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Relationships between advance oak regeneration and biotic and abiotic factors†

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Summary Relationships between advance regeneration of four tree species (red maple (*Acer rubrum* L.), white oak (*Quercus alba* L.), chestnut oak (*Q. montana* Willd.) and northern red oak (*Q. rubra* L.)) and biotic (non-tree vegetation and canopy composition) and abiotic (soil series and topographic variables) factors were investigated in 52, mature mixed-oak stands in the central Appalachians. Aggregate height was used as a composite measure of regeneration abundance. Analyses were carried out separately for two physiographic provinces. Associations with tree regeneration were found for all biotic and abiotic factors both in partial models and full models. Red maple was abundant on most of the sites, but high red maple abundance was commonly associated with wet north-facing slopes with little or no cover of mountain-laurel (*Kalmia latifolia* L.) and hay-scented fern (*Dennstaedtia punctilobula* (Michx.) Moore). Regeneration of the three oak species was greatly favored by the abundance of overstory trees of their own kind. White oak regeneration was most abundant on south-facing, gentle, lower slopes with soils in the Buchanan series. Chestnut oak regeneration was more common on south-facing, steep upper slopes with stony soils. There was a positive association between chestnut oak and huckleberry (*Gaylussacia baccata* (Wangh.) Koch) cover classes. Northern red oak was more abundant on north-facing wet sites with Hazleton soil, and was associated with low occurrence of mountain-laurel and hay-scented fern.

Keywords: Appalachians, red maple.

Introduction

Abundance of tree regeneration in mixed-oak forest stands may be affected by both biotic and abiotic factors at stand and landscape scales. Previous observational studies have shown that abiotic factors such as soil series and landform may strongly influence the composition of hardwood forests (Robles et al. 1976, Honeycutt et al. 1982, Host et al. 1987). Similarly, experimental studies have shown that seedlings in mixed-oak stands may exhibit pronounced responses to manipulations of abiotic factors such as prescribed fire, soil scarification and fertilization (Brose and VanLear 1998, Ward and Gluck 1999, Zaczek 2002, Adams and Rieske 2003).

Biotic factors comprise species interactions, manifest through negative and positive associations, that may affect regeneration establishment and survival and, eventually, forest overstory composition. In the mixed-oak forests of the central Appalachians, dense ground covers of blueberry (*Vaccinium* spp.), hay-scented fern (*Dennstaedtia punctilobula* (Michx.) Moore), and other non-tree species can interfere with the development of advance oak regeneration (Allen and Bowersox 1989, Horsley et al. 1992, Steiner and Joyce 1999). Overstory trees play a twofold role in the establishment and survival of regeneration. They provide the necessary seed source for the new cohort, but they reduce understory irradiance and compete for underground resources that are important for tree regeneration.

Throughout eastern Northern America, the natural regeneration of oaks (*Quercus* spp.) appears to be declining and has proved difficult to duplicate artificially. Although the causes of this decline are probably complex (Lorimer 1992), increased regional knowledge of associations between oak regeneration and measurable stand variables is needed to improve silvicultural prescriptions. The objective of our study was to investigate those associations in the central Appalachian region of Pennsylvania based on observational data gathered from 52 forest stands.

Materials and Methods

Study area

The study area crosses the Allegheny Plateau and the Ridge and Valley physiographic provinces of Pennsylvania (Figure 1). In both physiographic provinces, soils in the study stands are derived from sandstone, siltstone, and shale and are typically well drained and support moderately productive forests. Stand elevations range from 250 m above sea level in the Ridge and Valley province to 700 m on the Allegheny Plateau. Precipitation, temperature, and length of growing season vary with latitude and topography. Mean annual precipitation ranges from 960 to 1070 mm and mean annual temperature

