

Analysis of temporal variation and species–site relationships of witness tree data in southeastern Pennsylvania

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Abstract: Witness tree species – site relationships are described with respect to parent material, soil drainage, and soil surface texture in Lancaster County, southeastern Pennsylvania. *Quercus velutina* Lam. and *Carya* were positively associated with “limestone” parent materials and well-drained, loamy sites. *Quercus velutina* was strongly associated with “acid shale and sandstone” parent materials and well-drained, upland soils. *Quercus alba* L. was most abundant on parent material classes associated with stream valleys and coves while *Quercus prinus* L. and *Castanea dentata* (Marsh.) Borkh. were positively associated with well-drained, rocky sites on “quartzite” parent materials. Procedures were then developed to test for significant changes in witness tree species frequencies over the 100-year period of metes and bounds surveys in Lancaster County. These tests revealed that *Quercus coccinea* L., *Nyssa sylvatica* Marsh., and early successional species were surveyed much later than *Quercus rubra* L., *Q. alba*, and *Carya* spp. Agricultural land clearing, cutting for firewood, selective logging, and the charcoal-iron industry all probably contributed these species changes. Overall, abundances of minor species appear to be much more sensitive to these early settlement land uses. Given the extent of metes and bounds surveys, these tests for temporal variations may be applied to witness tree data throughout the eastern United States.

Résumé : Les relations entre les espèces d’arbres-témoins et le site sont décrites en fonction de la roche-mère, du drainage et de la texture de surface du sol pour le comté de Lancaster dans le sud-est de la Pennsylvanie. *Quercus velutina* Lam. et *Carya* étaient positivement associés à une roche-mère calcaire et des sites loameux bien drainés. *Quercus velutina* était étroitement associé à une roche-mère composée de schiste acide et de grès et des sols bien drainés des hautes-terres. *Quercus alba* L. était le plus abondant sur les classes de roches-mères associées aux cours d’eau des vallées et des vallons encaissés tandis que *Quercus prinus* L. et *Castanea dentata* (Marsh.) Borkh. étaient positivement associés aux sites rocheux et bien drainés sur des roches-mères de quartzite. Des procédures ont ensuite été développées pour détecter les changements significatifs dans la fréquence des espèces d’arbres-témoins sur la période de 100 ans couverte par les relevés de bornage dans le comté de Lancaster. Ces tests révèlent que *Quercus coccinea* L., *Nyssa sylvatica* Marsh. et les espèces de début de succession ont été notées beaucoup plus tard que *Quercus rubra* L., *Q. alba* et *Carya* spp. Le défrichage des terres agricoles, les coupes pour le bois de chauffage, les coupes sélectives et l’industrie du charbon ont probablement tous contribué à ces changements d’espèces. Globalement, l’abondance des espèces secondaires semble être beaucoup plus sensible à ces usages des terres du début de la colonisation. Compte tenu de l’ampleur des relevés de bornage, ces tests pourraient être appliqués aux données d’arbres-témoins partout dans l’est des États-Unis pour détecter les variations temporelles.

[Traduit par la Rédaction]

Introduction

In early land surveys throughout the eastern and midwestern United States, surveyors frequently relied on witness (boundary) trees to mark property corners. Over the past century, ecologists have utilized these trees recorded in surveyors’ notes to reconstruct forest composition at the time of early European settlement (Lutz 1930; Spurr 1951; Bourdo 1956; McIntosh 1962; Siccama 1971; Seischab 1990; Abrams and Ruffner 1995). Species–site relationships may

be analyzed using witness tree data, and the role of disturbances such as windthrow and fire can be established (Lorimer 1977; Grimm 1984; Seischab and Orwig 1991; Abrams and Ruffner 1995; Abrams and McCay 1996). Also, with this baseline information, the impacts of Native American and European land uses on forest change can be investigated (Ruffner 1999; Black and Abrams 2001). Thus, witness trees provide a valuable quantitative resource for describing the ecology of early settlement forests and the impacts of humans on the landscape, especially in regions where original forests have been cleared or altered.

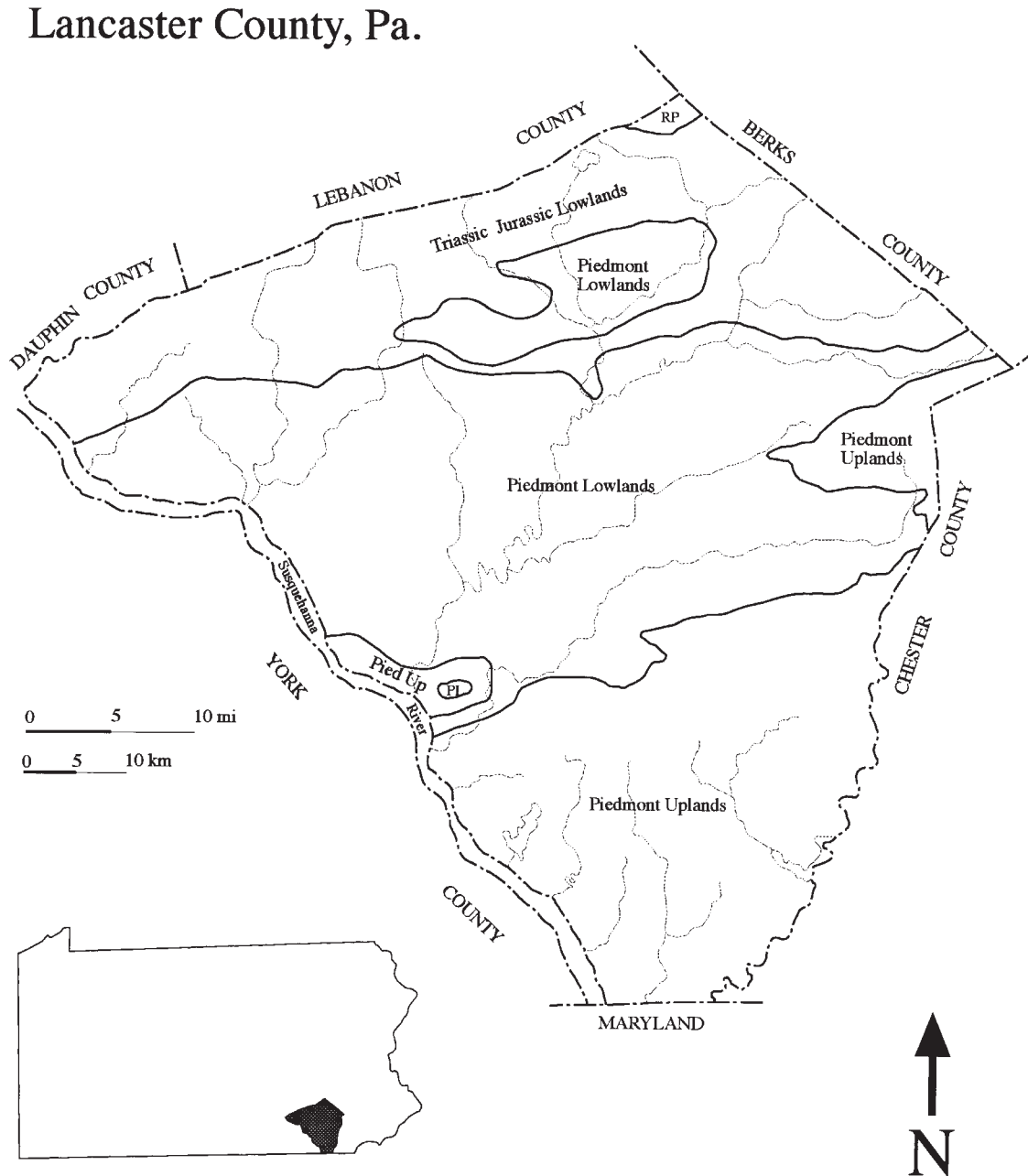
Because of the fact that witness trees represent an unintentional vegetation survey, a number of biases and errors may occur in the data. Occasionally, scientific names and common colonial species names are impossible to associate, and some witness trees may have been misidentified (Siccama 1971; Loeb 1987; Seischab 1990). However, the most serious problem associated with witness tree data is

