

Competitive success of natural oak regeneration in clearcuts during the stem exclusion stage

Robert C. Morrissey, Douglass F. Jacobs, John R. Seifert, Burnell C. Fischer, and John A. Kershaw

Abstract: We sampled dominant and codominant regeneration on 70 clearcuts, 21–35 years old, on the Hoosier National Forest in southern Indiana, USA, to evaluate influence of site variables on the competitive success of natural oak (*Quercus* L.) over time. Collected data was compared with data collected on these same sites 20 years prior. Regression tree analysis indicated aspect, natural region, and oak abundance in preharvest stands had the greatest influence on competitive success (relative density, RD) of oak species in the latter sampling, which was then examined across sites as defined by these three variables. Oak RD increased across all mid- and some lower-slope positions, sites on which oaks are expected to be replaced by faster growing species. Drought events between sampling periods apparently contributed to a decline in RD and vigor of yellow-poplar (*Liriodendron tulipifera* L.), a major competitor for growing space. Stump sprouts contributed 45% of dominant oak stems. Mean oak diameters were not significantly lower than those of other species groups, with the exception of yellow-poplar in younger stands and at mid-slope positions. Oak species drought tolerance, relative to more mesic species found on these sites, and the large proportion of oak stump sprouts likely contributed to oak competitive success.

Résumé : La régénération dominante et codominante a été échantillonnée dans 70 coupes totales âgées entre 21 et 35 ans afin d'évaluer l'influence des conditions de site sur la compétitivité du chêne (*Quercus* L.) à long terme dans la forêt nationale Hoosier, Indiana, États-Unis. Les données recueillies ont été comparées avec des données prises sur les mêmes sites 20 ans auparavant. L'analyse par arbre de régression basée sur les données récentes a indiquée que l'aspect, la région et l'abondance du chêne avant coupe ont eu la plus grande influence sur la compétitivité du chêne (densité relative, RD). La RD a par la suite été examinée en fonction de ces trois variables. Le chêne a augmenté en RD en milieu de pente sur tous les sites ainsi qu'en bas de pente sur certains sites : deux positions où l'on s'attend à ce que le chêne soit remplacé par des essences à croissance plus rapide. Des périodes de sécheresse ont apparemment contribué à la diminution de la RD et de la vigueur du tulipier de Virginie (*Liriodendron tulipifera* L.), un compétiteur important pour l'espace de croissance. Les rejets de souche de chêne représentaient 45 % des tiges dominantes. Le diamètre moyen du chêne n'était pas significativement plus bas que celui des autres groupes d'essences à l'exception du tulipier de Virginie dans les peuplements plus jeunes ainsi qu'en milieu de pente. La tolérance du chêne face à la sécheresse en comparaison avec d'autres essences moins tolérantes, combinée à la proportion élevée de rejets de souche de chêne ont pu contribuer à la forte compétitivité du chêne observée dans cette étude.

Introduction

In the Central Hardwood Forest Region (CHFR) of the USA, decline of natural oak (*Quercus* L.) regeneration is a source of concern for forest managers, and the topic has garnered much interest in recent years. Oak timber is economically valuable for use in numerous wood products and is important to secondary and tertiary producers. Oaks are also critical components of wildlife habitat, aesthetics, and cultures of the region.

Oak ecosystems have developed as a result of changes in

stand structure arising from interactions among growth, mortality, and tree recruitment within stands, which is further supplemented by regional disturbance regimes and site considerations. Natural regeneration of oak species in mesic forests has been considered a problem across the CHFR for more than half a century (Johnson et al. 2002). Lack of success of natural oak regeneration has often been attributed to anthropogenic influences; those most commonly cited are past silvicultural practices (Smith 1992; Parker and Ruffner 2004) and fire suppression (Lorimer 1993).

Roach and Gingrich (1968) recommended even-aged sil-

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R.C. Morrissey, D.F. Jacobs,¹ and J.R. Seifert.² Department of Forestry and Natural Resources, Hardwood Tree Improvement and Regeneration Center, Purdue University, West Lafayette, IN 47907, USA.

B.C. Fischer. The School of Public and Environmental Affairs, Indiana University, 1315 East 10th Street, Bloomington, IN 47405, USA.
J.A. Kershaw. Faculty of Forestry and Environmental Management, University of New Brunswick, P.O. Box 44555, 28 Dineen Drive, Fredericton, NB E3B 6C2, Canada.

¹Corresponding author (e-mail: djacobs@purdue.edu).

²Present address: Indiana Division of Forestry, Department of Natural Resources, Room W296, 402 West Washington Street, Indianapolis, IN 46204, USA.

viculture as the most reliable method to promote oak regeneration in the CHFR where advance regeneration and good potential for oak stump sprouts exists. Numerous studies have monitored stand development after clear-cutting and expressed concern regarding low levels of oak reproduction relative to various other regenerating species (Standiford and Fischer 1980; Ward and Heiligmann 1990); however, these studies examined development for a period of <20 years. If advance oak regeneration is inadequate at time of harvest, the result may be a change in species composition. Pioneer species, such as yellow-poplar (*Liriodendron tulipifera* L.) and black cherry (*Prunus serotina* Ehrh.), may invade the stand after harvest and dominate stand development, as has been commonly reported in harvested oak stands (Beck and Hooper 1986; Jenkins and Parker 1998). Site differences may also influence species composition, as higher quality sites are commonly dominated by less valuable species, such as sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), yellow-poplar, and white ash (*Fraxinus americana* L.); whereas oak species compete best on poorer sites (Hilt 1985a; Fischer 1987). Varying combinations of differential species growth, reaction to competition, site factors, and external influences (e.g., animal browsing, drought, wind, etc.) determine the developmental pattern of a stand (Oliver and Larson 1996). There is little data available to examine long-term trends of oak populations and competing species interactions across a variety of sites during the competitive stem exclusion stage of stand development (Oliver and Larson 1996).

We examined influence of site variables on natural oak regeneration and competitive success of oaks 21–35 years old following harvest. This study compared the current population of oaks with an investigation conducted within the same stands in 1986 (Fischer 1987), hereinafter referred to as the 2004 and 1986 data sets, respectively. These two data sets provided a unique opportunity to evaluate the competitive ability of oak species across different site conditions during the stem exclusion stage after clear-cutting. The data includes 1329 plots throughout 556 ha of 70 clear-cut sites on the Hoosier National Forest (HNF) in south-central Indiana, USA.

Specific objectives of this study were to (i) examine site factors that influenced relative density (RD) of oaks 21–35 years old following harvest, (ii) contrast the change in oak composition relative to the change in other species groups between the 1986 and 2004 data sets, and (iii) compare growth of oaks with growth of competing species groups during that same period. Like many observational, long-term studies (Clatterbuck and Hodges 1988; Williams and Heiligmann 2003), we make inferences from our findings and relate them to knowledge of species silvics and the regional environment to evaluate factors that may have influenced our findings.

