COMMUNITY AND EDAPHIC ANALYSIS OF MIXED OAK FORESTS IN THE RIDGE AND VALLEY PROVINCE OF CENTRAL PENNSYLVANIA

Gregory J. Nowacki and Marc D. Abrams[1]

Abstract: Forty-two relatively undisturbed mixed oak stands on nine different physiographic units in the Ridge and Valley Province of central Pennsylvania were surveyed to investigate the ecological status of oak species in the region. *Quercus* species were primarily restricted to the canopy, with the exception of *Quercus ilicifolia* Wangenh. (a shrub). The most species rich forest stands were located along an indented stream and on fine-textured, valley floor sites where *Quercus alba* L., *Quercus velutina* Lam. and/or *Quercus rubra* L. dominated the overstories and *Acer rubrum* L. and *Prunus serotina* Ehrh. dominated the understories. The importance of *Quercus prinus* L. was positively correlated with percent sand and elevation, and this species dominated steep inclines and xeric ridgetop communities. *Quercus velutina*, *Carya* spp. and *Q. rubra* occurred on all topographic sites, however the latter was most abundant on cool, north-facing slopes.

Most present-day stands were initiated following heavy cutting and fire around the 1900's, and the oak component tended to be even-aged. Regeneration data suggest that succession to more shade tolerant species, primarily *A. rubrum*, is occurring in all but the most xeric oak stands. Frequent understory associates with *A. rubrum* included *P. serotina*, *Acer saccharum* Marsh. and *Fraxinus americana* L. on mesic toe slopes, indented stream bank and valley floor sites and *Betula lenta* L. and *Acer pensylvanicum* L. on and near ridgetops. Although *Quercus* species were well represented as seedlings in most stands, recruitment into larger classes was infrequent, except on the driest sites.

INTRODUCTION

The topography of Ridge and Valley Province of central Pennsylvania leads to an diverse floristic pattern across the landscape, in which *Quercus* species predominate. Typical of most eastern forests, large-scale logging and subsequent fires following European settlement drastically altered the original vegetation in central Pennsylvania (Hough and Forbes 1943, Whitney 1987, Crow 1988, Nowacki et al. 1990). Braun (1950) had classified this area as oak-chestnut (*Castanea dentata* [Marsh.] Borkh.) forest type, though most ecologists now consider it an oak-hickory (*Carya* spp.) or mixed-oak association (Keever 1953, McCormick and Platt 1980, Johnson and Ware 1982). Braun also suggested that the mixed mesophytic

[1]Graduate Student and Assistant Professor of Forestry, respectively, Pennsylvania State University, University Park, PA 16802.

forest is the potential climax in the region, but that topographic diversity would lead to physiographic or edaphic climaxes, including mixed oak communities on mountain slopes, hemlock-dominated (*Tsuga canadensis* [L.] Carr.) communities within mountain coves, white oak (*Q. alba*) forests on valley floors and mixed mesophytic communities on ravine slopes along indented streams. Whether the oak communities are actually true or edaphic climaxes in this or other regions of eastern North America is uncertain. Recent studies indicate a transition from oak to more shade tolerant species in many forests (Christensen 1977, Lorimer 1984, Parker et al. 1985, Abrams 1986, McGee 1986, Nowacki et al. 1990). Successional trends in oak forests of central Pennsylvania have not been well established, although regional surveys indicate poor oak development under shaded conditions (Lorimer 1984, Russell and Schuyler 1988, Abrams and Downs 1990).

In this study, mixed oak stands on nine different physiographic units in the Ridge and Valley Province in central Pennsylvania were surveyed to investigate the effect of edaphic factors on stand composition and structure. From these data we attempt to predict the successional status of mixed oak forests in the region and how successional pathways may vary with physiographic changes.

METHODS

During the summers of 1988-1989, 42 relatively undisturbed mixed oak forests in central Pennsylvania were surveyed. Stands selected for sampling were 1) relatively homogeneous vegetative units located on uniform topography and restricted to a single soil type and 2) showed little or no evidence of recent disturbance by fire, cutting, etc. Trees ($\geq$ 10 cm dbh) were sampled using the point-quarter method (Cottam and Curtis 1956) at 20 points within each stand. Points were systematically located along transects at intervals of 20 to 30 m depending on stand size. Transects were positioned to avoid forest edges. Tree information included distance from the sample point, dbh, species name and canopy position (dominant, codominant, intermediate, or overtopped). Crown class definitions followed those of Smith (1986).

Saplings and seedlings were recorded by species at each sampling point within nested circular plots of 10 and 5 m^2, respectively. Saplings were classified as tree species < 10 cm at dbh but $\geq$ 1.5 m in height, whereas seedlings were < 1.5 m in height. Average slope and aspect were estimated for each stand using a clinometer, compass and topographic maps.

Soils were described at a centrally-located pit within each stand. Horizons comprising the upper 50 cm solum were identified and their depth recorded. Soil samples were collected form the mineral surface (A or E horizon) for particle-size analysis using the Hydrometer Method (Bouyoucos 1962). Soil pH was also recorded by use of a pH meter (calibrated at pH 4.0) and a prepared soil slurry consisting of 5 g soil and 10 ml distilled water.

Species importance percentages were calculated from the tree data for each stand (importance percentage = [relative density + relative dominance + relative frequency]/3; Cottam and Curtis

1956). Statistical analyses were accomplished using simple correlation, ANOVA and Scheffe's mean separation procedure at $p < 0.05$.

