SITE AND CANOPY CHARACTERISTICS ASSOCIATED WITH OAK ADVANCE REPRODUCTION IN MATURE OAK-HICKORY FORESTS IN THE RIDGE AND VALLEY PROVINCE IN TENNESSEE

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ABSTRACT.—To investigate hypotheses regarding effects of competitors and site quality on oak regeneration, we documented site factors and oak seedling composition, size, and abundance in the Ridge and Valley Province of Tennessee. Small oak seedlings were most abundant on productive soils and mesic landform positions, whereas large oak seedlings were most abundant on less productive soils and drier landform positions. Patterns in the abundance of large oak seedlings and saplings were consistent with the hypothesis that oaks are most competitive on drier and poorer sites. Results were mixed with regard to existing hypotheses concerning particular competitors and competition for light.

Reduced oak regeneration in the eastern U.S. remains a significant problem despite more than two decades of research on potential causal factors and solutions. Most oak regeneration research has focused on the evaluation of different management techniques for releasing existing natural oak advanced reproduction, or on increasing the success and competitive potential of planted oaks (Beck 1970, Sander 1972, Loftis 1990, Buckley and others 1998). Fewer studies have investigated the underlying factors that affect the presence, absence, and abundance of oak advanced reproduction available for subsequent management on sites with little disturbance (Weitzman and Trimble 1957, Carvell and Tryon 1961, Lorimer and others 1994).

Oak forest types and mixtures of oaks and other species are considered the most abundant forest types in the U.S., but forest management techniques used over the past 50 years have favored species that are more shade tolerant or faster growing than oak (Clark 1993). Tennessee forests are 71 percent oak-hickory forest type, 12 percent oak-pine forest type, and 4 percent oak-gum-cypress forest type (Schweitzer 2000). Since forest types containing oak cover 87 percent of the forested land in Tennessee, a continued lack of oak regeneration will cause changes to forest composition that will negatively impact the forest products industry and wildlife. Little information has been published on the severity of the oak regeneration problem in Tennessee. To our knowledge, this is the first study of this kind to take place in the Ridge and Valley Province of Tennessee.

Results of previous research suggest that drought, fire suppression, competition, increased consumption of acorns by wildlife, defoliation, and various soil properties have contributed to oak regeneration failures (Lorimer 1989, LeBlanc 1998, Cook and others 1998, Rogers and Johnson 1998). McGee (1984) found that on average and productive sites, established oak seedlings in the understory were unable to capture small or large canopy gaps. Due to increased competition with species such as red maple (*Acer rubrum* L.), sugar maple (*A. saccharum* Marsh.), yellow-poplar (*Liriodendron tulipifera* L.), and beech (*Fagus grandifolia* Ehrh.), it is uncertain whether oaks will remain the dominant species in hardwood forests in the future.

In the northern Appalachian hardwoods of West Virginia, oak regeneration tends to be more widespread on intermediate to poor sites, with a

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decreasing proportion of oak with increasing site quality (Weitzman and Trimble 1957). Thus, oak species may be more competitive on intermediate and poor sites where competitors are limited (Lorimer 1993). Soil texture, litter depth, pH, and soil moisture may not directly lead to regeneration declines, but they do have an effect on the germination, growth, and mortality of hardwood species (Meiners and others 1984, Meredieu and others 1996).

Past research has generated two primary hypotheses concerning oak regeneration. The first is that the amount of oak reproduction should increase with reduced abundance of potential competitors. The second hypothesis is that oak regeneration should be more successful on drier, poorer soils, warmer aspects, and upper slope positions where competitors are limited by growing conditions. The overall objectives of this study were:

1) to quantify natural oak regeneration in the Ridge and Valley Province of Tennessee in untreated, closed-canopy forests, and
2) to examine effects of competition and site factors associated with greater abundance of oak reproduction.

