TREE SPECIES ASSOCIATIONS OF *PINUS ECHINATA* MILL. OVER A LARGE-SCALE SAMPLING REGIME ON THE INTERIOR HIGHLANDS OF ARKANSAS

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ABSTRACT.—The Interior Highlands physiographic province of Arkansas is considered the ecological center of the geographic distribution of shortleaf pine (*Pinus echinata* Mill.). I used data from the U.S. Forest Service, Forest Inventory and Analysis (FIA) program to identify the major tree species associates of *P. echinata* across this 66,700-km^2 landscape. Across the region, 41,207 km^2 were covered by timberland. The study population was represented by 434 relatively undisturbed upland sample plots from the 1995 forest survey of Arkansas. *P. echinata* ≥12.7 cm in diameter at breast height (DBH) occurred on 211 of these sample plots. Additionally, it ranked first in basal area on 119 plots, second on 39 plots, and third on 19 plots. Where P. echinata was dominant, stand basal area averaged 23.1 m^2 ha^{-1} (± 0.57 SEM). I used chi-square to test for degree of association between the stand dominants and to test for positive and negative associations. There was a positive association between *P. echinata* and *Quercus alba* L. (χ^2 = 0.490; 1df). In contrast, there was a negative association between *P. echinata* and *Q. velutina* Lam. (χ^2 = 15.571; 1df). These results demonstrate that the chi-square test of association is effective even on the larger scales of sampling where lack of sample homogeneity may sometimes complicate analysis. Such quantitative tests for species associations offer meaningful insights into *P. echinata* communities at the landscape scale of sampling.

INTRODUCTION

Shortleaf pine (*Pinus echinata* Mill.) has an extensive range that covers an area from New Jersey to southeast Texas. In the northern part of its range, it stretches from New Jersey to southern Missouri and eastern Oklahoma. In the southern portion of its range, it is found from South Carolina all the way to east Texas. Much autecological work has been done on *P. echinata* and a summarization of its silvics can be found in Burns and Honkala (1990). Somewhat lacking, however, are detailed descriptions of species associates in specific *P. echinata* communities. Some of the few botanical and silvical descriptions of this species typically offer only brief general listings of community associates (Barrett 1995, Fralish and Franklin 2002, Harlow and others 1996, Burns and Honkala 1990, Eyre 1980, Braun 1950, Vankat 1979). Tree species associations are a theme central to much of ecological community analysis. These repeating patterns of species associations are the basis of the classification of vegetation communities. However, species with wide ecological amplitude, such as *P. echinata*, may often have different associates over different parts of their range. Usually, detailed descriptive work is done on small localized studies, often of stands that are unique in some respect such as stand history, species rareness, possibility of becoming endangered, etc. Lacking are studies that outline specific tree species associations over large geographic areas. Such studies will add to the full complement of information necessary to classify vegetation composed of species with wide ecological amplitude.

The center of highest ecological development of *P. echinata* is in the Interior Highlands physiographic province of Arkansas. This area contains the highest concentration of *P. echinata* volume in the U.S. As of the 1995 survey of Arkansas, there were 3.8 billion cubic feet of volume in *P. echinata* (Rosson 2002), far above any other state in the U.S. Most of the volume is concentrated in Montgomery, Scott, Yell, Perry, and Polk Counties, accounting for 43 percent of all *P. echinata* volume in Arkansas. Volume and relative ecological importance of *P. echinata* decreases north and south of this area. For instance, moving north onto the Salem-Plateaus province, the volume of *P. echinata* in Missouri is only 0.8 billion cubic feet (Miles 2006). The ecological importance of *P. echinata* in Arkansas on the Interior Highlands presented an opportunity to study its primary species associations across this large landscape. The objectives of the study were to determine the common tree associates of *P. echinata* across this region and determine whether these associations are positive or negative.

