RESEARCH ARTICLE

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American Chestnut (*Castanea dentata*) in the Pre-settlement Vegetation of Mammoth Cave National Park, Central Kentucky, USA

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ABSTRACT: The loss of American chestnut (*Castanea dentata*) due to the fungal pathogen *Cryphonectria parasitica* had a considerable effect on the ecology of eastern forests. Because of its historical importance, researchers have worked to develop a blight-resistant variety of American chestnut for establishment into its former range. Chestnut breeders now predict that such varieties will be available within a decade. Information on forest communities in which chestnut was abundant prior to the blight should provide historical legitimacy to restoration efforts and increase the likelihood of success. We analyzed "witness" trees from settlement-era land deeds in order to guide site selection for chestnut restoration at Mammoth Cave National Park, Kentucky. Chestnut was the ninth most important species in our sample and was positively associated with white oak (*Quercus alba*) and black oak (*Quercus velutina*) and negatively associated with post oak (*Quercus stellata*) and blackjack oak (*Quercus marilandica*). Non-metric multidimensional scaling indicated that chestnut was associated with chestnut oak (*Quercus prinus*), black gum (*Nyssa sylvatica*), and white oak in the overstory of pre-blight forests, and with serviceberry (*Amelanchier arborea*) and sourwood (*Oxydendrum arboreum*) in sub-canopy layers. We suggest targeting restoration sites which contain these species and avoiding sites where post oak or blackjack oak are currently dominant. Witness tree analysis allows for the identification of vegetation associations that historically had a chestnut component, increasing the potential for restoration success. Even so, silvicultural considerations and the introductions of pests and pathogens other than the blight fungus may inhibit chestnut restoration.

Index Terms: American chestnut, land deed, reference conditions, restoration, witness tree

INTRODUCTION

One of the most important events in the history of the post-glacial Eastern Deciduous Forest was the loss of the American chestnut (*Castanea dentata* [Marsh.] Borkh.) due to the pathogenic fungus *Cryphonectria parasitica* (Murrill) Bar. When *C. parasitica* was introduced from Asia in the early 1900s (Brooks 1937), the American chestnut was an important forest species throughout much of the eastern United States (Braun 1950, Nelson 1955). By 1950, chestnut blight (*C. parasitica*) had dispersed throughout much of the Appalachian Mountains and, by 1960, the American chestnut was practically extinct as a canopy tree (Keever 1953, Good 1968, Mackey and Sivec 1973, McCormick and Platt 1980). Throughout the native range of the American chestnut, all that remains of this once dominant species are seedling and stump sprouts which grow into small trees and are killed back by the blight (Paillet 1984, 1988, 2002).

Prior to the arrival of the blight, American chestnut occupied a wide range of soil types and landscapes positions and occurred in a variety of forest communities. For instance, in the Cumberland Mountains of eastern Kentucky, chestnut reached it greatest dominance on xeric sandstone ridge tops in association with pitch pine (*Pinus echinata* Miller.), where it comprised up to 50% of the canopy in some stands (Braun 1935, 1950; Rhoades and Park 2001). Chestnut also occurred in finer texture soils on mesic, north-facing slopes in association with basswood (*Tilia americana* L.) and buckeye (*Aesculus flava* Aiton.; Braun 1935, 1950). In Great Smoky Mountain National Park, American chestnut was found in 27 forest types including pine-oak and mixed-mesophytic communities (Woods and Shanks 1959). Studies of coarse woody debris document the presence of chestnut on ridges and upper slopes and in mesic coves (Muller and Liu 1991) and riparian zones (Vandermast and Van Lear 2002).

