Bulletin of the Torrey Botanical Club 117(2), 1990, pp. 106–122

Effects of environment and land-use history on upland forests of the Cary Arboretum, Hudson Valley, New York

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ABSTRACT

GLITZENSTEIN, J. S., C. D. CANHAM, M. J. MCDONNELL AND D. R. STRENG (Institute of Ecosystem Studies, Millbrook, NY 12545). Effects of environment and land-use history on upland forests of the Cary Arboretum, Hudson Valley, New York. Bull. Torrey Bot. Club 117: 106–122. 1990.—Relationships of vegetation to environment and land-use history were investigated in forests of the Mary Flagler Cary Arboretum in the Hudson Valley of New York. Vegetation data were obtained from 76 $\frac{1}{20}$ ha circular plots randomly located within the forest. Environmental data collected at each plot included slope, aspect, canopy openness, soil texture and nutrients, topographic position, and presence of exposed rock; gravimetric soil moisture was determined weekly during 1985 for a subsample of 25 stands. Land-use history information came from historical records (land deeds and U.S. and N.Y.S. census records), stone-fence locations, landscape patterns in stand ages, an old aerial photograph, and soils data.

Vegetation analyses identified three major community types. One group of stands, dominated by chestnut oak (*Quercus prinus* L.) and northern red oak (*Quercus rubra* L.), occurred on steep, rocky, upper slope sites never cleared for agriculture. Distinct vertical stratification of dominant canopy species in these stands is consistent with a probable history of intensive selective cutting early in this century. Both of the other major community types occurred primarily on abandoned agricultural land. Stands dominated by white oak (*Quercus alba* L.), black oak (*Quercus velutina* Lam.) and pignut hickory (*Carya glabra* (Mill.) Sweet) tended to occur at lower elevations on rocky, nutrient poor sites probably derived from abandoned pastures. The significantly more open canopy in these stands, less distinct vertical stratification of canopy trees, and a diverse herbaceous understory frequently including grasses and sedges, also suggests very gradual invasion of these forests onto old pasture sites. The third major vegetation type, dominated by red maple (*Acer rubrum* L.) and white pine (*Pinus strobus* L.), tended to occur on finer textured, less rocky old field sites possibly abandoned from cultivation. Comparison of current vegetation with witness tree data from early land survey records suggests that the white oak-black oak-hickory type was prevalent on lower slope sites prior to forest clearing, but has declined in importance relative to the red maple type during the past 100 years of abandonment of land from agriculture.

Key words: environment, forest vegetation, land-use history, Hudson Valley, New York.

Environment and history can be regarded, in the most general terms, as the two preeminent factors determining the distribution of plant communities across a landscape. The role of environment is widely appreciated, and many studies have demonstrated relationships between important environmental variables (e.g., elevation, topography, soils, nutrients) and the distribution of plant species and communities (e.g., Whittaker 1956; Loucks 1962; Peet and Loucks 1977; Marks and Harcombe 1981; Bergeron and Bouchard 1983; Tilman 1987). The role of history, while also widely recognized, is usually not documented as thoroughly (Hamburg and Sanford 1986; Whitney and Davis 1986). In most vegetation studies successional development is the only aspect of history to be considered; this is usually measured simply as stand age (e.g., Marks and Harcombe 1981) or through an index based on relative importance of "early successional" species (e.g., Peet and Loucks 1977; Bergeron

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We would like to thank Dan Spada, Carolyn Wilczynski, Carl Glitzenstein and Harold Fraleigh for their able assistance in the field and laboratory. We also thank D. M. Smith and D. R. Foster for educational walks through the Cary Arboretum forests, G. G. Parker for stimulating discussion of the subject material, and Peter Marks and Wm. Niering for useful comments on earlier drafts of the manuscript. Financial support was provided by the Mary Flagler Cary Charitable Trust. This manuscript is a contribution to the program of the Institute of Ecosystem Studies, The New York Botanical Garden.

Received for publication October 5, 1988 and in revised form September 29, 1989.

and Bouchard 1983). Other aspects of history, such as those related to conditions at the time of stand initiation (e.g., Keever 1950), are rarely quantified.