Materials and methods

Study area

This study was conducted on the HNF, which is dominated by upland hardwood forests in the unglaciated, central portion of southern Indiana. Overstory species composition of the HNF was strongly influenced by anthropogenic dis-

turbance in the early 1800s, with the intensification of European settlement and associated land clearing for agriculture, mining, and timber harvesting (Ponder 2004). Many agricultural areas were later abandoned due to low productivity, but widespread burning and grazing continued until the 1930s. Since that period, fire suppression has greatly reduced understory disturbance within these forests and periodic timber harvest has been the primary disturbance mechanism (Parker and Ruffner 2004).

The HNF is located within the Shawnee Hills and Highland Rim ecological sections of the interior low plateau (Homoya et al. 1985). The Shawnee Hills section includes the Crawford Uplands and Crawford Escarpment subsections. The Crawford Uplands subsection is characterized by rugged hills of acid silt loams of the Wellston–Zanesville–Berks association formed from sandstone and loess, marked by sandstone outcrops and rock shelters. Broad ridges and flats with moderately deep to deep soils are found throughout the subsection. Oak–hickory is the dominant forest type on the upland slopes, with typical species such as white oak (*Quercus alba* L.), black oak (*Quercus velutina* Lam.), scarlet oak (*Quercus coccinea* Muenchh.), chestnut oak (*Quercus montana* Willd.), and hickory spp. (*Carya* L.). Mesic species such as American beech (*Fagus grandifolia* Ehrh.), sugar maple, white ash, yellow-poplar, and black walnut (*Juglans nigra* L.) are common in coves (Homoya et al. 1985). It is likely that more frequent fire intervals during the preharvest period of stand initiation and early development limited the proliferation of mesic species such as yellow-poplar and black cherry. In the Crawford Escarpment subsection, sandstone outcrops and rock shelters are not present as in the Crawford Uplands subsection, although much of the upland sections are otherwise similar in soils and topography. However, the lower areas may contain limestone-derived soils and karst topography. In the upland areas, post oak (*Quercus stellata* Wangenh.) and black oak tend to replace chestnut oak on drier sites, whereas some of the cove species present on the Crawford Uplands subsection are absent in the Crawford Escarpment subsection (Homoya et al. 1985). Preharvest volumes of the study stands indicate that yellow-poplar was a relatively minor component of these stands, composing approximately 8% of volume removed, while the black cherry–white ash–black walnut species group (hereinafter referred to as cherry–ash–walnut species group) accounted for only 3% of total volume (Table 1).

The Highland Rim section includes the Brown County Hills and Mitchell Karst Plain subsections (Homoya et al. 1985). The Brown County Hills subsection is composed of shallow, well-drained acid silt loams of the Berks–Gilpin–Weikert association that were formed from weathered bedrock and minor amounts of loess. Topography of the area is typically composed of deeply dissected uplands, steep slopes, and narrow hollows. Oak–hickory is the major forest association on upland sites with chestnut oak dominating the overstory of the ridge tops. The lower areas are composed of more mesic species such as American beech, northern red oak (*Quercus rubra* L.), sugar maple, and white ash. The Mitchell Karst Plain subsection is characterized by irregular topography with larger portions of rolling slopes with karst features intermixed with areas of steep hillsides, bedrock

Table 1. Mean preharvest relative volumes by USDA Forest Service species groupings harvested from study sites by natural region.

Natural region	No. of stands	Species group					
		White oak	Red oak	Other oaks	Yellow-poplar	Cherry–ash–walnut	Mixed hardwood
Shawnee Hills	52	0.23±0.02	0.27±0.02	0.06±0.01	0.08±0.01	0.03±0.01	0.33±0.02
Highland Rim	18	0.18±0.03	0.25±0.03	0.20±0.03	0.08±0.02	0.00±0.00	0.28±0.05

outcrops, and cliffs (Homoya et al. 1985). Yellow-poplar was a minor component of the study stands within the Highland Rim section as well, with mean preharvest volume of 8%, whereas the cherry–ash–walnut species group accounted for <1% of the preharvest volume (Table 1); episodic fire during the early periods of stand initiation and development likely served to limit the widespread distribution of these species within the region.

Sample sites were chosen based on previous selections made during the 1986 study conducted by Fischer (1987). In the 1986 study, mature upland hardwood sites on the HNF were selected that were clear-cut harvested between 1969 and 1982; clearcuts were 5–17 years old at time of first measurement. Season of harvest could not be determined, as harvesting could have been conducted at any time during the 2 year contracts granted. No data existed that described the distribution or amount of advance regeneration prior to harvest. Records were incomplete regarding possible stand tending treatments during the period between the two samples, although it is suspected that some stands in the Highland Rim section may have been treated to reduce grapevines (*Vitis* L.).

Field methods

Stands were sampled using 0.04 ha plots with a sampling intensity of 2.5 plots·ha⁻¹. The 1986 plot centers could not be relocated, so new permanent plots were established based on grid sampling, similar to the method used in 1986 (Table 2). Within each plot, all trees with a diameter at breast height (dbh; at tree height of 1.37 m on uphill side) >2.54 cm were tallied by species. The dbh, crown class (dominant, intermediate, or suppressed), and origin (sprout or seed) were recorded for each tree; stump sprout origin was assumed if the cut stump was still present and intact or where it was evident that a clump of stems had originated from a single, harvested stump. Yellow-poplar presumed to have been injured or killed by drought and (or) disease were also tallied and measured.

Aspect at each plot was recorded to the nearest 5° of azimuth. Slope percentage to the nearest 5% was recorded, and slope position was classified as either upper, mid-, or lower-slope. Plots were also assigned a category based on the amount of surface rock present (<1%, 1–10%, >10%). These methods are similar to those used in the 1986 sampling period (Fischer 1987), except that they used plots 0.004 ha in size.

Table 2. Number of plots by natural region, aspect code, slope position, and sample year.

Aspect code	Lower position		Mid-position		Upper position	
	1986	2004	1986	2004	1986	2004
Shawnee Hills section						
1	44	52	204	114	34	50
2	53	52	230	147	56	57
3	71	46	274	177	44	60
4	36	36	282	161	33	27
Highland Rim section						
1	3	7	20	34	51	27
2	8	11	26	33	62	34
3	19	14	32	48	105	40
4	17	17	32	56	64	29

Note: Discrepancies in the number of plots by aspect code and slope position between sample years may be explained by sample grid starting point and orientation or the subjective nature of the slope position variable.

