SITE CHARACTERISTICS OF AMERICAN CHESTNUT, OAK, AND HICKORY WITNESS TREES ON THE MONONGAHELA NATIONAL FOREST, WEST VIRGINIA

Melissa Thomas-Van Gundy and Michael Strager1

Abstract.—Early metes and bounds surveys of the area that would become the Monongahela National Forest in West Virginia were used to create a digital database of corner witness trees. With these electronic and geo-referenced data, physical characteristics were obtained to describe species’ locations on the landscape. To characterize the physical environment, variables associated with the corner points were extracted from existing spatial datasets and derived from a digital elevation model. The terrain components that were assessed included topographic roughness, moisture index, aspect, and landform. Calculations were made for American chestnut, several oak species, and hickory species. Species-site associations differed by subsection. American chestnut, chestnut oak, and scarlet oaks, however, were generally found in areas of low moisture and at moderate elevations. White oak was more likely on areas of high moisture and valley floor landforms. Northern red oaks were more likely on S-SE facing benches with low moisture levels. While few differences between subsections were noted for these species, construction of predictive models should consider subsectional differences.

INTRODUCTION

Information is lacking for much of the eastern United States on historical forest conditions due to almost complete forest clearing at the turn of the 19th century. Descriptions and quantitative assessments of early forests are useful in restoration ecology and can come from many sources, such as deeds, traveler’s accounts, and photographs. Although these descriptions represent a static point in time, they can be a source of information for the time of European settlement (Whitney and DeCant 2001).

The recording of witness trees in deeds as corner markers for parcel boundaries has often been used to describe European settlement-era vegetation (Abrams and Ruffner 1995; Black and Abrams 2001a, 2001b; Whitney and DeCant 2003; Rentch and Hicks 2005). Land transfers in most eastern forests followed survey methods called “metes and bounds,” consisting normally of bearings, distances, and species of tree used to witness property corners. Several authors have discussed the possibility of bias in witness tree databases, mainly pertaining to rectangular land surveys. Nonetheless, the usefulness of the data has been shown to generally outweigh the potential biases (Bourdo 1956, Siccama 1971, Whitney 1994).

Previous witness tree analysis in the Monongahela National Forest (MNF) determined that pre-European settlement Northern Ridge and Valley Section forests were dominated by mixed oak (Quercus spp.),

1Research Forester (MT-VG), Northern Research Station, USDA Forest Service, P.O. Box 404, Parsons, WV 26287; Assistant Professor (MS), West Virginia University, Morgantown, WV 26506-6108. MT-VG is corresponding author: to contact, call (304)478-2000 or email at mthomasvangundy@fs.fed.us.
pine (*Pinus* spp.), American chestnut (*Castanea dentata* [Marsh.] Borkh.), and hickories (*Carya* spp.) on ridges while the valley floors were dominated by white oak (*Q. alba* L.), sugar maple (*Acer saccharum* Marsh.), pine, basswood (*Tilia* spp.), and hemlock (*Tsuga canadensis* [L.] Carrière) (Abrams and McCay 1996). In the Allegheny Mountains Section, beech (*Fagus grandifolia* Ehrh.)-hemlock-pine forests dominated mountain tops and hemlock-maple-birch (*Betula* spp.) forests were found on valley floors (Abrams and McCay 1996).

In the 1930s, staff of the MNF collected deeds and land grants of the earliest granted tracts of land within the MNF proclamation boundary. Dates of these deeds and land grants range from 1752 to 1910. Between 2005 and 2009, these data were converted to a spatial database in a geographic information system (GIS). With these geo-referenced data, physical characteristics associated with species locations can be obtained to describe where species were found on the landscape.