METHODS

The inclusive area of the study is the Interior Highlands Physigraphic Division in Arkansas (Fenneman 1938). This

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area is divided into two provinces, the Ozark Plateaus Province and the Ouachita Province. These two provinces contain two Sections: the Springfield-Salem Plateaus and the Boston Mountains Sections in the Ozark Plateaus Province, and the Arkansas Valley and Ouachita Mountains Sections in the Ouachita Province (Fig. 1). The Interior Highlands covers approximately 66,700 km^2 of which 41,207 km^2 are forested. Using GIS software, I selected U.S. Forest Service Inventory and Analysis (FIA) plots that fell within each of these physiographic regions.

The data came from forest surveys conducted by FIA in 1968, 1978, 1988, and 1995. The sample plot study population was extracted from these four surveys by the following criteria. First, a plot had to fall within the Interior Highlands. Second, the plot had to be forested during all four surveys. Third and fourth, plots that showed evidence of disturbance (e.g. cutting) or were artificially regenerated were excluded. Fifth, the plot had to occur on an upland site. Evidence of cutting disturbance or planting was obtained by examination of the repeated-measures plots over time, where individual trees were tracked with descriptive tree histories. There were 1,179 plots that met the first two criteria, and 434 that met all five.

The total plot population, from which the 434 study plots were selected, came from a 4.8 km square sample grid. The same plots were visited and measured at each of the four surveys. Only trees ≥12.7 cm in diameter at breast height (DBH) were included in the study. These trees were tallied using an 8.6 m^2 per hectare basal area factor (BAF) prism on 10 points dispersed over an area of approximately 0.4 hectares (see Rosson 2002 for more details on sampling methods for these Arkansas surveys). Nomenclature follows Little (1979).

A 2 x 2 contingency table was used to define the tree species associations. The data entry for each cell was the presence or absence of two select species on each plot. In this study all species that occurred in the 434 sample plots across the Interior Highland were compared with *P. echinata* in the contingency table.

Species B

		P	A	
Species A		P	A	
	P	a	b	m
	A	c	d	n
		r	s	tot

Where

P = plots where species is present
A = plots where species is absent
a = number of plots species where A and B co-occur

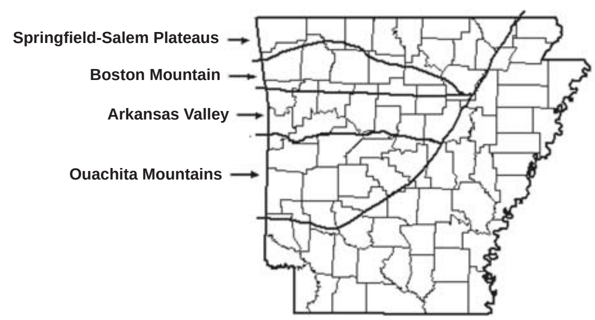

Figure 1.—The four physiographic sections on the Interior Highlands of Arkansas (after Fenneman 1938).

b = number of plots where species A is present and species B is absent
c = number of plots where species A is absent and species B is present
d = number of plots where species A and species B are both absent
m = a + b
n = c + d
r = a + c
s = b + d
tot = total number of plots in sample (a + b + c + d)

The chi-square test statistic was then applied to the data in the 2 x 2 contingency table. This formula includes the Yates correction that corrects for bias when any cell in the 2 x 2 contingency table has an expected frequency of <1 or if two or more of the table cells have expected frequencies of <5 (Zar 1984).

$$\chi^2 = \frac{N[|(ad) - (bc)| - (N/2)^2}{mnrs}$$

The null hypothesis is that the species are independent, i.e., there is no association between the two species being tested. If the chi-square value is >3.84, the null hypothesis is rejected and it is concluded that the species are associated. In addition, the chi-square value may be used as a measure of the degree of association, the higher the value the stronger the association (Causton 1988). There are two types of association possible (see Ludwig and Reynolds 1988):

Positive—the pair of species occurred more often than expected if independent. $a > E(a)$
Negative—the pair of species occurred less often than expected if independent. $a < E(a)$