Data analysis

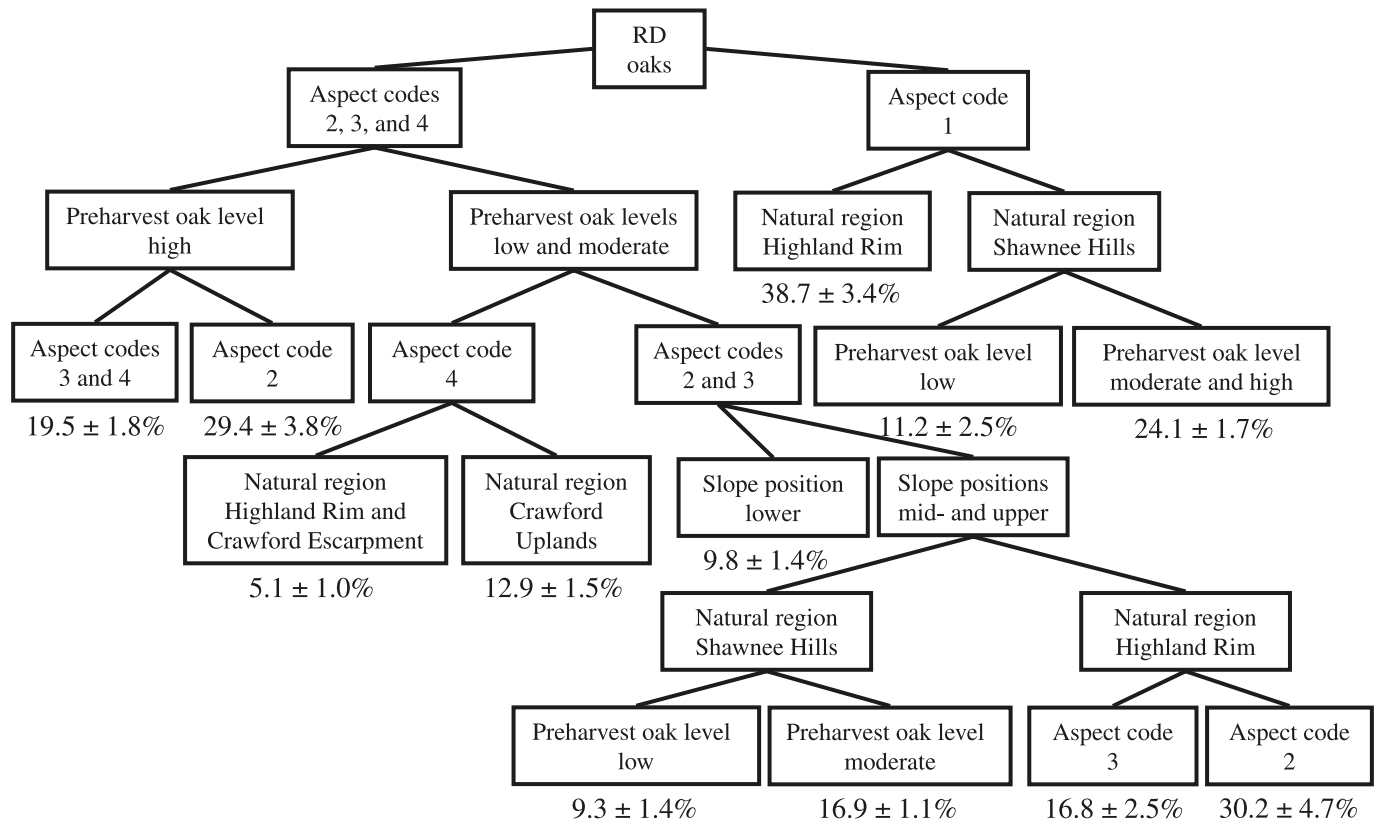
For purposes of this study, the focus was on dominant and codominant trees from the 1986 and 2004 data sets. Dominant and codominant trees are the best indicators of the species established on a site, and given that the stem exclusion stage is well underway, this may provide a clearer picture of future stand composition (Hilt 1985a); hereinafter, the term dominant will be used to refer to both dominant and codominant trees.

Species were assigned to six groups: oak species, black cherry, yellow-poplar, maple species, mixed species, and noncommercial species (Table S1)³; discussion of maple species and noncommercial species groups are not included in the following report. Considering that density of dominant trees is largely a function of stand age and site quality, we used RD (number of stems of a given species group/total number of stems tallied) to quantify species composition; change in RD indicated a corresponding change in competitive status of a species group.

Species groups were stratified by natural region and a combination of transformed aspect code (hereinafter referred to as aspect code) and slope position. Aspect code was determined using Beers et al. (1966) aspect transformation procedure, which was reduced to four aspect codes. Aspect codes 1 (185°–265°) and 2 (135°–185° and 265°–315°)

³Species groups used to classify trees found in 1986 and 2004 may be found in supplementary table. Supplementary data for this article are available on the journal Web site (cjfr.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3743. For more information on obtaining material refer to cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

Fig. 1 Regression tree showing mean (± 1 SE) dominant oak relative density (RD, %) by site and stand history attributes for stands 21–35 years old on the Hoosier National Forest (HNF).