A blight-resistant hybrid chestnut possessing the form and fruiting attributes of the native American species is projected to be available for planting within a decade (Anagnostakis 1982, Griffin 2000). In anticipation of resistant varieties, establishment trials using pure American chestnut genetic material are currently underway (Brosi 2001; McCament 2004; Hewitt et al., in press). Public interest in American chestnut suggests that large-scale reintroduction may follow (Ronderos 2000). Information about the general distribution and abundance of American chestnut (Braun 1950, Russell 1987, Rhoades and Park 2001) provides approximate guidelines for future reintroduction. However, to maximize the likelihood of success, planting efforts need to identify specific landscape conditions and species associations that favor chestnut. Because chestnut is now scarce or absent throughout its native range, there are few opportunities to define such conditions in present-day forests. These target conditions can only be established through historical reconstruction of pre-blight forest composition.

A technique frequently used to reconstruct historic vegetation patterns is the analysis of "witness" trees that marked corners or other boundaries in land deeds created during European settlement (McIntosh 1962, Seischab 1990, Fralish et al. 1991, Dyer 2001, Schulte and Mladenoff 2001). Witness tree data are most often used to reconstruct vegetation patterns, but they also provide a means to examine the ecological history of individual species (Abrams 2001). Though witness tree data can be limited by errors in species identification, use of parochial nomenclature, and biases in tree selection, they are adequate for defining the historic abundance of common forest species (Rhoades and Park 2001, Schulte and Mladenoff 2001, Whitney and DeCant 2001).

In order to facilitate site selection for chestnut restoration at Mammoth Cave National Park, in central Kentucky, we analyzed land deeds spanning a 53-year period (1824-1877) prior to arrival of the chestnut blight. Our objectives were to: (1) describe the species composition of pre-settlement forests and (2) identify the species most commonly associated with American chestnut in the pre-blight forest landscape.

METHODS

Site Description

Mammoth Cave National Park (MCNP) lies within the Shawnee Hills physiographic region in central Kentucky, near the western edge of the pre-blight range of American chestnut. The area has a humid continental climate with warm summers, cool winters, and no distinct dry season. Soils at Mammoth Cave National Park are derived from either alkaline limestone (Alfisols) or acidic sandstone and shale (Ultisols) parent materials. Topographic aspect and slope position combine with these soil types to generate complex forest associations relating to edaphic and microclimatic conditions. On acidic substrate, lower slope positions and north-facing slopes support white oak (*Quercus alba* L.), black oak (*Q. velutina* Lam.), and hickory (*Carya* spp.), while more xeric locations support chestnut oak (*Q. prinus* L.) and post oak (*Q. stellata* Wangenh.). Mesic limestone sites are occupied by yellow-poplar (*Liriodendron tuliperifera* L.) and other mesophytic species. Drier limestone sites feature blackjack oak (*Q. marilandica* Muenchh.), post oak (*Q. stellata*), chinkapin oak (*Q. muhlenbergii* Englem.), and shingle oak (*Q. imbricaria* Michx.). All botanical nomenclature follows Gleason and Cronquist (1991).

American chestnut is known to have been a component of forests in and around MCNP. European explorers mentioned the abundance and stature of American chestnut, in the vicinity of what is now MCNP, before the arrival of chestnut blight (DeFriese 1884, Hussey 1884).

> *On leaving Glasgow Junction, toward Mammoth Cave, plenty of white oak is found in the sinks; post oak, black oak, scarlet oak, and red oak are found on the higher grounds and as soon as the Chester sandstone, which caps the so-called hills, is reached, chestnut is found in great abundance. This is the first chestnut worthy of note found, and all that has been found, so far [from Mississippi River to here]* (DeFriese 1884).

Within MCNP, Braun (1950) recorded tree species in five forest types. The greatest density of chestnut was found on an oak-poplar (*Quercus-Liriodendron*) site that contained 8.1% chestnut along with 31% white oak, 17% black oak, and 24% yellow-poplar. In mesophytic coves and American beech (*Fagus grandifolia* Ehrh.) bottomlands, chestnut represented 1 and 2.5% of the forest, respectively. Chestnut was also present on ravine slopes (0.8 to 2.2%) dominated by yellow-poplar, white oak, chestnut oak, and American beech. Beech-maple (*Fagus-Acer*) and white oak-hickory forests located on limestone bluffs did not support chestnut.