METHODS

Stand Types and Study Region

We sampled 33 mature mixed oak/hardwood stands within five counties of the Ridge and Valley Physiographic Province in Tennessee, also known as The Great Valley of East Tennessee. All sampled stands had oak as the dominant canopy species and had not been significantly disturbed (canopies have remained intact) within the last 50 years. Highgrading is common in the region, however, and the possibility of past highgrading of some of the stands sampled cannot be ruled out. The Ridge and Valley Province constitutes 18 percent of the total land area in Tennessee (Springer and Elder 1980). The region is characterized by its folded rock formations oriented in a northeast-southwest direction, comprising nearly 5 million acres of land.

There are seven soil provinces within the region, each further divided into soil associations (table 1). Three soil provinces were not sampled because of limited forest cover. There were a total of eight different soil associations within the four soil provinces sampled. Two of the eight soil associations were not sampled due to soils such as calcareous shales and calcareous sandstones that were not characteristic of the region. Soils within the soil associations included in the study ranged from moderately high productivity to strongly acidic soils low in fertility (Springer and Elder 1980).

Transect Design and Measurements

For sampling, belt transects 60 m long and 5 m wide were placed parallel to the contour of the stand (fig. 1). Three landform positions (southeast mid-slope, northwest mid-slope, and ridgetop) were sampled within each soil association. Each of these three landform positions was

Table 1.—*Comparison of the soil associations sampled in the Tennessee portion of the Ridge and Valley Physiographic Province. Adapted from Springer and Elder (1980) and Owenby and Ezell (1992).*

Soil Association	Parent Material	Landscape	Soil Productivity	AnnualP recip. (in)	Temp.* (°C)
Fullerton-Dewey	Dolomitic Limestone	Hilly and rolling	Mod. High	53	1 I 24
Fullerton-Bodine	Dolomitic Limestone	Hilly	Strongly acid; low fertility	54	2 I 24
Dunmore-Dewey	Dolomitic Limestone	Rolling and hilly	Moderate	42	1 I 24
Talbott-Rock-Etowah	Clayey Limestone	Undulating to hilly	Moderate	55	3 I 23
Litz-Sequoia-Talbott	Shale	Undulating and rolling	Mod.; lots of coarse fragments	55	3 I 23
Wallen-Talbott-Montevallo	Sandstone, Shale, & Dolomitic Limestone	Steep ridges and rolling valleys	Low; shallow soil	53	3 I 24

* First number is mean temperature in January, second number is mean July temperature.

sampled in two geographic locations within the same soil association for replication. The southeast or northwest-facing aspects coincide with the dominant northeast-southwest orientation of the ridges in the Ridge and Valley Province.

Oak reproduction was sampled within three 5 m x 20 m subplots along the length of each transect. Species and size class were tallied for all oak seedlings and saplings within each subplot. The four size classes used were defined as

1) 0 to 25 cm tall;
2) 26 to 50 cm tall;
3) 51 to 150 cm tall; and
4) greater than 150 cm tall, but less than 8 cm dbh.

Variables measured within transects included slope; percent cover of understory herbs, shrubs, and tree seedlings; litter depth; litter composition; basal area; density of non-oak tree saplings greater than 150 cm tall, but less than 8 cm dbh; percent full photosynthetically active radiation (PAR); the number, composition, and width of canopy layers; and percent canopy cover. All site factor measurements, except for percent full PAR, density of non-oak saplings, and canopy cover percent, were recorded at three sampling points located at 10 m, 30 m, and 50 m down the center of the transect (fig. 1). Percent full PAR and canopy cover percent were recorded every 10 m along the center of the transect. Non-oak sapling density was measured within the three 5 m x 20 m subplot areas along the transect.

We estimated cover of understory herbs, shrubs, and tree seedlings less than 1 m tall within 1 m^2 quadrat frames located on transect sampling points. The species comprising canopy strata over each sampling point were recorded and the thickness of each stratum was quantified using a height pole and clinometer to measure the height of the top and bottom of each stratum > 1 m thick. For analysis, the canopy profile was separated into two sections, upper canopy (> 13 m above the ground) and mid-canopy (4 to 13 m above the ground). Litter depth was measured to the nearest centimeter at each sampling point. Basal area of the stand was determined at each sample point with a 10 BAF prism. The species and diameter at breast height for all 'in' trees were also recorded. Importance values (relative density + relative frequency + relative dominance) for each species were calculated from basal area data for each transect as described in Krebs (1985).

