch and red maple may also decline at around this time. In many stands, particularly in the RV province where sweet birch mortality was high (D.H., personal observation of birch snags (2007)), sweet birch also declined in relative height by around age 15 years. This is in keeping with observations that sweet birch may be able to colonize sites on which it will not be able to ultimately compete and thus sustain dominance (Leupold and Parker 1985) and with the tendency for the importance or density of sweet birch to rapidly decline with crown closure (Beck and Hooper 1986; Brashears et al. 2004). Red maple also lost its early height advantage over dominant oaks by age 15, perhaps as stump sprouts failed to develop new root systems (Wilson 1968; Del Tredici 2001).

Conclusions

Although the results of this study demonstrate the verity of latent dominance in oak, they also show that trees destined to become canopy dominants were never more than 1–2 m shorter than their direct competitors, while currently subordinate oaks were commonly more than 1–2 m behind their sweet birch and black cherry neighbors during development. The growth dynamics of currently subordinate trees were indistinguishable from those of currently dominant trees during their first decade, but currently subordinate trees had already fallen well behind their competitors by age 15 years in the AP province and age 10 years in the RV province of the Northern Appalachians. These results suggest that although oaks are able to compete effectively against sweet birch, red

maple, and black cherry, there is a point of height deficiency from which they are not able to recover. Although interspecific competition during early stand development varies by site and region, it should be possible in many areas to identify oaks at risk of becoming perpetually overtopped during the narrow window of opportunity for evaluation of 10–15 years of age.

Acknowledgements

Special thanks to Greg Sanford, Eric Baxter, Bob Brown, Dave Cole, Josh Hanson, Lance Meyer, John Schwartz, Kevin Cook, and Derek Larson for their dedicated field and laboratory work. The manuscript was improved by the insights of Chad Oliver and an anonymous reviewer. We also thank the Pennsylvania Department of Conservation and Natural Resources, Bureau of Forestry, and Pennsylvania Agricultural Experiment Station Project PEN-4225 for financial support.