Evaluation of Historical Data

We randomly selected 575 settlement era land deeds from Edmonson County, Kentucky, which contains the vast majority of Mammoth Cave National Park. These deeds span a 53-year period (1824-1877) during settlement of west-central Kentucky and contained information from 6965 boundary markers or "corners." This time period preceded arrival of the chestnut blight by approximately 60 years. For each deed, we tallied the corner trees and recorded ownership, parcel size and location, and corner markers (e.g., posts, stakes).

Forest associations were examined using a variety of techniques. First, we compared the species composition of deeds where chestnut occurred with those in which it was absent. This comparisonwas made using the relative importance value (RIV = (relataive density + relataive frequency) / 2). We then used Spearman's rank correlation to examine relationships among chestnut and co-occurring species. We chose Spearman correlation because the data was irrevocably non-normal. We also analyzed the deed data using non-metric multidimensional scaling (NMS) ordination (PC-ORD ver. 4; McCune and Mefford 1999). NMS ordination performs well with data matrices that contain a large number of zeros and which may be non-normal, making it particularly useful for our application (Minchin 1987, McCune and Grace 2002).

RESULTS AND DISCUSSION

Size distribution of deeds was consistent over the sample period. Land parcels ranged from less than two to more than 400 hectares in size (Table 1). Deeds from 40.5 to 80 ha made up the largest portion of the sample during five out of the six decades examined. Across all years, 47% of the deeds covered from 20.3 to 80 ha (Table 1). The largest deeds were catalogued from 1850 to 1870; however, there was no other clear trend in parcel size across the sample

Table 1. Size distribution of European settlement-era land deeds from the vicinity of Mammoth Cave National Park, Kentucky, expressed as total number (#) and percent of total (%).

	1820		1830		1840		1850		1860		1870		All years	
Deed Area (ha)	#	%	#	%	#	%	#	%	#	%	#	%	#	%
≤ 2	1	1.4	0	0	1	1.1	2	3.2	6	3.4	4	2.8	14	2.4
2.1 - 4	2	2.7	0	0	2	2.3	1	1.6	8	4.5	1	0.7	14	2.4
4.1 - 10.1	2	2.7	4	13.8	3	3.4	7	11.1	5	2.8	9	6.2	30	5.2
10.2 - 20.2	14	19.2	5	17.2	9	10.2	7	11.1	28	15.8	30	20.7	93	16.2
20.3 - 40.4	6	8.2	5	17.2	20	22.7	11	17.5	23	13	29	20	94	16.3
40.5 - 80	28	38.4	6	20.7	30	34.1	18	28.6	58	32.8	37	25.5	176	30.6
80.1 - 200	10	13.7	7	24.1	10	11.4	8	12.7	24	13.6	18	12.4	77	13.4
201-400	3	4.1	0	0	3	3.4	0	0	3	1.7	3	2.1	12	2.1
> 400	0	0	0	0	0	0	1	1.6	2	1.1	2	1.4	5	0.9
Unknown size	7	9.6	2	6.9	10	11.4	8	12.7	20	11.3	12	8.3	59	10.3
Total	73	100	29	100	88	100	63	100	177	100	145	100	575	100

period (Table 1).

The 575 deeds contained 50 tree species (Table 2). Overall, hickory (*Carya* spp.), white oak, black oak, and post oak were the most important species, having a cumulative relative importance value (RIV) of 45.1. These species, along with blackjack oak (*Q. marilandica*), which ranked seventh in importance, are all typical of xeric forest conditions (Table 2). American chestnut occurred on 119 of the deeds (21%), and was the ninth most abundant species overall, exhibiting an RIV of 3.6 (Table 2). Although hickory and white oak had the largest RIV values overall, post oak was the most important species in the 1820s and was among the most important species in the first four decades examined (Table 2). Post oak importance declined in the last three decades of the sampling period, and by the 1870s, both hickory and white oak had importance values two times higher than post oak. This trend is mirrored in blackjack oak, which exhibited greatest importance during the 1820s and 1830s. In contrast, white oak and chestnut oak (Table 2) exhibited their largest importance values in the last two decades of the sample.