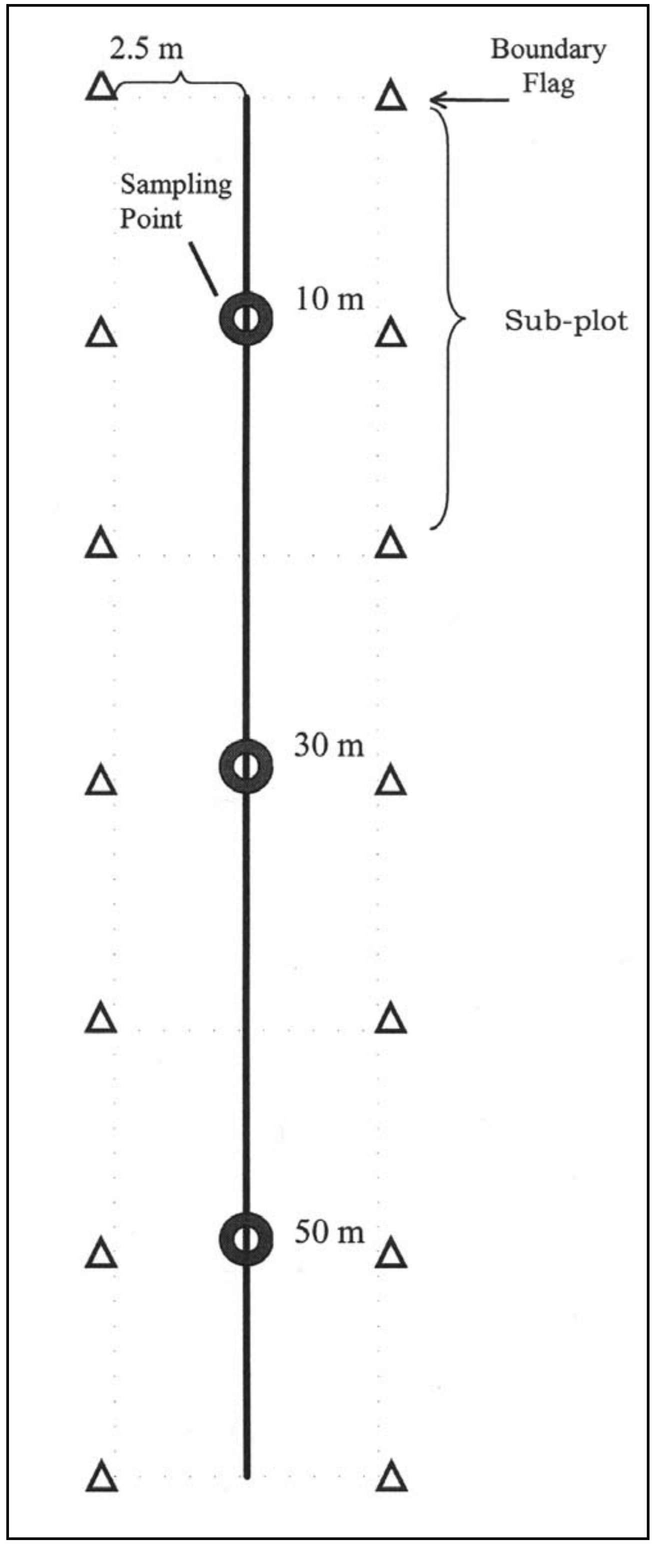

Figure 1.—*Transect design placed parallel to the contour at each sampling site, used to sample stand and oak measurements on the different soil associations and landform positions.*

PAR consists of all wavelengths of light that are used in photosynthesis, and was measured with an AccuPAR Ceptometer (Decagon; Pullman, WA). PAR measurements were taken 1 m above each sampling point along a given transect between 11:00 AM and 3:00 PM EDST. All PAR measurements were taken on clear days, and reference measurements were taken in completely open areas before and after sampling transects. The ratio of below canopy PAR to mean PAR in the open was used to calculate percent full PAR. Percent canopy cover was measured with a CI-110 Digital Plant Canopy Imager (CID, Inc.; Vancouver, WA), which measured the fraction of sky that was visible from beneath the canopy. The Plant Canopy Imager was held 1 m above each sampling point while facing north.

