Two chesnut fruit on an understory *Castanea dentata* growing in the Hi Lewis Pine Barrens State Nature Preserve on Pine Mountain, Kentucky. Photograph by Tracy S. Hawkins, USDA Forest Service. See article on page 73 of this issue.

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A Forest Transect of Pine Mountain, Kentucky: Changes Since E. Lucy Braun and Chestnut Blight

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ABSTRACT

In 1997, forest composition and structure were determined for Hi Lewis Pine Barrens State Nature Preserve, a 68-ha tract on the south slope of Pine Mountain, Harlan County, Kentucky. Data collected from 28 0.04-ha plots were used to delineate forest types. Percent canopy compositions were compared with those reported by Dr. E. Lucy Braun prior to the peak of chestnut blight. Four forest types were identified: *Liriodendron-Acer, Quercus-Tsuga,* Mixed *Quercus,* and *Pinus-Quercus.* Post-blight, little change has occurred in the *Pinus-Quercus* forest type on ridges and SSE aspects. On more mesic aspects, canopy gaps created by chestnut death were filled primarily by existing canopy species (*Quercus* spp.) and to a lesser degree by non-canopy species. Near the crest of the mountain, *Acer rubrum* has replaced *Castanea dentata* and assumed secondary importance to *Liriodendron tulipifera. Castanea dentata* remains an important component in the subcanopy of the four forest types and is present in the groundcover in three types. Except for the absence of *C. dentata,* species composition of Braun's forest types has remained relatively unchanged during the past 70 years; however, loss of *C. dentata* initiated changes in the relative importance of these species resulting in varying degrees of transition to post-blight forest types. Contribution of existing canopy species to importance values for the subcanopy and woody groundcover strata is less than that of fire-sensitive species, suggesting future changes in these post-blight forest communities.

KEY WORDS: Lucy Braun, *Castanea dentata,* chestnut blight, forest types, Pine Mountain

INTRODUCTION

Prior to the 20th century, American chestnut [*Castanea dentata* (Marsh.) Borkh.] was a dominant or codominant species of many hardwood forests of the eastern United States (Braun 1942, 1950; Gravatt 1949; Stephenson 1986; Schwadron 1995) and contributed up to 84.6% to the canopy composition in these mixed mesophytic forests (Braun 1942). However, introduction of chestnut blight [*Cryphonectria parasitica* (Murr.) Barr] to the United States in the early 1990's (Merkel 1905; Shelford 1963; Anagnostakis 1987) precipitated forest changes as *C. dentata* died out. In some forests, canopy gaps created from *C. dentata* death were filled by existing codominant species, while in others, subordinate species invaded the canopy (Braun 1950; Keever 1953; Woods and Shanks 1959; Good 1968).

Dr. E. Lucy Braun (1935) provided perhaps the best qualitative and quantitative information for pre-blight forests of the Cumberland Plateau in the Appalachian Plateaus Physiographic Province (Fenneman 1938) of Kentucky. She considered the extreme southeastern portion of Kentucky the geographic center of her "Mixed Mesophytic Forest Region" (Martin 1992). At the time of her research, *C. dentata,* although dying, was still present in

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the forest strata; therefore, she was able to include the species in her assessment of forest communities. The descriptions of Pine Mountain, in southeastern Kentucky, included percent canopy composition relative to topography and edaphic factors, as well as qualitative descriptions of lower forest strata and herbaceous groundcover. Further, Braun's (1935) study identified four complex forest associations on Pine Mountain that she further subdivided into sixteen forest types. *Castanea dentata* was present in all forest types, was a dominant canopy species in eight, and was described as "important" in two.