American chestnut was associated with species known to inhabit sandy xeric uplands while being negatively correlated with post oak and blackjack oak. For example, the RIV of both post oak and blackjack oak was nearly three times lower on deeds that contained chestnut as compared to deeds without chestnut (Figure 1). Red oak (*Quercus rubra* L.) and hickory were also more important on deeds where chestnut was absent. In contrast, white oak importance was greater on deeds that contained chestnut. These species patterns were mirrored by the Spearman rank correlation analysis. For instance, chestnut RIV was most strongly correlated with white oak and black oak (both, $P < 0.0001$), and most negatively correlated with blackjack oak ($P < 0.001$) and post oak ($P < 0.001$; Figure 2).

Non-metric multidimensional scaling further emphasized these patterns (Figure 3). The first ordination axis explained 34% of the variability in the data set and arrayed species along a gradient from the xerophytes post oak and blackjack oak near the far left of the diagram to the more typically mesic species paw-paw (*Asimina triloba* (L.) Dunal.) and boxelder (*Acer negundo* L.) on the far right. American chestnut was found near the middle of the diagram (labeled CADE) in the vicinity of serviceberry (*Amelanchier arborea* (Michx. F.) Fern.), white and chestnut oak, and sourwood (*Oxydendrum arboreum* (L.) DC.).

Restoration Target Areas

Our witness tree data from the pre-blight forests of Mammoth Cave National Park indicate that American chestnut was associated with species common on moderately acidic, upper slopes. In particular, our analysis identified chestnut oak, white oak and black oak, and the understory species sourwood and serviceberry as associates of chestnut. Chestnut was negatively associated with red oak (a typically mesic oak), and all three analyses indicated a strong negative association with post oak and blackjack oak. In order to begin restoration of American chestnut, we suggest establishing seedlings on sites that currently support white oak, black oak, and chestnut oak as canopy species and include serviceberry and sourwood in the sub-canopy layers. Restoration efforts should avoid sites where post oak or blackjack oak is an important species.

Although witness tree analysis can be used to target restoration sites, creating the conditions necessary for chestnut restoration may prove difficult. Chestnut establishment and growth are apparently enhanced by the high light conditions that follow forest disturbance (Hewitt et al., in press). For instance, the coppice forests of early 20th

Table 2. Relative importance value (RIV) of tree species (or taxa only identified to genus) found in European settlement-era land deeds from the vicinity of Mammoth Cave National Park in Edmonson County, Kentucky.