Where

$$E(a) = \frac{(a+b)(a+c)}{N}$$

Goodall (1953) was the first to measure the association between species. The 2 x 2 contingency table with chi-square test of significance is the most commonly used approach. Testing for association between species has been called association analysis, species association analysis, interspecific association analysis, and species correlation analysis (Ludwig and Reynolds 1988, Causton 1988, Kershaw 1973, Greig-Smith 1983). Such species association constructions have been used in a variety of contexts beyond association analysis. One application is in multivariate analysis, where it is commonly applied in various ordination techniques. The association between two species is the degree and measure to which they occupy the same sample sites across the landscape and is an extremely important ecological indicator in multivariate techniques (Pielou 1984, Gauch 1982, Greig-Smith 1983).

RESULTS AND DISCUSSION

Overstory stand basal area averaged 19.3 m^2 ha^{-1} in the 434 post-stratified plots on the Interior Highlands. Fifty-two tree species ≥12.7 cm DBH were recorded. Often, these 10 species accounted for just over 90 percent of overstory basal area. *P. echinata* was the most dominant species, accounting for 22 percent of basal area, followed by *Quercus alba* L., *Q. rubra* L., *Carya* spp. Nutt., *Q. stellata* Wangenh., *Q. velutina* Lam., *Nyssa sylvatica* Marsh., *Liquidambar styraciflua* L., *Q. falcata* Michx., and *Juniperus virginiana* L. (Table 1).

There were some shifts in dominance by physiographic regions. *P. echinata* was strongly dominant in the Ouachita Mountains, accounting for 41 percent of basal area. *Q. alba* was second, accounting for 17 percent of basal area. Across the Arkansas Valley, *P. echinata* shared dominance with *Q. stellata*, each species accounting for 20 percent of stand basal area. Stand basal area in the Boston Mountains averaged 19.5 m^2 ha^{-1}. *Q. alba* was dominant there, followed by *Q. rubra*, accounting for 25 and 16 percent of basal area, respectively. *P. echinata* was fifth in dominance, accounting for 8 percent of stand basal area in this region. On the Salem-Plateaus, *Q. velutina* was dominant, with 22 percent of basal area, followed by *Q. alba* and *Q. stellata* with 16 and 14 percent, respectively. *P. echinata* ranked sixth there, accounting for 9 percent of basal area.

P. echinata's adaptation to a wide range of soils and sites contributes to its wide distribution. It favors and is most prevalent on acid soils, but is also very competitive on other soils with southern aspects, drier sites, and nutrient-deficient soils (Burns and Honkala 1990). *P. echinata* is most common on the Ouachita Province, where it is most competitive on the numerous southern exposure slopes and more acidic soils derived from sandstone bedrock. It declines in importance in the provinces to the north probably because of habitat limitations—fewer south-exposed slopes and more limestone-derived soils. In addition, the degree of past disturbance (fire and cutting) has played a large role in the trajectory of forest composition that currently occupies the Interior Highlands of Arkansas (Batek and others 1999, Chapman and others 2006, Stambaugh and others 2002).

Across the Interior Highlands, *P. echinata* occurred on 211 of the 434 upland plots and was the stand dominant on 119 plots (Table 2). *Q. alba* was the leading, second dominant tree, on these plots, occurring on 37 sample plots. Ranked third in dominance was *Q. stellata*, occurring on 25 plots. By physiographic region within the Interior Highlands, *P. echinata* occurred on 130 of the 152 Ouachita Mountain plots, on 26 of the 55 Arkansas Valley plots, on 41 of the 159 Boston Mountain plots, and on 14 of the 68 Salem-Plateaus plots.

Across the Interior Highlands the relative stand dominance of *P. echinata* varied. Thirty-eight percent of the plots had 50 to 75 percent of basal area in *P. echinata*, while 35 percent had basal area in the 25 to 50 percent range. Twenty-seven percent had basal area ranging from 75 to 100 percent. Less than 1 percent of the plots had *P. echinata* basal area in the 0 to 25 percent range. In the order of ranked dominance, 119 plots had *P. echinata* as the number 1 stand dominant, 39 plots had *P. echinata* ranked second in dominance, 19 plots had *P. echinata* ranked third, and the remaining 34 plots had a ranking of fourth or higher in *P. echinata* dominance. (Table 2).