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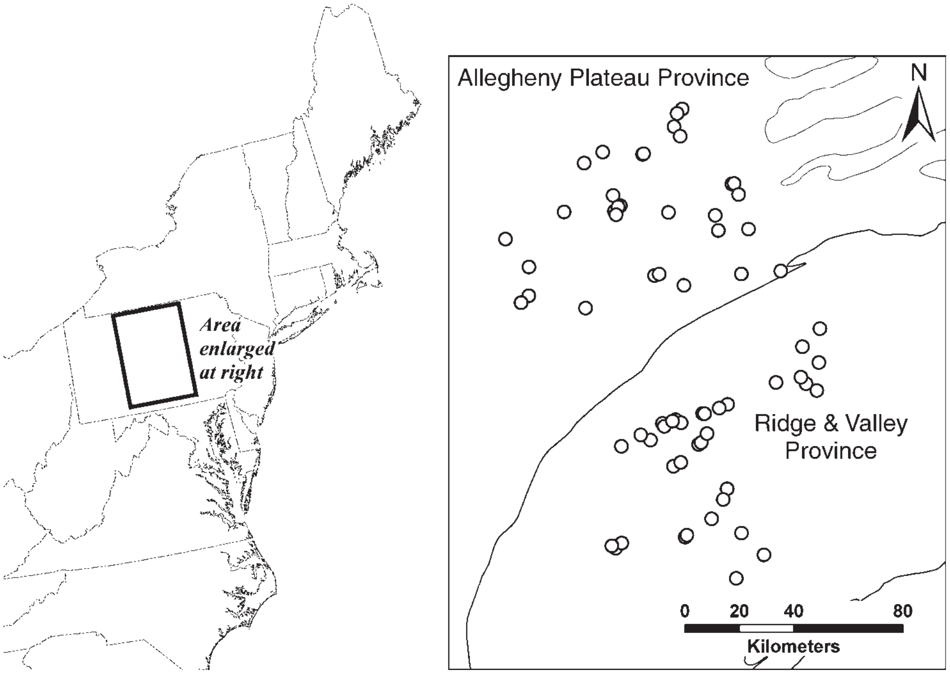

Figure 1. Distribution of study stands in the Ridge and Valley and Allegheny Plateau physiographic provinces in Pennsylvania, USA.

ranges from 8 to 11 °C. The growing season ranges from 120 to 140 days in the northwest, and from 140 to 180 days in the southeast. Forests containing a majority of basal area in oak are the dominant natural vegetation in the Ridge and Valley region. Oak forests transition into Allegheny hardwoods moving from south to north on the Allegheny Plateau, though oaks continue to be locally important in the northern part of Pennsylvania (Bailey et al. 1994, Stout 1991). Most stands in the region regenerated following turn-of-the-century logging, and mature oak stands are typically even aged and between 80 and 100 years old (Stout 2000).

Data collection

Field measurements were made on 52 mixed-oak stands (> 50% of basal area in oak species) comprising a total area of 966 hectares during 1996–2006. Seventeen stands are located on the Allegheny Plateau and 35 stands in the Ridge and Valley physiographic province. Depending on stand size, 15 to 30 permanent, circular plots with an 8.02 m radius were systematically installed in a square grid to represent the whole stand. Four permanent subplots with a radius of 1.13 m were established within each main plot in a systematic arrangement. In total, 5732 subplots were established in the study area. On each subplot, tree seedlings (< 5.1 cm in DBH) were recorded by species and height class. Eight height classes were used (< 5.1, 5.1–15.2, 15.3–30.5, 30.6–61.0, 61.1–91.4, 91.5–121.9, 122.0–152.4 and > 152.4 cm).

Biotic and abiotic conditions were recorded at the stand, plot and subplot scale. Slope position was recorded at the stand scale. At the plot scale, we measured slope shape (sum of percentage slope uphill, down hill and at 90° to aspect), slope percentage, exposure angle (the angle between the visible east horizon and west horizon), slope aspect, and diameter at breast height (DBH) of all overstory trees (≥ 5.1 cm in DBH) by species. At the subplot scale, we measured cover percentage for species or species groups for plants other than tree regeneration. Soil type and elevation for each plot were obtained by superimposing the coordinates of each sampled plot onto the National Soil Information System (USDA-NRCS; http://nasis.usda.gov/) and the 30-meter resolution National Elevation Dataset (USGS; http://ned.usgs.gov/).

Data analysis

Because the Allegheny Plateau and the Ridge and Valley physiographic provinces have different regeneration compositions (Fei et al. 2005), analyses of the relationships between tree regeneration and biotic and abiotic factors were carried out separately for each province. Two biotic factors (non-tree vegetation and overstory trees) and two abiotic factors (soil series and topographic variables) were studied for their relationships with advance regeneration of red maple (*Acer rubrum* L.), the most abundant advance regeneration species, and three oak species (white oak (*Quercus alba* L.), chestnut oak (*Q. montana* Willd.) and northern red oak (*Q. rubra* L.)). First, partial models that included only one biotic or one abiotic factor as the independent variable were applied, and then full models were fit using the significant variables derived from the partial models.

Aggregate height, defined as the total height of all the individuals of a species or species group per unit area (Fei et al. 2006), was used as a measure of regeneration abundance. Aggregate height provides an efficient measure of the relative prevalence of a species at a given stage of development and its ability to persist into future stages (Fei et al. 2006, Gould et al.