Preliminary analysis indicated that landform positions and soil associations were important across all species and size classes. Thus, analyses were run within landform position-soil association combinations. Regeneration data were averaged over each transect and analyzed with R^2 Variable Selection, Response Surface Analysis, and General Linear Model (GLM) analysis (CD version 8, SAS Institute, Cary, NC). Transects were assumed to be independent ecological units. GLM was used as a final step in the analysis because landform position and soil association were class variables and were not appropriate for variable selection or Response Surface analysis. Separate models were developed for each oak species due to differences in their habitat requirements, as well as for each size class of oak due to potential differences in requirements and interactions at different developmental stages.

RESULTS

Eight species of oak were encountered: white oak (*Quercus alba* L.), chestnut oak (*Q. Montana* Willd.), black oak (*Q. velutina* Lam.), northern red oak (*Q. rubra* L.), scarlet oak (*Q. coccinea* Muenchh.), southern red oak (*Q. falcate* Michx.), post oak (*Q. stellata* Wangenh.), and chinkapin oak (*Q. muehlenbergii* Engelm.). Post oak and chinkapin oak were omitted from individual species analyses because of low abundance and spotty distribution, but were included in analysis of all oak species and size classes combined. Scarlet and southern red oaks have similar habitat requirements and were less abundant. Thus, they were analyzed as a combined group.

The white oak group represented 76 percent of the total number of oak seedlings tallied in the region (table 2). The smallest size class of seedlings comprised 88 percent of the oak seedlings tallied, while the largest size class comprised only 0.5 percent. By far, white oak and chestnut oak were the most abundant species in the 0 to 25 cm and 26 to 50 cm size classes. White oak, chestnut oak, black oak, and northern red oak in the 51 to 150 cm and > 151 cm, but less than 8 cm dbh size classes were fairly comparable. Only two individuals in the scarlet/southern red oak group were found in the 51 to 150 cm size class, and no scarlet/southern red oak individuals were tallied in the > 151 cm, but less than 8 cm dbh size class.

The 12,220 oak seedlings tallied in the 0.99 ha total area sampled suggests densities of 12,341 seedlings/ha, which exceeds the 9,100 seedlings/ha average reported previously for the Southern Appalachians (Cook and others 1998). Only 61, 0.5 percent, of the total numbers of seedlings sampled, however, were greater than 150 cm in height. This suggests a density of 62 seedlings/ha taller than 150 cm, which is well below the previously reported, tentative estimate of 1,000+ seedlings/ha that exceed 140 cm in the Southern Appalachians (Cook and others 1998).

Table 2.—*Total number of oak seedlings tallied by species and size class.*

Species	Size class* 1st	2nd	3rd	4th	Percent
White oak	1675	318	49	11	16.8
Chestnut oak	6742	425	69	10	59.3
Black oak	1034	197	49	23	10.7
N. red oak	806	220	65	17	9.1
Scarlet/S. red oak	458	50	2	0	4.2

*1st = seedlings 0 – 25 cm tall, 2nd = seedlings 26-50 cm tall, 3rd = seedlings 51-150 cm tall, and 4th = seedlings 151 cm tall up to 8 cm dbh.

Soil association was a significant variable (P < 0.05) in at least one size class for all oak species. Consequently, soil association was included as a variable in all subsequent models developed. Similarly, landform position was found to be significant for most of the oak species and was also included in all models. Small seedlings (up to 50 cm tall) were most abundant on the Fullerton-Dewey, Wallen-Talbott-Montevallo, and Talbott-Rock-Etowah soil associations (fig. 2), which spanned the range of soil productivity (table 1).