Chestnut persistence and replacement have been well documented for forests in Braun's (1950) Oak-Chestnut Forest Region (Keever 1953; Woods and Shanks 1959; Good 1968; Christensen 1977; Karban 1978; Arends 1981; Johnson and Ware 1982; Stephenson 1986; Stephenson et al. 1991; Hannah 1993; Parker et al. 1993). Braun's (1950) Beech-Maple (Schwadron 1995) and Western Mesophytic (Schibig et al. 2003; Myers et al. 2004) Forest Regions have received attention, as well. However, post-blight forest succession has gone largely undescribed in the Mixed Mesophytic Forest Region. The purposes of this study were to 1) delineate forest types and determine forest structure for a section of the southeastern dip slope of Pine Mountain, 2) compare post-blight canopy species percent composition with pre-blight values reported by Braun (1935), and 3) describe chestnut persistence and/or replacement in forest types on Pine Mountain during the post-chestnut blight era.

THE STUDY AREA

Pine Mountain is a prominent, monoclinal ridge extending approximately 200 km in a northeast-southwest direction, from West Virginia into Tennessee and, within its Kentucky range, forms the western border of the Cumberland Mountains. Formed from the Pine Mountain thrust fault, its strata dip southeastward forming a dip slope ranging in altitude from approximately 488 to 975 m over a distance of 1.6 to 2.4 km. Small southerly flowing streams that drain into the Poor Fork of the Cumberland River occur at about 0.8 km intervals along the extent of the dip slope (Braun 1935). The eroded edges of the strata make up a steep scarp slope on the northeast aspect of Pine Mountain that is characterized by decreases in altitude of 305 m over a distance of 402 m to 603 m (Braun 1935).

THE STUDY SITE

Hi Lewis Pine Barrens State Nature Preserve is a 68-ha forested tract on the south slope of Pine Mountain, Harlan County, Kentucky. It lies approximately 8 km southwest of the vicinity where Braun (1935) made the majority of her pre-blight observations. Elevation is 488 m at the base of the slope, and increases along a 1.6 km gradient to 792 m at the crest of the mountain. The most widely distributed soil in the transect is an Alticrest-Totz-Helechawa complex described by Childress (1992) as acidic, highly permeable and low in natural fertility. A Helechawa-Varilla-Jefferson complex, a slightly deeper, acidic soil, is also present; however, it is found only in the ravine formed by Ashhopper Branch on the east boundary of the preserve. Underlying bedrock consists of Pennsylvanian sandstones, siltstones and shales (Childress 1992). On average, Harlan County receives 127 cm of precipitation annually, with 50% of this falling in April through September. Mean annual temperature is 12.7 °C (Childress 1992). The growing season is from April through September, with first and last freeze dates occurring in October and April, respectively (Childress 1992).

METHODS

Post-blight Forest Types and Structure

Following observation of topographic maps and aerial photographs and reconnaissance of the area, nine temporary transects (designated 1 through 9) and five permanent (designated P1 through P5) 0.04 ha plots were established. In June and July 1997, data were collected from each of the permanent plots and from 0.04 ha circular sampling plots placed at 30 m intervals along each transect. During data collection, coordinates for each plot were recorded on a Trimble® GPS. Within each 0.04 ha plot, woody stems with a dbh $\geq$ 10.16 cm (canopy) were measured and recorded by species. In a 0.02 ha circular plot nested in the center of each 0.04 ha plot, woody stems with a dbh of 2.54–10.15 cm (subcanopy) were measured and recorded by species, with the exception of oaks, pines, and hickories, which were identified by genus. These data collected for the canopy and subcanopy strata were used to calculate percent composition, density, relative density, basal area, relative basal area, frequency, and relative frequency. Summation of the relative values gave an importance value (IV) with a maximum of 300 (Curtis and McIntosh 1950; Barbour et al. 1987). Woody groundcover (tree species; dbh < 2.54 cm) within a 0.0025 ha circular plot nested in the center of each 0.04 ha plot were counted and recorded by genus. The data were used to obtain density, relative density, frequency, relative frequency, and importance values (maximum 200) for the woody groundcover stratum.

Community coefficients (CC) for pairwise comparison of all transects and permanent plots were calculated using Horn's index (Horn 1966), with subsequent cluster analysis of CCs to identify distinct forest types. A threshold CC of 0.50 was used to delineate forest types (Barbour et al. 1987). The Shannon-Weiner Index of Species Diversity was calculated for each post-blight forest type for comparison with other forests in the Mixed Mesophytic Region.