2006). Relationships between regeneration abundance and non-tree vegetation were tested at the subplot scale. The four most abundant non-tree vegetation categories: hay-scented fern, mountain-laurel (*Kalmia latifolia* L.), huckleberry (*Gaylussacia baccata* (Wangh.) Koch), and blueberry were selected for inclusion in the analysis. Percentage cover by these four categories of vegetation was defined by four classes: none, low (1 to 10% cover), moderate (11 to 30%), and heavy (over 30%). The heavy class reflects the threshold value of competing vegetation considered problematic by Marquis (1994). Data were subjected to analysis of variance (ANOVA) and means of aggregate height in each cover class were compared by Duncan's multiple range tests (Neter et al. 1996).

The relationship between regeneration abundance and overstory trees was studied at the plot scale. Mean aggregate height was calculated based on the associated four subplots. Basal area of overstory tree species or species groups was calculated for each plot. To minimize the complexity and maximize the degrees of freedom, only the three most abundant non-oak overstory species (red maple, blackgum (*Nyssa sylvatica* Marsh.) and black birch (*Betula lenta* L.)) and three oak species (white oak, chestnut oak and northern red oak) were included in the analysis. Another variable, basal area of other species (BAOT), was created for each regeneration species to assess the crowdedness of overstory species not of its own kind. For example, BAOT for red maple regeneration is calculated by subtracting overstory red maple basal area from the total basal area on a given plot. Multiple linear regressions were applied by setting mean aggregate height of a given species as the response variable and basal areas of overstory tree species as the independent variables. Backward stepwise elimination procedure was applied to achieve the best-fit models.

Because there were 74 soil types in the surveyed stands, an ANOVA with all the soil types would lack statistical power and be hard to comprehend. Therefore, to facilitate the analysis and to minimize errors associated with map resolution, soil types were grouped into soil series or associations. Soil series or associations that occurred on fewer than 3% of the surveyed plots or in fewer than two stands were excluded from the analysis. Six soil series and one soil association in the Ridge and Valley and four soil series on the Allegheny Plateau were included in the analysis. Their general properties are summarized in Table 1. The resulting data were subjected to ANOVA and means of aggregate height in each soil series were compared by Duncan's multiple range tests.

Mixed models were applied to study the relationship between regeneration abundance and topographic variables. Slope aspect, θ, is a circular variable, and attention must be given to its periodic nature during model building. In this analysis, the effect of aspect was modeled through a linear combination of the two variables, $\sin\theta$ (which measures east–west effects) and $\cos\theta$ (which measures north–south effects). Slope percent (SL), slope shape (SH), $\sin\theta$ (AX), $\cos\theta$ (AY), exposure angle (EX) and elevation (EL) were set as numerical independent variables, slope position (PO) was set as a categorical independent variable, and mean plot aggregate height was set as the response variable. Backward stepwise elimination procedure was applied to achieve the best fit models. Because 16 of the 17 stands on the Allegheny Plateau had the same slope position, this variable was omitted from models of Allegheny Plateau stands.

Finally, full models for the four regeneration species were developed at the plot scale by pooling all significant biotic and abiotic factors derived from the partial models. Mixed models

Table 1. Summary of general properties of common soil series and associations in the study area (USDA Soil Conservation Service 1981, 1993).

Type	Depth	Drainage	Parent material	Permeability	Slope (%)
Berks	Moderate	Good	Residuum of shale, siltstone, and fine sandstone	Moderate to moderately rapid	0–80
Buchanan	Very deep	Poor to moderate	Sandstone colluvium	Slow to moderate	0–45
Clymer	Deep	Good	Residuum from sandstone, shale and siltstone	Moderate	0–80
Cookport	Deep to very deep	Moderate	Residuum from sandstone, shale and siltstone	Slow to moderate	0–25
Hazleton	Deep to very deep	Good	Residuum of acid gray, brown, or red sandstone	Moderately rapid to rapid	0–80
Hazleton-Dekalb	Moderate to deep	Excessive to good	Residuum of acid gray and brown sandstone	Moderately rapid to rapid	0–80
Laidig	Very deep	Good	Colluvium from sandstone, siltstone, and some shale	Moderate to moderately rapid	0–55
Meckesville	Very deep	Good	Colluvium, glacial till, or congeliturbate from red acid sandstone, siltstone, and shale	Moderately slow	0–60
Ungers	Deep to very deep	Good	Residuum of red sandstone and shale	Moderate	0–60
Wharton	Deep to very deep	Moderate	Residuum from interbedded clay shale, siltstone, and fine sandstone	Slow to moderately slow	0–35

were applied in model building. Multicollinearity was checked between the independent variables before fitting the models. To simplify the analysis, interaction terms were omitted.