Table 1.--Edaphic features of the nine physiographic units studied in the Ridge and Valley Province of central Pennsylvania.

Physio. Unit	% sand	% silt	% clay	pH	Predominant texture	Representative soil type	% slope[1]	Elev.[1] (m)
Stream	46^{ab}	41^{ab}	14^{a}	6.1^{b}	loam	Ultic Hapludalfs	19±6	306±6
Fine-Valley	26^{a}	59^{a}	15^{a}	4.9^{a}	silt loam	Typic Hapludalfs	7±1	344±6
Cove	65^{ab}	27^{b}	8^{a}	3.5^{c}	sandy loam	Typic Fragidults	7±3	547±21
North-Lower	52^{ab}	34^{b}	14^{a}	4.3^{ac}	loam	Typic Fragidults	28±3	464±4
South-Lower	53^{ab}	34^{ab}	14^{a}	4.4^{ac}	loam	Typic Fragidults	30±0	472±1
North-Upper	60^{ab}	30^{ab}	10^{a}	3.9^{ac}	loam	Typic Dystrochrepts	35±6	501±21
South-Upper	67^{b}	26^{b}	7^{a}	3.7^{c}	sandy loam	Typic Dystrochrepts	28±7	568±16
Coarse-Valley	70^{b}	21^{b}	9^{a}	4.1^{ac}	sandy loam	Ultic Hapludalfs	6±1	407±9
Crest	75^{b}	19^{b}	6^{a}	4.1^{ac}	sandy loam	Typic Dystrochrepts	4±0	598±22

[1] Mean±S.E.
Values in a column with the same letter are not significantly different at $p < 0.05$.

RESULTS

Stand Classification Based On Edaphic Factors

Forty-two forest stands were grouped into nine physiographic units based on topographic position and soil characteristics (Table 1). The physiographic groups were indented stream bank, fine textured-valley floor, coarse textured-valley floor, cove, northern-lower slope, northern-upper slope, crest, southern-upper slope, and southern-lower slope (Fig. 1). Soil factors were correlated with changes in elevation. In particular, percent sand increased and percent silt, clay and pH decreased with elevation ($p < 0.05$, $r = .58, -.57, -.49$ and $-.77$, respectively). Fine textured-valley sites contained significantly less sand and more silt than coarse textured-valley, crest, and southern-upper sites (Table 1). Average soil pH was highest

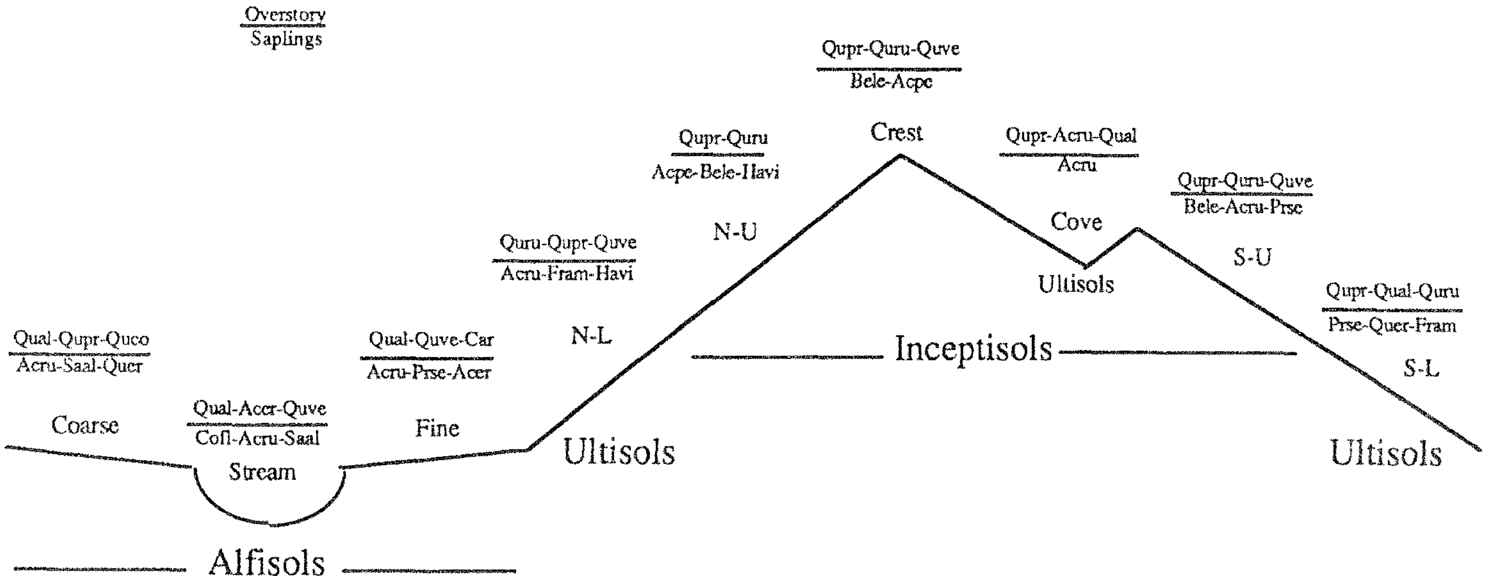

Figure 1. Dominant overstory and regenerating species on nine physiographic areas in the Ridge and Valley Province of central Pennsylvania arranged along a topographic gradient.
Acer=*Acer saccharum/platanoides*, Acpe=*Acer pensylvanicum*, Acru=*Acer rubrum*, Bele=*Betula lenta*, Car=*Carya* spp., Cofl=*Cornus florida*, Fram=*Fraxinus americana*, Havi=*Hamamelis virginiana*, Prse=*Prunus serotina*, Qual=*Quercus alba*, Quco=*Quercus coccinea*, Quer=*Quercus* spp., Qupr=*Quercus prinus*, Quru=*Quercus rubra*, Quve=*Quercus velutina*, Saal=*Sassafras albidum*.

along streams, intermediate on valley sites and lower slopes and lowest on upper slopes and coves. A general shift in soil type occurred with elevation, with Alfisols dominating valley floor and stream bank sites, Ultisols along lower slopes and coves and Inceptisols located on upper slopes and ridgetops (Fig. 1).