Pre- and Post-blight Comparison

A proportional similarity index was used for comparison of post-blight forest types with the 16 pre-blight forest types described by Braun (1935). The author recognizes that Dr. Braun did not give canopy size class diameter. However, she documented percent composition in several different stands and augmented this information with descriptions of elevation, slope, aspect, and edaphic factors. Collectively, this information permits reasonable comparison of pre- and post-blight forest types.

RESULTS

Post-blight Forest Types and Structure

A total of sixteen canopy (dbh ≥ 10.16 cm) species were identified. Cluster analysis of species data collected from transects and permanent plots yielded four distinct forest types: *Liriodendron-Acer, Quercus-Tsuga,* Mixed *Quercus,* and *Pinus-Quercus.* Canopy species diversity was greatest in the *Quercus-Tsuga* and Mixed *Quercus* forest types and least in the *Liriodendron-Acer* and *Pinus-Quercus* forest types (Table 1).

Table 1. Proportional similarity comparison of pre- and post-chestnut blight forest types, and species diversity indices for post-blight forest types of Hi Lewis Pine Barrens State Nature Preserve on Pine Mountain, Harlan County, Kentucky.

1935[a]	1997	Similarity (%)	H′ [b]
Chestnut-Tulip	Tuliptree-Red Maple	55.5	1.35
Hemlock	Oak-Hemlock	49.5	2.61
Chestnut Oak-Chestnut-Tulip	Mixed Oak	45.7	3.12
Chestnut Oak-Pine	Pine-Oak	72.9	1.93

[a] Braun, 1935.
[b] 1997.

A narrow, wet-mesic longitudinal trough (Transect 1; N_{plot} = 2; altitude, 768 m) near the crest of the mountain supported a *Liriodendron* dominant canopy (IV = 187.6) with *Acer rubrum* L. (IV = 64.2) second in importance (Table 2). *Liriodendron tulipifera* L. (IV = 50.0) was codominant with *Sassafras albidum* (Nutt.) Nees (IV = 47.3) in the subcanopy (Figure 1A). *Sassafras albidum, A. rubrum,* and *Carya* spp. contributed equally to the woody groundcover stratum (Figure 1A).

In the dip slope ravine (Transect 9; N_{plot} = 4; elevation, 570–573 m) on the east boundary of the preserve, *Quercus alba* L. (IV = 66.0), *Q. rubra* L. (IV = 55.5), and *Tsuga canadensis* (L.) Carr. (IV = 45.5) were codominants in the *Quercus-Tsuga* forest type (Table 2). *Acer rubrum* and *L. tulipifera* also contributed heavily to the canopy with importance values of 45.0 and 44.6, respectively (Table 2). *Acer rubrum* (IV = 45.0) was the most important species in the subcanopy, followed by *Oxydendrum arboreum* (L.) DC. (IV = 39.2), and *S. albidum* (IV = 37.2; Figure 1B). *Acer rubrum* was the dominant woody groundcover species with an importance value of 64.3. Species of lesser importance in this stratum were *S. albidum* (IV = 30.8), *T. canadensis* (IV = 28.7), and *Quercus* spp. (IV = 27.1; Figure 1B).

A mixed *Quercus* forest type (Transects 5, 6; N_{plot} = 5; elevation, 658–768 m) was found on mesic, ESE aspects of the dip slope. *Quercus velutina* Lam. (IV = 71.4) and *Q. montana* L. (IV = 44.8) were codominant canopy species (Table 2). *Quercus* spp. (IV = 25.9) were less important in the subcanopy, where the

Table 2. Canopy (dbh ≥ 10.16 cm) composition and structure for four post-blight forest types of Hi Lewis Pine Barrens State Nature Preserve on Pine Mountain, Harlan County, Kentucky.