Results

Advance regeneration abundance versus non-tree vegetation

Associations between non-tree vegetation cover class and advance tree regeneration abundance were found in both physiographic provinces (Figure 2). Red maple regeneration abundance was significantly associated with the abundance of all of the non-tree vegetation categories in the Ridge and Valley, and was significantly associated with the abundance of huckleberry, mountain-laurel, and hay-scented fern on the Allegheny Plateau. In both provinces, red maple regeneration abundance was significantly reduced under heavy cover of mountain-laurel and hay-scented fern.

White oak regeneration abundance was significantly associated with the abundance of all non-tree vegetation categories in the Ridge and Valley, but no significant association was found on the Allegheny Plateau (probably because there was so little white oak regeneration). White oak regeneration was significantly more abundant when associated with low to moderate cover of huckleberry or moderate cover of blueberry, and was significantly lower when associated with moderate to heavy cover of mountain-laurel or hay-scented fern.

Chestnut oak regeneration abundance was significantly associated with the abundance of all non-tree vegetation categories in the Ridge and Valley, and was significantly associated with the abundance of huckleberry and mountain-laurel on the Allegheny Plateau. Consistent associations of chestnut oak regeneration and huckleberry and cover were found across the physiographic provinces. Chestnut oak regeneration abundance increased monotonically as huckleberry cover thickened, and chestnut oak regeneration abundance was significantly higher when associated with heavy huckleberry cover.

An association between northern red oak regeneration and huckleberry abundance was found in the Ridge and Valley. Higher northern red oak abundance was observed on plots with moderate cover of huckleberry. On the Allegheny Plateau, northern red oak regeneration abundance was signifi-