Stand Composition and Structure

The overstory of all groups was dominated by *Quercus* (Fig. 1 and 2), however significant differences in species importance occurred among groups (Table 2). The three most abundant oaks, *Q. alba*, *Q. rubra*, and *Q. prinus*, varied with elevation. *Quercus alba* was most important on gently sloping, valley and indented stream locations, although it was also important in mesic cove forests. *Quercus alba* importance was negatively correlated with slope ($r = -.38$), elevation ($r = -.50$) and the importance of *Q. rubra* and *Q. prinus* ($r = -.66$ and -.67, respectively). *Quercus rubra* and *Q. prinus* were most abundant on lower slopes and crest sites, respectively. *Quercus prinus* importance was correlated with percent sand, silt, clay, elevation, and pH ($r = .56, -.54, -.49, .79$ and -.58, respectively). Similar to *Q. alba*, *Quercus coccinea* Muenchh. was most frequent on valley sites, although it was associated with coarser soils. *Quercus velutina* was fairly common on all sites, but its highest importance occurred at lower elevations. Overstory trees other than *Quercus* were primarily *A. rubrum*, *A. saccharum*, *Pinus strobus* L., *P. serotina*, and *Carya* spp. Most of these species were infrequent, intermediate in crown size, and restricted to stream bank, valley floor and/or cove sites.

A larger number of species were present as understory trees, including *Quercus*, *Carya*, *Acer*, *Prunus* and *P. strobus* (Fig. 2). In general, understory trees of *Quercus* were most abundant on xeric areas (i.e. coarse textured-valley, crest, and upper slope sites) and in younger stands regardless of physiographic location. *Carya*, *Acer*, *Prunus* and *P. strobus* were most abundant in the understory on stream banks and fine textured-valley sites. *Acer rubrum* was a common understory tree in most stands.

Regeneration Trends Across An Environmental Gradient

Total seedling number tended to be greatest on the coarse textured-valley sites and least on the upper slopes (Table 3). Seedling number was negatively correlated with stand basal area and percent slope ($p < 0.05$, $r = -.43$ and -.41). *Quercus* species were well represented as seedlings in all physiographic units and seedling density closely followed importance values of the overstory species. Seedlings of *Q. alba* were most abundant on stream bank and valley sites, *Q. rubra* on slopes and *Q. prinus* on slopes, ridges and coarse textured-valley sites. *Quercus prinus* seedlings were significantly correlated with percent sand, silt and clay ($p < 0.05$, $r = .50, -.47$ and -.42, respectively), as exhibited with its overstory importance. *Acer rubrum* and *P. serotina* were common seedlings on all sites, however the latter were most