In contrast, large seedlings (from 51 cm tall up to 8 cm dbh) were most abundant on the Litz-Sequoia-Talbott and Dunmore-Dewey soil associations (fig. 2), which have soils generally ranked as moderate in productivity (table 1). Mean percent full PAR and mean overstory basal areas varied little across soil associations, and showed no clear relationships to the number of small or large oak seedlings (fig. 2).

Small seedlings were most abundant on the northwest aspect/mid-slope position, whereas large seedlings were most abundant on the southeast aspect/mid-slope position (fig. 3). However, differences in the mean number of large seedlings between landform positions were small due to the low numbers of large seedlings. Changes in mean percent full PAR and mean basal area were slight across landform positions, but mean PAR was greatest on the southeast aspect/mid-slope position and least on the northeast aspect/mid-slope position. Mean basal area was lowest on the southeast aspect/mid-slope position. Thus, small seedlings were most abundant on the landform position with high basal area and the lowest mean PAR, whereas large seedlings were most abundant on the landform position with the greatest mean PAR and lowest mean basal area.

Three-dimensional plots of the abundance of individual size classes within species (not presented) indicated a concentration of seedlings 51 to 150 cm tall and 151 cm tall up to 8 cm dbh for all species but scarlet/southern red oak on the southeast aspect/mid-slope and ridge top landform positions and the Litz-Sequoia-Talbott soil association. Models developed for all species and size classes of oak seedlings combined indicated positive relationships between the number of oak seedlings and the importance value of chestnut oak and the number of oak seedlings and the mean depth (combined thickness of all strata > 1 m thick) of the mid-canopy (table 3). A negative relationship was indicated between the number of oak seedlings and the number of hickory seedlings 151 cm tall up to 8 cm dbh.