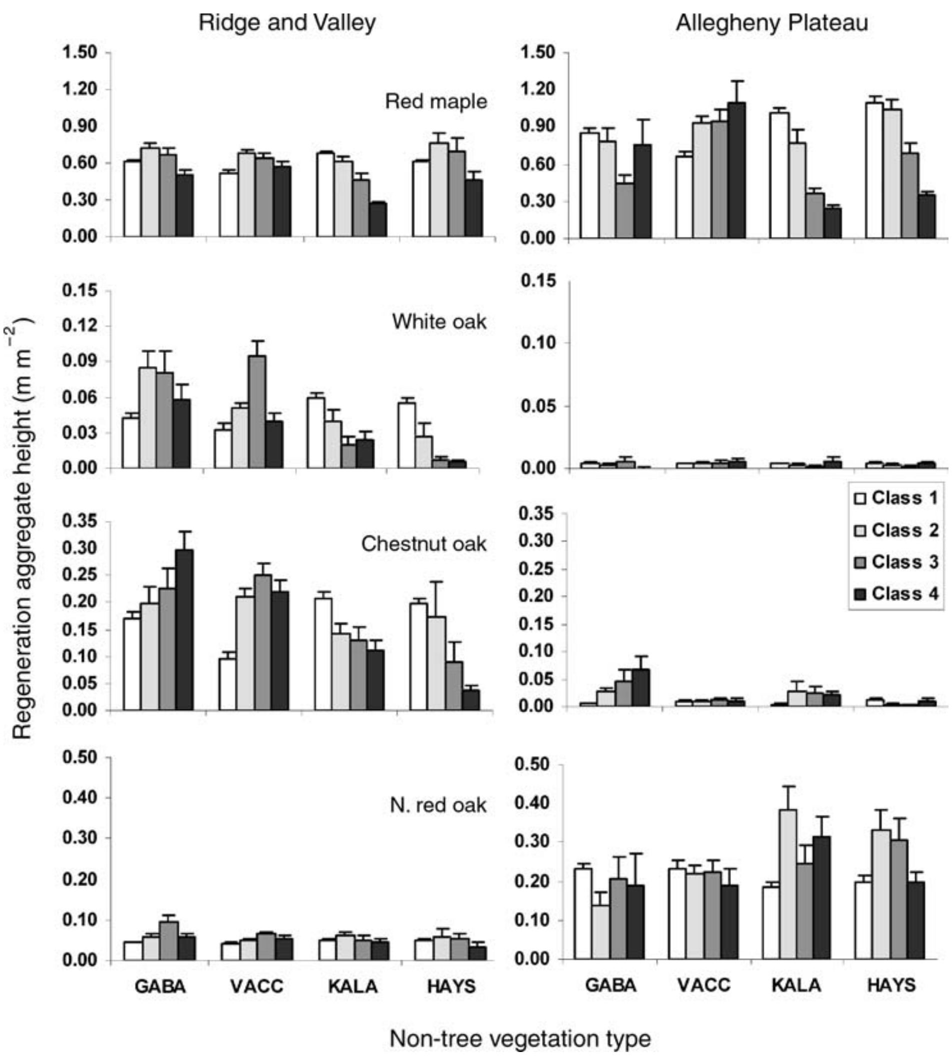

Figure 2. Mean and stand deviation of advanced regeneration abundance of four tree species, as expressed as regeneration aggregate height, under different cover classes (Class 1: no cover; Class 2: 1–10%; Class 3: 11–30%; Class 4: > 30%) of four non-tree vegetation species (GABA, huckleberry; VACC, blueberry; KALA, mountain-laurel; and HAYS, hay-scented fern) in the Ridge and Valley and the Allegheny Plateau physiographic provinces.

cantly affected by mountain-laurel and hay-scented fern abundance. Northern red oak regeneration was most abundant with moderate mountain-laurel or hay-scented fern cover.

Advance regeneration abundance versus overstory trees

The oak species studied had positive associations with overstory trees of their own species, and negative associations with total basal area not of their own kind (Table 2). That is, their regeneration aggregate height increased as the total basal area of their own kind increased, and decreased as the total basal area of species other than their own increased. This trend held for the three oak species in both provinces. Red maple, blackgum and black birch did not qualify to enter the final models as individual overstory tree species because they did not significantly associate with oak regeneration abundance in either physiographic province.

Relationships between red maple regeneration abundance and overstory trees differed with physiographic province. Red maple regeneration was unaffected by overstory trees of its own species or by the total basal area not of its own kind. Red maple regeneration had negative associations with chestnut oak and northern red oak in the Ridge and Valley province, but a positive association with northern red oak on the Allegheny Plateau province. Because it is possible that different mechanisms are operating on red maple regeneration in the two provinces, the overstory tree associations were omitted from the final full models for red maple regeneration.

Advance regeneration abundance versus soil types

Regeneration abundance for different soil series is shown in Table 3. No direct comparisons can be made between the provinces because these provinces share only one common soil series (Hazleton series). In the Ridge and Valley province, red maple occurred on almost all the surveyed plots. Its mean aggregate height was greatest on the Ungers series, followed by the Hazleton-Dekalb association and the Meckesville series, and was the lowest on the Berks series. White oak had a low occurrence frequency overall. Although white oak occurrence frequency was highest on the Ungers soil, its mean aggregate height was significantly greater on the Buchanan soil than the other soil series. Chestnut oak regeneration had the greatest mean aggregate height on the Hazleton-Dekalb association, followed by the Meckesville series. Chestnut oak had the lowest occurrence frequency and the least mean aggregate height on the Berks series. Northern red oak had relatively similar occurrence frequency on all the soil series. Its mean aggregate height was greatest on the Hazleton series, followed by the Hazleton-Dekalb association, and least on the Berks series. Although each species was most abundant on different soil series, all species had their poorest regeneration on the Berks series.

On the Allegheny Plateau, red maple regeneration abundance was highest on the Cookport series, followed by the Wharton and the Clymer series. Both white oak and chestnut oak had low mean aggregate height and occurrence frequency on all the soil series. White oak had some regeneration on the Wharton series, and virtually none on the other three soil series. Chestnut oak had some regeneration on the Cookport series, and virtually none on the other three soil series. Northern red oak regeneration was least on the Wharton series both in mean aggregate height and occurrence frequency, but there were no significant differences in mean aggregate height among the other soil series.

Advance regeneration abundance versus topographic factors

Relationships between regeneration abundance and topographic factors were more complicated than with other biotic or abiotic factors. Results derived from the mixed models are presented in Table 4 for numerical topographic variables in both physiographic provinces, and in Table 5 for the categorical factor slope position in the Ridge and Valley.

In the Ridge and Valley region, red maple regeneration was most abundant on valley bottoms or lower slopes with a north-facing aspect (positive association with $\cos \theta$). Abundant white oak regeneration was associated with low elevation, valley bottom gentle slopes with a south-facing aspect. Abundant chestnut oak regeneration was also associated with south-facing slopes, but it was more commonly associated with steep slopes and upper-slope positions. Northern red oak was more abundant on north-facing slopes with a relative

Table 2. Relationship between advance regeneration abundance and basal area of overstory tree species (OT: other species not of its own kind). Symbols: 0 denotes no significant association; + denotes positive association; and – denotes negative association between advance regeneration abundance and basal area of overstory trees. Significant values are indicted by asterisks: *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$).