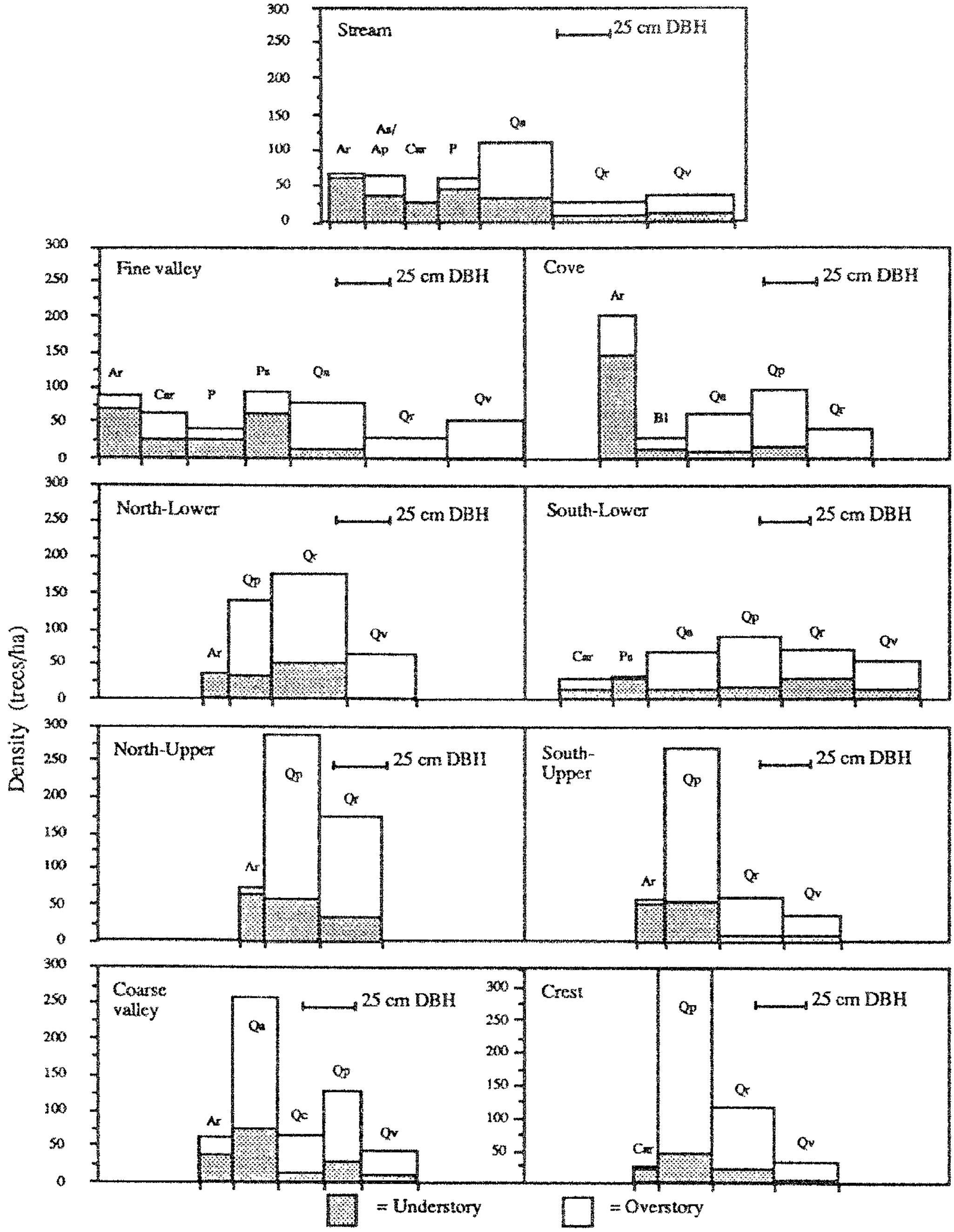

Figure 2. Stand structure on nine physiographic areas in the Ridge and Valley Province of central Pennsylvania based on mean density of overstory and understory trees and mean diameter of principal species (mean importance percentages of 5 or greater). Ar=*Acer rubrum*, As/Ap=*Acer saccharum/platanoides*, Bl=*Betula lenta*, Car=*Carya* spp., P=*Pinus strobus*, Ps=*Prunus serotina*, Qa=*Quercus alba*, Qc=*Quercus coccinea*, Qp=*Quercus prinus*, Qr=*Quercus rubra*, Qv=*Quercus velutina*.

Table 2.--Mean importance percentages[1] (±S.E.) of principal species and mean stand density (trees/ha) and basal area (m^2/ha) of 42 mixed oak forest stands organized by physiographic unit.

	Stream	Fine Valley	Cove	North Lower	South Lower	North Upper	South Upper	Coarse Valley	Crest
Acru	10±3[ab]	15±2[ab]	30±5[b]	6±2[a]	1±0[a]	9±7[ab]	10±4[ab]	10±2[a]	2±1[a]
As/Ap	8±6[a]	2±1[a]	0±0[a]	0±0[a]	1±1[a]	0±0[a]	0±0[a]	0±0[a]	0±0[a]
Bele	0±0[ab]	0±0[a]	6±4[b]	2±1[ab]	0±0[ab]	1±1[ab]	1±1[ab]	0±0[a]	2±1[ab]
Carya*	5±1[a]	11±3[a]	3±3[a]	1±1[a]	9±5[a]	1±1[a]	3±3[a]	2±1[a]	5±1[a]
Pist*	9±4[a]	8±3[a]	0±0[a]	1±1[a]	1±1[a]	4±2[a]	2±2[a]	1±1[a]	0±0[a]
Prav	1±1[a]	3±2[a]	0±0[a]	0±0[a]	1±0[a]	0±0[a]	0±0[a]	0±0[a]	0±0[a]
Prse	4±2[b]	15±2[a]	1±1[b]	1±1[b]	7±2[ab]	0±0[b]	0±0[b]	1±1[b]	1±1[b]
Qual	27±9[ab]	20±5[ab]	15±9[ab]	1±1[b]	18±3[ab]	0±0[ab]	1±1[b]	38±9[a]	1±1[ab]
Quco	4±2[ab]	1±1[a]	2±2[ab]	0±0[a]	1±0[ab]	0±0[a]	1±0[a]	14±3[b]	0±0[a]
Qupr	0±0[ab]	0±0[a]	22±1[abc]	32±6[abc]	22±5[abc]	47±1[bc]	52±8[c]	17±9[abc]	54±4[c]
Quru	9±3[ac]	8±4[a]	11±4[ac]	39±4[b]	19±3[ab]	34±6[bc]	17±5[ab]	3±2[a]	27±1[ab]
Quve	11±4[a]	15±5[a]	5±3[a]	13±5[a]	14±5[a]	1±1[a]	10±4[a]	10±3[a]	8±2[a]
# of Stands	4	7	3	5	3	3	5	9	3
Density	507[a]	498[a]	501[a]	478[a]	390[a]	575[a]	472[a]	617[a]	530[a]
Basal Area	34[ab]	35[a]	24[ab]	37[a]	30[ab]	31[ab]	24[ab]	20[b]	31[ab]

[1] Importance percentage = (relative density + relative dominance + relative frequency)/3. Values in a row with the same letter are not significantly different at $p < 0.05$.
* Significant differences based on ANOVA, but not detected by Scheffe's mean separation procedure.
Acru=*Acer rubrum*, As/Ap=*Acer saccharum/platanoides*, Bele=*Betula lenta*, Carya=*Carya* species, Pist=*Pinus strobus*, Prav=*Prunus avium*, Prse=*Prunus serotina*, Qual=*Quercus alba*, Quco=*Quercus coccinea*, Qupr=*Quercus prinus*, Quru=*Quercus rubra*, Quve=*Quercus velutina*.

abundant on southern lower slopes and fine textured-valley sites. *Acer saccharum*, *Acer platanoides* L. and *Prunus avium* L. seedlings were restricted primarily to mesic sites, specifically fine textured-valley and stream bank sites. In contrast, *A. pensylvanicum* and *B. lenta* seedlings occurred primarily on more severe, ridge sites.