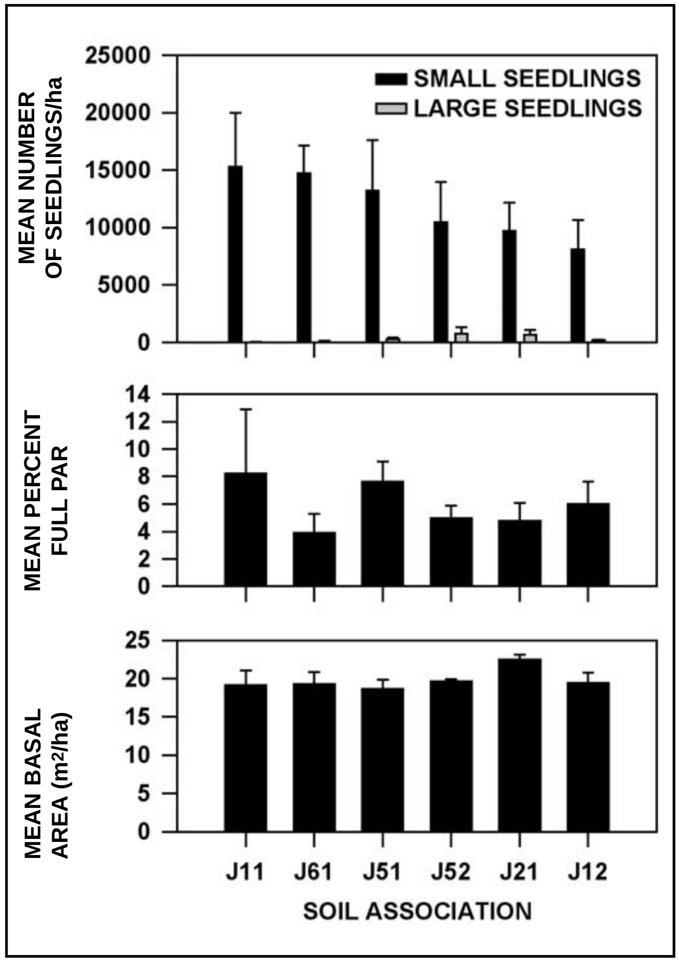

Figure 2.—*Mean number of oak seedlings, mean percent full PAR, and mean overstory basal area by soil association. Small seedlings represent oak seedlings of all species measuring 1 - 50 cm in height and large seedlings represent seedlings of all species measuring 51 cm tall up to 8 cm dbh. For soil associations, J11 = Fullerton-Dewey, J61 = Wallen-Talbott-Montevallo, J51 = Talbott-Rock-Etowah, J52 = Litz-Sequoia-Talbott, J21 = Dunmore-Dewey, J12 = Fullerton-Bodine. Error bars represent 1 standard error.*

Models for each individual oak species (all size classes combined) indicated positive relationships between the number of seedlings and the importance value of mature oaks of the same species (table 3). The number of white oak seedlings also showed a positive relationship with the importance value of beech and the depth of the canopy. The depth of the canopy was positively related to the number of chestnut oak seedlings, and other positive relationships

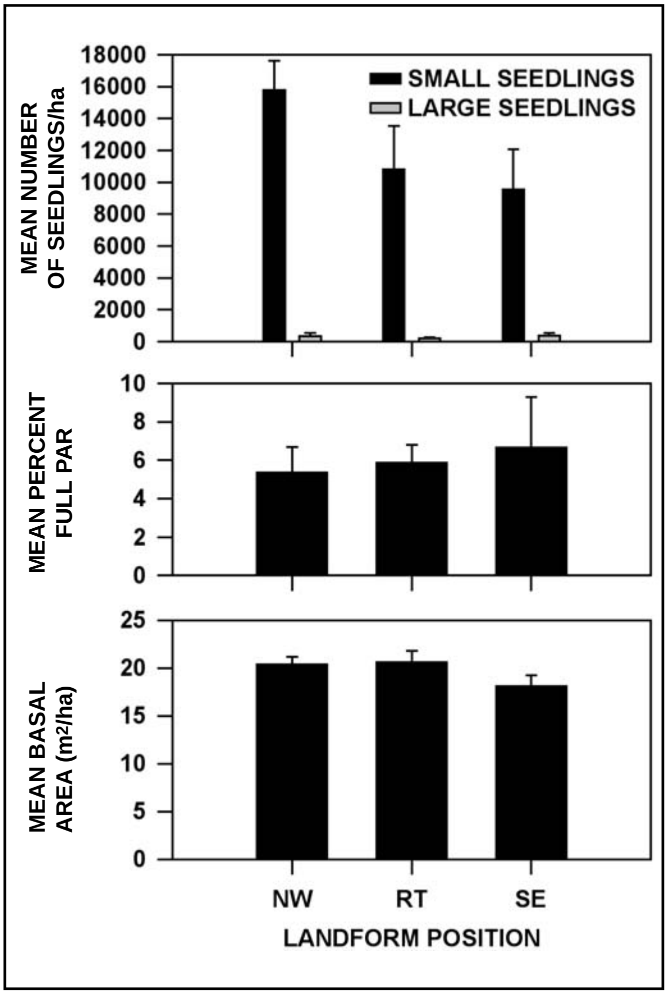

Figure 3.—*Mean number of oak seedlings, mean percent full PAR, and mean overstory basal area by landform position. Small and large seedlings and error bars as in figure 2. NW = northwest aspect, mid-slope position, RT = ridge top, and SE = southeast aspect, mid-slope position.*

were indicated between the numbers of chestnut oak, black oak, and northern red oak seedlings and potential competitors such as blackgum (*Nyssa sylvatica* Marsh.) seedlings and mature pines (table 3). Negative relationships were indicated between percent full PAR and the number of chestnut oak and scarlet/southern red oak seedlings.

Negative relationships between potential competitors and the number of oak seedlings were indicated for chestnut oak, northern red oak, and scarlet/southern red oak (table 3). These potential competitors included sassafras (*Sassafras albidum* (Nutt.) Ness), mature white oak, and mature black oak.