In forests of the northeastern United States, perhaps the most important historical influence on vegetation has been the history of land use by humans (Robichaud and Buell 1973; Vale 1982; Hamburg and Sanford 1986). Burning by Indians prior to European settlement (Bromley 1935; Day 1953; Niering and Goodwin 1962; Cronon 1983); agricultural use and decline (Lutz 1928; Bromley 1935; Raup and Carlson 1941; Bormann 1982; Whitney and Davis 1986; Whitney and Foster 1988) and patterns of cutting associated with particular forest industries (Winer 1956; Spurr 1956; Smiley and Huth, personal communication) have all been implicated in altering patterns of forest regeneration and selectively favoring the reproduction of certain kinds of trees. However, with a few notable exceptions (e.g., Raup and Carlson 1941; Winer 1956; Bormann 1982; Whitney and Foster 1988), surprisingly few studies have directly related land-use patterns to patterns of forest structure or community composition.

The Hudson Valley of New York presents a diverse pattern of physical environments as well as a complex land-use history spanning more than three centuries. Vegetation in the most prominent mountains of the region has been well described (Raup 1938; McIntosh and Hurley 1964; McIntosh 1972; Olsvig 1980), but vegetation at lower elevations has received little attention. The Mary Flagler Cary Arboretum encompasses 795 ha of the ancient Taconic Mountains in the Mid-Hudson Valley at elevations between 90 and 220 meters (Fig. 1). In the present study, we describe the major plant communities in the upland forests of the Arboretum, and evaluate the relative importance of environment and land-use history in determining structural and compositional differences among these community types.

Study Area. The Mary Flagler Cary Arboretum is located in the Town of Washington in Dutchess County, New York (41°50'N, 73°45'W). Closed forests within the Arboretum occupy about 325 ha distributed among a number of discontinuous patches, with the largest area of continuous forest located on and around three steep hills known locally as the Canoo Hills (Fig. 1). The east branch of Wappingers Creek flows through the SE corner of the Canoo Hills tract (Fig. 1). The Arboretum lies within a forested region variously described as Appalachian oak (Küchler 1964), Central hardwoods-hemlock-white pine (Westveld *et al.* 1956) and oak-chestnut (Braun 1950). As a whole, this region is characterized by the former abundance of chestnut (*Castanea dentata* (Marsh.) Borkh.), and the past and present importance of several species of oaks (*Quercus* spp.) and hickories (*Carya* spp.). Mature hemlock (*Tsuga canadensis* (L.) Carr.) and shade tolerant hardwoods (e.g., beech, *Fagus grandifolia* Ehrh., and sugar maple, *Acer saccharum* Marsh.) are typically confined to moist habitats such as ravines and streamsides. Braun (1950) recognized two distinct oak dominated forest types within the oak-chestnut region: an oak-chestnut forest type, formerly dominated by chestnut, chestnut oak (*Quercus prinus,* L.), red oak (*Q. rubra,* L.), and black oak (*Q. velutina* Lam.), and now dominated by the three oaks, and an oak-hickory type dominated by white oak (*Q. alba* L.), with black oak, hickories (*Carya glabra* (Mill.) Sweet and *C. ovata* (Mill.) K. Koch) and red maple (*Acer rubrum* L.) as important associates. The oak-chestnut type is usually found on steep, rocky upper slopes and ridgetops, while the oak-hickory type is more important in valley bottoms and mesic upland sites (e.g., Niering 1953; Goodlett 1954).

Climate, Topography, and Soils. Mean annual precipitation at the nearest weather station (Poughkeepsie, NY) is 1020 mm/yr. Mean annual temperature is 9.4°C, with a January mean of −4.2°C and a July mean of 22.4°C. Topography within the Arboretum varies from a wide stream valley at approximately 90 m elevation to rocky uplands rising to 220 m in the Canoo Hills. The upland forests of the Arboretum are underlain by late Cambrian-early Ordovician shales and slates of the ancient Taconic Mountains. Soils are principally shallow, well drained silt loams of the Nassau and Woodlawn series formed from the acidic and relatively infertile glacial till (Secor *et al.* 1955). Bedrock outcrops are common throughout the upland forests and till depth generally ranges from 0–75 cm.