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Fig. 1. Physiographic sections and hydrology of Lancaster County, Pennsylvania. RP, Reading Prong (not included in this study).



that surveyors could have biased their selection of trees on criteria of economic value, ease of inscription, size, vigor, longevity, age, or relative abundance (Russell 1981; Grimm 1984; Schulte and Barnes 1996). A number of statistical tests have been developed to evaluate these biases in rectangular surveys, such as the public land surveys (PLS). Although these tests are criticized because they make the unrealistic assumption that trees are randomly distributed throughout the study area, their results suggest an absence of species or size bias (Kenoyer 1930; Bourdo 1956; Hushen et al. 1966; Siccama 1971; Delcourt and Delcourt 1974; Delcourt 1976). Another indication that bias was insignificant is that surveyors usually identified a large number of tree species. Furthermore, qualitative forest descriptions of-

ten agree with species frequencies derived from witness tree data (Siccama 1971; Lorimer 1977; Whitney 1986).

Much of the East Coast was surveyed before the PLS procedures were standardized in 1785, and no species or size bias tests exist for these older, colonial surveys. Also, in this irregular "metes and bounds" system, surveyors often followed a seemingly haphazard course along stream banks, "Indian paths," or ridgetops (Munger 1991; Abrams and Ruffner 1995). As a result, witness trees were not systematically sampled across the landscape (Black and Abrams 2001). In a systematic rectangular system, all topographic regions and landforms would roughly have been sampled with equal intensity. But in metes and bounds surveys, certain topographic regions and landforms may be overly repre-

sented in the witness tree record (Black and Abrams 2001). For example, in Lancaster County, surveyors recorded a significantly greater number of witness trees in the mountainous regions. In addition, surveyors preferred to locate property corners on ridgetops and in stream valleys while avoiding difficult side-slope terrain (Black and Abrams 2001). Thus, metes and bounds witness tree data must be subdivided with respect to topographic region, and into landforms within each topographic region before the data may be interpreted.

Metes and bounds witness trees are not only irregularly distributed across the landscape but also through time. Unlike PLS, which were short in duration and usually completed before settlement, metes and bounds surveys were often conducted over a much longer period and while settlement was occurring. Therefore, European settlers may have had the opportunity to alter local forest composition by the time the last surveys were completed. The few studies that have attempted to quantify species differences between early and late metes and bounds surveys have suggested that species frequency shifts occurred (Glitzenstein et al. 1990; Orwig and Abrams 1994). However, these studies do not include geologic and topographic factors that may have interacted with vegetation and settlement patterns. For example, in Lancaster County, Pennsylvania, settlement began in the most fertile regions and later expanded into the more rugged and less desirable terrain. Without accounting for these environmental variables, temporal analysis of witness tree data would reveal a distinct shift from species characteristic of the fertile lowlands to those species common on the uplands, which could have been falsely attributed to the effects of European disturbance.

In this study, we propose techniques to test for human impacts on forest composition over the survey period, while accounting for interactions among environmental variables, settlement patterns, witness tree densities, and vegetation distribution. Lancaster County in southeastern Pennsylvania is well suited for this research, since it contains a diverse physiography and a high density of metes and bounds witness trees that were recorded over a period spanning more than 100 years. Also, techniques have been described to eliminate the effects of interactions between physiography and witness tree density specifically for the study area (Black and Abrams 2001). Therefore, the objectives of this study are to (i) describe early settlement forest species–site relationships with respect to soil parent material, drainage, and soil surface texture and (ii) propose techniques for investigating temporal variations in metes and bounds witness tree data.

Study area

Lancaster County occupies approximately 2453 km² in southeastern Pennsylvania and is located almost entirely within the Piedmont Physiographic Province (Fenneman 1938; Custer 1985). Three distinct sections of the Piedmont occur in Lancaster County: the Piedmont Uplands, the Piedmont (Conestoga) Lowlands, and the Triassic–Jurassic (Gettysburg–Newark) Lowlands (Fig. 1). The Piedmont Uplands extend across the southern third of the county. Broad, gently rolling hills dissected by relatively deep, steeply sloping, and often rocky stream valleys typify the topography of

Table 1. Lancaster County witness tree environmental analysis classification scheme.

Surficial geology	Drainage
(1) Alluvial	(1) Well
(2) Loam	(2) Moderately well
(3) Silt loam	(3) Somewhat poorly
(4) Channery, gravel	(4) Poor
(5) Very stony	
(6) Extremely stony	

this area (Custer 1985; Ciolkosz et al. 1989). The northern third of the county lies within the Triassic–Jurassic Lowlands. Abrupt “trap” ridges of igneous diabase interrupt rolling lowlands formed from soft, easily weathered sandstone and shale (Fenneman 1938; Custer 1985). Above the Triassic–Jurassic Lowlands, the northernmost tip of the county falls within the Reading Prong section of the New England Province and is excluded from this study (Fig. 1).

Little topographic relief and well-drained calcareous Ultisols make the Piedmont Lowlands of central Lancaster County some of the best agricultural land in the eastern United States (Cuff et al. 1989). To the north, acidic Silurian sandstone and shale underlie the soils of the Bedington association (Custer 1985; Ciolkosz et al. 1989). Although this soil association is generally classified with the Piedmont Lowlands, the sedimentary parent materials and well-defined topography are most similar to those of the Triassic–Jurassic Lowlands. For these reasons, the Bedington association was included with the Triassic–Jurassic Lowlands in this study.