One of the strongest patterns of group associations was in the *P. echinata*—*Q. alba*—*Carya* spp. type. Twelve percent of all plots were in this category. Stand composition of shade-intolerant pine in association with shade-tolerant species (oaks and hickories) is most likely a result of stand initiation from past disturbance. *P. echinata* probably became established after past logging or natural disturbance, but if succession proceeds without further disturbance, it will begin to drop out of these stands. *P. echinata* is moderately intolerant as a seedling but loses that tolerance after just a few years. Without major disturbance, hardwoods will take over the site. *P. echinata* may maintain some minor presence by taking advantage of canopy gaps and the ability to reach the canopy by high growth rates (Barrett 1995). *P. echinata* stands >100 years old begin to deteriorate rapidly and more tolerant hardwoods will take over the site without some kind of disturbance (Walker 1999). Table 2 illustrates other strong patterns described by the first three ranked species. These involve *P. echinata*, *Q. alba*, *Carya* spp., and *Q. stellata*. Involving first and second ranked species, there were 32 plots with *Q. alba*, 25 plots with *Q. stellata*, and 21 plots with *Carya* spp. (Table 2), together accounting for 66 percent of all plots dominated by *P. echinata*. Although Table 2 shows only the top three dominant species, it illustrates the high variability in dominance ranking, especially in the third dominant position, and beyond.

Table 1.—Basal area (m^2 ha^{-1}) by species, Interior Highland Physiographic Division, and four Interior Highland Sections; n=434 for the Interior Highlands, n=152 for the Ouachita Mountains, n=55 for the Arkansas Valley, n=159 for the Boston Mountains, and n=68 for the Salem-Plateaus. Data are from 1995.