Local Agricultural History. Active European settlement in the vicinity of the Arboretum did not begin until after 1730 (Reynolds 1940a; Buck and McDermott 1979; McDermott 1980) and the clearing of original forest was not extensive as late as 1760 (Reynolds 1940b). After this, forest clearing proceeded rapidly, however, and most of the land in Dutchess County had

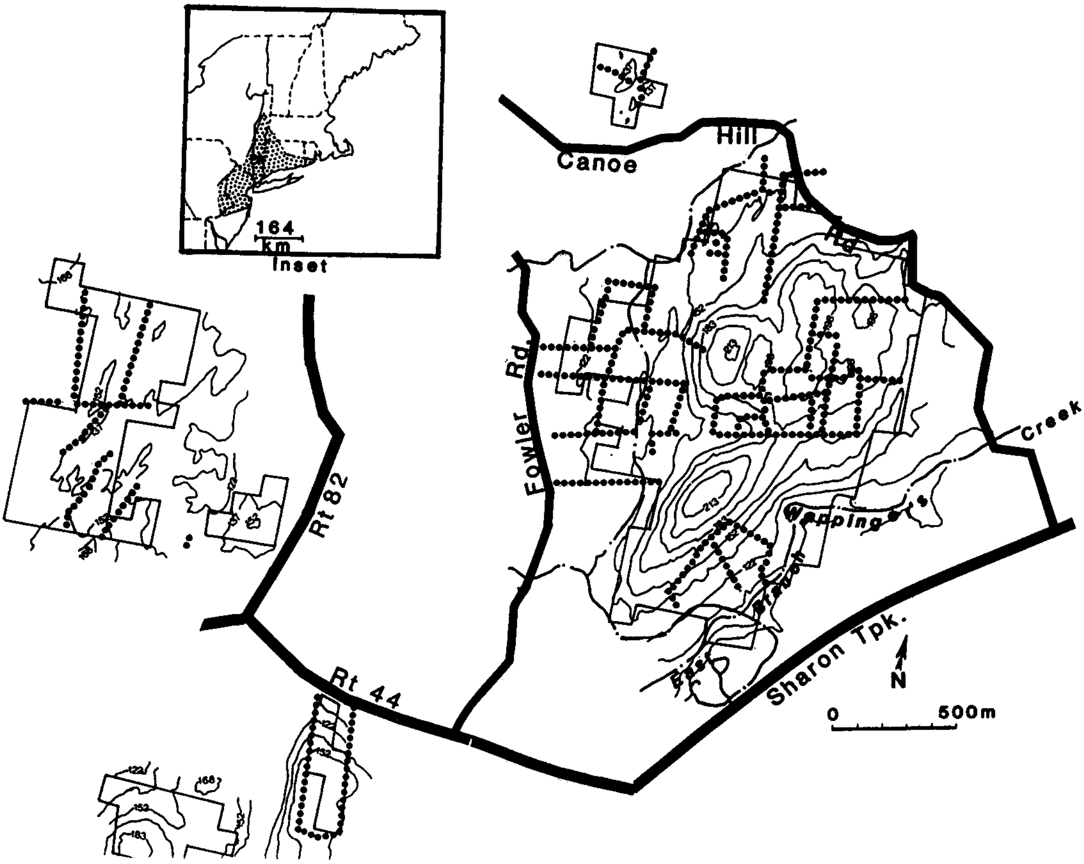

Fig. 1. Topographic map of forested areas in the Cary Arboretum included in the present study. The Canoo Hills are the high peaks within the large area to the east of Fowler Road. Stone fences (dotted lines) within the study area are included for comparison with Fig. 2. Contour interval = 15.24 m. Insert shows location of the Cary Arboretum east of the Hudson River in the glaciated section of the oak-chestnut forest region (shaded; after Braun 1950).

been converted to improved farmland by the mid-19th century (Roberts and Reynolds 1938). Farm prosperity began to decline in some areas of New York State after 1870 (Gates 1969), but in Dutchess County, 95% of the county was in farmland as late as 1880 (Roberts and Reynolds 1938). Economic conditions for farmers worsened statewide during the 1880's, and abandonment of marginal farmland began in earnest towards the end of the decade (Gates 1969). By 1930, acreage in farms in Dutchess County had declined 32% from the high point of the previous century (Roberts and Reynolds 1938). Farming in what is now the Cary Arboretum largely ended between 1925 and 1939 as the remaining operating farms (including the Petit, Knapp, Hall, Henry and Saccomanda farms; see Fig. 2) were purchased by Mary and Melbert Cary (Broach 1985; J. Henry personal communication).