Sapling density was not consistent among species, although higher density was skewed towards shade tolerant species (Table 4). The most prevalent sapling was *A. rubrum*, which commonly occurred on all physiographic sites. *Prunus serotina* saplings were similar in number to *A. rubrum* on all sites except for coarse textured-valley and cove sites. *Acer saccharum*, *A. platanoides* and *Cornus florida* L. were frequent saplings in mesic, fine

Table 3.--Mean seedling number (stems/ha) of principal species of 42 mixed oak forest stands organized by physiographic unit.

	Stream	Fine Valley	Cove	North Lower	South Lower	North Upper	South Upper	Coarse Valley	Crest
Acpe	0^{a}	0^{a}	900^{ab}	380^{a}	0^{a}	6733^{ab}	1180^{a}	11^{a}	13600^{b}
Acru	20200^{a}	6329^{a}	57033^{a}	15440^{a}	4100^{a}	7767^{a}	10980^{a}	36322^{a}	9200^{a}
As/Ap	3225^{a}	3886^{a}	0^{a}	20^{a}	33^{a}	0^{a}	0^{a}	0^{a}	0^{a}
Bele*	0^{a}	0^{a}	1567^{a}	420^{a}	0^{a}	433^{a}	480^{a}	11^{a}	4333^{a}
Carya*	1125^{a}	857^{a}	0^{a}	1560^{a}	1733^{a}	467^{a}	200^{a}	633^{a}	367^{a}
Cade*	0^{a}	0^{a}	0^{a}	60^{a}	0^{a}	33^{a}	20^{a}	244^{a}	0^{a}
Cofl	925^{a}	386^{a}	33^{a}	100^{a}	67^{a}	0^{a}	0^{a}	89^{a}	267^{a}
Fram	3025^{ab}	1171^{ab}	33^{ab}	10700^{b}	11067^{ab}	467^{ab}	500^{ab}	222^{a}	0^{ab}
Havi*	600^{a}	43^{a}	633^{a}	1520^{a}	0^{a}	1067^{a}	500^{a}	33^{a}	500^{a}
Nysy	0^{a}	0^{a}	300^{a}	100^{a}	0^{a}	0^{a}	340^{a}	0^{a}	0^{a}
Osvi*	1650^{a}	43^{a}	0^{a}	200^{a}	0^{a}	0^{a}	0^{a}	44^{a}	0^{a}
Pist	425^{a}	0^{a}	200^{a}	0^{a}	0^{a}	33^{a}	0^{a}	67^{a}	0^{a}
Prav*	325^{a}	6629^{a}	0^{a}	20^{a}	67^{a}	0^{a}	20^{a}	56^{a}	0^{a}
Prse	5075^{ab}	14457^{ab}	2933^{ab}	2660^{a}	27333^{ab}	2333^{ab}	5420^{b}	6100^{ab}	3067^{ab}
Prvi	0^{ab}	8686^{a}	0^{ab}	60^{ab}	67^{ab}	0^{ab}	80^{ab}	11^{b}	0^{ab}
Qual*	3575^{a}	3557^{a}	3800^{a}	200^{a}	4233^{a}	0^{a}	20^{a}	29589^{a}	0^{a}
Quco	325^{a}	29^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	2200^{b}	0^{a}
Quil	0^{ab}	0^{a}	0^{ab}	0^{ab}	0^{ab}	0^{ab}	0^{ab}	2933^{b}	0^{ab}
Qupr	0^{a}	43^{a}	3700^{a}	6560^{a}	26267^{a}	19333^{a}	14640^{a}	28756^{a}	10207^{a}
Quru*	400^{a}	271^{a}	533^{a}	2200^{a}	1333^{a}	1600^{a}	1880^{a}	756^{a}	1100^{a}
Quve*	1050^{a}	314^{a}	233^{a}	780^{a}	2133^{a}	333^{a}	1020^{a}	2178^{a}	1533^{a}
Saal*	4450^{a}	0^{a}	200^{a}	20^{a}	133^{a}	267^{a}	720^{a}	6444^{a}	67^{a}
Total	51675^{ab}	48786^{a}	96000^{ab}	44280^{a}	82667^{a}	42467^{ab}	39060^{ab}	124744^{b}	44700^{ab}