FIA species code and name	Ouachita	Arkansas Valley	Boston Mountains	Salem-Plateaus	Interior Highland
	Average basal area (m^2 ha^{-1})				
68 *Juniperus virginiana* L.	0.153	1.126	0.249	0.847	0.420
110 *Pinus echinata* Mill.	8.515	3.503	1.585	1.050	4.171
131 *Pinus taeda*	0.215	0.000	0.027	0.000	0.085
311 *Acer barbatum* Michx.	0.000	0.000	0.005	0.000	0.002
313 *Acer negundo* L.	0.000	0.000	0.011	0.000	0.004
316 *Acer rubrum* L.	0.164	0.109	0.281	0.051	0.182
318 *Acer saccharum* L.	0.000	0.000	0.325	0.190	0.149
341 *Ailanthus altissima* (Mill.) Swingle	0.000	0.000	0.005	0.013	0.004
381 *Bumelia* sp.	0.000	0.000	0.000	0.013	0.002
400 *Carya* sp. Nutt.	1.256	2.220	2.585	1.669	1.930
404 *Carya illinoensis* (Wangenh)K.Koch	0.000	0.000	0.005	0.000	0.002
420 *Castanea* sp. Mill.	0.000	0.000	0.005	0.000	0.002
461 *Celtis laevigata* Willd.	0.017	0.000	0.000	0.000	0.006
462 *Celtis occidentalis* L.	0.000	0.000	0.022	0.013	0.010
471 *Cercis canadensis* L.	0.000	0.000	0.038	0.051	0.022
491 *Cornus florida* L.	0.011	0.000	0.022	0.063	0.022
521 *Diospyros virgininana* L.	0.017	0.016	0.016	0.000	0.014
531 *Fagus grandifolia* Ehrh.	0.011	0.000	0.335	0.000	0.127
541 *Fraxinus Americana* L.	0.057	0.078	0.227	0.266	0.155
544 *Fraxinus pennsylvanica* Marsh.	0.034	0.031	0.016	0.025	0.026
546 *Fraxinus quadrangulata* Michx.	0.000	0.000	0.000	0.025	0.004
552 *Gleditsia triacanthos* L.	0.011	0.031	0.005	0.000	0.010
602 *Juglans nigra* L.	0.006	0.031	0.076	0.139	0.055
611 *Liquidambar styraciflua* L.	0.656	0.891	0.633	0.038	0.581
621 *Liriodendron tulipifera* L.	0.000	0.000	0.000	0.025	0.004
651 *Magnolia acuminata* L.	0.000	0.000	0.049	0.025	0.022
682 *Morus rubra* L.	0.017	0.016	0.011	0.025	0.016
693 *Nyssa sylvatica* Marsh.	0.549	0.563	0.952	0.392	0.674
731 *Platanus occidentalis* L.	0.023	0.109	0.059	0.013	0.046
762 *Prunus serotina* Ehrh.	0.124	0.188	0.130	0.126	0.135
802 *Quercus alba* L.	3.491	1.673	4.911	2.795	3.672
812 *Quercus falcata* Michx.	0.436	0.579	0.254	0.683	0.426
813 *Quercus falcata* var. *pagodifolia* Ell.	0.023	0.360	0.005	0.000	0.055
823 *Quercus macrocarpa* Michx.	0.000	0.000	0.000	0.025	0.004
824 *Quercus marilandica* Muenchh.	0.232	0.266	0.114	0.468	0.230
825 *Quercus michauxii* Nutt.	0.000	0.000	0.000	0.013	0.002
826 *Quercus muehlenbergii* Engelm.	0.006	0.063	0.141	0.443	0.131
827 *Quercus nigra* L.	0.011	0.031	0.005	0.000	0.010
830 *Quercus palustris* Muenchh.	0.000	0.000	0.005	0.000	0.002
831 *Quercus phellos* L.	0.028	0.000	0.000	0.000	0.010
833 *Quercus rubra* L.	1.709	0.813	3.132	1.518	2.087
834 *Quercus shumardii* Buckl.	0.000	0.016	0.011	0.013	0.008
835 *Quercus stellata* Wangenh.	1.765	3.440	1.028	2.491	1.821
837 *Quercus velutina* Lam.	0.837	0.797	1.801	3.832	1.655
901 *Robinia pseudoacacia* L.	0.006	0.031	0.114	0.038	0.054
931 *Sassafras albidum* (Nutt.)Nees	0.000	0.000	0.005	0.051	0.010
951 *Tilia americana* L.	0.017	0.000	0.054	0.051	0.034
971 *Ulmus alata* Michx.	0.192	0.219	0.103	0.152	0.157
972 *Ulmus americana* L.	0.062	0.047	0.049	0.051	0.054
973 *Ulmus crassifolia* Nutt.	0.000	0.016	0.005	0.000	0.004
975 *Ulmus rubra* Muhl.	0.000	0.031	0.022	0.000	0.012
976 *Ulmus serotina* Sarg.	0.000	0.078	0.000	0.000	0.010
999 Unidentified trees	0.000	0.016	0.038	0.025	0.020
All species	20.651	17.388	19.472	17.706	19.344

Table 2.—The number of plots by dominant species. Listed are all plots where *P. echinata* was dominant. The species codes in the three dominant categories are identified in the species list, Table 1. Data are from 1995; n = 119.