Methods. VEGETATION. In 1984, we defined a 235 ha sampling area, subdivided into 1 ha cells, encompassing most of the upland forests of the Arboretum (Fig. 1). Within this area, 76 1 ha cells were randomly chosen, within each of which we randomly located a $\frac{1}{20}$ ha circular plot. Species, diameter at breast height (DBH), and crown class (canopy, subcanopy, understory and standing dead) were then tallied for all live and standing dead trees (stems > 10 cm DBH) in each $\frac{1}{20}$ ha plot. The largest tree in each plot was cored at 1 m height to provide an estimate of plot age. The percent of the sky hemisphere unobscured by canopy foliage was measured at four randomly chosen locations in each plot through the use of a 35 mm camera with a grid of 25 points marked on its focusing screen.

Saplings (stems >1 m in height and <10 cm DBH) were sampled in two randomly chosen 125

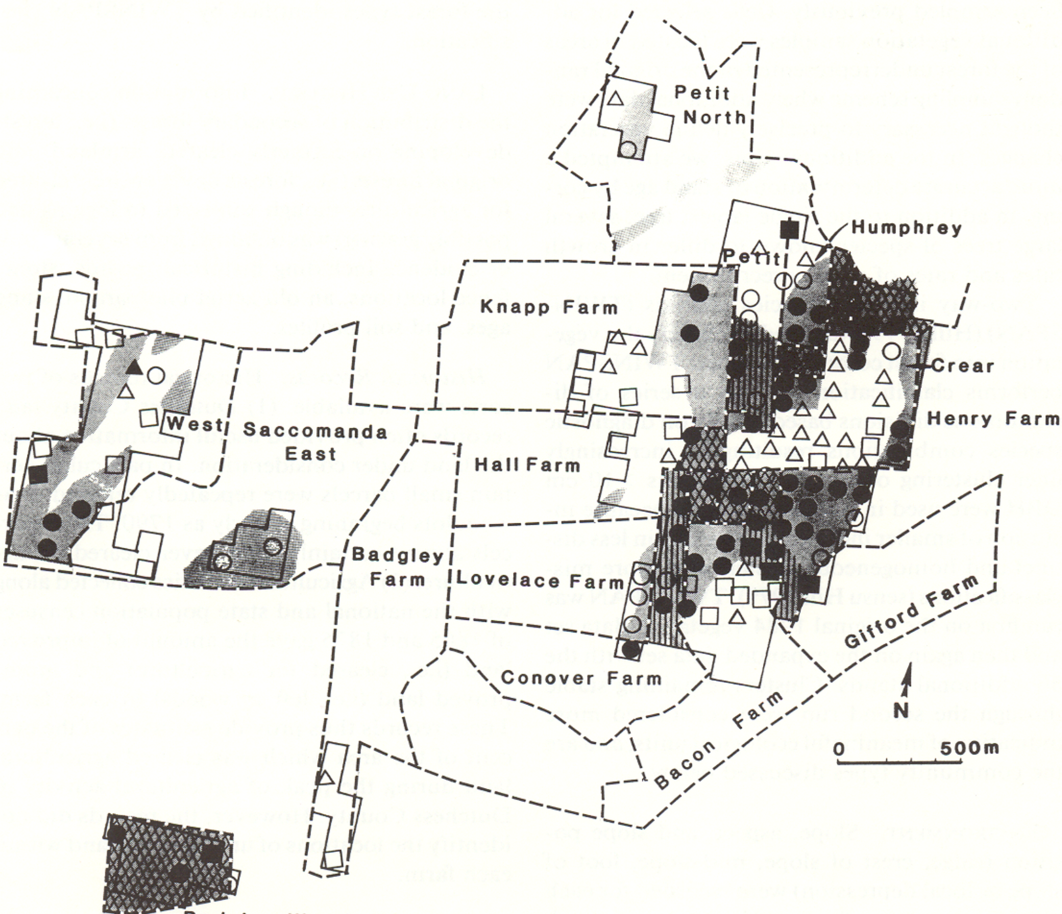

Fig. 2. Map of the Cary Arboretum showing: 1) boundaries of the study area as in Fig. 1 (heavy solid lines); 2) ownership boundaries in 1875 corresponding to parcel names given in Table 6 (thin dashed lines); 3) presumed areas of original forest (shaded); and 4) symbols showing locations of plots sampled in the field. The following subdivisions are indicated within the area of presumed original forests, corresponding to the kind of evidence used in making the determination of land-use history: 1) cross-hatching = well established woodlots repeatedly indicated in land records; 2) vertical hatching = areas indicated as woods in the early 1800's and presently containing trees originating before 1890; and 3) light shading = original forest areas as inferred from field evidence (see text) and contiguous with areas of original forest determined as in 1) or 2) above. The key to symbols is as follows: circles = chestnut oak forests; squares = oak-hickory forests; and triangles = red maple forests. Filled symbols are plots where the oldest tree cored originated prior to 1890; open symbols indicate stands originating after 1890.

m^2 quadrats within the main circular plot. Shrub cover was recorded as total projected cover along an east-west transect running the entire length of the plot (25.23 m). The density of tree seedlings and the projected cover of herbaceous species were sampled in eight 1 m × 0.5 m rectangular quadrats randomly located along the transect running east-west through the plot. A species list of all vascular plants present in the plot was also compiled. Nomenclature largely follows Gleason and Cronquist (1963).