Values in a row with the same letter are not significantly different at $p < 0.05$.
* Significant differences based on ANOVA, but not detected by Scheffe's mean separation procedure.
Acpe=*Acer pensylvanicum*, Acru=*Acer rubrum*, As/Ap=*Acer saccharum/platanoides*, Bele=*Betula lenta*, Carya=*Carya* spp., Cade=*Castanea dentata*, Cofl=*Cornus florida*, Fram=*Fraxinus americana*, Havi=*Hamamelis virginiana*, Nysy=*Nyssa sylvatica*, Osvi=*Ostrya virginiana*, Pist=*Pinus strobus*, Prav=*Prunus avium*, Prse=*Prunus serotina*, Prvi=*Prunus virginiana*, Qual=*Quercus alba*, Quco=*Quercus coccinea*, Quil=*Quercus ilicifolia*, Qupr=*Quercus prinus*, Quru=*Quercus rubra*, Quve=*Quercus velutina*, Saal=*Sassafras albidum*.

textured-valley and stream bank communities, whereas *Hamamelis virginiana* L., *A. pensylvanicum*, and *B. lenta* saplings were common on slopes and ridgetops. The latter two species were positively correlated with elevation ($p < 0.05$, $r = .36$ and $.37$, respectively). *Sassafras albidum* (Nutt.) Nees saplings frequently occurred on coarse textured-valley sites.

Table 4.--Mean sapling number (stems/ha) of principal species of 42 mixed oak forest stands organized by physiographic unit.

	Stream	Fine Valley	Cove	North Lower	South Lower	North Upper	South Upper	Coarse Valley	Crest
Acpe*	0^{a}	0^{a}	0^{a}	170^{a}	0^{a}	1467^{a}	50^{a}	0^{a}	1017^{a}
Acru	187^{a}	1136^{a}	2250^{a}	420^{a}	100^{a}	67^{a}	440^{a}	1333^{a}	50^{a}
As/Ap	62^{a}	321^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}
Bele	0^{a}	0^{a}	87^{a}	146^{a}	29^{a}	987^{a}	442^{a}	17^{a}	2330^{a}
Carya	25^{a}	50^{a}	0^{a}	110^{a}	133^{a}	0^{a}	20^{a}	33^{a}	0^{a}
Cade	0^{a}	0^{a}	0^{a}	10^{a}	10^{a}	0^{a}	0^{a}	89^{a}	0^{a}
Cofl	475^{b}	129^{ab}	0^{a}	40^{a}	50^{a}	17^{a}	0^{a}	28^{a}	0^{a}
Fram	25^{a}	250^{a}	0^{a}	280^{a}	150^{a}	33^{a}	0^{a}	6^{a}	0^{a}
Havi	0^{ab}	0^{a}	17^{ab}	270^{b}	0^{ab}	100^{ab}	20^{ab}	0^{a}	67^{ab}
Nysy	0^{a}	0^{a}	33^{a}	10^{a}	20^{a}	0^{a}	0^{a}	0^{a}	0^{a}
Osvi	87^{a}	14^{a}	0^{a}	40^{a}	0^{a}	0^{a}	0^{a}	22^{a}	0^{a}
Pist	13^{a}	7^{a}	0^{a}	0^{a}	30^{a}	0^{a}	0^{a}	44^{a}	0^{a}
Prav	0^{a}	71^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}
Prse	62^{a}	729^{a}	33^{a}	80^{a}	1850^{b}	67^{a}	190^{a}	128^{a}	17^{a}
Prvi*	0^{a}	129^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}
Qual	13^{a}	0^{a}	0^{a}	0^{a}	50^{a}	0^{a}	0^{a}	83^{a}	0^{a}
Quco	13^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	83^{a}	0^{a}
Quil	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	94^{a}	0^{a}
Qupr	0^{a}	0^{a}	0^{a}	10^{a}	50^{a}	0^{a}	10^{a}	78^{a}	0^{a}
Quru	13^{a}	14^{a}	0^{a}	30^{a}	33^{a}	17^{a}	10^{a}	6^{a}	0^{a}
Saal	187^{ab}	7^{a}	0^{ab}	0^{a}	10^{a}	0^{ab}	0^{ab}	456^{b}	0^{ab}
Total	1350^{a}	3000^{a}	2400^{a}	1580^{a}	2917^{a}	2450^{a}	1050^{a}	2583^{a}	2667^{a}

Values in a row with the same letter are not significantly different at $p < 0.05$.
* Significant differences based on ANOVA, but not detected by Scheffe's mean separation procedure.
Acpe=*Acer pensylvanicum*, Acru=*Acer rubrum*, As/Ap=*Acer saccharum/platanoides*, Bele=*Betula lenta*, Carya=*Carya* spp., Cade=*Castanea dentata*, Cofl=*Cornus florida*, Fram=*Fraxinus americana*, Havi=*Hamamelis virginiana*, Nysy=*Nyssa sylvatica*, Osvi=*Ostrya virginiana*, Pist=*Pinus strobus*, Prav=*Prunus avium*, Prse=*Prunus serotina*, Prvi=*Prunus virginiana*, Qual=*Quercus alba*, Quco=*Quercus coccinea*, Quil=*Quercus ilicifolia*, Qupr=*Quercus prinus*, Quru=*Quercus rubra*, Quve=*Quercus velutina*, Saal=*Sassafras albidum*.

DISCUSSION

Mixed oak forests of the Ridge and Valley Province of central Pennsylvania differ appreciably in composition and structure due to differences in edaphic factors. General decreases in soil moisture with increasing elevation from mesic indented stream sites to xeric ridgetops occurred due to increases in percent sand and slope, decreases in soil thickness and percent silt and clay, and changes in substrate (limestone to sandstone) and soil type (Alfisols to Inceptisols)(cf. Whittaker 1956). This gradient is rather uniform across the landscape except for two physiographic outliers, the coarse textured-valley floor and cove units. These units encompass xerophytic and mesophytic communities, respectively, which contrast sharply with surrounding forests. Otherwise, changes in forest composition were rather subtle between adjoining physiographic units, representing a continuum of community organization (Gleason 1926). Although changes in forest composition seemed to be closely linked with moisture availability, changes in fertility and pH may also play important roles (Peet and Loucks 1977, Balter and Loeb 1983, Campbell 1987).