Common name	Scientific name	1820	1830	1840	1850	1860	1870	All Years
Hickory	*Carya* spp.	11.9	12.3	12.7	10.6	13.2	14.2	12.5
White Oak	*Quercus alba*	11.5	10.4	11	10	12.9	14	11.6
Black Oak	*Quercus velutina*	10.1	8.8	11.2	9.9	11.5	11.8	10.6
Post Oak	*Quercus stellata*	12.1	11.7	12.7	11.5	8.3	5.7	10.4
Red Oak	*Quercus rubra*	7.7	10.2	8	7.3	5.9	5.4	7.4
Beech	*Fagus grandifolia*	6.5	2.4	7.2	7.6	7.4	6	6.2
Blackjack Oak	*Quercus marilandica*	6.9	7.8	3	5.9	2.3	3.1	4.8
Poplar	*Liriodendron tulipifera*	4.7	4.9	3.9	3.5	4.1	4	4.2
Chestnut	*Castanea dentata*	2.8	6.1	2.4	2.6	4.2	3.6	3.6
Spanish Oak	*Quercus falcata*	1.8	6.2	5.7	2.4	2.3	1.7	3.3
Dogwood	*Cornus florida*	1.5	3.1	3.9	2.8	3.7	3.5	3.1
Sugar Tree	*Acer saccharum*	3.4	1.7	2	3.7	3.4	2.8	2.9
Black gum	*Nyssa sylvatica*	2	1	1	2.2	3.7	3.8	2.3
Ash	*Fraxinus americana, F. pennsylvanica*	2.1	1	1.5	2.8	2.5	2.5	2.1
Walnut	*Juglans nigra*	2.1	2.1	2.1	1.9	1.1	1.3	1.8
Sycamore	*Platanus occidentalis*	1.8	2.8	1.4	0.9	1.6	1.2	1.6
Maple	*Acer saccharinum, A. rubrum*	0.8	1.2	1.9	2.3	1.4	1.9	1.6
Elm	*Ulmus americana*	1.8	1.7	0.7	1.7	0.5	1.8	1.4
Chestnut Oak	*Quercus prinus*	0.2	0	0.7	1	1	3.4	1.1
Ironwood	*Carpinus caroliniana*	0.2	0.5	0.3	1	1.1	0.9	0.7
Sassafras	*Sassafras albidum*	0.2	0	1.4	0.6	0.7	1	0.7
Butternut	*Juglans cinerea*	0.9	0	0.8	0.8	0.5	0.9	0.7
Sweet gum	*Liquidambar styraciflua*	0.2	0.5	0.5	1	0.7	0.6	0.6
Mulberry	*Morus rubra*	0.6	0.7	0.9	0	0.2	0.4	0.5

Minor species (and taxa indentified only to genus) rank ordered by RIV for all years: water oak (*Quercus nigra*), gum (unknown), hornbeam (*Ostrya virginiana*), sour-wood (*Oxydendrum arboreum*), pin oak (*Quercus palustris*), oak (*Quercus* spp.), redbud (*Cercis canadensis*), boxelder (*Acer negundo*), red elm (*Ulmus rubra*), persimmon (*Diospyros virginiana*), hackberry (*Celtis occidentalis*), honeylocust (*Gleditsia triacanthos*), hemlock (*Tsuga canadensis*), buckeye (*Aesculus glabra*), service-berry (*Amelanchier arborea*), locust (*Robinia pseudoacacia*), black hickory (*Carya texana*), scarlet oak (*Quercus coccinea*), birch (*Betula nigra*), basswood (*Tilia americana*), pawpaw (*Asimina triloba*), black ash (*Fraxinus nigra*), cherry (*Prunus serotina*), black haw (*Viburnum prunifolium*), cedar (*Juniperus virginiana*), apple (*Pyrus malus*).

century New England were apparently well suited to chestnut growth and establishment (Paillet 2002). Even so, public opinion regarding forest harvesting and other forms of forest disturbance, particularly on National Park Service land, may prevent the stand manipulations necessary to recreate these conditions. Moreover, the introduction of forest pests and pathogens other than the blight fungus (Rhoades et al. 2003, Rieske et al. 2003) and changes in fire regime may alter the ability of chestnut to succeed on sites where it once occurred. Thus, although historical analysis may aid in targeting areas conducive to chestnut success, experimental studies, including silvicultural manipulations, are needed to refine our understanding of the structural and micro-environmental conditions necessary for successful chestnut restoration (Brosi 2001, McCament 2004).