Additional models developed for individual size classes within oak species (not presented) indicated negative relationships between dogwood (*Cornus florida* L.) and the numbers of chestnut oak, black oak, and northern red oak, and between mature maples (red and sugar maple combined) and scarlet/southern red oak. A negative relationship was also indicated between the number of 151 cm tall up to 8 cm dbh northern red oak seedlings and the amount of canopy cover. Finally, a positive relationship was indicated between percent slope and the number of black oak seedlings 151 cm tall up to 8 cm dbh.

R^2 variable selection indicated percent cover of understory herbs, shrubs, and tree seedlings less than 1 meter, litter depth, and litter were not significantly related to the amount of oak regeneration that occurred on the site ($P > 0.05$).

Table 3.— *Models and variables explaining the number of oak seedlings of all species and size classes combined and the number of seedlings of each species (all size classes combined). Signs indicate positive or negative relationships between variables and numbers of oak seedlings. Y-intercepts in the models vary across landform position/soil association combinations. Variable coefficients and Y-intercepts have been omitted for the purpose of efficient presentation.*

Species	Model	R^2 (Percent)	P-value
All Species	**LFP[1] Soil[2] +Coiv[3] +Midcan[4] -Hick[5]**	**54.2**	**0.0297**
White oak	**LFP Soil +Woiv[6] +Bchiv[7] +Candep[8]**	**86.9**	**<0.0001**
Chestnut oak	**LFP Soil +Coiv -PAR[9] +Candep +Blgm[10] -Sass[11]**	**69.6**	**0.0041**
Black oak	**LFP Soil +Boiv[12] +Pineiv[13]**	**73.2**	**<0.0001**
N. red oak	**LFP Soil +Nroiv[14] -Woiv +Blgmiv[15] -Sassiv[16] -Midcan**	**61.0**	**0.0280**
Scarlet/S. red oak	**LFP Soil +Scsroiv[17] -Boiv -PAR**	**71.1**	**0.0005**

[1]Landform position; [2]Soil association; [3]Chestnut oak importance value; [4]Average midcanopy depth (m); [5]Hickory saplings, 4th size class; [6]White oak importance value; [7]Beech importance value; [8]Average total canopy depth (m); [9]Average percent full PAR; [10]Blackgum saplings, 4th size class; [11]Sassafras saplings, 4th size class; [12]Black oak importance value; [13]Pine importance value; [14]Northern red oak importance value; [15]Blackgum importance value; [16]Sassafras importance value; [17]Scarlet and Southern red oak importance value.p

DISCUSSION

The dominance of small seedlings in the white oak group on the study sites may have been due to greater seedling shade tolerance in white oak and chestnut oak than in the red oaks. In hardwoods, the shade tolerance of younger seedlings is often greater than that of older saplings (Burns and Honkala 1990). An alternative explanation is that red oak seed sources may have been reduced by past highgrading, which tended to remove the more commercially important species in the red oak group. A final possibility is that conditions and seed crops in recent years were more favorable for establishment of species in the white oak group than in the red oak group. Provided that size can be reasonably correlated with age, the comparable number of all species except scarlet/southern red oak in the large size classes suggest that long-term survival of white, chestnut, black, and northern red oak measuring 151 cm tall and up to 8 cm dbh is comparable.

It is likely that the importance of landform position and soil association in explaining the abundance of oak seedlings was due to strong relationships between these variables and the availability of light and soil moisture (Geiger 1966). As a rule, northern aspects (NW, N, and NE) are typically more moist and cool than southern aspects (SW, S, and SE) due to lower amounts of incoming radiation (Barnes and others 1998).

The disparity between the patterns of abundance in small and large seedlings across soil associations and landform positions suggests that the relative importance of factors influencing survival may change with seedling development. Greater mean number of small oak seedlings on the northwest/mid-slope landform positions suggests that the moist and cool conditions associated with northwest-facing sites may be more important than light for germination and early survival. Greater number of large oak seedlings on the drier and warmer southeastern/mid-slope positions suggests that conditions associated with this slope position may be the most favorable for recruitment into larger seedling size classes. This pattern supports the assertion that oaks are better adapted to droughty conditions than many other hardwoods, and therefore may compete more successfully with other hardwood species on the drier, poorer sites (Thor and others 1969, Abrams 1990).