Physiographic province	Regeneration species	Association with overstory species				
		Red maple	White oak	Chestnut oak	Northern red oak	OT
Ridge and Valley	Red maple	0	0	–**	–**	0
	White oak	0	+**	0	0	–**
	Chestnut oak	0	0	+**	0	–**
	N. red oak	0	0	0	+***	–**
Allegheny Plateau	Red maple	0	0	0	+**	0
	White oak	0	+**	0	0	–*
	Chestnut oak	0	0	+**	0	–*
	N. red oak	0	0	0	+**	–*

Table 3. Mean aggregate height (AvgAH; m m^{-2}) and occurrence frequency (Freq.; % of plots with AvgAH > 0) of four regeneration species on common soil series or associations in the Ridge and Valley and Allegheny Plateau physiographic provinces. (n = number of plots; N = number of stands). Statistical tests were based on plots. Within the same column in each province, mean aggregate height values not sharing the same letters are significantly different at $P < 0.05$.

Soil series or associations	Red maple		White oak		Chestnut oak		Northern red oak	
	AvgAH	Freq.	AvgAH	Freq.	AvgAH	Freq.	AvgAH	Freq.
Ridge and Valley								
Berks (n = 37, N = 4)	0.226 d	100	0.002 b	14	0.007 c	8	0.009 c	59
Buchanan (n = 114, N = 12)	0.618 bc	100	0.100 a	51	0.187 b	65	0.050 bc	60
Hazleton (n = 61, N = 5)	0.420 cd	100	0.002 b	3	0.141 bc	59	0.126 a	72
Hazleton-Dekalb (n = 141, N = 13)	0.898 ab	99	0.026 b	30	0.362 a	79	0.066 ab	79
Laidig (n = 309, N = 18)	0.479 cd	99	0.019 b	26	0.152 bc	71	0.037 bc	71
Meckesville (n = 60, N = 3)	0.834 ab	100	0.001 b	10	0.216 ab	82	0.041 bc	57
Ungers (n = 33, N = 3)	0.936 a	100	0.041 b	58	0.129 bc	58	0.032 bc	73
Allegheny Plateau								
Clymer (n = 130, N = 9)	0.854 ab	99	0.002 b	10	0.004 b	12	0.229 a	82
Cookport (n = 120, N = 9)	1.106 a	99	0.002 b	13	0.018 a	18	0.152 a	87
Hazleton (n = 99, N = 7)	0.547 b	99	0.003 b	8	0.004 b	10	0.270 a	96
Wharton (n = 54, N = 3)	0.866 ab	100	0.011 a	33	0.005 b	13	0.011 b	61

small exposure angle, and was more commonly associated with high-elevation ridge top, upper-slope positions, or benches.

In the Plateau region, red maple regeneration was more commonly associated with north-facing slopes, small exposure angles, and high elevations. Abundant white oak regeneration was associated with concave slopes and a southern aspect. Chestnut oak regeneration was more abundant on steeper slopes, and northern red oak regeneration was more abundant on west-facing slopes. Although different association patterns were identified across provinces, they still share some similarity. In both provinces, red maple regeneration was positively associated with north-facing slopes, whereas white oak was positively associated with south-facing slopes, and chestnut oak was positively associated with steep slopes.

Table 4. Relationships between advance regeneration abundance and topographic factors in the Ridge and Valley and Allegheny Plateau physiographic provinces. Abbreviations and symbols: SL, slope percent; SH, slope shape; AX, sin θ; AY, cos θ, where θ is the slope aspect; EX, exposure angle; EL, elevation; 0 denotes no significant association; + denotes a positive association; and – denotes a negative association ($P < 0.05$).

Regeneration Species	Association with topographic factors					
	SL	SH	AX	AY	EX	EL
Ridge and Valley						
Red maple	0	0	0	+	0	0
White oak	–	0	0	–	+	–
Chestnut oak	+	0	0	–	0	0
N. red oak	0	0	0	+	–	+
Allegheny Plateau						
Red maple	0	0	0	+	–	+
White oak	0	+	0	–	0	0
Chestnut oak	+	0	0	0	0	0
N. red oak	0	0	–	0	0	0

Full model of advance regeneration with biotic and abiotic factors

Biotic and abiotic factors included in the full models for red maple and three oak species are listed in Table 6. Full models provided a comprehensive view of the association between regeneration abundance and biotic and abiotic factors. Full models for the oak regeneration species were similar among species and between the two physiographic provinces. Regardless of province, oak regeneration was positively associated with the abundance of overstory trees of its own kind and was significantly related to soil series. Models for red maple regeneration showed little consistency, except that in both regions red maple decreased in abundance as mountain-laurel cover increased.