References

- Abrams, M.D., and Nowacki, G.J. 1992. Historical variation in fire, oak recruitment, and post-logging accelerated succession in central Pennsylvania. *Bull. Torrey Bot. Club*, **119**(1): 19–28.
- Arthur, M.A., Muller, R.N., and Costello, S. 1997. Composition in a central hardwood forest in Kentucky 11 years after clear-cutting. *Am. Midl. Nat.* **137**(2): 274–281. doi:10.2307/2426846.
- Bakker, J.P., Olf, H., Willems, J.H., and Zobel, M. 1996. Why do we need permanent plots in the study of long-term vegetation dynamics? *J. Veg. Sci.* **7**(2): 147–156. doi:10.2307/3236314.
- Beck, D.E., and Hooper, R.H. 1986. Development of a southern Appalachian hardwood stand after clearcutting. *South. J. Appl. For.* **10**: 168–172.
- Brashears, M.B., Fajvan, M.A., and Shuler, T.M. 2004. An assessment of canopy stratification and tree species diversity following clearcutting in central Appalachian hardwoods. *For. Sci.* **50**: 54–64.
- Brose, P. 2008. Root development of acorn-origin oak seedlings in shelterwood stands on the Appalachian Plateau of northern Pennsylvania: 4-year results. *For. Ecol. Manage.* **255**(8–9): 3374–3381. doi:10.1016/j.foreco.2008.02.021.
- Brose, P. 2011. A comparison of the effects of different shelterwood harvest methods on the survival and growth of acorn-origin oak seedlings. *Can. J. For. Res.* **41**(12): 2359–2374. doi:10.1139/x11-143.
- Brose, P., Gottschalk, K., Horsley, S., Knopp, P., Kochenderfer, J., McGuinness, B., Miller, G., Ristau, T., Stoleson, S., and Stout, S. 2008. Prescribing regeneration treatments for mixed-oak forests in the Mid-Atlantic region. U.S. For. Serv. Gen. Tech. Rep. NRS-33.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodal inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.
- Caspersen, J.P., and Kobe, R.K. 2001. Interspecific variation in sapling mortality in relation to growth and soil moisture. *Oikos*, **92**(1): 160–168. doi:10.1034/j.1600-0706.2001.920119.x.
- Cook, J.E., Sharik, T.L., and Smith, D.W. 1998. Oak regeneration in the Southern Appalachians: potential, problems, and possible solutions. *South. J. Appl. For.* **22**: 11–18.
- Crow, T.R. 1988. Reproduction mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*) — a review. *For. Sci.* **34**: 19–40.
- Del Tredici, P. 2001. Sprouting in temperate trees: a morphological and ecological review. *Bot. Rev.* **67**(2): 121–140. doi:10.1007/BF02858075.
- Della-Bianca, L. 1983. Sixty years of stand development in a southern Appalachian cove-hardwood stand. *For. Ecol. Manage.* **5**(3): 229–241. doi:10.1016/0378-1127(83)90074-9.
- Dey, D.C., Miller, G.W., and Kabrick, J.M. 2007. Sustaining northern red oak forests: managing oak from regeneration to canopy dominance in mature stands. In *Integrated Restoration of Forested Ecosystems to Achieve Multi-Resource Benefits: Proceedings of the 2007 National Silviculture Workshop*. Edited by R.L. Deal. U. S. For. Serv. Gen. Tech. Rep. PNW-733. pp. 91–105.
- Drobyshev, I., Linderson, H., and Sonesson, K. 2007. Relationship between crown condition and tree diameter growth in southern Swedish oaks. *Environ. Monit. Assess.* **127**(1–3): 61–73. doi:10.1007/s10661-006-9415-2. PMID:17171283.
- Fei, S., Kong, N., Steiner, K.C., Moser, W.K., and Steiner, E.B. 2011. Change in oak abundance in the eastern United States from 1980 to 2008. *For. Ecol. Manage.* **262**(8): 1370–1377. doi:10.1016/j.foreco.2011.06.030.
- Gould, P.J., Steiner, K.C., Finley, J.C., and McDill, M.E. 2005. Developmental pathways following the harvest of oak dominated stands. *For. Sci.* **51**: 76–90.
- Heggenstaller, D.J., Zenner, E.K., Brose, P.H., and Peck, J.E. 2012. How much older are Appalachian oaks below-ground than above-ground? *North. J. Appl. For.* In press.
- Hibbs, D.E. 1983. Forty years of forest succession in central New England. *Ecology*, **64**(6): 1394–1401. doi:10.2307/1937493.
- Kobe, R.K., Pacala, S.W., Silander, J.A., Jr, and Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* **5**(2): 517–532. doi:10.2307/1942040.
- Kopas, F.A. 1993. Soil survey of Cameron and Elk counties, Pennsylvania. U.S. Soil Conservation Service, Washington, D.C.
- Lamson, N.I. 1987. D.B.H./crown diameter relationships in mixed Appalachian hardwood stands. U.S. For. Serv. Res. Pap. NE-610.
- Larsen, D.R., and Johnson, P.S. 1998. Linking the ecology of natural oak regeneration to silviculture. *For. Ecol. Manage.* **106**(1): 1–7. doi:10.1016/S0378-1127(97)00233-8.
- Leupold, D.J., and Parker, G.P. 1985. Vegetation patterns on a southern Appalachian watershed after successive clearcuts. *Castanea*, **50**: 164–186.
- Liptzin, D., and Ashton, P.M.S. 1999. Early-successional dynamics of single-aged mixed hardwood stands in a southern New England forest, USA. *For. Ecol. Manage.* **116**(1–3): 141–150. doi:10.1016/S0378-1127(98)00448-4.
- Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., and Schabenberger, O. 2006. SAS for mixed models. 2nd ed. SAS Institute Inc., Cary, N.C.
- Lockhart, B.R., Ezell, A.W., Hodges, J.D., and Clatterbuck, W.K. 2006. Using natural stand development patterns in artificial mixtures: a case study with cherrybark oak and sweetgum in east-central Mississippi, USA. *For. Ecol. Manage.* **222**(1–3): 202–210. doi:10.1016/j.foreco.2005.09.029.
- Loftis, D.L. 1990. Predicting post-harvest performance of advance northern red oak reproduction in the southern Appalachians. *For. Sci.* **36**: 908–916.
- Loftis, D.L. 1992. Regenerating northern red oak on high-quality sites in the southern Appalachians. In *Oak regeneration: serious problems, practical recommendations*. Edited by D.L. Loftis and C.E. McGee. U.S. For. Serv. Gen. Tech. Rep. SE-84. pp. 202–210.
- Lorimer, C.G. 1983. Eighty-year development of northern red oak after partial cutting in a mixed species Wisconsin forest. *For. Sci.* **29**: 371–383.
- Merkel, E.J. 1978. Soil survey of Huntingdon County, Pennsylvania. U.S. Soil Conservation Service, Washington, D.C.
- Miller, G.W. 2000. Effect of crown growing space on the development of young hardwood crop trees. *North. J. Appl. For.* **17**: 25–35.