Quercus species were consistently the largest and presumably oldest individuals on all sites, and dominated the overstories of all physiographic units. These attributes seem to be quite characteristic of *Quercus* in other eastern forests (Cottam 1949, Parker et al. 1985, Abrams 1986, McGee 1986, Nowacki et al. 1990). General shifts in *Quercus* dominance from *Q. alba* through *Q. rubra* to *Q. prinus* occurred from mesic to xeric sites, and is consistent with regional surveys (Niering 1953, Keever 1973, Overlease 1978, Russell and Schuyler 1988). In contrast, both coarse textured-valley and cove sites had overstories dominated by *Q. alba* and *Q. prinus*. This is rather unusual considering that these two physiographic units occur at the opposite extremes of the moisture spectrum and the co-occurrence of these two species on other sites is infrequent.

The mixed oak forests in this study are considered early- to mid-successional on most sites based on regeneration trends. Replacement of the oak component to varying degrees by more shade tolerant species seems likely in the future, though the transition may be rather gradual due to long life span of *Quercus* species (Abrams and Downs 1990). Understory trees and saplings are probably the best predictor of future composition, barring large-scale disturbances to the site (cf. Ohmann and Buell 1968). On mesic sites, *A. rubrum* and *P. serotina* were the most abundant understory species, which is consistent with other forests in the region (Gysel and Arend 1953, Crow and Miller 1983, Lorimer 1984, Russell and Schuyler 1988, Abrams and Downs 1990). The distribution of *A. rubrum* on a wide variety of sites in central Pennsylvania can be explained, in part, by genotypic variation and physiological plasticity (Abrams and Kubiske 1990). Some studies indicate poor performance of *P. serotina* in understory conditions (cf. Mackey and Sivec 1973), however we found this species growing rather vigorously and recruiting well in most cases. *Acer saccharum*, usually a dominant understory species in other *Quercus* forests (Crow and Miller 1983, Parker et al. 1985, Nowacki et al. 1990), was lacking on most mesic areas, probably due to its low overstory importance in the area. On the drier upper slopes, trends towards *A. pensylvanicum, H. virginiana, B. lenta, A. rubrum* were apparent, though only the latter two species have overstory potential. Regeneration on the crest was primarily made up of *B. lenta* and *A. pensylvanicum*. Successful seedling-to-sapling recruitment of *Quercus* species occurred only on coarse textured-valley floor locations, combining with *A. rubrum, P. strobus* and *S. albidum* to form the understory. Abundant *Quercus* regeneration on xeric sites has been documented elsewhere (Gysel and Arend 1953, Overlease 1978, McCune and Cottom 1985, Abrams 1986), and may be explained by higher light levels at the forest floor and fewer competing seedlings of less drought tolerant species. We conclude from these data that future decreases of *Quercus* will probably occur, with corresponding increases of *A. rubrum* and *P. serotina* on mesic sites and *A. rubrum* and *B. lenta* on drier slopes and ridgetops. In the most xeric communities, *Quercus* seems to be a rather stable component, although slight increases in *A. rubrum, S. albidum* and/or *B. lenta* may occur.

Betula lenta often dominates recently disturbed areas in central Pennsylvania, however it can also occur in shaded forest understories (Fowells 1965). Successional trends in this and other studies of northeastern forests suggest that *B. lenta* has been increasing in importance over the past few decades, possibly in response to canopy gaps (Good 1968, Russell and Schuyler 1988, Loeb 1990). Nonetheless, the distribution of *B. lenta* in this study was restricted to high-elevational or xeric valley-floor forests.

Present-day mixed oak stands seem to be intrinsically linked with intense anthropogenic disturbances. Most stands included in the survey are associated with recurring logging and fire from 1760 to 1900. Even though *Quercus* species were an important component in eastern presettlement forests (Sears 1925, Braun 1950, Spurr 1951, Russell 1981, Abrams and Downs 1990), it seems likely that their dominance has been maintained or even promoted from recurring disturbances due to their resistence to fire and competitiveness in post-disturbance environments (Lorimer 1985, Crow 1988, Lorimer 1989, Nowacki et al. 1990). However, decreased disturbance this century has led to conditions favoring shade tolerant species, with few opportunities for *Quercus* establishment and canopy recruitment. Under today's low-disturbance regime, *Quercus* species will most likely decline on all but the most xeric sites.

LITERATURE CITED

Abrams, M. D. 1986. Historical development of gallery forests in northeast Kansas. Vegetatio 65:29-37.

Abrams, M. D. and J. A. Downs. 1990. Successional replacement of old-growth white oak by mixed-mesophytic hardwoods in southwest Pennsylvania. Can. J. For. Res. (In Press).

Abrams, M. D. and M. E. Kubiske. 1990. Photosynthesis and water relations during drought in *Acer rubrum* L. genotypes from contrasting sites in central Pennsylvania. Functional Ecology (in press).

Balter, H. and R. E. Loeb. 1983. Arboreal relationships on limestone and gneiss in northern New Jersey and southeastern New York. Bull. Torrey Bot. Club 110:370-379.