Historical context

Settlement of Lancaster County began early in the 18th century. Early colonists purchased large parcels of the most desirable land in the Piedmont Lowlands and quickly established farms. By 1740, settlers began to experience a shortage of land in the Piedmont Lowlands as reflected by a sharp decrease in the number and size of surveys and a dramatic increase in land prices (Ellis and Evans 1883; Henderson 1989). As survey dates indicate, settlement shifted to the less desirable Piedmont Uplands in the 1750s and then to the Triassic–Jurassic Lowlands in the 1760s. During settlement of these more mountainous sections, few large tracts of land were purchased, and survey sizes steadily decreased over time (Henderson 1989; Black 1998). By 1770, land prices had quadrupled from what they were in 1736, and few surveys were conducted in the county (Henderson 1989).

Spared the extensive clearing experienced by the Piedmont Lowlands during early settlement, the forests of the Piedmont Uplands and Triassic–Jurassic Lowlands fueled the charcoal-iron industry. Soon after the first furnace opened in 1742, six additional charcoal-iron furnaces opened in Lancaster County and two more opened just across what is now the county’s northern border. In conjunction with the furnaces, 14 forges used charcoal as fuel to process pig iron in Lancaster County. Under these demands, forests were depleted by the mid-19th century (Ellis and Evans 1883). The charcoal-iron industry in combination with agriculture eventually resulted in the clearing of all forest lands in Lancaster County.

Methods

Witness tree environmental analysis

Early European settlement forest conditions of Lancaster County were reconstructed using original warrant (survey) maps. The county surveyor, after completing the first survey of a tract of land, drew a warrant map showing property boundary lengths and bearings, the location and nature of corner markers (whether a tree,

Table 2. Parent material classification schemes within physiographic provinces.

Triassic–Jurassic Lowlands	Piedmont Lowlands	Piedmont Uplands
(1) Acid sandstone and shale	(1) Limestone	(1) Mica schist, granitized schist
(2) Red sandstone and shale	(2) Limestone and siltstone	(2) Mica schist, quartzite
(3) Metamorphosed sandstone	(3) Micaceous limestone and schist	(3) Sandstone and quartzite
(4) Diabase		

post, or stone), and any significant geographic landmarks, including streams, mountains, Indian paths, or roads (Munger 1991; Abrams and Ruffner 1995). In Lancaster County, a total of 9880 witness (bearing) trees were recorded by vernacular name on some 3400 survey maps. These warrant maps have been connected into contiguous township warrantee maps for all 42 townships in Lancaster County and are available at the Pennsylvania State Archives in Harrisburg. We transcribed these township warrantee maps onto 27 U.S. Geological Survey (USGS) 7.5' quadrangles, and the location of each witness tree was tallied with respect to three environmental parameters: parent material, surface soil texture, and soil drainage class. Parent material, drainage class, and surface textures of the soils were obtained from the Lancaster County Soil Survey (Custer 1985) and each environmental parameter was divided into discrete classes. Parent material was divided into 10 classes (Table 1), surface soil texture was divided into 6 classes, and soil drainage into 4 classes (Table 2). The soil survey drainage classes "excessively well drained" and "well drained" were combined into "well drained"; and "poorly drained" and "very poorly drained" were combined into "poorly drained" so sample sizes would be more equal across the soil drainage classes. For all analyses, soils disturbed beyond classification and areas flooded by dams were excluded from the sample set. Additionally, alluvial soils were excluded from parent material analysis. Drainage and soil surface texture parameters were analyzed within each physiographic section. Environmental classes with too small a sample set were dropped from analysis.

Contingency table analysis was used to evaluate positive or negative association of a species with each class of environmental parameter (Strahler 1978). First, we constructed presence and absence contingency tables for each combination of species and environmental parameter. We then used the G^2 statistic to test for independence between species distribution and environmental parameter in each contingency table (Sokal and Rolf 1969). At this point, species with fewer than six individuals in more than two thirds of the "expected" contingency table cells were excluded from analysis because of inadequate sample size (Steel et al. 1997). After calculation of the G^2 statistic, we removed species without a significant response ($\alpha = 0.05$) from further analysis. For significant species, table cells were converted from frequency counts to standardized residuals, and the standardized residuals were then further corrected with respect to cell variance according to the method of Haberman (1973). A positive corrected standardized residual indicated a positive association with the environmental parameter, while a negative corrected standardized residual indicated a negative association (Strahler 1978).

Temporal analysis

Witness trees were tallied with respect to survey year and soil series in the relatively level Piedmont Lowlands and mountainous Piedmont Uplands of Lancaster County. Within each soil series, the survey dates of all witness trees were averaged to calculate the mean witness tree survey date. Once soil series were classified with respect to an environmental parameter, mean witness tree survey dates in each soil series were compared in successively larger physiographic scales: within parent material classes, within physiographic sections, and among physiographic sections. We deter-

mined significant differences in survey dates using analysis of variance followed by Tukey's mean separation tests.

To compare mean survey dates among species, witness trees were grouped with respect to parent material to eliminate as many edaphic variables as possible while maintaining a relatively large sample size. Grouping with respect to parent material also reduced variations in witness tree density (Black and Abrams 2001). Two closely related parent material classes, "limestone and siltstone" and "limestone," did not significantly differ in time of survey and were combined to increase sample size. Within each of these revised parent material classes, the mean survey date of each major tree species was calculated and mean survey dates of species within each parent material class were compared using analysis of variance followed by Tukey's mean separation tests.

Results

Species–site relationships

Castanea dentata (Marsh.) Borkh., *Quercus prinus* L., *Quercus alba* L., *Quercus coccinea* Muench., and *Nyssa sylvatica* Marsh. were positively associated with soil classes of the Piedmont Uplands (Table 3, Fig. 2). Within that section, *Castanea dentata*, *Q. prinus*, and *Q. coccinea* were most abundant on the rugged "schist and quartzite" and "sandstone and quartzite" parent materials. In contrast, *N. sylvatica* and *Q. alba* were most positively associated with the relatively level "schist" parent material class. On the Triassic–Jurassic Lowlands, *Quercus velutina* Lam. and *Q. coccinea* were positively associated with the "acid shale and sandstone" parent material class (Table 3, Fig. 2). *Quercus alba* was most abundant in the "sandstone and siltstone" class, a parent material generally occurring in valleys and coves. Of those species positively associated with soils of the Piedmont Lowlands, *Carya* spp. and *Q. velutina* were most abundant on the "limestone" parent material class, while *Q. alba* exhibited a positive association with the "limestone and siltstone" parent material class (Table 3, Fig. 2). *Castanea dentata* and *Q. prinus* were negatively associated with parent materials of the relatively level and calcareous terrain of the Piedmont Lowlands.