The goal of this research is to characterize the European settlement-era forests based on these witness tree data. Specifically, we intend to: 1) characterize the spatial distribution of selected species; and 2) characterize the early forests of the MNF in terms of relationships between species and physical variables. The tree species assessed were American chestnut, white oak, chestnut oak (*Q. prinus* L.), northern red oak (*Q. rubra* L.), scarlet oak (*Q. coccinea* Münchh.), black oak (*Q. velutina* Lam.), and hickory species. The oak and hickory species were selected for analysis because they often dominate the central hardwoods forest (Fralish 2003) and American chestnut was selected because of its historical extent in the central hardwoods forest and study area. This information may then be used in studies for occurrence modeling and future restoration efforts.

**STUDY AREA**

Most of the witness tree locations are within 5 km of the proclamation boundary, creating a study area of approximately 689,000 ha. The MNF in eastern West Virginia consists of complex topography in both the Allegheny Mountains and Northern Ridge and Valley physiographic sections (Fig. 1). The MNF includes the highest point in West Virginia and many valleys which quickly drop more than 800 m in elevation. This complexity results in a great variety of landforms and conditions for vegetative diversity.

Subsections represented on the MNF include: Eastern Allegheny Mountain and Valley (EAMV), Eastern Coal Fields (ECF), Northern High Allegheny Mountain (NHAM), Ridge and Valley (RV), Southern High Allegheny Mountain (SHAM), Western Allegheny Mountain (WAM), and Western Allegheny Mountain and Valley (WAMV) (Cleland and others 2007).

The moisture and temperature regimes of the subsections are described in detail in Table 1 (Cleland and others 2007). In general, the RV subsection is warm and dry and the WAMV subsection dry with moderate temperatures. The ECF subsection is warm and moderate in overall moisture. The EAMV subsection is moderate in both moisture and temperature regimes, and the WAM subsection is cool with moderate moisture. The SHAM and NHAM subsections are both wetter than the other subsections; however, NHAM has the lowest average temperatures while SHAM is more moderate.

Appalachian oak forest is the primary potential natural vegetation for the RV, EAMV, and WAMV subsections. In contrast, Northern hardwood is the primary potential natural vegetation for the NHAM and SHAM subsections. The mixed mesophytic type is the primary potential natural vegetation for the WAM and ECF subsections (Cleland and others 2007; Table 1).
Figure 1.—Study area location with corner locations. Thicker line is boundary between Northern Ridge and Valley and Allegheny Mountains Sections. EAMV = Eastern Allegheny Mountain and Valley, ECF = Eastern Coal Fields, NHAM = Northern High Allegheny Mountain, RV = Ridge and Valley, SHAM = Southern High Allegheny Mountain, WAM = Western Allegheny Mountain, and WAMV = Western Allegheny Mountain and Valley.
Table 1.—Selected subsection climate and potential natural vegetation attributes (Cleland and others 2007).

<table>
<thead>
<tr>
<th></th>
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<th></th>
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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>RV</td>
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<td>4.1</td>
<td>-7.1</td>
<td>82.6</td>
<td>102.3</td>
</tr>
<tr>
<td>NHAM</td>
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<td>2.0</td>
<td>-9.4</td>
<td>263.5</td>
<td>128.2</td>
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<tr>
<td>WAM</td>
<td>15.1</td>
<td>3.0</td>
<td>-8.8</td>
<td>187.8</td>
<td>122.2</td>
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<td>SHAM</td>
<td>15.2</td>
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<td>-9.0</td>
<td>224.5</td>
<td>138.1</td>
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<td>111.0</td>
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<tr>
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<td>85.6</td>
<td>99.7</td>
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<tr>
<td>ECF</td>
<td>17.5</td>
<td>4.5</td>
<td>-6.8</td>
<td>94.9</td>
<td>113.7</td>
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Potential Natural Vegetation (%)