In the Ridge and Valley region, slope aspect and position were the other factors that had significant associations with re-

Table 5. Regeneration abundance on different slope positions (1, ridge top; 2, upper slope; 3, mid slope; 4, lower slope; 5, bench; and 7, bottom) by species in the Ridge and Valley physiographic provinces. Within a column, mean aggregate height values not sharing the same letters are significantly different at $P < 0.05$.

Slope position	Mean aggregate height (m m^{-2})			
	Red maple	White oak	Chestnut oak	N. red oak
1 (n = 79)	0.58 b	0.00 c	0.03 c	0.09 ab
2 (n = 130)	0.40 b	0.01 c	0.35 a	0.11 a
3 (n = 401)	0.56 b	0.06 b	0.16 bc	0.03 c
4 (n = 126)	0.84 a	0.04 bc	0.22 b	0.02 c
5 (n = 77)	0.83 a	0.04 bc	0.12 bc	0.09 ab
7 (n = 45)	0.93 a	0.18 a	0.11 bc	0.07 b

Table 6. Biotic and abiotic factors (non-tree vegetation cover (GABA, huckleberry; VACC, blueberry; KALA, mountain-laurel; and HAYS, hay-scented fern); basal area of mature overstory trees (BAQA, white oak basal area; BAQM, chestnut oak basal area; BAQR, northern red oak basal area; and BAOT, basal area of trees not of its own species)); soil series or association (SS); and topographic factors (PO, slope position; SL, slope percent; SH, slope shape; AX, sin θ; AY, cos θ, where θ is the slope aspect; EX, exposure angle; and EL, elevation)) that significantly associated with regeneration abundance of red maple, white oak, chestnut oak, and northern red oak ($P < 0.05$). Superscript "+" denotes positive association and superscript "–" denotes negative association).

Regeneration species	Influential factors ($P < 0.05$)	
	Biotic	Abiotic
Ridge and Valley		
Red maple	KALA, VACC	SS, AY $^+$, PO
White oak	BAQA $^+$	SS, AY $^-$, SL $^-$
Chestnut oak	BAQM $^+$, BAOT $^-$, GABA, KALA	SS, AY $^-$, PO
N. red oak	BAQR $^+$, BAOT $^-$	SS, AY $^+$, PO, EL $^+$
Allegheny Plateau		
Red maple	KALA, HAYS	EX $^-$, EL $^+$
White oak	BAQA $^+$	SS, SH $^+$
Chestnut oak	BAQM $^+$, GABA	SS
N. red oak	BAQR $^+$, HAYS, KALA	SS

generation abundance, other than slope position for white oak. Both chestnut oak and northern red oak abundance decreased as the total basal area for species not of their own kind increased. Chestnut oak regeneration abundance was positively associated with huckleberry cover classes.

Models for the Allegheny Plateau were simpler than for the Ridge and Valley region. Regeneration of the three oak species was favored by the abundance of overstory trees of their own kind, but it was not significantly associated with species not of its own kind. Soil was the only abiotic factor that was significantly associated with the regeneration abundance of chestnut oak and northern red oak.

Discussion

Forest composition and structure are shaped by interactions with the physical environment (abiotic factors), biotic interaction (competition, facilitation), and disturbance (natural or anthropogenic). Because of changes in the physical environment (e.g., climate change and increased CO_2 concentrations), disturbance regimes (e.g., wildfire and forest management practice) or biotic interactions (e.g., wildlife population and invasive species), forest composition and structure as they have existed historically may be undergoing perceptible shifts. Therefore, it is not surprising to observe within the same stand patches that differ in regeneration composition and abundance even though the overstory stand composition is relatively uniform.

Results from the partial models and full models indicated that non-tree vegetation, overstory composition, soil and topographic variables all influence regeneration abundance. However, relationships varied among species and between regions, and some factors were more influential than others as indicated by the number of times they qualified to enter the full model. Soil series or association, which is a composite representation not only for parent materials drainage and permeability, but also for slope position and slope percent, was significant in all models for all species in both regions, except red maple on the Allegheny Plateau. White oak regeneration was most abundant on the Buchanan series, chestnut oak regeneration was most abundant on the Hazleton-Dekalb association, northern red regeneration was most abundant on the Hazleton soils, where red maple had relatively abundant regeneration on almost every soil series except the Berks series.