Upland species *Castanea dentata* and *Q. prinus* were positively associated with well-drained, stony soils (Figs. 3 and 4). *Quercus velutina* was also positively associated with well-drained soils, but was more positively associated with loamy soil than stony soils. In contrast, *Q. alba* and *Acer* were positively associated with poorly drained, alluvial soils. *Nyssa sylvatica* was also most abundant on poorly drained soils, yet was positively associated with both alluvial and stony soil surface textures. *Carya* spp. and *Q. coccinea* exhibited only weak associations with drainage class and surface soil texture (Figs. 3 and 4).

Table 3. Common witness tree species counts and frequencies (%) within parent material classes of three physiographic sections in Lancaster County, Pennsylvania.

Species	Piedmont Uplands			Piedmont Lowlands			Triassic–Jurassic Lowlands			
	Mica schist, granitized schist	Mica schist, quartzite	Sandstone, quartzite	Limestone	Limestone, siltstone	Schist, micaceous limestone	Acid shale, sandstone	Sandstone, siltstone	Metamorphosed sandstone	Diabase
<i>Acer</i> spp.	4.8	0.9	0.0	0.0	0.0	1.1	0.1	1.2	0.0	0.7
<i>Betula</i> spp.	0.6	0.4	0.0	0.0	3.9	0.0	0.0	0.1	0.0	1.3
<i>Carya</i> spp.	11.3	12.7	9.2	30.3	20.5	24.6	11.5	16.1	21.9	22.9
<i>Castanea dentata</i>	9.4	20.5	23.1	0.2	0.0	1.1	10.8	7.9	5.3	6.5
<i>Fagus grandifolia</i> Ehrh.	0.0	0.1	0.0	0.2	0.0	1.6	0.0	0.3	1.3	1.3
<i>Fraxinus</i> spp.	1.0	0.1	0.0	0.3	1.6	2.1	0.2	0.7	1.3	1.3
<i>Juglans</i> spp.	0.8	0.2	0.0	0.2	1.6	1.6	0.0	0.2	0.0	0.7
<i>Liriodendron tulipifera</i>	1.3	0.4	0.0	0.2	0.0	2.1	0.3	0.6	0.7	1.3
<i>Nyssa sylvatica</i>	2.5	1.1	0.8	0.2	0.8	1.6	0.9	1.3	0.7	2.0
<i>Pinus</i> spp.	0.4	0.2	0.8	0.0	0.0	0.0	0.1	0.1	0.0	0.0
<i>Quercus alba</i>	38.8	23.3	9.2	28.4	41.7	25.7	22.9	32.2	27.8	28.1
<i>Quercus coccinea</i>	6.3	5.9	12.3	3.1	4.7	3.2	7.9	5.1	6.6	3.9
<i>Quercus prinus</i>	3.3	6.2	18.5	0.2	0.0	0.0	3.3	2.6	2.6	3.9
<i>Quercus rubra</i>	0.8	1.4	0.0	0.1	0.0	0.0	0.0	0.1	0.0	1.3
<i>Quercus velutina</i>	17.7	26.1	26.2	35.9	23.6	32.1	41.8	30.9	31.1	22.9
<i>Robinia pseudoacacia</i>	0.4	0.4	0.0	0.0	0.0	1.6	0.0	0.0	0.0	0.0
<i>Ulmus</i> spp.	0.0	0.0	0.0	0.2	0.8	1.1	0.0	0.1	0.0	1.3
Other	0.6	0.2	0.0	0.5	0.8	1.6	0.3	0.5	0.7	0.7
Tree count	480	3620	130	1243	127	187	1019	1778	151	153

Fig. 2. Significant associations ($\alpha = 0.01$) of species to parent material classes in Lancaster County, Pennsylvania. Positive corrected standardized residuals indicate a positive association with the parent material class, while negative residuals indicate a negative association.

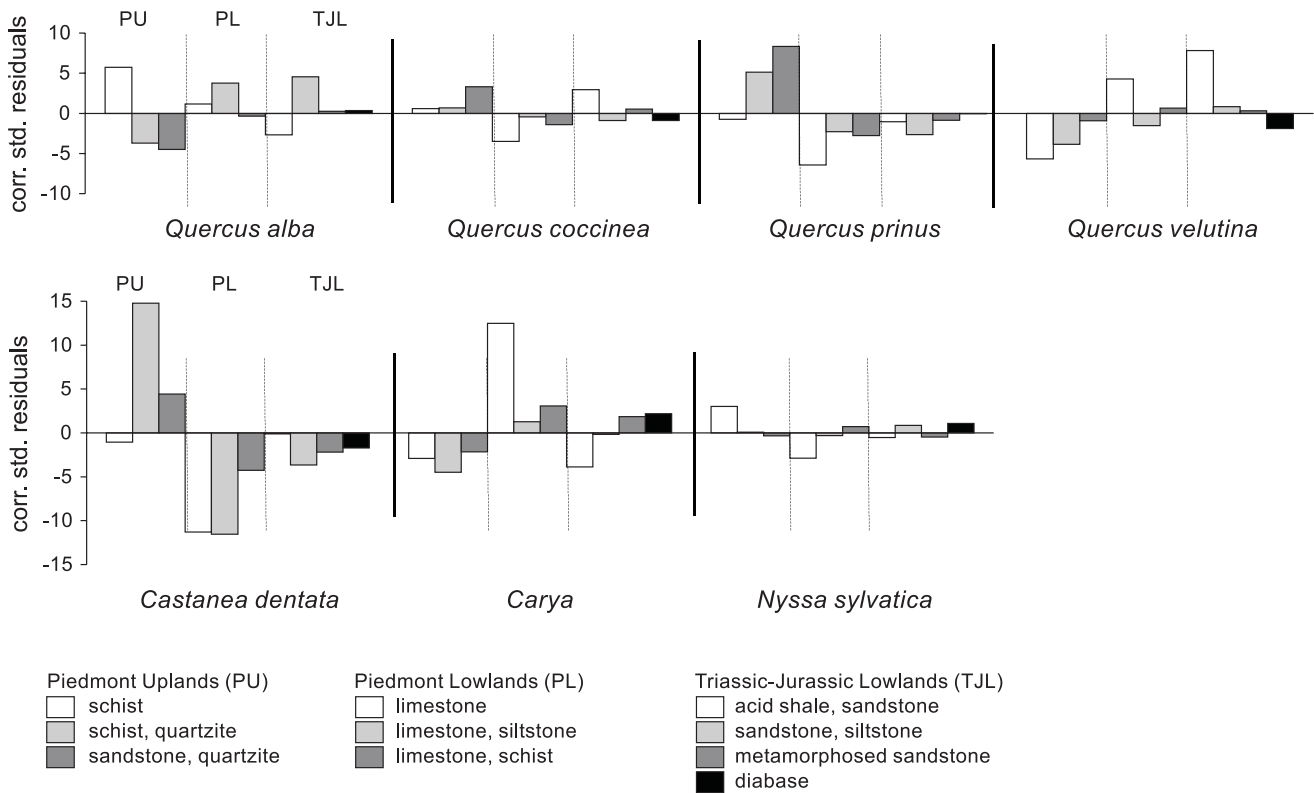


Fig. 3. Significant associations ($\alpha = 0.01$) of species to soil drainage classes in Lancaster County, Pennsylvania. Positive corrected standardized residuals indicate a positive association with the soil drainage class, while negative residuals indicate a negative association. NS, not significant.