<table>
<thead>
<tr>
<th></th>
<th>Appalachian oak forest</th>
<th>Mixed mesophytic forest</th>
<th>Northeastern spruce-fir forest</th>
<th>Northern hardwoods</th>
<th>Oak-hickory-pine forest</th>
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<tr>
<td>RV</td>
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<td>0.7</td>
<td>9.2</td>
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<tr>
<td>NHAM</td>
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<td>14.3</td>
<td>80.4</td>
<td>5.4</td>
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<tr>
<td>WAM</td>
<td>26.6</td>
<td>38.0</td>
<td>35.3</td>
<td>0.1</td>
<td></td>
</tr>
<tr>
<td>SHAM</td>
<td>4.5</td>
<td>23.3</td>
<td>21.1</td>
<td>51.2</td>
<td></td>
</tr>
<tr>
<td>EAMV</td>
<td>58.9</td>
<td>0.2</td>
<td>40.9</td>
<td></td>
<td></td>
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<tr>
<td>WAMV</td>
<td>85.9</td>
<td>1.1</td>
<td>13.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ECF</td>
<td>28.1</td>
<td>51.7</td>
<td>20.2</td>
<td></td>
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</tr>
</tbody>
</table>

EAMV = Eastern Allegheny Mountain and Valley, ECF = Eastern Coal Fields, NHAM = Northern High Allegheny Mountain, RV = Ridge and Valley, SHAM = Southern High Allegheny Mountain, WAM = Western Allegheny Mountain, and WAMV = Western Allegheny Mountain and Valley.

METHODS

DATA COLLECTION

The parcel descriptions from the old deeds (1752 to 1910) were used in the 1930s to plot the parcels on maps. The resulting 83 planimetric maps of uniquely identified individual parcels cover an area of approximately 10,832 ha each; the maps overlap and non-MNF area was included. The full dataset includes deeds up to 1910, but this analysis includes deeds/corners up to 1900.

In 2005, the 1930s maps were scanned and geo-referenced, using at least four tie points. Geo-referencing was done using the GIS software in ArcMap (ESRI, Redlands, CA, 2002) by linking coordinates on the scanned maps to the 1:4800 State Addressing Mapping Board orthophotos. The maps were used as a base for digitizing the corners of each parcel. In 2009, manual digitizing of corners was completed using GIS at a scale of 1:5000. The hand-drawn features and printed map line of the 1930s maps, now scanned, were used to create and place corners, creating points in a digital file. The deeds were used to determine corners on the maps and enter tree species or other markers in the attribute field. Trees mentioned in the deeds as rock oak were treated as chestnut oaks (Strausbaugh and Core 1977), and those named span, Spanish, or pin oaks were tallied as scarlet oak (Burns and Honkala 1990).

At each corner, a relative frequency of each species was calculated by dividing the number of trees of each species at the corner by the total number of trees at the corner (Wang and others 2009). The relative compositions of the corners allowed for the use of spatial autocorrelation statistics. For indicator species analyses these relative frequencies were converted to presence or absence of a species at each corner.
SPATIAL AND STATISTICAL ANALYSES

To assess the diverse topography, climate, and soils of the study area, the analyses were stratified by ecological sub-section (Black and Abrams 2001a). This stratification should also address the possible bias for some landforms (Black and Abrams 2001a). Spatial statistics were used to describe the distribution of the witness trees by species and to discern patterns in the distribution.

To identify overall patterns in the witness trees, Moran’s I was calculated in ArcGIS (ESRI, Redlands, CA 2002) using the species’ relative frequency as the attribute value and calculating the spatial autocorrelation from just those points with the selected species present (the number of points used differed by species). This measure of spatial autocorrelation is a broad comparison of the study locations to a theoretical random distribution of points and associated values. Moran’s I ranges from -1 to +1. Scores closer to +1 indicate clustered distributions, scores closer to -1 identify uniform or dispersed patterns, and values close to 0 indicate random patterns. The strength of any pattern discerned in the spatial data is reflected in a calculated Z-score; a 95-percent confidence interval was used (α = 0.05).

To characterize the physical site characteristics associated with tree species of the European settlement-era forests, environmental variables at the corner points were extracted from existing spatial datasets and variables derived from an 18-m digital elevation model (DEM). Physical components assessed were topographic roughness, a moisture index, aspect, landform, and elevation. The corner points were buffered by 21 m, which is the spatial error of the dataset calculated from measurements of images on the scanned maps used to place digital points.