Number of plots	Percent of all plots	No. 1 dominant	No. 2 dominant	No. 3 dominant
14	11.8	110	802	400
6	5.0	110	802	835
5	4.2	110	802	833
4	3.4	110	802	693
3	2.5	110	802	837
1	0.8	110	802	812
1	0.8	110	802	131
1	0.8	110	802	611
1	0.8	110	802	531
1	0.8	110	802	316
8	6.7	110	835	400
5	4.2	110	835	802
1	0.8	110	835	833
1	0.8	110	835	693
3	2.5	110	835	0
2	1.7	110	835	812
1	0.8	110	835	131
1	0.8	110	835	611
2	1.7	110	835	68
1	0.8	110	835	762
7	5.9	110	400	802
4	3.4	110	400	835
1	0.8	110	400	833
1	0.8	110	400	693
2	1.7	110	400	837
2	1.7	110	400	131
1	0.8	110	400	611
1	0.8	110	400	68
2	1.7	110	400	824
1	0.8	110	68	400
1	0.8	110	68	802
1	0.8	110	68	835
1	0.8	110	68	491
1	0.8	110	68	521
2	1.7	110	833	400
1	0.8	110	833	802
1	0.8	110	833	835
1	0.8	110	833	0
1	0.8	110	837	400
3	2.5	110	837	802
1	0.8	110	837	693
1	0.8	110	611	400
1	0.8	110	611	802
1	0.8	110	611	833
1	0.8	110	611	693
1	0.8	110	611	831
2	1.7	110	812	802
1	0.8	110	812	835
1	0.8	110	812	813
1	0.8	110	693	835
1	0.8	110	693	837
1	0.8	110	693	824
1	0.8	110	824	835
1	0.8	110	824	833
2	1.7	110	131	812
2	1.7	110	0	0
1	0.8	110	541	611
1	0.8	110	971	400
1	0.8	110	316	0

Table 3 shows the chi-square values and the type of association for each species in relation to its occurrence (or lack thereof) with *P. echinata*. This chi-square value is a measure of the degree of association, where the higher the value, the stronger the association (Causton 1988). It is also important to consider the number of plots that contain neither species. If this cell is 0, then a chi-square value cannot be calculated (Kershaw 1973). So, species with wide amplitude (typically those that occurred on every plot or a high number of plots) may demonstrate a weak chi-square value. Examples are *Carya* spp., where 352 of the 434 plots were occupied by this genus; and *Q. alba*, which occurred on 332 sample plots.

Of the 52 tree species tallied on various portions of the 434 sample plots, *P. echinata* had a positive association with 20 of them. The strongest positive associations were with *P. taeda*, *Liquidambar styraciflua*, and *Q. stellata*. In contrast, *P. echinata* had a negative association with 32 species. However, many of these are the result of much too small of a tally. For example, see *Acer negundo*, where it was tallied on only one sample plot. Some of the stronger negative associations were *A. saccharum*, *Cercis canadensis*, *Fraximus Americana*, *Q. muehlenbergii*, *Q. rubra*, *Q. velutina*, and *R. pseudoacacia*.

An interesting finding is that even though different species may have the same affinity for particular site and habitat conditions, the species associations between the two may be negative. The two species may be in direct competition for resource space or there may be something in the past history of the site that has given advantage to one species over the other. For example, both *P. echinata* and *Q. velutina*. prefer the same xeric sites and soils, but studies on the Interior Highland have shown that *P. echinata* dominance increased with increasing fire frequency while *Q. velutina* decreased with increasing fire frequency (Batek and others 1999, Chapman and others 2006, Stambaugh and others 2002). Selective cutting with preference for *P. echinata* arguably could produce an opposite effect, where *Q. velutina* dominance would then prevail on such sites.

When the chi-square coefficient is used to study species associations it is important to be aware of the scale of the sample domain from which the sample is drawn because sample plots without either species in the test are construed as similar (Causton 1988). Therefore, the larger the domain that contains plots outside the range of interest, the more artificially similar the chi-square values will be. While this situation will not directly impact the results of studies that stand alone, comparing studies from different size sample domains and varying degrees of species homogeneity across the landscape would result in a less rigorous comparison. The sample domains should be as close to the same size and homogeneity as possible for direct comparison of chi-square values. Unfortunately, sample homogeneity (or lack thereof) is a problem for all aspects of multivariate analyses,

Table 3.—Chi-square values and species association of 52 tree species with *P. echinata* on the Interior Highland of Arkansas. Data are from 1995; n = 434. A + indicates a positive association, a – indicates a negative association. Column labeled 'Plots both present' indicates the number of plots where the respective species occurred with *P. echinata*. 'Total plots present' indicates the total number of plots where each species occurred.