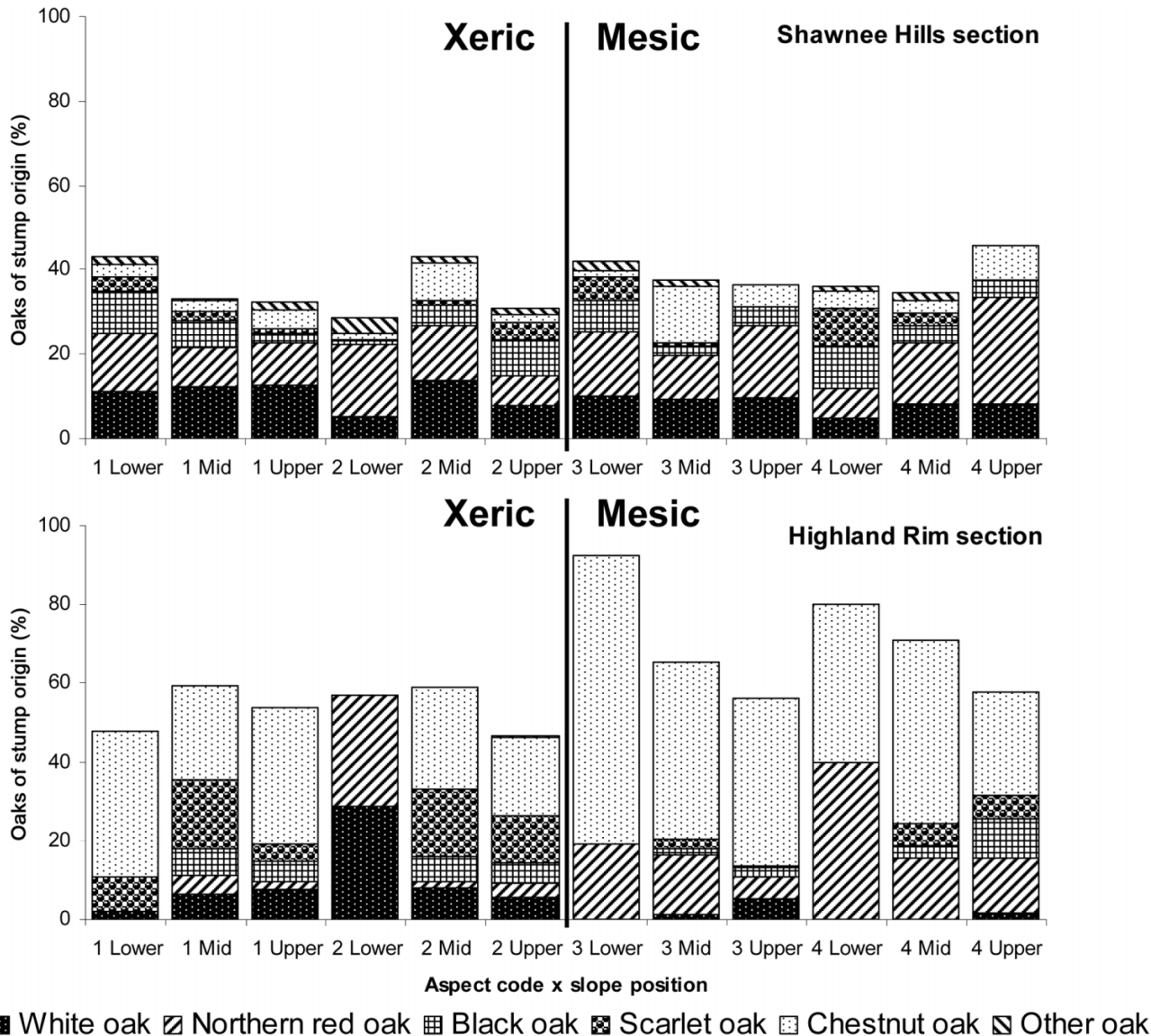


range from southeast to northwest, typically drier sites, while aspect codes 3 (85° – 135° and 315° – 5°) and 4 (5° – 85°), more mesic sites, denote aspects ranging from northwest to southeast. Slope position was grouped according to lower-, mid-, and upper-slope positions, which is an approach adopted by Bowersox and Ward (1972). The plot distribution for the two sample periods by natural region, aspect code, and slope position is shown in Table 2. Preharvest oak levels (high, moderate, and low) were derived from preharvest volumes; mean oak volume per area of all 70 stands was determined, and high, moderate, and low levels were assigned to each stand according to their location relative to the mean; one or more standard deviations below the mean indicated a low level, while one or more standard deviations above the mean indicated a high level. Thus, all plots within that stand were assigned the same preharvest level rating. Each plot was also classified according to time since harvest (21–25, 26–30, or 31–35 years) of the parent stand in contrast with species groups' mean dbh values as another measure of oak competitiveness.

The RD values of oak species groups across plots did not meet the assumptions of parametric statistics; thus, we used JMP version 5.1 (SAS Institute Inc., Cary, North Carolina) to analyze the data using regression tree analysis to evaluate factors that contributed to higher oak RD in the 2004 data set (Fan et al. 2006). Regression trees use an iterative process called binary recursive partitioning to split data into partitions. The algorithm selects the factor to split that partitions data into two groups such that it takes magnitude

of an effect on our continuous variable, RD, into account, rather than residual variance. Partitioning is then applied to each of the new branches and continues until each node reaches a user-specified minimum node size (20 plots) and becomes a terminal node, or further splits do not justify complexity of the tree relative to increased explanation of the variance of the variable of interest. All site-related variables were initially entered into the analysis, although all did not significantly contribute to oak RD according to the parameters set out in the regression tree analysis. Assuming that RD of dominant oaks is an indicator of oak competitiveness, the explanatory site-related variables yielded from the regression tree were then used to frame further exploration of competitive success of oaks in relation to site. Significantly different RD values of species groups in 1986 and 2004 were explored using *t*-tests. The ability of dominant oaks to compete for growing space was further evaluated by contrasting the species groups' mean arithmetic dbh values using the statistical analysis package SAS version 9.1 (SAS Institute Inc.) under the assumption that dbh was a strong indicator of ability of oak crowns and roots to compete for growing space. Dbh values were transformed using a natural log transformation to better meet normality assumptions. The transformed dbh values and the large sample size (32 064 trees) justified the use of parametric statistical methods to analyze the data. Transformed dbh values were then compared using one-way ANOVA and Tukey's pairwise multiple comparison test; all tests of significance were determined at $P \leq 0.05$.

Fig. 2 Percentage of dominant oak stems that originated from stump sprouting and relative percentages of five major oak species stratified by natural region, aspect code, and slope position in the 1986 and 2004 data sets across 70 clear-cut stands on the HNF.



Results

Site variables and oak RD

According to the regression tree analysis (Fig. 1), aspect code, natural regions, and preharvest oak level had the greatest influence in determining oak species group RD in the 2004 data set; slope percentage and amount of surface rock present were not found to be important within the parameters of the model. While the overall variation of oak RD explained is relatively low ($r^2 = 0.14$), consistent patterns are evident throughout the regression tree. The first split of the root node along the variable aspect code accounted for 32.6% of the total sum of squares (SS) of the regression tree, with a total of 48.6% SS explained by the aspect code variable throughout. Aspect code was the single strongest variable influencing oak species group RD, with drier aspects consistently yielding higher mean RD values. Natural regions and preharvest oak levels accounted for a combined 46.7% SS (24.5% and 22.2%, respectively), while

slope position accounted for only 4.8% SS. The natural region tended to split, with sites in the Highland Rim section consistently producing higher oak species RD values, with the exception of aspect code 4, in which oaks tended to have higher mean RD values in the Crawford Uplands subsection of the Shawnee Hills section. Those plots within stands that had high levels of preharvest oaks consistently produced higher mean oak RD values across both natural regions.

Preharvest oak level, represented by mean oak volume per hectare of all 70 stands, was determined to be a significant factor in predicting oak species group RD of the 2004 data set. An examination of the percentage of dominant oak stems of stump sprout origin by aspect code and slope position in both natural regions and composition of those stems by the five major oak species, indicates the importance of stump sprouting of oak as a source of natural regeneration in these stands (Fig. 2). In total, 45% of all dominant oak stems tallied were of stump sprout origin, which varied by

natural region. In the Highland Rim section, 57% of all dominant oak stems tallied arose from stump sprouts, compared with 37% for the Shawnee Hills section. In the Shawnee Hills section, the proportion of oak stump sprouts was similar across all sites, and a large proportion of stump sprouts were either white oak or northern red oak across most sites. In contrast, in the Highland Rim section, the higher proportion of oaks of stump sprout origin appeared to be related to species as well as site. Chestnut oak was the most prominent sprouting species, though scarlet oak also contributed on the xeric aspect codes, whereas northern red oak was more prevalent on mesic aspect codes. On mesic sites, notably lower slope positions and mesic aspect codes, where oak RD values are low in the Highland Rim section, stump sprouts accounted for more than half of all dominant oak stems (Fig. 2).