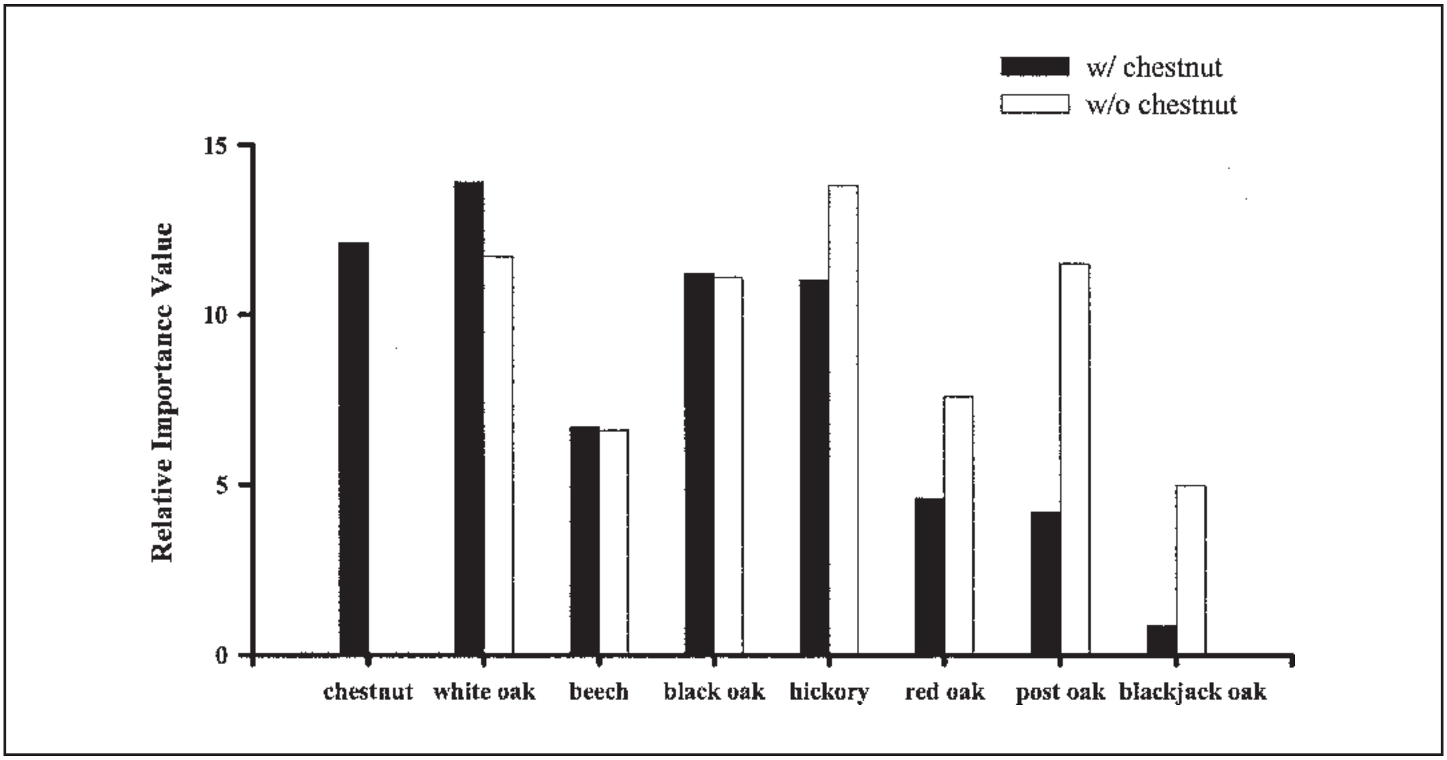

Figure 1. Relative importance value (RIV) of the seven most important tree species on settlement-era land deeds from the vicinity of Mammoth Cave National Park. Comparison is between deeds that contained American chestnut (*Castanea dentata*) (w/chestnut) and those that did not (w/o chestnut).