Species	Chi-sq. value	Association	Plots both present	Total plots present
Juniperus virginiana L.	0.071	–	40	86
Pinus echinata Mill.				211
Pinus taeda L.	11.014	+	12	12
Acer barbatum Michx.	2.081	–	0	3
Acer negundo L.	0.001	–	0	1
Acer rubrum L.	4.413	–	38	98
Acer saccharum L.	12.740	–	5	31
Ailanthus altissima (Mill.) Swingle	0.449	–	0	2
Bumelia sp.	0.449	+	1	2
Carya sp. Nutt.	0.161	+	169	352
Carya illinoensis (Wangenh)K.Koch	0.449	+	1	2
Castanea sp. Mill.	0.001	+	1	1
Celtis laevigata Willd.	0.005	+	4	7
Celtis occidentalis L.	5.856	–	0	8
Cercis canadensis L.	17.228	–	1	23
Cornus florida L.	9.162	–	46	125
Diospyros virgininana L.	0.142	+	8	14
Fagus grandifolia Ehrh.	3.474	–	4	17
Fraxinus americana L.	24.175	–	11	60
Fraxinus pennsylvanica Marsh.	0.009	–	6	11
Fraxinus quadrangulata Michx.	0.449	+	0	2
Gleditsia triacanthos L.	0.200	–	1	4
Juglans nigra L.	9.955	–	4	25
Liquidambar styraciflua L.	10.473	+	59	92
Liriodendron tulipifera L.	0.449	+	1	2
Magnolia acuminata L.	1.359	–	1	6
Morus rubra L.	0.214	–	5	13
Nyssa sylvatica Marsh.	1.263	–	88	194
Platanus occidentalis L.	0.763	–	6	17
Prunus serotina Ehrh.	1.557	+	30	52
Quercus alba L.	0.490	+	165	332
Quercus falcata Michx.	0.795	+	44	82
Quercus falcata var. *pagodifolia* Ell.	0.118	+	3	6
Quercus macrocarpa Michx.	0.449	–	0	2
Quercus marilandica Muenchh.	0.617	+	33	61
Quercus michauxii Nutt.	0.449	–	0	2
Quercus muehlenbergii Engelm.	12.131	–	7	36
Quercus nigra L.	0.004	+	3	5
Quercus palustris Muenchh.	0.001	–	0	1
Quercus phellos L.	0.312	+	3	4
Quercus rubra L.	23.669	–	90	238
Quercus shumardii Buckl.	0.117	–	2	6
Quercus stellata Wangenh.	5.453	+	122	226
Quercus velutina Lam.	15.571	–	83	214
Robinia pseudoacacia L.	14.189	–	1	20
Sassafras albidum (Nutt.) Nees	0.763	–	6	17
Tilia americana L.	3.028	–	2	11
Ulmus alata Michx.	0.001	+	59	121
Ulmus americana L.	4.716	–	6	24
Ulmus crassifolia Nutt.	0.449	+	1	2
Ulmus rubra Muhl.	5.856	–	0	8
Ulmus serotina Sarg.	0.449	–	0	2

especially where endpoint references are essential (Legendre and Legendre 1998).

Studies such as this are important in uncovering specific species associations, especially those species with wide ecological amplitude such as *P. echinata*. Further work is needed on species associations of *P. echinata* across the eastern and southern part of its range to compare patterns of association with those of the Interior Highlands of Arkansas.

LITERATURE CITED

Barrett, J.W. 1995. Regional silviculture of the United States. Third edition. New York: John Wiley and Sons, Inc. 643 p.

Batek, M.J.; Rebertus, A.J.; Schroeder, W.A.; Haithcoat, T.L.; Compas, E.; Guyette, R.P. 1999. Reconstruction of early nineteenth-century vegetation and fire regimes in the Missouri Ozarks. Journal of Biogeography. 26: 397-412.