Overstory composition by site

The regression tree framed site variable analysis to facilitate evaluation of the competitive nature of oak in developing clearcuts. Although slope position explained little variation in mean dominant oak species group RD in the regression tree analysis, it was included because of its role in the 1986 analysis, prevalence in relevant literature, and important differences found in the Highland Rim section. Figure 3 highlights the change in mean RD of important species groups from the 1986 data set to the 2004 data set as delineated by natural region, aspect code, and slope position. Noncommercial species group is not shown, because it exhibited significant declines across all sites and was reduced to a mean of <2% RD of the main canopy within both sections, and maple species group accounted for a mean RD of 10% in both 1986 and 2004 with little change.

Within the Shawnee Hills section, mean dominant oak species group RD increased significantly on mid-slope positions across all aspect codes between 1986 and 2004, as well as all lower-slope positions, with the exception of aspect code 2. Mean oak RD did not significantly increase on any upper-slope positions but was sufficiently competitive to maintain its presence within the canopy relative to other species groups. The mixed species group exhibited a similar pattern except that it showed significant decreases on those same sites, yet it still occupies a significant portion of the main canopy (mean RD 32% across all sites); overall, 77% of the group is composed of four species, including sassafras (*Sassafras albidum* (Nutt.) Nees), white ash, red elm (*Ulmus rubra* Muhl.), and largetooth aspen (*Populus grandidentata* Michx.) (29%, 22%, 15%, and 11%, respectively). Yellow-poplar RD showed a relatively even distribution throughout most sites and no strong trends toward aspect code or slope position for the 1986 and 2004 data sets. Yellow-poplar increased significantly on all mid-slope positions and on upper-slope positions of aspect codes 1 and 4; whereas black cherry exhibited significantly increased mean RD values on most sites.

The Highland Rim section displayed a different dynamic among the various species groups. Mean dominant oak species group RD increased significantly on mid-slope positions across all aspect codes between 1986 and 2004, as well as all upper-slope positions, yet, not on any lower-slope positions (Fig. 3). The mixed species group decreased signifi-

cantly on most sites, yet it still occupied a significant portion of the main canopy (mean RD 27% across all sites); on average, 79% of the group was mainly composed of three species, including largetooth aspen, sassafras, and red elm (45%, 23%, and 11%, respectively). In the Highland Rim section, there was no strong relationship between yellow-poplar RD and slope position in 1986, but RD was generally higher on more mesic aspect codes. However, in 2004, yellow-poplar RD displayed a trend of decreasing RD levels from lower- to upper-slope positions, but maintained the trend of higher RD levels in association with more mesic aspect codes. Yellow-poplar displayed large significant increases on all lower- and upper-slope positions of aspect codes 2, 3, and 4. Black cherry displayed few significant increases across sites and no significant decreases.

Figure 4 illustrates mean density of dominant oak trees by site in 2004, compared with estimated mean levels of dominant oaks at time of harvest as derived from USDA Forest Service records of harvested volumes; the mean density estimate ranged from a low of 25 trees·ha⁻¹ to a high of 75 trees·ha⁻¹. The 2004 data set indicates that all sites of the Shawnee Hills section fall within or exceed the estimated preharvest density range of dominant oaks; similarly, most sites of the Highland Rim section have sufficient stocking of dominant canopy oaks with exception of lower-slope positions of aspect codes 2 and 4, and possibly 3.