- Moser, W.K., Hansen, M., McWilliams, W., and Sheffield, R. 2006. Oak composition and structure in the eastern United States. *In* Fire in Eastern Oak Forests: Delivering Science to Land Managers, Proceedings of a Conference, 15–17 November 2005, Columbus, Ohio. *Edited by* M.B. Dickinson. U.S. For. Serv. Gen. Tech. Rep. NRS-P-1. pp. 49–61.
- Norland, E.R., and Hix, D.M. 1996. Composition and structure of a chronosequence of young, mixed-species forests in southeastern Ohio, USA. *Vegetatio*, **125**(1): 11–30. doi:10.1007/BF00045201.
- O'Hara, K. 1986. Developmental patterns of residual oaks and oak yellow-poplar regeneration after release in upland hardwood stands. *South. J. Appl. For.* **10**: 244–248.
- Oliver, C.D. 1978. The development of northern red oak in mixed stands in central New England. *School For. Environ. Stud. Bull.* 91. Yale University, New Haven, Conn.
- Oliver, C.D. 1980. Even-aged development of mixed species stands. *J. For.* **78**: 201–203.
- Oliver, C.D. 1981. Forest development in North America following major disturbances. *For. Ecol. Manage.* **3**: 153–168. doi:10.1016/0378-1127(80)90013-4.
- Oliver, C.D., and Stephens, E.P. 1977. Reconstruction of a mixed-species forest in central New England. *Ecology*, **58**(3): 562–572. doi:10.2307/1939005.
- Palik, B.J., and Pregitzer, K.S. 1993. The vertical development of early successional forests in northern Michigan, USA. *J. Ecol.* **81**(2): 271–285. doi:10.2307/2261497.
- Steiner, K.C., Finley, J.C., Gould, P.J., Fei, S., and McDill, M. 2008. Oak regeneration guidelines for the central Appalachians. *North. J. Appl. For.* **25**: 5–16.
- Stokes, M.A., and Smiley, T.L. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago, Ill.
- Tift, B.D., and Fajvan, M.A. 1999. Red maple dynamics in Appalachian hardwood stands in West Virginia. *Can. J. For. Res.* **29**(2): 157–165. doi:10.1139/x98-190.
- Trimble, G.R. 1974. Response to crop-tree release by 7-year-old stems of red maple stump sprouts and northern red oak advance reproduction. U.S. For. Serv. Res. Pap. NE-303.
- Ward, J.S. 2009. Intensity of precommercial crop tree release increases diameter growth and survival of upland oaks. *Can. J. For. Res.* **39**(1): 118–130. doi:10.1139/X08-165.
- Ward, W.W. 1966. Oak-hardwood reproduction in central Pennsylvania. *J. For.* **11**: 744–749.
- Ward, J.S., and Stephens, G.R. 1999. Influence of cutting methods on 12 year old hardwood regeneration in Connecticut. *In* Proceedings, 12th Central Hardwood Forest Conference, 28 February 28 – 1–2 March 1999, Lexington, Kentucky. *Edited by* J.W. Stringer and D. L. Loftis. U.S. For. Serv. Gen. Tech. Rep. SRS-24. pp. 204–208.
- Wilson, B.F. 1968. Red maple stump sprouts: development the first year. Harvard For. Pap. No. 18. Harvard University, Petersham, Mass.