Topographic roughness (TRI) was calculated as the square root of the sum of squared differences in elevation between a cell and its eight neighboring cells (Riley and others 1999). A moisture index was calculated as the natural log of flow accumulation +1, divided by slope +1 of a target cell (Anderson and Merrill 1998). Elevation, moisture index, and topographic roughness index were all calculated as an average for a 21-m radius around the corner location. These averages were then classified into high, medium, and low groups based on quantiles. Low elevations ranged from 1 to 698 m, moderate elevations were between 698 and 872 m, and more than 872 m was considered high elevation. Low TRI ranged from 1 to 32.4 m, moderate TRI from 32.5 to 68.1 m, and high from 68.2 to 224.7 m.

Aspect, elevation, topographic roughness, and the moisture index were derived from the 18-m DEM of the study area. Landforms were extracted from an existing spatial dataset of the MNF. Landforms include: ridge/peak, bench/plateau, toe slope, side slope, cove, and valley floor. Buffering the corners by 21-m resulted in species-landform tallies that duplicated some corners as the buffer could encompass more than one landform.

To determine significant associations, indicator species analysis on the presence/absence of species by site variable was conducted in PC-ORD (McCune and Mefford 2006). Indicator species analysis is a multivariate, non-parametric method to describe relationships between species and environmental groups based on proportional frequencies of the species by groups; groups are based on the categorical site variables. Statistical significance (α = 0.05) is computed through a Monte Carlo permutation method where the data matrix is shuffled 4,999 times with results compared to the results from real data (McCune and Grace 2002). While only results for selected species are reported here, the indicator species analysis and significance testing included all major species (n>30) found in the dataset.
RESULTS

The analysis was made on 15,591 corners (1,279 included markers other than trees) representing 22,107 witness trees. Each corner represented up to six witness trees; about 8 percent of the corners were not witnessed by any trees. About 24 percent of the corners date to the late 1700s. The greatest numbers of corners were established in the 1840s through the 1850s, at 17.8 percent and 29.3 percent, respectively.

The selected species constituted 44 percent of all tallied witness trees (Table 2). All oak species combined totaled 32 percent of species tallied, with white oak making up the majority.

Of the 49 combinations of subsections and species, 28 were found to have a clustered pattern (positive spatial autocorrelation), 20 were found to have random patterns (no spatial autocorrelation), and one (scarlet oak in ECF) had too few occurrences to calculate spatial autocorrelation (Table 2). All species showed a clustered pattern when assessed across the study area.

In the RV subsection, no significant associations with aspect, TRI, and moisture were found based on the Monte Carlo tests. Monte Carlo tests found no significant correlation between frequencies of any species and moisture index or TRI in the ECF subsection. Frequencies of the selected species were not found to be correlated with aspect in the WAMV and WAM subsections. Table 3 contains the summarized results for all indicator species analyses.

AMERICAN CHESTNUT

American chestnut witness trees were associated with areas of low moisture (WAM and EAMV) and high (RV and EAMV) and moderate (WAM) elevations. American chestnut witness trees were more likely to occur on areas with moderate TRI in the EAMV subsection. American chestnut was significantly associated with ridge landforms (WAM, ECF, WAMV, and EAMV). In the SHAM subsection the species was more likely on toe slopes and in the NHAM subsection it was more likely on benches. On the study area as a whole, American chestnut trees were more likely found on ridges with high TRI, low moisture, and high elevations.