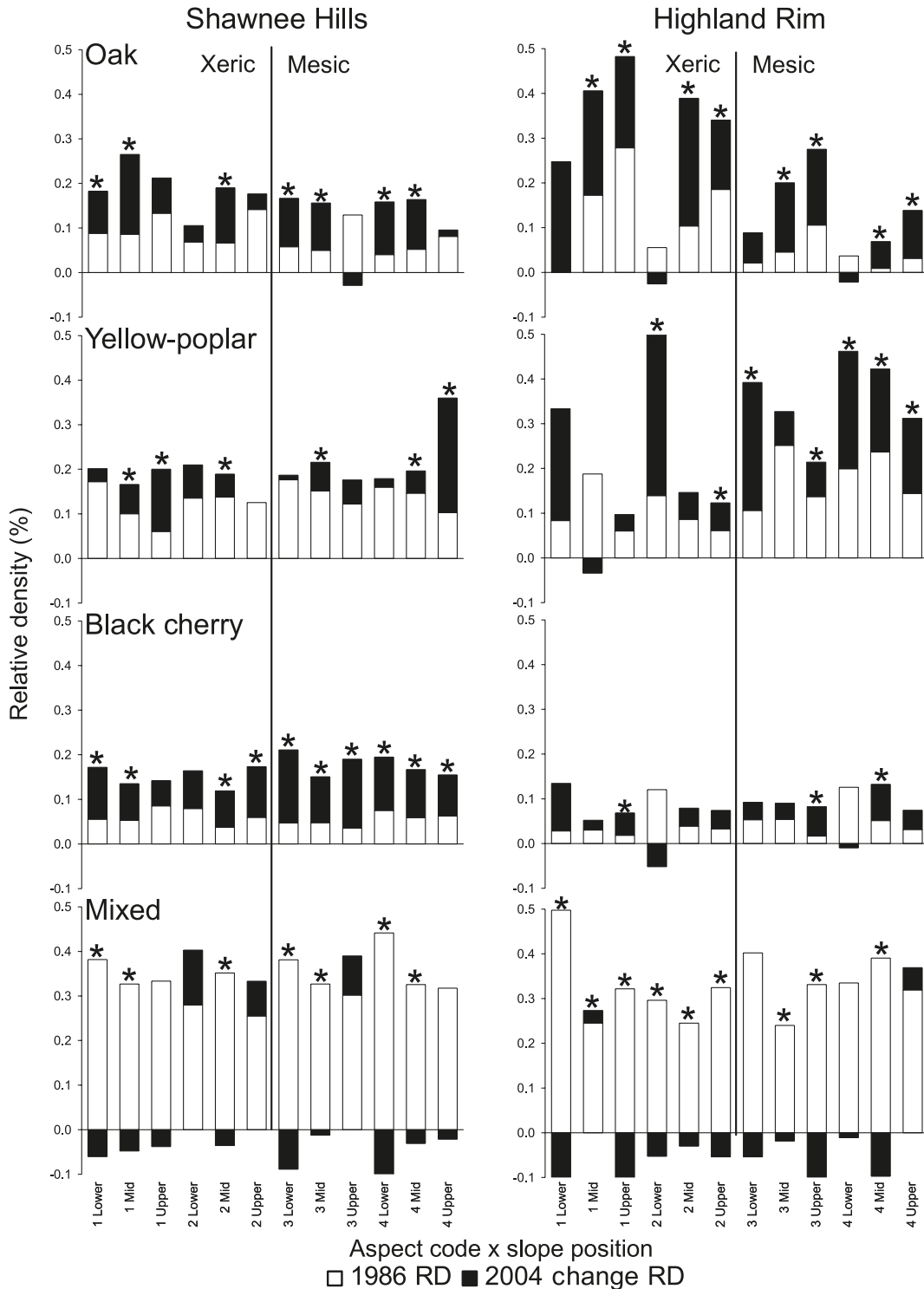
Oak dbh means by site

Tables 3 and 4 indicate significant differences between arithmetic mean dbh values of dominant yellow-poplar, black cherry, and mixed species group trees in contrast with the oak species group trees stratified by aspect code and slope position and further divided by age class to account for age distribution of plots in both natural regions. Yellow-poplar was the only group in both regions that showed significantly higher arithmetic mean tree dbh values compared with the oak species group across several sites, most notably on mid-slope positions and mesic aspect codes in stands ≤30 years old. The oldest stands, 31–35 years after harvest, had only a few instances of significantly higher mean tree dbh values of yellow-poplar, all of which occurred on aspect codes 3 or 4 and on mid-slope positions. Some differences may have been masked on those sites where numbers of observed oak stems were low, but broad trends indicated the oak species group had lower mean dbh values compared only with yellow-poplar on mid-slope positions and more mesic aspect codes in younger age classes in both natural regions.

Discussion

Our results suggest that competitive success of the oak species group has increased since the 1986 sample period, indicating that oaks have aggressively persisted and grown sufficiently to compete for growing space during the stem exclusion stage. Because of constant redistribution of growing space as stands develop, it is difficult to precisely identify causes of species differentiation. However, in this study, competitive success of oaks over this period exhibited a strong relationship with site variables, including natural region, aspect code, preharvest oak levels, and, to a lesser de-

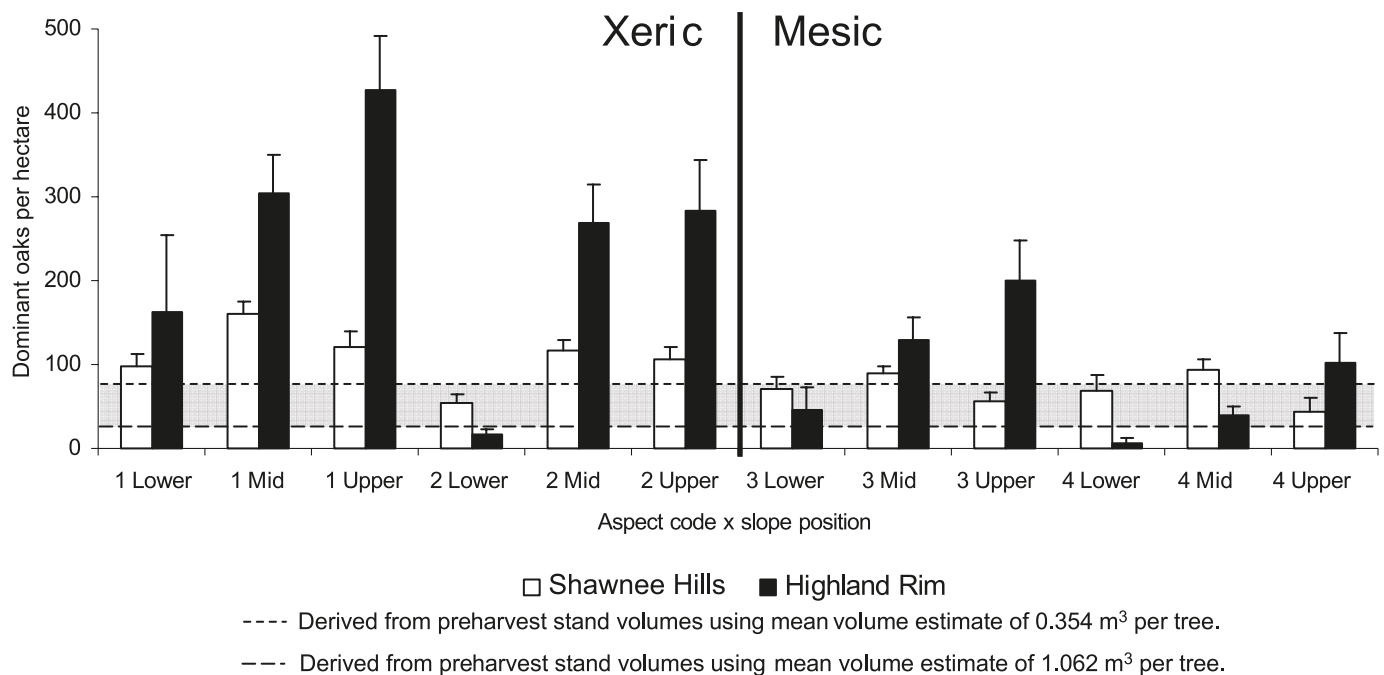
Fig. 3 Main species groups mean dominant relative densities (RD, %) from 1986 and changes as of 2004 stratified by natural region, aspect code, and slope position. *, significant change in mean RD between sampling years using *t*-tests ($\alpha = 0.05$).



gree, slope position (Fig. 1). It is also noteworthy that from 1986 to 2005, there were at least six drought events during the growing season that likely influenced species' competitive success and stand dynamics. Monthly Palmer drought severity index (PDSI) values for the period 1969–2005 were obtained for Indiana climate district VIII from the climate visualization system (CLIMVIS) website of NCDC/NOAA

(2007). Three consecutive growing seasons, from 1986 to 1988, were subject to drought events rated incipient, moderate, and severe, respectively, and consecutive mild and incipient events in 1991 and 1992, respectively, presumably served as strong selection factors against drought intolerant species. Krecik and Marshall (S.G. Krecik and P.T. Marshall, 2007). Forest health evaluation of yellow-poplar de-

Fig. 4 Mean dominant oak density by natural region, aspect code, and slope position, compared with estimated mean preharvest oak densities derived from USDA Forest Service harvest volumes. Error bars represent 1 SE.



cline in Indiana. USDA For. Serv. Grant NC-EM-04-01, unpublished data) reported yellow-poplar decline events in south-central Indiana during 1995–2004 and concluded that drought was the inciting factor. Yellow-poplar decline symptoms included bark splits and cankers in the lower crown, sparse crowns and dieback, chlorosis of leaves, and root and epicormic sprouting, all of which were observed in this study to varying degrees, as well as numerous dead standing stems presumed to have succumbed to similar stresses.