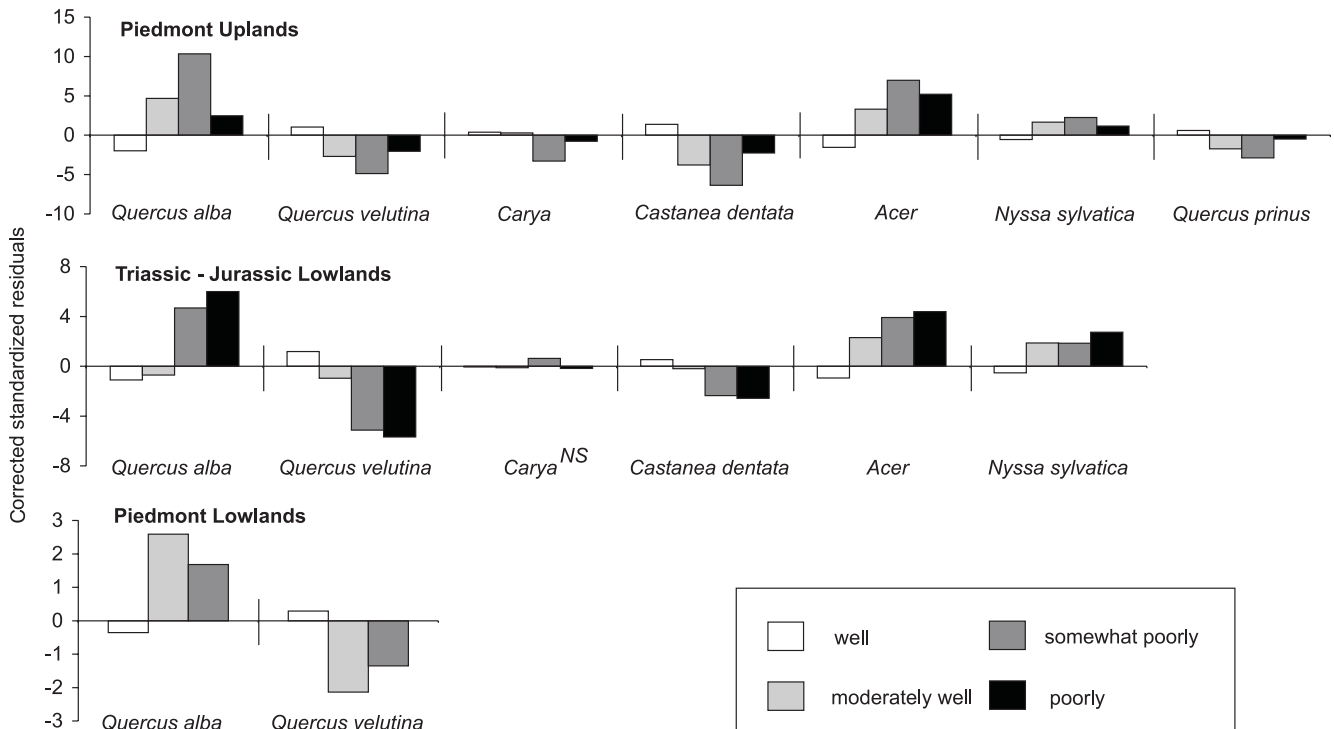
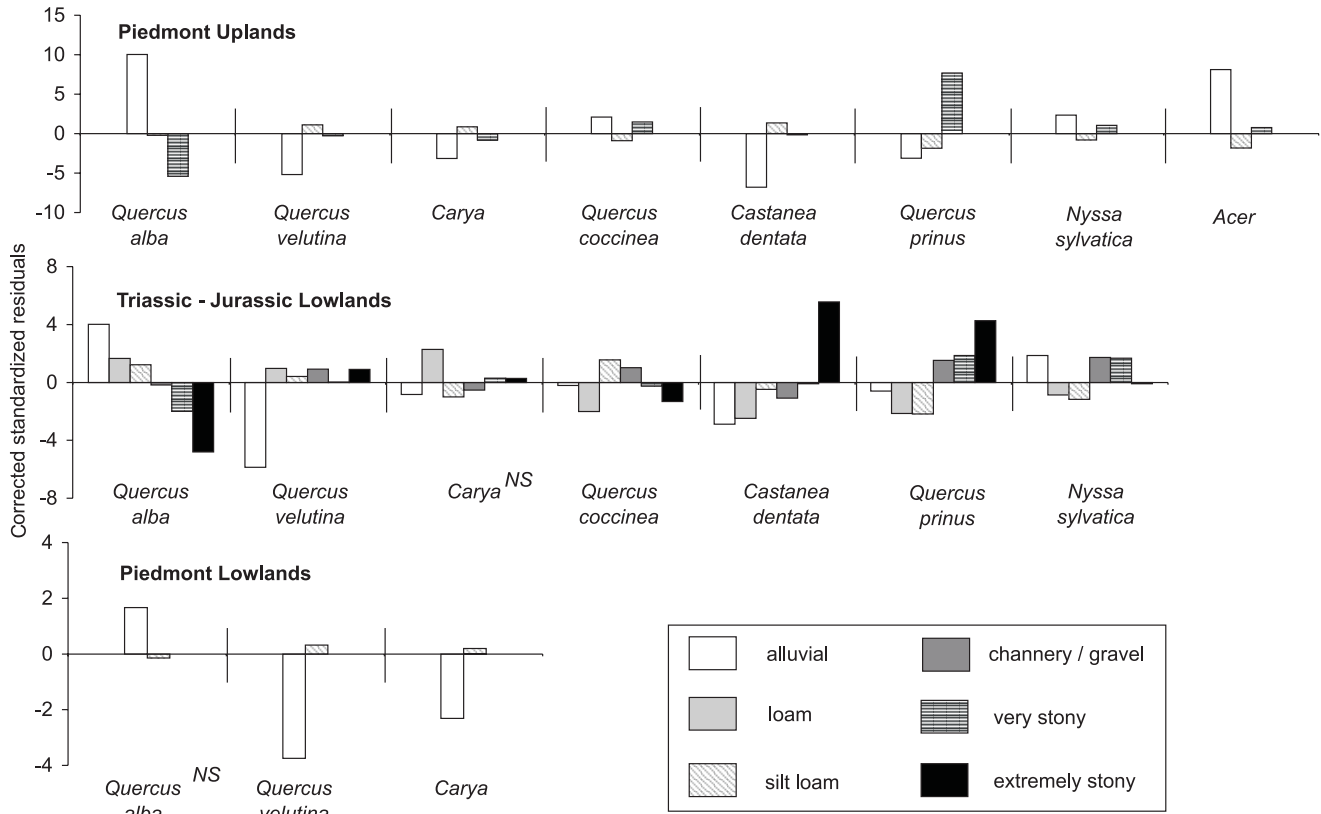