Table 2.—Species’ relative frequency by subsection. Highlighted estimates denote random spatial pattern; all others occurred as clustered spatial pattern (global Moran’s I; α = 0.05)

<table>
<thead>
<tr>
<th>Species</th>
<th>EAMV</th>
<th>ECF</th>
<th>NHAM</th>
<th>RV</th>
<th>SHAM</th>
<th>WAMV</th>
<th>WAM</th>
<th>Study area</th>
</tr>
</thead>
<tbody>
<tr>
<td>American chestnut</td>
<td>6.4</td>
<td>18.4</td>
<td>4.0</td>
<td>4.0</td>
<td>4.7</td>
<td>6.1</td>
<td>9.3</td>
<td>6.3</td>
</tr>
<tr>
<td>White oak</td>
<td>32.5</td>
<td>10.7</td>
<td>5.7</td>
<td>28.3</td>
<td>3.9</td>
<td>38.2</td>
<td>17.0</td>
<td>19.4</td>
</tr>
<tr>
<td>Chestnut oak</td>
<td>6.1</td>
<td>3.0</td>
<td>2.3</td>
<td>12.3</td>
<td>1.0</td>
<td>2.2</td>
<td>7.6</td>
<td>5.2</td>
</tr>
<tr>
<td>Northern red oak</td>
<td>2.9</td>
<td>2.9</td>
<td>3.3</td>
<td>4.8</td>
<td>3.1</td>
<td>2.2</td>
<td>2.6</td>
<td>3.1</td>
</tr>
<tr>
<td>Scarlet oak</td>
<td>0.9</td>
<td>0.5</td>
<td>2.1</td>
<td>2.0</td>
<td>0.9</td>
<td>3.8</td>
<td>4.3</td>
<td>2.0</td>
</tr>
<tr>
<td>Black oak</td>
<td>2.8</td>
<td>4.0</td>
<td>0.2</td>
<td>5.6</td>
<td>0.7</td>
<td>5.0</td>
<td>1.4</td>
<td>2.2</td>
</tr>
<tr>
<td>Hickory</td>
<td>6.1</td>
<td>2.2</td>
<td>1.3</td>
<td>4.5</td>
<td>1.7</td>
<td>5.1</td>
<td>5.3</td>
<td>4.1</td>
</tr>
</tbody>
</table>

EAMV = Eastern Allegheny Mountain and Valley, ECF = Eastern Coal Fields, NHAM = Northern High Allegheny Mountain, RV = Ridge and Valley, SHAM = Southern High Allegheny Mountain, WAM = Western Allegheny Mountain, and WAMV = Western Allegheny Mountain and Valley.
Table 3.—Indicator species analysis results for witness trees and moisture index, TRI, elevation, aspect, and landform across the study area. Differences between subsections noted in parentheses.

<table>
<thead>
<tr>
<th>Species</th>
<th>Moisture</th>
<th>TRI</th>
<th>Elevation</th>
<th>Aspect</th>
<th>Landform</th>
</tr>
</thead>
<tbody>
<tr>
<td>American chestnut</td>
<td>low</td>
<td>high</td>
<td>moderate (high RV, EAMV)</td>
<td>none (N-NW-W EAMV)</td>
<td>ridge (toe slopes SHAM; bench NHAM)</td>
</tr>
<tr>
<td>White oak</td>
<td>high</td>
<td>low (low NHAM and SHAM)</td>
<td>low (low NHAM; moderate EAMV)</td>
<td>none (SW SHAM)</td>
<td>valley floor (toe slopes SHAM, RV, WAMV)</td>
</tr>
<tr>
<td>Chestnut oak</td>
<td>low</td>
<td>high</td>
<td>moderate (high RV, ECF, EAMV)</td>
<td>none (N-NW-W EAMV)</td>
<td>ridge (bench NHAM)</td>
</tr>
<tr>
<td>Northern red oak</td>
<td>low</td>
<td>high</td>
<td>high (moderate WAM)</td>
<td>S-SE</td>
<td>bench (toe slope RV; ridge EAMV; valley ECF)</td>
</tr>
<tr>
<td>Scarlet oak</td>
<td>low</td>
<td>high</td>
<td>moderate (high WAM, EAMV)</td>
<td>none (SW NHAM; S-SE SHAM)</td>
<td>none (cove RV)</td>
</tr>
<tr>
<td>Black oak</td>
<td>low</td>
<td>none (high EAMV)</td>
<td>low (high EAMV)</td>
<td>none (S-SE EAMV)</td>
<td>none (toe slope RV; ridge EAMV; valley ECF)</td>
</tr>
<tr>
<td>Hickory</td>
<td>none</td>
<td>high</td>
<td>low</td>
<td>none (SW NHAM and ECF; S-SE SHAM)</td>
<td>none (side slope SHAM)</td>
</tr>
</tbody>
</table>