The random sampling scheme was intended to provide a representative sample of the forest vegetation of the Arboretum. Preliminary analysis of this data set suggested distinct spatial patterns in tree species composition and stand ages. In order to further clarify these patterns, we located an additional 56 $\frac{1}{20}$ ha plots, and censused the trees (i.e., stems >10 cm DBH) as in the original survey. For convenience in vegetation mapping, each new plot was located precisely at the center of one of the 1 ha cells which had not been sampled previously. Cells selected for additional vegetation samples were located in areas of the forest underrepresented in the original random sampling scheme where additional data were thought necessary to precisely define vegetation changes. In the additional plots, we attempted a more accurate determination of stand age by coring, in addition to the single largest tree, several large trees of species known to differ in growth rates and rates of canopy recruitment.

Two-way indicator species analysis (TWINSPAN) (Hill 1979) was used to classify the vegetation into forest community types. TWINSPAN performs classification through a series of dichotomous divisions based largely on diagnostic species combinations resulting in increasingly finer clustering of stands. Only stems >10 cm DBH were used in our classification because inclusion of smaller individuals resulted in less distinct and homogeneous clusters and more misclassifications (sensu Hill 1979). TWINSPAN was run first on the original 1984 vegetation data set and then again on the expanded data set with the 56 additional stands. Clusters remaining stable through the second run were considered more indicative of meaningful ecological units, and are the community types discussed below.

ENVIRONMENT. Slope, aspect, and slope position (ridge, crest of slope, mid-slope, foot of slope or local depression) were recorded for each plot. The presence of exposed bedrock was noted, as was the presence or evidence of permanent or ephemeral streams or ponds. The depth of the forest floor (L, F, and H horizons combined) was measured at four randomly chosen distances along the transect running from east to west across the plot. Soil samples from the top 10 cm of mineral soil were also collected at the four locations and combined for an aggregate sample. The soil samples were frozen until ready to be processed, then air dried for 1 week and passed through a 2 mm sieve. Soil pH was measured in water and extractable 1N NH_4OAc cations (Ca, Mg, K, Mn, Zn, and Fe) were analyzed with atomic emission spectrophotometry. An index of the organic matter content of the mineral soil was obtained from weight loss of the mineral soil following ignition at 600°C for 2 hours. Soil texture was determined by a hydrometer method. Gravimetric soil moisture levels were determined weekly for an 11 week period during the summer of 1985 for 25 of the original sample of 76 stands. The 25 stands were randomly chosen from the groups of stands representing each of the forest types identified by TWINSPAN classification.