Fig. 4. Significant associations ($\alpha = 0.01$) of species to soil surface texture classes in Lancaster County, Pennsylvania. Positive corrected standardized residuals indicate a positive association with the soil surface texture class, while negative residuals indicate a negative association. NS, not significant.



Temporal analysis

Mean soil series survey dates were significantly ($\alpha = 0.05$) later in the Piedmont Uplands than in the Piedmont Lowlands (Figs. 5–7). Also, mean survey dates were significantly ($\alpha = 0.05$) later in the “sandstone and quartzite” parent material class of the Piedmont Uplands than the rest of the physiographic section (Figs. 5 and 6). Because the soil series in the “sandstone and quartzite” class represent rocky, upland, well-drained sites, the soil surface texture class “very stony” and the soil drainage class “well-drained” had relatively late survey dates in the Piedmont Uplands. In the Piedmont Lowlands, mean survey year did not significantly vary among soil series within parent material classes; however, witness trees on the Conestoga soil series of the “micaceous limestone and schist” were surveyed significantly earlier than those surveyed on the Hagerstown soil series of the “limestone” parent material class (Fig. 5). Despite this difference among parent material classes, there was no significant variation among soil drainage or soil surface texture classes within the Piedmont Lowlands (data not shown).

Analysis of mean species survey dates revealed significant differences within the “sandstone and quartzite,” “schist and quartzite,” and “micaceous limestone and schist” parent material classes (Figs. 6 and 7). In each of these three parent material classes, early successional species, including *Liriodendron tulipifera* L., *Robinia pseudoacacia* L., *Prunus* spp., and *Betula* spp., were among the latest tree species surveyed (Figs. 6 and 7). *Nyssa sylvatica* was surveyed latest in the “sandstone and quartzite” class, while *Q. prinus* was sur-

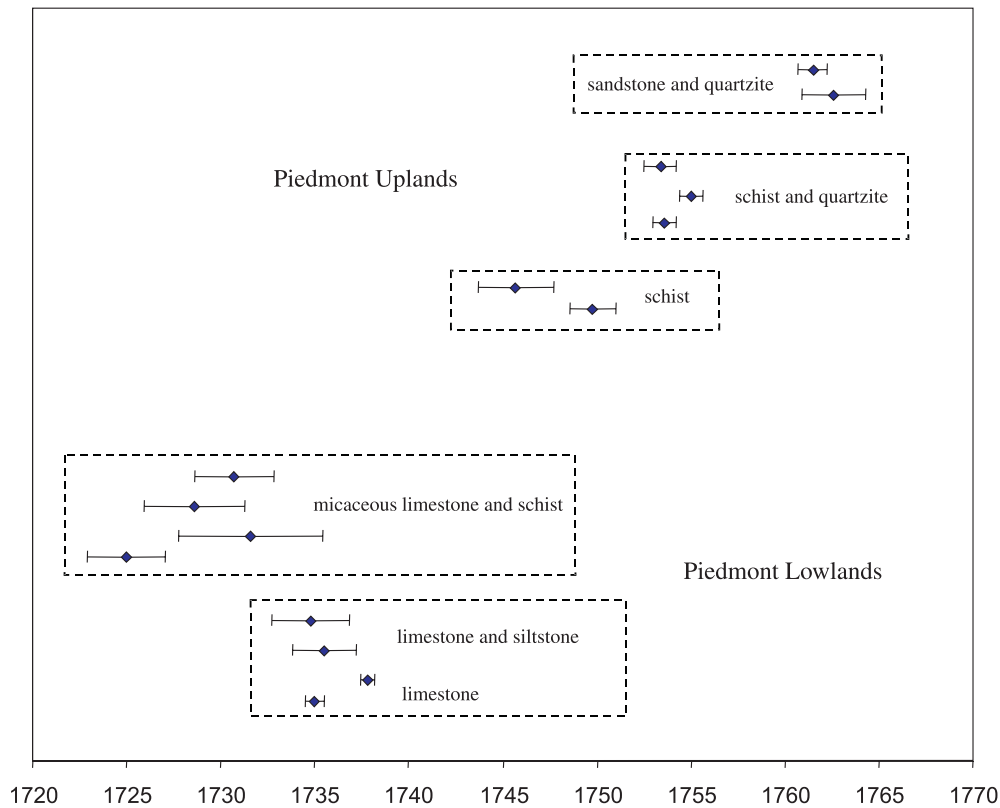
veyed late in both parent material classes of the Piedmont Uplands (Fig. 2). *Carya* spp. was most frequently recorded early in both parent material classes of the Piedmont Uplands (Fig. 6). In contrast, *Q. coccinea* was recorded latest in the survey records of the “micaceous limestone and schist,” while *Q. alba* was recorded earliest in that parent material class (Fig. 7).

Discussion

Witness tree – site relationships

Quercus velutina dominated the presettlement forests of the Pennsylvania Piedmont (Mikan et al. 1994). As was expected, it was positively associated with soils of shale origin, yet it was also positively associated with, and dominated, soils of limestone residuum (Burns and Honkala 1990) (Fig. 2). In contrast to *Q. velutina* dominance, the Piedmont of northern Virginia and New Jersey was dominated by *Q. alba* as were other physiographic provinces of Pennsylvania, West Virginia, and New York that supported *Quercus*–*Carya*–*Castanea* forests (Russell 1981; Abrams and Downs 1990; Glitzenstein et al. 1990; Nowacki and Abrams 1991; Mikan et al. 1994; Abrams and Ruffner 1995; Abrams and McCay 1996). In Lancaster County, *Q. alba* was the second most abundant species. Consistent with its reputation, *Q. alba* grew optimally on mesic sites and dominated soil types associated with stream valleys and coves throughout the study area (Niering 1953; Carvell and Tryon 1961; Mc-

Fig. 5. Mean survey dates (± 1 SE) of soil series in the Piedmont Lowlands and Piedmont Uplands of Lancaster County, Pennsylvania. Parent material groupings are enclosed by broken lines.