EAMV = Eastern Allegheny Mountain and Valley, ECF = Eastern Coal Fields, NHAM = Northern High Allegheny Mountain, RV = Ridge and Valley, SHAM = Southern High Allegheny Mountain, WAM = Western Allegheny Mountain, and WAMV = Western Allegheny Mountain and Valley.

**WHITE OAK**

White oaks were more likely on areas of low moisture (NHAM and SHAM). The association of white oaks with TRI varied by subsection with white oaks significant on low TRI areas in the WAM subsection, high TRI areas in the NHAM subsection, and moderate TRI in the EAMV subsection. On the NHAM, SHAM, and WAMV subsections, white oaks were associated with areas of moderate elevation. They were significantly associated with low elevations on the WAM and RV subsections. White oaks were more likely to be located on SW aspects (SHAM). White oaks were associated with valley floors (WAM) and toe slopes (SHAM, RV, and WAMV). Across the study area white oaks were more likely on valley floor landforms at low elevations with high moisture and low TRI.

**CHESTNUT OAK**

Chestnut oaks were associated with areas of low moisture and areas of high TRI (WAM, NHAM, and EAMV). Chestnut oaks were more likely on high (RV, ECF, and EAMV) or moderate (WAM) elevations and were associated with ridges (EAMV and ECF). Across the study area chestnut oak witness trees were more likely to be found on ridge landforms with high TRI, low moisture, and moderate elevations.
NORTHERN RED OAK
Northern red oaks were found on areas of low moisture (WAMV, SHAM, and EAMV) and high (RV and EAMV) to moderate (WAM) elevations. Associations with landforms varied between subsections. Toe slopes were significant in the RV subsection, benches in the SHAM and NHAM subsections, and ridges in the EAMV subsection. Taken across the study area, northern red oak witness trees were more likely on S-SE facing benches at high elevations, with high TRI and low moisture.

SCARLET OAK
Surprisingly, the cove landforms were found to be significant for scarlet oak in the RV subsection. Scarlet oaks were more likely on SW (NHAM) and S-SE (SHAM) aspects. In the WAM subsection, scarlet oaks were associated with higher elevations and high TRI. An association with areas of high TRI was also found for the EAMV subsection. Across the study area low moisture index, moderate elevation, and high TRI were found to be significant for describing the site-species relationship for scarlet oak.

BLACK OAK
Black oak was associated with areas of low moisture and high TRI (EAMV). Black oak was associated with low elevations in the NHAM subsection and areas of high elevation in the EAMV subsection. Black oak was associated with toe slopes (RV), valleys (ECF), and ridges (EAMV). In the EAMV subsection, black oaks were more likely on S-SE slopes. Across the study area, black oaks were associated with low moisture and low elevations.

HICKORY
Hickory witness trees were associated with areas of high TRI (NHAM) and low elevations (NHAM and EAMV). Hickories were more likely to occur on SW (NHAM and ECF) and S-SE aspects (SHAM). Hickory was more likely to be found on side slopes (SHAM). Across the study area, hickories were more likely to be found on low elevations with high TRI.

DISCUSSION AND CONCLUSIONS
All species locations were found to be spatially auto-correlated when assessed across the study area. This is not surprising as tree species are not generally randomly located across a landscape as large as the study area. The lack of spatial autocorrelation in some combinations of species and subsections was not expected and may be due to low numbers of points in some subsections (ECF) or the shape of the subsections (RV).