Bouyoucos, G. J. 1962. Hydrometer method improved for making particle size analysis of soils. Agro. J. 54:464-465.

Braun, E. L. 1950. Deciduous forests of eastern North America. Hafner Press, New York, NY, 596 p.

Campbell, J. J. N. 1987. Gradients of tree species composition in the central hardwood region. In Proc. Central Hardwood Forest Conf. VI, R. L. Hay, F. W. Woods and H. DeSelm (eds.), Knoxville, TN, p. 325-346.

Christensen, N. L. 1977. Changes in structure, pattern and diversity associated with climax forest maturation in Piedmont, North Carolina. Am. Midl. Nat. 97: 176-188.

Cottam, G. 1949. The phytosociology of an oak woods in southwestern Wisconsin. Ecology 30:271-287.

Cottam, G. and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37: 451-460.

Crow, G. R. and C. A. Miller. 1983. Woody plant composition of a southwestern Pennsylvania upland deciduous forest. Proc. Penn. Acad. Sci. 57:177-180.

Crow, T. R. 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*) - a review. For. Sci. 34: 19-40.

Fowells, H. A. 1965. Silvics of forest trees of the United States. USDA Agric. Handb. 271, 762 p.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bull. Torrey Bot. Club 53:7-26.

Good, N. F. 1968. A study of natural replacement of chestnut in six stands in the Highlands of New Jersey. Torrey Bot. Club 95:240-253.

Gysel, L. W. and J. L. Arend. 1953. Oak sites in southern Michigan: their classification and evaluation. Mich. Tech. Bull. 236, 57 p.

Hough, A. F. and R. D. Forbes. 1943. The ecology and silvics of forests in the High Plateaus of Pennsylvania. Ecol. Monogr. 13: 299-320.

Johnson, G. G. and S. Ware. 1982. Post-chestnut forests in the central Blue Ridge of Virginia. Castanea 47: 329-343.

Keever, C. 1953. Present composition of some stands of the former oak-chestnut forest in the southern Blue Ridge Mountains. Ecology 34: 44-54.

Keever, C. 1973. Distribution of major forest species in southeastern Pennsylvania. Ecol. Monogr. 43:303-327.

Loeb, R. E. 1990. Measurement of vegetation changes through time by resampling. Torrey Bot. Club 117:173-175.

Lorimer, C. G. 1984. Development of the red maple understory in northeastern oak forests. For. Sci. 30:3-22.

Lorimer, C. G. 1985. The role of fire in the perpetuation of oak forests. In Proceedings, Challenges in oak management and utilization, J. E. Johnson (ed.). Coop. Extension Service, Univ. of WI-Madison, p. 8-25.

Lorimer, C. G. 1989. The oak regeneration problem: new evidence on causes and possible solutions. Forest Resource Analyses No. 8, Dept. of For., Univ. of WI-Madison, 31 p.

Mackey, H. E. Jr. and N. Sivec. 1973. The present composition of a former oak-chestnut forest in the Allegheny Mountains of western Pennsylvania. Ecology 54:915-919.

McCormick, J. F. and R. B. Platt. 1980. Recovery of an Applachian forest following the chestnut blight or Catherine Keever-You were right! Am. Midl. Nat. 104: 264-273.

McCune, B. and G. Cottam. 1985. The successional status of a southern Wisconsin oak woods. Ecology 66:1270-1278.

McGee, C. E. 1986. Oaks lose dominance in an undisturbed old-growth forest. In Proceedings of annual hardwood symposium (Issue 14th), Hardwood Research Council, Memphis, TN, p. 115-121.

Niering, W. A. 1953. The past and present vegetation of High Point State Park, New Jersey. Ecol. Monogr. 23:127-148.

Nowacki, G. J., M. D. Abrams and C. G. Lorimer. 1990. Composition, structure, and historical development of northern red oak stands along an edaphic gradient in north-central Wisconsin. For. Sci. 36:276-292.

Ohmann, L. F. and M. F. Buell. 1968. Forest vegetation of the New Jersey Highlands. Torrey Bot. Club 95:287-298.

Overlease, W. R. 1978. A study of forest communities in southern Chester County, Pennsylvania. Proc. Penn. Acad. Sci. 52:37-44.

Parker, G. R., D. J. Leopold and J. K. Eichenberger. 1985. Tree dynamics in an old-growth, deciduous forest. For. Ecol. Manage. 11: 31-57.

Peet, R. K. and O. L. Loucks. 1977. A gradient analysis of southern Wisconsin forests. Ecology 58:485-499.

Russell, E. W. B. 1981. Vegetation of northern New Jersey before European settlement. Am. Midl. Nat. 105:1-12.

Russell, E. W. and A. E. Schuyler. 1988. Vegetation and flora of Hopewell Furnace National Historic Site, eastern Pennsylvania. Bartonia 54:124-143.

Sears, P. B. 1925. The natural vegetation of Ohio. Ohio J. Sci. 25:139-149.

Smith, D. M. 1986. The practice of silviculture. John Wiley and Sons, New York, NY, 527 p.

Spurr, S. H. 1951. George Washington, surveyor and ecological observer. Ecology 32: 544-549.

Whitney, G. G. 1987. An ecological history of the Great Lakes forest of Michigan. J. Ecol. 75: 667-684.

Whittaker, R. H. 1956. Vegetation of the Great Smokey Mountains. Ecol. Monogr. 26:1-80.