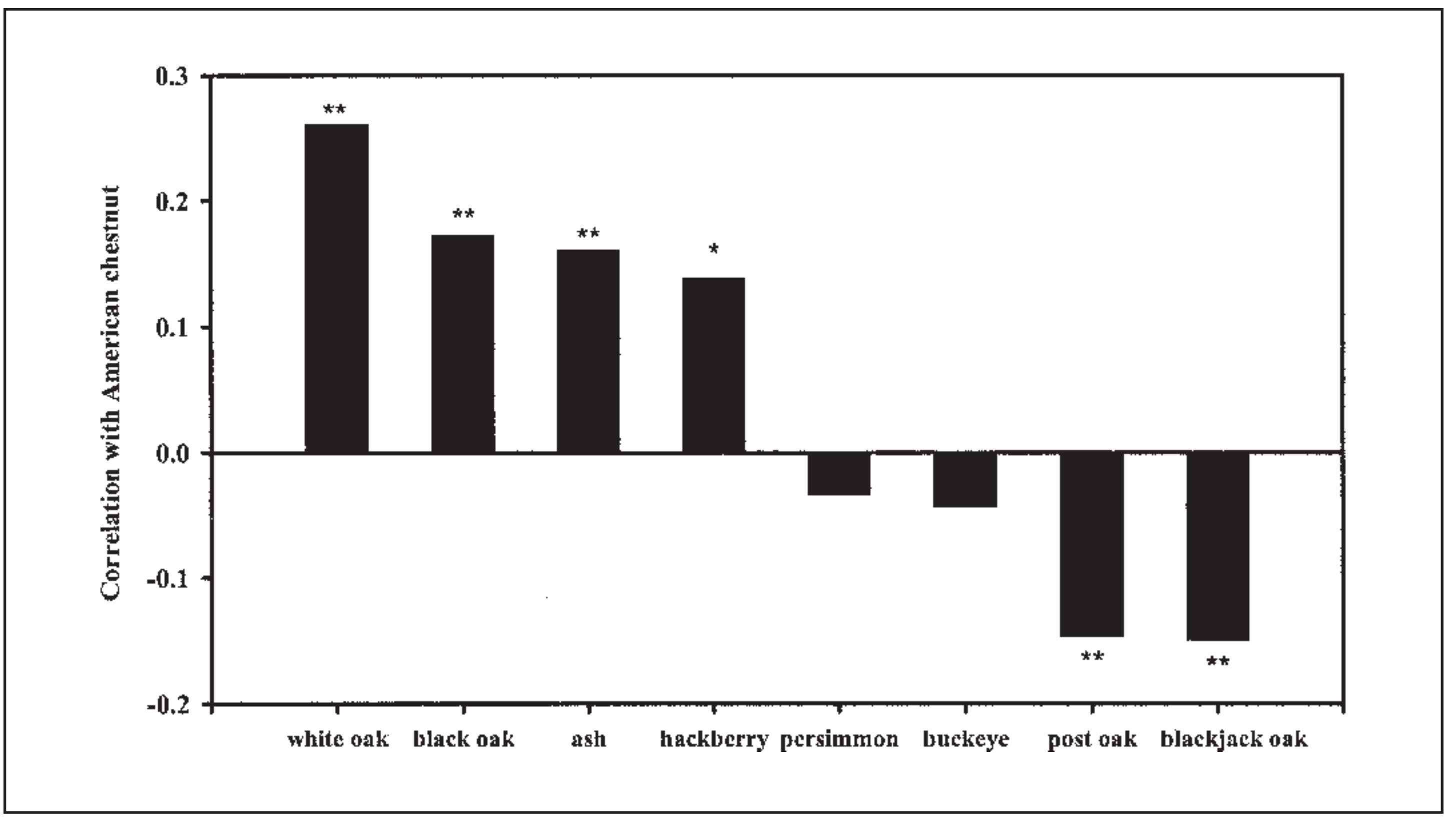

Figure 2. Spearman rank-correlation coefficients for the four species most positively and negatively correlated with American chestnut (*Castanea dentata*) in settlement-era land deeds from the vicinity of Mammoth Cave National Park. Note: * denotes significance at $P < 0.05$, ** denotes significance at $P < 0.001$.