Overstory composition was the other highly influential factor for tree regeneration. It was significant in the full model for all three oak species in both regions. The associations between overstory oak trees and understory oak regeneration were overwhelmingly consistent among species and across regions, even though oaks (primarily chestnut oak and northern red oak) comprised more than 50% of the overstory basal area in every stand studied. Oak regeneration was favored by the presence of mature overstory trees of its own species within the same plot and was inhibited by other species. This association is presumably attributable to the reproductive characteristics of oak species. Although small mammals and birds may disperse acorns long distances (Barnett 1977, Johnson and Adkisson 1986), most acorns that are not eaten necessarily remain in the vicinity of the mother tree. More adult oak trees produce more acorns that likely germinate to produce more oak seedlings. Another biological characteristic of oaks is that oak seedlings are intolerant of shade (Johnson et al. 2002), and presumably grow better under the shade cast by oaks than that of trees that are more shade-tolerant, such as red maple and blackgum, and that have higher leaf area indices.

Red maple showed no tendency to regenerate better near trees of its own kind. However, red maple seeds are winged and dispersed by wind, and red maple was generally abundant in the stands we studied: there were 222 red maple trees per ha or one red maple tree per 45 m^2 grid on average. In our stands, seed source appears not to be a limiting factor for red maple regeneration even at the scale of an 8.02-m-radius plot. Red maple is a shade-tolerant species (Walters and Yawney 1990), a characteristic that helps red maple seedlings to establish regardless of canopy density. A combination of these factors may explain the lack of association between red maple overstory and red maple regeneration.

Non-tree vegetation had a major influence on tree regeneration but in ways that varied among species. Subplots with moderate blueberry and huckleberry cover had the highest or second highest white oak regeneration abundance, and subplots with heavy huckleberry cover and moderate blueberry cover had the highest chestnut oak regeneration abundance in both regions. Rogers (1974) pointed out that heath communities dominated by blueberry and huckleberry have an affinity for infertile sites with well-drained acidic soils. The affinity of some oaks for similar environmental conditions may at least partially explain why regeneration of white oak and chestnut oak was associated with blueberry and huckleberry. Regeneration of all species was inhibited to some degree by the presence of moderate to heavy cover of mountain-laurel and hay-scented fern. Competition from hay-scented fern has been identified as an important factor contributing to the decline in regeneration of mixed-oak forests in Pennsylvania (McWilliams et al. 1995, Steiner and Joyce 1999). Hay-scented fern has been classified as a competitor species because of its ability to respond aggressively to sudden increases in resource availability with vegetative expansion through rhizomes and sexual reproduction (Groninger and McCormick 1991, Hughes and Fahey 1991). Mountain-laurel is another strong regeneration competitor because of its aggressive vegetative growth habit (Moser et al. 1996). Chapman (1950) reported that irradiances underneath mountain-laurel canopies may be only about 2% of full sunlight. Although mountain-laurel has little effect on regeneration establishment, it suppresses the growth of small seedlings (Waterman et al. 1995). The competition from heavy cover of hay-scented fern or mountain-laurel, or both, was so intense that even the relatively shade-tolerant red maple was greatly inhibited under these species in our study area.

Although different topographic factors were included in the full models, they can be grouped by their effects on regeneration. Low-slope positions, gentle slopes, and low elevations are characteristics of the valley floor and are favored by white oak. South-facing slopes, large exposure angles, and convex slopes provide dry and sunny conditions that are favored by white oak. Abundant chestnut oak regeneration was associated with south-facing and relatively steep, upper slopes, whereas northern red oak was associated with wet north-facing slopes. Although red maple regeneration can be found on any site, it was more abundant on wet north-facing slopes. Not all physiographic variables entered into the full model, perhaps because of the co-linearity between soil types and some of the physiographic variables mentioned above.

Other factors such as deer browsing, seed crop fluctuation, disturbance history, and stochastic variation in climate are also important to tree regeneration. These factors could change the regeneration patterns that we observed. Because we lack good information on these and other factors, caution is needed when applying our results to field management. Furthermore, the statistical associations we have described do not necessarily imply biological significance, because the associations might arise from shared relationships with other, unmeasured factors rather than direct, biological interactions. In addition, interaction terms were excluded from the full model to minimize model complexity. The interaction between overstory tree and understory non-tree vegetation could have a significant effect on tree regeneration, and it deserves further investigation. Despite these shortcomings, our study provided specific regional knowledge of the advantages and limitations associated with biotic and abiotic factors for tree regeneration. When time and resources are limited, forest managers should focus on areas that have good regeneration potentials and work to control or reduce limiting factors such as fern and mountain-laurel covers.

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