The contrasting patterns observed in small and large seedlings suggest that the importance of soil moisture may decrease relative to the importance of light as seedlings develop into the larger size classes. This is difficult to determine definitively from our data, however, because the sample size of larger size class seedlings was very low and the difference in mean abundance of large seedlings between the northwest/mid-slope position and southeast/ mid-slope position was slight.

The importance of seed source to oak regeneration is illustrated by the continual occurrence of the importance value of mature oaks of the same species as regenerating oak seedlings in the smaller size class models. In the analyses of the larger oak seedling individual size classes (results not presented), the importance value of seed sources tended to drop out of the regression models, whereas the potential influence of competitors in the overstory and understory tended to become significant.

Positive relationships between the abundance of oak seedlings and abundance of potential competitors such as beech, blackgum, and pine may have resulted from an affinity of these species for the same site conditions as the oak seedlings. The positive relationship between the number of black oak seedlings and pine, for example, may be explained by a similar tolerance of dry sites shared by pine and black oak (Ashton and Berlyn 1994). Positive relationships between oak seedling abundance and canopy depth, and negative relationships between oak seedling abundance and PAR were unexpected. These relationships may have occurred due to the large proportion of total oak reproduction comprised of oak seedlings that were in the small size classes and relatively shade tolerant (particularly seedlings in the white oak group), and the narrow ranges of PAR and canopy cover present on the study sites.

The negative relationships between oak seedling abundance and the abundance of potential competitors such as hickory, sassafras, dogwood, maple, and mature oaks of other species support the current hypothesis that oak reproduction decreases with increasing abundance of competitors (Lorimer 1993, Hodges and Gardiner 1993). Red maple is replacing oaks in many oak-dominated forests (Lorimer 1984) and dogwood and sassafras are ubiquitous throughout the Ridge and Valley Province. The future of dogwood populations is uncertain, however, due to the spread of dogwood anthracnose throughout the region.

CONCLUSION

While seedling density of smaller size class seedlings is above what has been previously reported, the larger size class seedlings and saplings are well below previous estimates for the Southern Appalachians (Cook and others 1998). For example, the low numbers of white, chestnut, black, and northern red oak seedlings in the larger size classes and the complete lack of scarlet/southern red oak seedlings 151 cm tall up to 8 cm dbh indicate that recapture of these sites by oak following future harvests is questionable. Oak stump sprouts would contribute to a portion of total regeneration, but pre-harvest establishment cuts or other treatments may be necessary to stimulate adequate amounts of larger oak advanced reproduction.

The concentration of large oak seedlings on the southeastern/mid-slope positions tends to support the hypothesis that oaks are more competitive on drier, poorer soils, warmer aspects, and upper slope positions where competitors are limited by growing conditions (Weitzman and Trimble 1957, Abrams 1990, Barnes and Van Lear 1998). Patterns in small seedlings, however, do not support this hypothesis. The hypothesis that oak regeneration should increase with the presence of fewer numbers of potential competitors was not supported by relationships between the abundance of oak seedlings and some potential competitors, PAR, and canopy structure. The negative relationships indicated between the number of oak seedlings and hickory, dogwood, sassafras, and maple are consistent with this hypothesis, and support previous assertions that control of these species may be necessary to facilitate oak regeneration in the region.

Whether the disparity in the abundance of large and small oak seedlings between soil associations and landform positions is due to a change in the relative importance of moisture and light as seedling development proceeds, or not, it appears that the abundance of small seedlings may be a poor indicator of the most favorable sites for obtaining larger oak seedlings and saplings in the future. Despite large differences between species in the number of seedlings less than 25 cm tall, the comparable numbers of seedlings in the larger size classes indicate that recruitment into larger seedling size classes is reasonably comparable for all species sampled except scarlet and southern red oak.

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