Positive spatial autocorrelation is common in ecological data. Ignoring spatial autocorrelation can cause problems in hypothesis testing, especially in studies that are not from planned experiments (Lennon 2000). There is a risk of inflating Type I errors (false positives) if simple confirmatory statistics are used on spatially auto-correlated data (Diniz-Filho and others 2003) because the degrees of freedom are overestimated (Lennon 2000). Permutation tests, where significance is based on random shuffling of the observations, are appropriate when positive spatial autocorrelation exists (Legendre 1993). For these reasons, analyses such as correlation and linear regression were not used to explain the relationships between species and sites. Regression models can be modified to account for spatial autocorrelation (Lennon 2000) and any future analysis of this dataset should include consideration of this spatial property.
While the subsection boundaries define areas based on observed ecological differences, there were relatively few differences in site-species associations between the subsections. Perhaps other physical or ecological variables such as soil series would show differences between subsections. Although few differences between subsections were noted for these species and site characteristics, construction of predictive models should consider subsectional differences.

One interesting difference between subsections is the variety of landforms associated with black oaks—ranging from toe slopes and valley to ridges. These differences are likely due to the different moisture regimes of the subsections; the RV is the driest of the study area. Another interesting difference between subsections but within a species is the association of northern red oaks to different landforms. Across the study area, northern red oaks are more likely on benches, but significant associations to ridges and toe slopes were also determined. These findings again may reflect the different moisture or temperature regimes in these subsections and the species' optimal habitat for competition.

As in the previous analysis of witness trees in the study area (Abrams and McCay 1996), chestnut oaks, northern red oak, scarlet oak, black oak, and American chestnut were found in areas of low moisture and ridge positions. In the current analysis, white oak was found to be more likely to occur on valley floors than in other landforms, while no landform preference was found to be significant previously.

Across its range, white oak can occur on all upland aspects and slope positions except for extremely dry ridges, poorly drained flats, and wet bottomland (Burns and Honkala 1990). This conclusion would seem counter to the findings presented here, where white oak was more likely on moist sites and valley floor landforms. White oak does not occur at higher elevations across its range (Burns and Honkala 1990) and this observation is reflected in the current analysis of witness trees.

Northern red oak currently occurs across all topographic positions, under mesic to dry-mesic conditions; it grows best on N and E aspects (Burns and Honkala 1990). Based on the variety of landforms found significant at the subsection level, the witness trees reflect the species’ suitability to many topographic positions. In contrast, S-SE aspects were found to be the only significant aspect for northern red oak trees.

These differences between current species distributions and this analysis of witness trees may be due to the comparison of the entire range with a portion of a species range. Comparing current distributions with past distributions also may explain these differences. The witness trees reflect species distributions before substantial influence of European settlement activities that may be responsible for the current distribution of the species, including fire suppression.

That American chestnut was associated strongly with ridge landforms and areas of low moisture is consistent with previous witness tree analysis (Abrams and McCay 1996). Before the near-elimination of the species from the chestnut blight, American chestnut was found on the hillsides in most of West Virginia (Hough 1878) and was dominant on ridges in western Maryland (Russell 1987). In West Virginia, the abundance of American chestnut dropped as elevation increased (Hough 1878). In this analysis, American chestnut was associated with moderate elevations. That no species was found to be significantly associated with side slopes, the most common landform in the study area, may indicate that side slopes were generally a mixture of these, and possibly other, species.
Indicator species analysis does not allow for the determination of site characteristics negatively associated with species, as can be made using the contingency table analysis. However, given that the witness tree corners exhibit positive spatial autocorrelation at the level of the study area—indicating the observations are not independent—the nonparametric indicator species analysis and Monte Carlo testing for significance are more appropriate.

Considering the possibility of confusion over common names used in the deeds, the creation of a red oak species grouping may be useful in future analyses. Future use of this database will include spatial interpolation of species occurrences between points to create continuous coverage and comparisons of past species abundances to current forest conditions.

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LITERATURE CITED


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