	Avg. no. (stems/ha)	Basal area (m^2/ha)	IV (300)
Liriodendron-Acer			
Liriodendron tulipifera	200	19.6	187.6
Acer rubrum	62	2.2	64.2
Morus rubra	25	0.4	26.6
Magnolia fraseri	13	0.1	21.5
Quercus-Tsuga			
Quercus alba	94	0.8	66.0
Quercus rubra	50	0.7	55.5
Tsuga canadensis	56	0.6	45.5
Acer rubrum	38	0.6	45.0
Liriodendron tulipifera	50	0.5	44.6
Quercus montana	50	0.2	34.6
Quercus velutina	6	0.1	8.6
Mixed *Quercus*			
Quercus velutina	35	1.1	71.4
Quercus montana	25	0.7	44.8
Nyssa sylvatica	25	0.4	37.4
Quercus alba	20	0.5	33.9
Liriodendron tulipifera	20	0.5	32.6
Quercus coccinea	20	0.4	31.3
Cornus florida	15	0.1	15.0
Sassafras albidum	10	0.1	12.6
Quercus rubra	5	0.2	12.6
Carya glabra	5	<0.1	8.4
Pinus-Quercus			
Pinus echinata	140	4.3	123.6
Pinus rigida	72	2.9	83.3
Quercus montana	13	0.7	32.0
Quercus coccinea	21	0.7	29.2
Quercus velutina	6	0.3	11.3
Quercus rubra	3	0.3	6.7
Carya glabra	6	0.1	6.6
Quercus alba	3	<0.1	4.3
Robinia pseudoacacia	1	<0.1	3.3

dominant species was *A. rubrum* (IV = 62.0), followed by *S. albidum* (IV = 53.2) and *Castanea dentata* (IV = 43.5). However, *Quercus* spp. (IV = 61.0) were dominant in the woody groundcover, followed by *S. albidum* (IV = 38.7) and *A. rubrum* (IV = 19.7; Figure 1C).

The most extensive forest type at the study site was *Pinus-Quercus* (Transects 2, 3, 4, 7, 8, P 1–5); N_{plot} = 17; elevation, 488–792 m), which was found on dry ridges and areas of the dip slope with a SSE aspect. *Pinus echinata* Mill. and *P. rigida* Mill. were codominant canopy species with importance values of 123.6 and 83.3, respectively (Table 2). Although individual importance values for each *Quercus* spp. appeared minimal relative to those of *Pinus* spp., importance values for five *Quercus* spp. totaled 83.5; therefore, the genus was considered codominant with *Pinus* (Table 2). *Quercus* spp. (IV = 62.5), *A. rubrum* (IV = 61.5), and *Pinus* spp. (IV = 50.8) were codominants in the subcanopy (Figure 1D). *Quercus* spp. (IV = 62.5) were the dominant woody groundcover species, followed in importance by *S. albidum* (IV = 41.4), and *Pinus* spp. (IV = 21.6; Figure 1D).

Pre- and Post-blight Comparison

Without *Castanea dentata* in the canopy, the four forest types delineated in this study showed moderate to high proportional similarity with four described by Braun (1935) at the onset of chestnut blight in southeastern Kentucky (Table 1). Braun's (1935) Chestnut-Tulip forest type, found in longitudinal troughs at the crest of Pine Mountain, had the greatest proportional similarity (55.5%) to the present-day Tuliptree-Red Maple (*Liriodendron-Acer*) type (Table 1). Pre-blight, *C. dentata* contributed up to one-third of the canopy in the Chestnut-Tulip forest type (Braun, 1935). In the present study, *C. dentata* was found only in the subcanopy of the *Liriodendron-Acer* forest type, where it ranked eighth in importance (IV = 20.9; Figure 1A).

The current Oak-Hemlock (*Quercus-Tsuga*) forest type showed greatest proportional similarity to Braun's (1935) Hemlock forest type (Table 1). *Castanea dentata* contributed only 4% to the pre-blight Hemlock forest (Braun 1935). In this study, it was not found in the *Quercus-Tsuga* canopy of the dip slope ravine (Table 2), ranked tenth in importance in the subcanopy, and was not found in the woody groundcover stratum (Figure 1B).