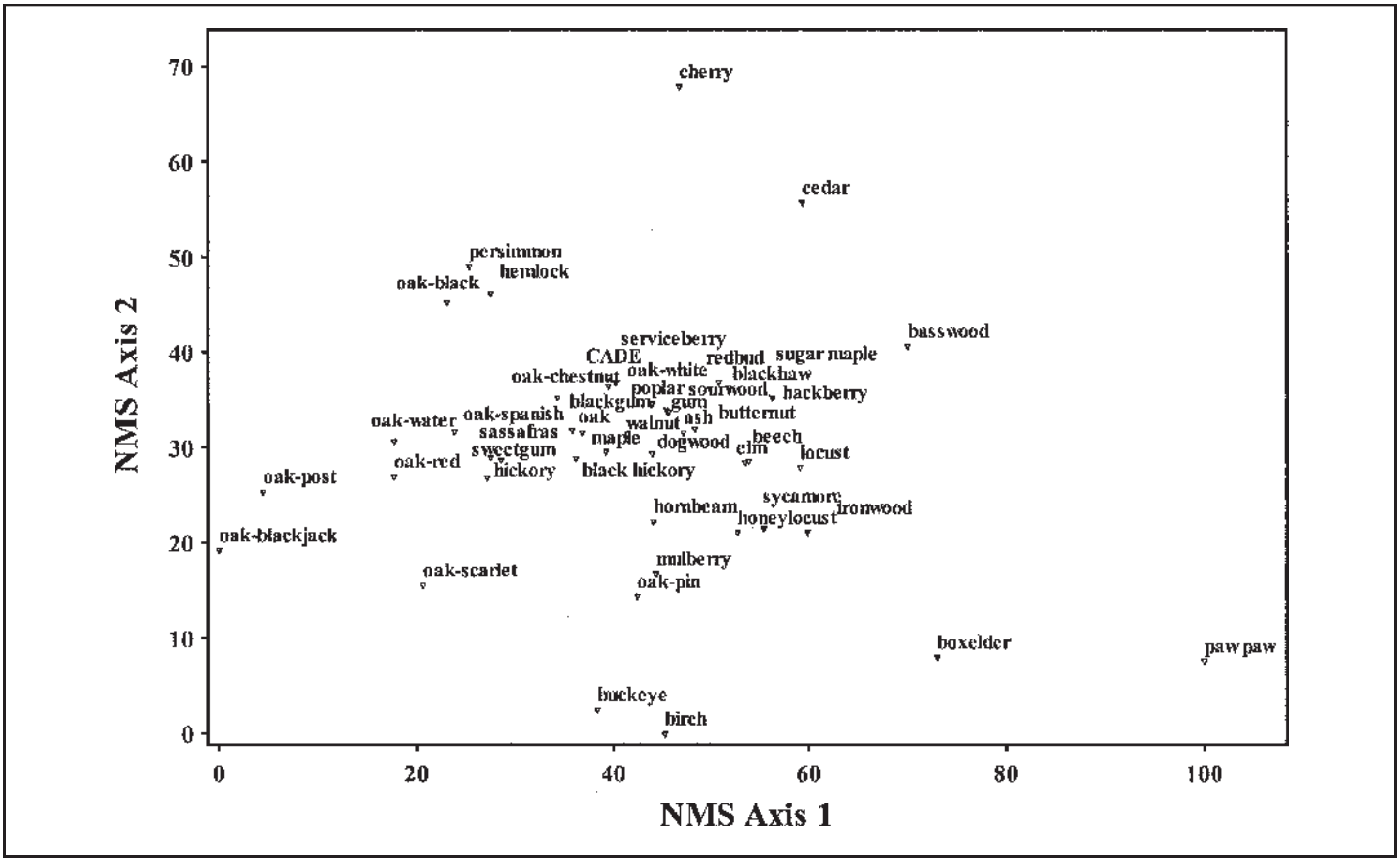

Figure 3. Non-metric multidimensional scaling ordination of settlement-era land deed data from the vicinity of Mammoth Cave National Park. Common names as listed on land deeds are presented and name order of oaks was reversed (e.g. oak-white) in order to elucidate species patterns. American chestnut (*Castanea dentata*) was labeled CADE for ease of recognition.

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