The deeper soils of the Shawnee Hills section, in contrast with the shallower soils of the Highland Rim section, provide greater capacity for soil moisture retention (Yeakley et al. 1998). This is further influenced by topographic features of aspect and slope position. Exposed aspects, south to west facing, receive greater incident solar radiation, resulting in increased temperatures, shallower soils, and more rapid soil drying, which may accentuate the effects of drought events (Fralish 1988), while lower-slope positions tend to have reduced rates of evapotranspiration and wind velocity, higher relative humidity, and deeper soils (Fralish 1988). Interaction between natural region soil characteristics and topographic features may have resulted in different dynamics of oak competitive success between the two natural regions.

The ability of oaks to compete on less productive sites, exposed aspects, and upper-slope positions, has been reported in several studies (Hilt 1985a; George and Fischer 1991); consistent with these findings, regression tree analysis of the 1986 data set showed that slope position was the most important factor in dominant oak RD, followed by aspect code (data not shown). Oak species competitive success on less productive sites is typically attributed to stress tolerance of many oak species, including morphological traits of deep rooting habits, leaf morphology, and xylem anatomy, as well as physiological characteristics, such as higher pho-

tosynthetic rates at low leaf water potentials and high vapor pressure as a result of osmotic and elastic adjustments (Abrams 1990). In contrast with the 1986 data set, aspect code rather than slope position was determined to be the primary driver of oak competitive success and would serve to intensify drought events of the period.

The shallow soils of the Highland Rim section are more prone to periods of drought; redistribution of growing space in the region throughout the several drought events favored morphological and physiological adaptations of oak species and their competitive status was improved on drought-prone sites. A strong linear relationship existed for lower- to upper-slope positions and mesic to more xeric aspect codes, sites increasingly prone to drought events, and the resultant increase in oak dominance and RD on those sites (Fig. 3). Yellow-poplar, a site-sensitive species (Beck 1990), exhibited large increases in RD on lower-slope positions and more protected aspects, sites that would be protected from higher temperatures and incident solar radiation (Fig. 3), but had lesser gains in RD on more exposed sites; Hilt (1985b) noted a trend of decreasing yellow-poplar densities in relation to drought years on clear-cut sites in Ohio, as did Parker and Swank (1982) on typically drier sites. Oak competitive success on lower-slope positions was more limited, which may be a result of a relatively low number of sample plots or related to intense competition from faster growing species (e.g., yellow-poplar) early in stand development.

Dominant oak species group dbh values were comparable to all other species groups across all stand ages, with the exception of yellow-poplar on some mid- and upper-slope positions in stands aged 26 to 30 years (Tables 3 and 4). Yellow-poplar growth rates typically greatly exceed those of most oaks; thus, it was surprising that more significant differences were not noted, especially on older stands and more productive sites. Krecik and Marshall (2007, unpub-

Table 3. Arithmetic mean diameter at breast height (dbh) of dominant stems of oak species group and number of sampled dominant oaks by aspect code, slope position, and time since harvest from 70 clearcuts in the Shawnee Hills section of the Hoosier National Forest (HNF).

Aspect code	Slope position	Mean oak dbh (cm)	No. of oaks	Yellow-poplar	Black cherry	Other species
21–25 years						
1	Lower	10.0±0.7	5	ns	ns	ns
1	Mid	13.6±0.4	143	ns	ns	ns
1	Upper	13.3±1.0	27	ns	ns	ns
2	Lower	14.0±0.6	55	ns	ns	ns
2	Mid	12.8±0.2	288	*	ns	ns
2	Upper	14.1±0.5	99	ns	ns	ns
3	Lower	13.5±0.6	48	ns	ns	ns
3	Mid	14.2±0.3	204	*	ns	ns
3	Upper	14.4±0.5	67	*	ns	ns
4	Lower	13.4±1.0	25	*	ns	ns
4	Mid	15.0±0.4	131	*	ns	ns
4	Upper	13.7±0.7	30	*	ns	ns
26–30 years						
1	Lower	16.1±0.6	77	ns	*	ns
1	Mid	16.8±0.3	277	*	ns	+
1	Upper	16.9±0.5	86	ns	ns	ns
2	Lower	16.2±1.0	22	ns	ns	ns
2	Mid	17.0±0.6	110	*	ns	ns
2	Upper	19.2±0.7	69	ns	ns	+
3	Lower	16.3±1.4	7	ns	ns	ns
3	Mid	15.5±0.4	167	*	ns	ns
3	Upper	16.4±1.0	26	ns	ns	ns
4	Lower	18.8±0.8	39	ns	ns	ns
4	Mid	16.2±0.3	327	*	ns	+
4	Upper	18.7±2.3	7	ns	ns	ns
31–35 years						
1	Lower	20.4±0.5	122	ns	ns	ns
1	Mid	20.5±0.4	318	ns	ns	+
1	Upper	21.2±0.6	132	ns	ns	+
2	Lower	19.2±0.8	39	ns	ns	ns
2	Mid	20.2±0.3	299	ns	ns	ns
2	Upper	21.4±0.8	78	ns	ns	+
3	Lower	21.3±0.8	76	ns	ns	ns
3	Mid	21.2±0.4	268	*	ns	+
3	Upper	20.4±1.0	42	ns	ns	ns
4	Lower	19.1±1.2	36	ns	ns	ns
4	Mid	20.9±0.5	157	*	ns	ns

Note: ANOVA ($P \leq 0.05$) followed by Tukey's multiple pairwise comparison ($\alpha = 0.05$) was used to compare mean oak species group dbh values to those of yellow-poplar, black cherry, and mixed species groups. *, applicable species group has significantly larger mean dbh than oak species group; +, oak species group has significantly larger mean dbh than applicable species group; ns, indicates not significantly different; na, no data available for comparison; 1, only one oak or applicable species group member was sampled. Analysis based on dominant and codominant stems only.

lished data, see above) measured reduced incremental growth of yellow-poplar during drought years, while oak species exhibited a variance only in the most severe drought year of the period studied. Several studies have reported similar findings, whereby yellow-poplar growth was reduced relative to oak species growth in periods of moisture stress (Elliott and Swank 1994; Orwig and Abrams 1997). However, extended effects of drought on yellow-poplar growth are uncertain, as studies have shown both lingering negative effects (Fekedulegn et al. 2003) as well as resumption of predrought growth patterns (Orwig and Abrams 1997). Repeated drought events may have had cumulative effects that

persisted and created different dominant species composition patterns than would occur under nondrought conditions.

High mean preharvest oak volumes in the Highland Rim section, approximately 65% of total volume, provided an abundant and important source of oak regeneration via stump sprouts. Beck and Hooper (1986) observed a 20-year-old clear-cut stand in North Carolina on which approximately 75% of the oaks considered free to grow originated from sprouts, though they made no distinction between stump and seedling sprouts. Gould et al. (2002) reported that oak stump sprouts contributed 68% of oak basal area on average, which was second only to red maple, on 65 formerly

Table 4. Arithmetic mean dbh of dominant stems of oak species group and number of sampled dominant oaks by aspect code, slope position, and time since harvest from 70 clearcuts in the Highland Rim section of the HNF.