Braun, E.L. 1950. Deciduous forests of eastern North America. Philadelphia, PA:The Blakiston Co. 596 p.

Burns, R,M.; Honkala, B.H., eds. 1990. Silvics of North America: Volume 1, conifers. Agric. Hndbk. 654. Washington, DC: U.S. Department of Agrigulture, Forest Service. 675 p.

Causton, D.R. 1988. Introduction to vegetation analysis: principles, practice, and interpretation. London: Unwin Hyman. 342 p.

Chapman, R.A.; Heitzman, E.; Shelton, M.G. 2006. Long-term changes in forest structure and species composition of an upland oak forest in Arkansas. Forest Ecology and Management. 236: 85-92.

Eyre, F.H., editor. 1980. Forest cover types of the Unites States and Canada. Washington, DC: Society of American Foresters. 148 p.

Fenneman, N.M. 1938. Physiography of eastern United States. New York: McGraw-Hill. 691 p.

Fralish, J.S.; Franklin, S.B. 2002. Taxonomy and ecology of woody plants in North American Forests (excluding Mexico and subtropical Florida). New York: John Wiley and Sons, Inc. 612 p.

Gauch, H.G. 1982. Multivariate analysis in community ecology. Cambridge, UK: Cambridge Cambridge University Press. 298 p.

Goodall, D.W. 1953. Objective methods for the classification of vegetation. I. The use of positive interspecific correlation. Australian Journal of Botany. 1: 39-63.

Greig-Smith, P. 1983. Quantitative plant ecology. Third edition. Berkeley and Los Angeles, CA: University of California Press. 359 p.

Harlow, W.M.; Harrar, E.S.; Hardin, J.W.; White, F.M. 1996. Textbook of dendrology. 8th edition. New York : McGraw-Hill. 534 p.

Kershaw, K.A. 1973. Quantitative and dynamic plant ecology. Second edition. New York: American Elsevier Publishing Co. 308 p.

Legendre, P.; Legendre, L. 1998. Numerical ecology. Second English edition. Amsterdam: Elsevier, B.V. 853 p.

Little, E.L., Jr. 1971. Atlas of United States trees, vol. 1, Conifers and important hardwoods. Misc. Publ. 1146. Washington, DC: U.S.Department of Agriculture, Forest Service.

Little, E.L., Jr. 1979. Checklist of United States trees. Agriculture Handbook No. 541. Washington, DC: U.S. Department of Agriculture, Forest Service. 375 p.

Ludwig, J.A.; Reynolds, J.F. 1988. Statistical ecology: a primer on methods and computing. New York: John Wiley and Sons. 337 p.

Pielou, E.C. 1984. The interpretation of ecological data: a primer on classification and ordination. New York: Wiley and Sons. 255 p.

Miles, P.D. 2006. Forest inventory mapmaker web-application version 2.1. St. Paul, MN: US Department of Agriculture, Forest Service, North Central Research Station. [Online only.] Available at: www.nrcs2.fs.fed.us/4801/fiadb/index.html

Rosson, J.F., Jr., 2002. Forest resources of Arkansas, 1995. Resour. Bull. SRS-78. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 82 p.

Stambaugh, M.C.; Muzika, R.-M.; Guyette, R.P. 2002. Disturbance characteristics and overstory composition of an old-growth shortleaf pine (*Pinus echinata* Mill.) forest in the Ozark Highlands, Missouri, USA. Natural Areas Journal. 22: 108-119.

Vankat, J.L. 1979. The natural vegetation of the North America: an introduction. New York: John Wiley and Sons. 261 p.

Walker, L.C. 1999. The North American forests: geography, ecology, and silviculture. Boca Raton, FL: CRC Press. 398 p.

Zar, J.H. 1984. Biostatistical analysis. Second edition. Englewood Cliffs, NJ: Prentice Hall. 718 p.