The proportional similarity index was greatest between the current Mixed Oak (*Quercus*) forest type and Braun's (1935) Chestnut Oak-Chestnut-Tulip forest type (Table 1). Prior to chestnut blight, *C. dentata* was a codominant contributing up to one-third to the Chestnut Oak-Chestnut-Tulip canopy composition (Braun, 1935). In the current Mixed Oak forest type, *C. dentata* is absent from the canopy (Table 2), a codominant (IV = 43.5) in the subcanopy, and ranked fifth (IV = 10.1) in importance among woody groundcover species (Figure 1C).

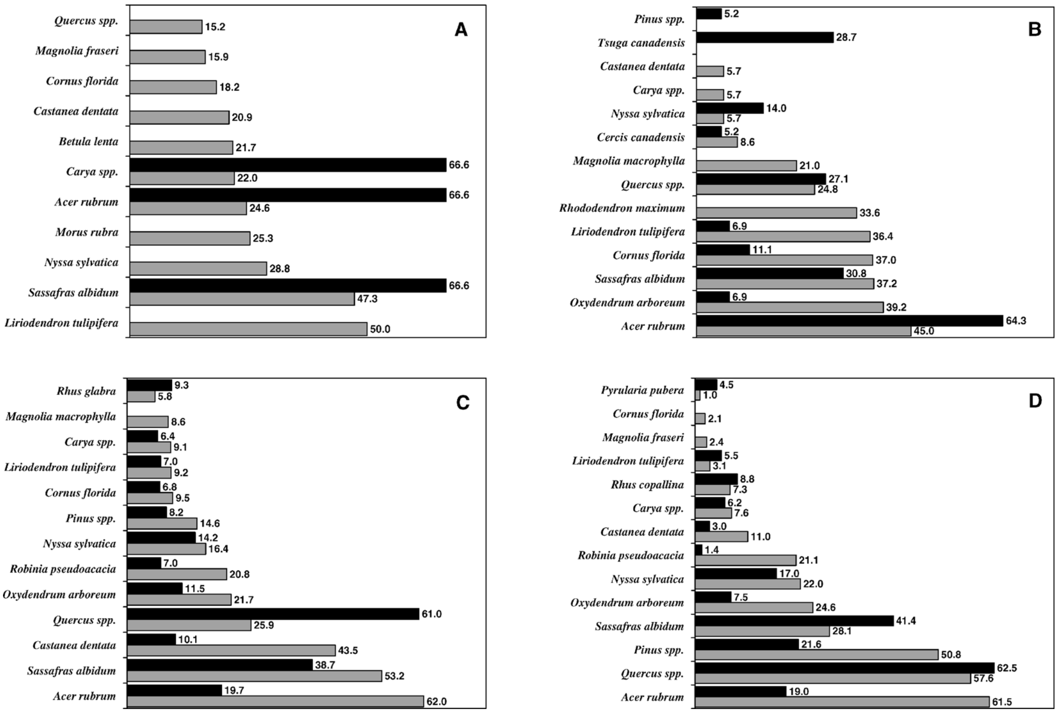

Figure 1. Importance values for subcanopy (dbh 2.54–10.15 cm; grey bars) and woody groundcover (<2.54 cm; black bars) strata in A) *Liriodendron-Acer,* B) *Quercus-Tsuga,* C) Mixed *Quercus,* and D) *Pinus-Quercus* post-chestnut blight forest types of Hi Lewis Pine Barrens State Nature Preserve on Pine Mountain, Harlan County, Kentucky.

Composition of the Pine-Oak (*Pinus-Quercus*) forest type identified in this study showed little difference (Proportional Similarity Index = 72.9%) to the Chestnut Oak-Pine forest described by Braun (1935; Table 1). Based on percent composition, *C. dentata* made up approximately 11% of the pre-blight Chestnut Oak-Pine canopy (Braun, 1935); however, *C. dentata* was not present in the *Pinus-Quercus* canopy and ranked eighth (IV = 11.0) and eleventh (IV = 3.0) in importance values in the subcanopy and woody groundcover layers, respectively (Figure 1D).