Carthy et al. 1987; Fralish 1988; Abrams and Downs 1990; Burns and Honkala 1990).

Carya spp., the third most abundant genus or species, was positively associated with limestone soils, yet was not significantly associated with drainage classes or soil surface texture classes (Figs. 2–4). Such lack of significant associations may exist because of the occurrence of several members of the *Carya* genus in Lancaster County. *Carya glabra* (Mill.) Sweet., *Carya tomentosa* Nutt., and *Carya ovata* (Mill.) K. Koch. would have been most abundant on upland sites while *Carya cordiformis* (Wang.) K. Koch. would have been associated with lowland sites (Burns and Honkala 1990). Likewise, *Q. coccinea* associated weakly, and occasionally inconsistently, with soil parameters (Figs. 2–4). For example, it was positively associated with upland and acid parent materials, yet was most common on alluvial soils of the Piedmont Uplands (Figs. 2–4). The shade-intolerant, prolifically sprouting, and drought-tolerant nature of *Q. coccinea* usually allows this species to maintain dominance on dry sites, even those too dry for *Q. prinus* or *Castanea dentata* (Baker 1949; Kramer et al. 1952; Brown 1960). A possible explanation for these inconsistent associations could be that surveyors had difficulty distinguishing *Q. coccinea* from *Quercus palustris* Muench., *Q. velutina*, or *Q. rubra*.

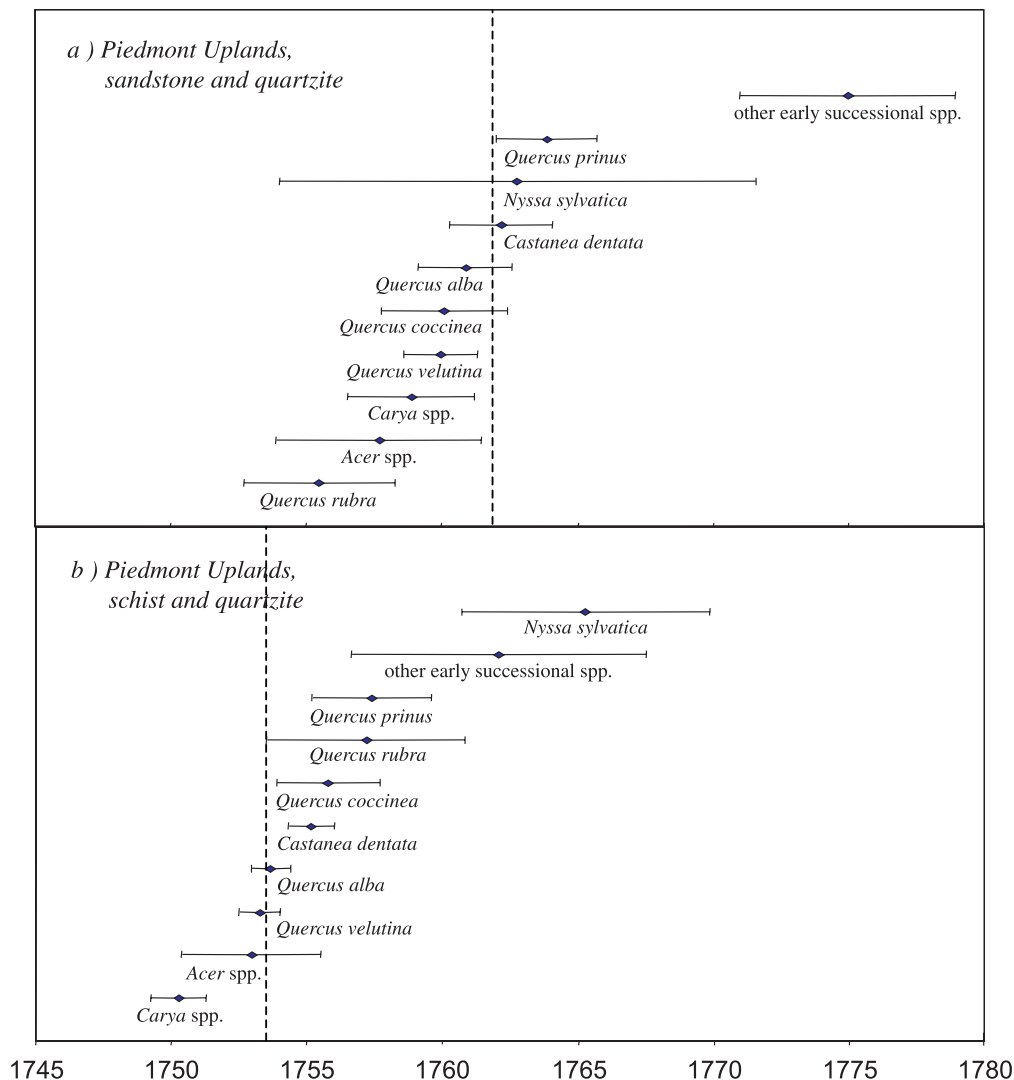
Of upland species, *Castanea dentata* was strongly associated with well-drained, stony sites. Before the chestnut blight of the early 20th century, *Castanea dentata* was generally most common on slope forests and rocky ridges with moist, well-drained acid loams (Russell 1987; Stephenson et al. 1991; Paillet 1992). The calciphobic nature of this spe-

cies has been well documented and was reflected in this study by its conspicuous absence from limestone soils (Fig. 2) (Russell 1987; Nowacki and Abrams 1991; Abrams and Ruffner 1995). Similar to *Castanea dentata*, *Q. prinus* has been found in greatest numbers on dry ridgetops and sandy, rocky soils. This species' drought tolerance is often cited for its ability to colonize steep upland sites (Niering 1953; Buell et al. 1954; Keever 1973; Burns and Honkala 1990; Mikan et al. 1994). Indeed, *Q. prinus* occupied well-drained, stony sites on the parent materials with the most rugged topography in Lancaster County (Figs. 2–4). *Nyssa sylvatica* also associated with stony, upland soils yet was found on alluvial soils. Such a broad edaphic distribution is characteristic of this species (Burns and Honkala 1990).