Aspect code	Slope position	Mean oak dbh (cm)	No. of oaks	Yellow-poplar	Black cherry	Other species
21–25 years						
1	Lower	11.3±0.0	1	1	1	1
1	Mid	15.6±0.5	104	ns	ns	ns
1	Upper	16.7±0.5	62	ns	ns	ns
2	Lower	na	0	na	na	na
2	Mid	16.7±0.8	49	ns	ns	ns
2	Upper	14.2±0.5	49	ns	ns	ns
3	Lower	na	0	na	na	na
3	Mid	17.3±2.1	2	ns	ns	ns
3	Upper	17.3±1.3	14	ns	ns	ns
4	Lower	na	0	na	na	na
4	Mid	22.7±5.0	3	ns	ns	ns
4	Upper	16.1±1.5	8	ns	ns	ns
26–30 years						
1	Lower	14.9±0.7	45	ns	ns	ns
1	Mid	14.4±0.3	228	ns	ns	*
1	Upper	14.2±0.2	376	ns	ns	ns
2	Lower	14.6±2.2	3	ns	ns	ns
2	Mid	16.7±0.3	209	*	ns	ns
2	Upper	14.2±0.3	241	*	ns	ns
3	Lower	15.2±0.6	26	ns	ns	ns
3	Mid	17.1±0.3	191	*	ns	*
3	Upper	16.1±0.4	260	*	*	*
4	Lower	21.8±6.7	2	ns	ns	ns
4	Mid	16.8±0.6	81	ns	ns	ns
4	Upper	15.1±0.6	104	*	ns	ns
31–35 years						
1	Lower	na	0	na	na	na
1	Mid	20.4±0.6	88	ns	ns	ns
1	Upper	20.0±1.3	29	ns	ns	ns
2	Lower	14.3±2.2	4	ns	ns	ns
2	Mid	19.1±0.5	101	ns	ns	ns
2	Upper	19.4±0.5	100	ns	ns	ns
3	Lower	na	0	na	na	na
3	Mid	18.5±0.9	58	*	ns	ns
3	Upper	19.2±0.8	50	ns	ns	+
4	Lower	20.0±4.6	3	ns	ns	ns
4	Mid	17.5±1.7	6	ns	ns	ns

Note: ANOVA ($P \leq 0.05$) followed by Tukey's multiple pairwise comparison ($\alpha = 0.05$) was used to compare mean oak species group dbh values to those of yellow-poplar, black cherry, and mixed species groups. *, applicable species group has significantly larger mean dbh than oak species group; +, oak species group has significantly larger mean dbh than applicable species group; ns, not significantly different; na, no data available for comparison; 1, only one oak or applicable species group member was sampled. Analysis based on dominant and codominant stems only.

oak-dominated stands 20 to 33 years after clear-cutting in Pennsylvania. Deep-rooted parent oaks provide a readily available source of carbon and greater access to soil water, which may have provided another competitive advantage through increased growth rates and reduced water stress during drought periods. The importance of oak stump sprouts is evident on more productive sites of the region, where greater early growth rates allowed them to persist and compete with species such as yellow-poplar that are well-suited to these sites.

In the Shawnee Hills region, with moderately deep to deep, more productive soils, a somewhat different dynamic exists. The more productive soils of the region provide for

a more complex interaction among species groups, and the oak species group is at a competitive disadvantage in relation to many co-occurring species at least during early stages of stand development when soil moisture is adequate. Deeper soils are better able to buffer drought events (Yeakley et al. 1998); thus, impacts on more site-sensitive species are less pronounced compared with the Highland Rim section and oaks presumably do not gain as strong an advantage in competing for growing space. Yet, oaks increased on mid- and lower-slope positions, sites where they typically do not compete well, but did not increase on upper-slope positions, sites where they would be expected to increase. Black cherry stems increased significantly in RD

across most sites but, surprisingly, yellow-poplar was not as successful in competing for growing space to assume a more dominant canopy position.

Drought events and associated yellow-poplar decline symptoms also occurred in the Shawnee Hills section. However, more productive sites were probably not as predisposed to drought effects as the Highland Rim section, though comparable rates of yellow-poplar density decline occurred over this period in the two sections. Overall, damaged and dead yellow-poplar stems were more prevalent in the Shawnee Hills section compared with the Highland Rim section, although this may be an artifact of time, as presumably the Highland Rim section would have been impacted sooner and to a greater extent; thus, many dead yellow-poplar stems would not have been tallied if they were already on the ground.

The deeper, more productive soils of the Shawnee Hills region would be expected to yield greater black cherry and yellow-poplar growth relative to the oak species group. Several studies suggested that if oaks are not in a dominant canopy position shortly after initiation of the stem exclusion stage, they likely will not attain a dominant canopy position (Hilt 1985a; George and Fischer 1991), as demonstrated in a long-term study in clearcut sites in Ohio (Williams and Heiligmann 2003). Stresses and associated reduction in growth of site-sensitive species, such as yellow-poplar and black cherry, would have provided a competitive advantage to oak species. Mean black cherry dbh values show essentially no significant differences across sites and stand ages in contrast to the oak species; however, yellow-poplar tends to exhibit higher mean dbh values on some mid-slope positions and more mesic aspect codes, with fewer differences in older stands. This trend suggests that decreased diameter growth of yellow-poplar over time allowed oaks to compete and grow in diameter to a comparable size, while in younger stands the competitive advantage associated with rapid initial growth typical of yellow-poplar is still evident. In contrast to the work of Williams and Heiligmann (2003), oak RD in 1986 was not a reliable indicator of future oak levels because of subsequent redistribution of growing space that served to select against typically faster growing species, such as yellow-poplar, and favored oak species thereby altering expected patterns of stand development.

Conclusions

The composition and structure of forest stands is determined by the competitive success of individual trees, which is dependent on species attributes, associated competitors, and environmental interactions (Oliver and Larson 1996). Our study suggests that the oak species group aggressively persisted and grew sufficiently to compete for growing space during the stem exclusion stage in association with yellow-poplar, a species that typically out-competes oaks via rapid early growth. Competitive success of oaks over this period exhibited a strong relationship with site variables including natural region, aspect code, preharvest oak levels, and, to a lesser degree, slope position, all of which may have further interacted with a series of drought events in the region during that period to favor the oak species group. Understanding stand dynamics is critical to achieving forest

management goals, as this knowledge helps explain stand developmental patterns and predict future stand structures, which may facilitate the ability to attain desired species compositions. Such information can also be used to identify necessary conditions for prescribing specific silvicultural operations, and to help realize management objectives at the landscape scale.

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