DISCUSSION

Keever (1953), Stephens and Waggoner (1980), and Russell (1987) have shown that *Castanea dentata* remains an important component of plant communities throughout its natural range. Further, its persistence in many post-blight forests results from root-crown sprouts from pre-blight root systems (Russell 1980; Paillet 1982, 1984; Schwadron 1995; Schibig et al. 2003). The present study identified four distinct forest types: *Liriodendron-Acer, Quercus-Tsuga,* Mixed *Quercus,* and *Pinus-Quercus.* Although *C. dentata* is no longer part of the canopy, it is found in the woody groundcover stratum in two of the four forest types and in the subcanopy in all four forest types. Further, it is likely that *C. dentata* will remain a part of these forest communities, persisting from root crown sprouts.

In the post-blight years, forest succession on this section of the dip slope of Pine Mountain has followed a pattern similar to that reported for forests in Braun's (1950) Western Mesophytic (Schibig et al. 2003; Myers et al. 2004) and Oak-Chestnut Region (Keever 1953; Woods and Shanks 1959; Good 1968; Christensen 1977; Karban 1978; Arends 1981; Johnson and Ware 1982; Stephenson 1986; Stephenson et al. 1991; Hannah 1993; Parker et al. 1993). In general, gaps created by dying chestnut have been filled by codominant pre-blight canopy species, with minor invasion by subcanopy species. However, the extent of change in canopy composition in the four forest types appears to be consistent with the extent to which chestnut was lost. For example, the forest type least changed by chestnut decline is the present-day *Pinus-Quercus* forest type that is very similar to Braun's (1935) Chestnut Oak-Pine forest type. Braun (1935) did not consider *C. dentata* to be an important component of the Chestnut Oak-Pine canopy. *Pinus echinata* and *P. rigida* were codominants, making up approximately 50% of canopy composition, and she described *Quercus montana* (~21% canopy composition) as important (Braun 1935). Based on importance values and percent composition from this study, these three species remain codominant.

Similarly, *C. dentata* was not important in Braun's (1935) Hemlock forest type found in the dip slope ravines of Pine Mountain. Currently, *Tsuga canadensis* remains important in the *Quercus-Tsuga* forest type of the dip slope ravine, although the species ranks slightly subordinate to *Q. alba* and *Q. rubra.* The results suggest that in the dip slope ravine, chestnut decline may have allowed for subordinate oak species to enter the canopy. This pattern of chestnut replacement was documented for post-blight forests in Braun's Oak-Chestnut region. Karban (1978), Johnson and Ware (1982), and Stephenson (1986) described chestnut replacement by a single oak species, such as *Q. rubra* or *Q. montana.* However, *C. dentata* was considered a codominant in those pre-blight forests; whereby it was of little importance to the pre-blight Hemlock forest type (Braun 1935).

Chestnut replacement was most apparent on ESE aspects of the dip slope where the Mixed-*Quercus* forest type is only remnant of Braun's (1935) Chestnut Oak-Chestnut-Tulip forest type descriptions. The importance of *C. dentata* to the pre-blight forest is still evidenced by its codominance in the subcanopy, as well as by being the sixth most important tree species in the woody groundcover. Within this forest type, *C. dentata* has been replaced by *Q. velutina,* and to a lesser degree, by *Q. montana.* Replacement of chestnut by codominant oaks also has been described for forests in the Great Smoky Mountains (Woods and Shanks 1959; Arends 1981; Golden 1981; Parker et al. 1993). Further, trees that Braun (1935) did not consider canopy species in the pre-blight Chestnut Oak-Chestnut-Tulip forest are found in the Mixed *Quercus* canopy, suggesting that some canopy gaps may have allowed for invasion of non-canopy species such as *Nyssa sylvatica* Marsh., *Cornus florida* L., and *Sassafras albidum.* This pattern of chestnut replacement has also occurred in mesic forests in West Virginia and North Carolina (Stephenson 1986; Hannah 1993) and in former chestnut occupied forests of the northern Highland Rim of Kentucky and Tennessee (Schibig et al. 2003). In these forests, species formerly considered non-canopy trees, such as *Acer rubrum, C. florida, Betula lenta* L., *Oxydendrum arboreum, N. sylvatica, Prunus serotina* Ehrend., and *Robinia pseudoacacia* L. entered the canopy following chestnut death (Stephenson 1986; Hannah 1993; Schibig et al. 2003).