Temporal analysis

Before comparisons of early and late forest composition can be made, the negative effects of variations in mean survey date and witness tree densities have to be mitigated. Previous research in Lancaster County indicated that witness tree density (number of trees per hectare) and landform bias (the surveyors' preference to mark witness trees on certain landforms) were homogenous within a physiographic section (Black and Abrams 2001). However, this present research indicates that soil series mean survey dates significantly vary within physiographic sections. Therefore, merely subdividing the study area into physiographic sections but not into parent material classes would have distorted the results of temporal analysis. For example, in the Piedmont Uplands, the Clymer soil series was surveyed relatively late during

Fig. 6. Mean survey dates (± 1 SE) for significant parent material classes of the Piedmont Uplands: (a) sandstone and quartzite parent material class and (b) schist and quartzite parent material class. Broken vertical line indicates mean witness tree survey date for the parent material class. Other early successional species include *Prunus* spp., *Betula* spp., *Liriodendron tulipifera*, and *Robinia pseudoacacia*.



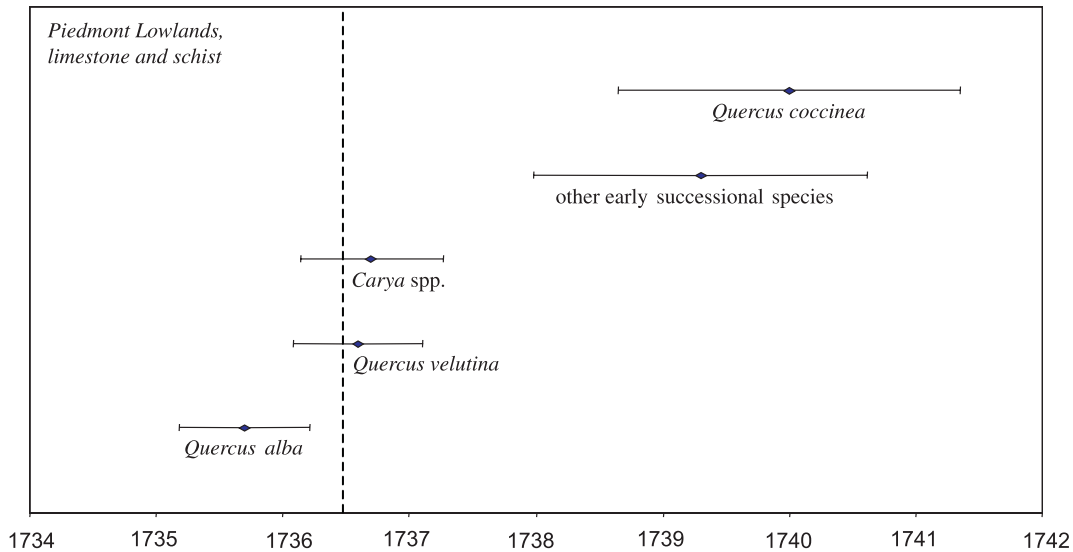
settlement, as would be expected, since this soil overlies some of the rockiest and most mountainous regions of the county (Custer 1985). If analyzed at the physiographic section level, *Castanea dentata* and *Q. prinus* would appear to be increasing in importance over time, when in reality, these increases would be a result of late surveys in the mountainous regions overlain by the Clymer soil series.

If subdivision of the study area into parent material classes is sufficient to mitigate negative effects of landform bias and minimize vegetation, topography, and survey date interactions, results of temporal analysis should reveal the impacts of European land uses. Given the results of the temporal analysis, one activity that could have led to the observed changes in vegetation is agricultural clearing on sites dominated by *Q. alba* in the "limestone and schist" of the Piedmont Lowlands, *Carya* in the "schist and quartzite" of the Piedmont Uplands, and *Q. rubra* in the "sandstone and quartzite" of the Piedmont Uplands. Avoidance of sites dominated by *Q. coccinea*, *N. sylvatica*, or various early

successional species would increase their representation in the witness tree record over time. Of these parent material classes, agricultural clearing would have been most widespread in the "limestone and schist," followed by the "schist and quartzite," and then the "sandstone and quartzite" classes.

Selective logging and harvesting for fuel may also have been instrumental in altering species frequencies. *Carya*, *Q. rubra*, and *Q. alba* are noted for their desirable qualities as lumber species and as a fuel source, given their high energy yield, and may have been selectively cut throughout the settlement period (Whitney 1994). Selective harvesting may also be the main reason for the late survey dates of *N. sylvatica* in the "schist and quartzite" parent material class, which contains some of the most mountainous topography in Lancaster County. It would have been poorly suited for agriculture and was probably used as a timber source for lumber or the charcoal-iron industry. *Nyssa sylvatica* has been recognized as a species of low economic value that was

Fig. 7. Mean survey dates (± 1 SE) for the micaceous limestone and schist parent material class of the Piedmont Lowlands. Broken vertical line indicates mean witness tree survey date for the parent material class. Other early successional species include *Prunus* spp., *Betula* spp., *Liriodendron tulipifera*, and *Robinia pseudoacacia*.



often avoided in early logging operations (Lutz 1930; Nowacki and Abrams 1994). Intense harvesting of associated species could explain its relative increase in abundance during the settlement period.

Opportunistic, light-seeded species such as *L. tulipifera*, *R. pseudoacacia*, and *Betula* spp. had relatively late mean survey dates in all significant parent material classes. Similar increases of opportunistic species such as *Fraxinus* spp., *Ulmus* spp., and *Acer* spp. occurred over the course of settlement in the Hudson Valley of New York and the Piedmont and Coastal Plain of northern Virginia (Glitzenstein et al. 1990; Orwig and Abrams 1994). Such shifts may be the result of intense harvesting for firewood or the charcoal-iron industry, and it may partially be due to forest fragmentation. Land clearing for agriculture would have dramatically increased the amount of edge habitat for these species to become established, and selective logging would have provided more light to the understory.

The exact causes of these variations in mean survey dates are difficult to assign. Differences in a species' abundance over time are probably not the consequence of any single land use but are likely the result of interactions among several land uses, including land clearing, selective harvesting, and altered fire frequencies. However, assigning causes to these variations is not as important as recognizing their existence in witness tree data. The results of this analysis suggest that in the Piedmont Uplands early successional species were probably over represented in the witness tree data. In the "schist and quartzite" parent material class, *N. sylvatica* may also have been less common before settlement (Fig. 6). The same was true of *Q. coccinea* and early successional species in the Piedmont Lowlands (Fig. 7).

One commonality among these species is that they composed less than 5% of forest cover in the regions where their mean survey dates were relatively late. Thus, early settlement land uses appear to have had the greatest effect on minor species. It is likely that this phenomenon is not unique to Lancaster County and slight over-representation of minor

species probably occurs in witness tree data throughout the eastern United States where metes and bounds surveys occurred (Marschner 1959; Black and Abrams 2001). In these areas, subdivision into physiographic sections and into landforms before analysis should be adequate to accurately estimate the frequencies of major species, but tests should be performed to describe temporal variations if there is an interest in accurately estimating frequencies of minor species.

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