In the longitudinal trough at the crest of Pine Mountain, the codominant *C. dentata* of Braun's Chestnut-Tulip forest type has been replaced primarily by *A. rubrum.* Although *Morus rubra* L. contributed to the present-day *Liriodendron-Acer* forest type, it is more often found on the northwest slope of Pine Mountain. On the other hand, presence of *Magnolia fraseri* Walt. in the subcanopy is typical of mesic areas in the mixed mesophytic forests of the Cumberland Plateau (Braun 1942).

Chestnut death appears to have precipitated relatively minor changes in forest composition on Pine Mountain; however, the influence of other factors such as aspect, physiography, and anthropogenic disturbance on post-blight succession should be taken into consideration in assessing current status and predicting future changes in these forest types. In the Appalachian Plateau Region the microclimate of a site is strongly influenced by its slope and aspect (Franzmeier et al. 1969; Hutchins et al. 1976). In turn, soil moisture (Whittaker 1956; Cooper and Hardin 1970; Day and Monk 1974; McEvoy et al. 1980) or a combination of soil moisture and fertility (Muller 1982) are important factors in determining patterns of species distribution and vegetation structure in southern Appalachian forests. Braun (1935) described a mosaic of forest communities on Pine Mountain resulting from variability in edaphic and topographic conditions over relatively short distances. Similarly, forest types identified in the present study changed with shifts in aspect, and change from one forest type to another was often abrupt. For example, sampling plots with a SSE aspect and those on ridges were xeric and supported a *Pinus-Quercus* canopy; whereby, *Liroden-dron-Acer* was found in the most mesic site at the crest of Pine Mountain. With change in aspect from SSE to ESE, *Pinus* spp. dropped out of the canopy and *Quercus* spp. were codominant in these more mesic plots.

Subcanopy composition appeared less influenced by changes in aspect and slope than the canopy. Although *Pinus* spp. were restricted to a single aspect (SSE), *Quercus* spp., *A. rubrum,* and *C. dentata* were found in all forest types. Species described as fire-sensitive, such as *N. sylvatica, O. arboreum,* and *S. albidum* (Martin 1989; Delcourt and Delcourt 1997) were part of the subcanopy and woody groundcover in at least three of four forest types. Frequency and importance of these latter three species may be attributed, in part, to frequent fire disturbance.

Diversity indices (H′) for the Mixed *Quercus* and *Quercus-Tsuga* forest types fall within the range of values (2.02–3.4) reported by Monk (1967) for forest types in the Mixed Mesophytic Forest Region. By contrast, forest types found on the most xeric (*Pinus-Quercus*) and most mesic (*Liriodendron-Acer*) areas of the dip slope had diversity indices below those recorded for forest types of the Mixed Mesophytic Forest Region (Monk 1967; Martin 1992; Clinton et al. 1993). Given that the *Liriodendron-Acer* forest type reflects chestnut replacement by a single species (*A. rubrum*), and little change occurred in the shift from Braun's Oak-Pine forest to the current Pine-Oak forest, these depressed diversity indices may well be the result of physiography, and not chestnut death.

Except for the absence of *C. dentata* in the canopy, forest composition on this section of Pine Mountain has remained relatively unchanged in the past 70 years. However, chestnut blight did create changes in the relative importance of pre-blight tree species, resulting in varying degrees of transition to post-blight forest types. Given the influence of aspect and physiography on species distribution and forest structure of southern Appalachian forests, current composition and relative importance of post-blight forest species would be expected to show minimal change in future years. However, the importance of fire-sensitive, as well as other non-canopy species, in the lower forest strata suggests that continued fire disturbance (i.e., arson) in conjunction with microhabitat may allow for subordinate tree species to enter the canopy and precipitate further change in the post-blight forest types.

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