LAND USE HISTORY. Information concerning the distribution of secondary forests (i.e., forests developing on formerly cleared farmland) and original forests (i.e., forests never entirely cleared for agriculture, though subjected to logging and possibly grazing) was obtained from several kinds of evidence including historical records, stone-fence locations, an old aerial photograph, stand ages, and soil profiles.

Historical Records. Historical records of two sorts were available. (1) Dutchess County land records often provided useful information about the land under consideration. In particular, certain small parcels were repeatedly referred to as woodlots beginning as early as 1790. These parcels almost certainly were never cleared for agriculture. (2) Agricultural statistics collected along with the national and state population censuses of 1865 and 1875 gave the amount of improved land (i.e., cleared for agriculture) and unimproved land (i.e., left in woods) in each farm. These records thus provide estimates of the percent of the area which was cleared agricultural land during the peak of agricultural activity in Dutchess County. However, the records did not identify the locations of unimproved land within each farm.

Stone Fences and Other Boundaries. Stone fences in colonial New England were commonly constructed around the borders of cleared fields, and their occurrence in presently forested areas is a clear indicator of abandoned farmland (Winer 1956; Cronon 1983). The locations of stone fences in the Cary Forest were in part available from maps based on aerial photos already on file at the Arboretum. Additional fences were located and mapped during the course of the present study. In addition to mapping stone fences, we also mapped wire fences, old roads, and stones apparently piled on the edges of plowed fields, especially where these additional features appeared to mark obvious changes in vegetation age or composition.

Plot Ages. Perhaps the most useful indicators of land-use history were the plot ages obtained during the course of vegetation sampling. Since virtually all land suitable for farming in Dutchess County was in cleared farmland prior to about 1890 (see Study Area: Local Agricultural History), plots containing trees originating before this date were very unlikely ever to have been entirely cleared for agriculture.

Aerial Photography. The oldest aerial photograph of the Arboretum grounds, apparently taken during the mid-1930's, was useful primarily in indicating areas presently forested which were at the time of the photo still clearly abandoned fields, and delineating points of obvious change in vegetation that corresponded with the locations of stone fences.

Soils. On the moderate to steep slopes and shallow soils characteristic of most of the Cary Forest, forest clearing and agricultural utilization resulted in substantial erosion, including loss of most of the original topsoil (L, O, and A horizons) and its replacement in some cases by a deep, dark brown Ap horizon composed largely of the original subsoil (Secor *et al.* 1955). These altered soils were mapped in the 1939 SCS soil survey of the Cary property as an eroded phase of Nassau slatey silt loam (Secor *et al.* 1955). In the present study, the 1939 SCS soils survey was used in conjunction with our own observations of soil profiles to help classify a few plots whose history could not be unambiguously determined by other methods.

PRESETTLEMENT VEGETATION. Lands presently occupied by the Arboretum fall within the Great Nine Partners Patent granted by the English crown to a group of New York businessmen in 1699. In the second subdivision of this area in 1734, the major part of the Nine Partners Patent was divided into 36 Great Lots of approximately 12.67 km^2 each (Buck and McDermott 1979). Lands now in the Arboretum were included in four of these Great Lots. In this study we recorded by decade the species of all witness trees given in land survey records prior to 1800 for the four Great Lots. Trees appearing in land records prior to 1760 can be considered representative of the pre-colonial forest (see Study Area: Local Agricultural History). Trees appearing after this date, but before 1800, may well be of second growth origin.

Results. VEGETATION CLASSIFICATION AND DESCRIPTION. A two-way table produced by the TWINSPAN classification of the original set of 76 plots is shown in Table 1. The primary division is between a set of 42 plots in which chestnut oak and red oak are consistent canopy dominants and a set of 34 plots largely dominated by either red maple or black oak.

Chestnut Oak Forests. The group of plots dominated by chestnut oak and red oak are very similar to the oak-chestnut forest type recognized by Braun (1950) as one of the primary forest types of the region. Because chestnut has been eliminated from canopy status, the type will be referred to as the "chestnut oak" type, to conform with other studies of vegetation in the region (e.g., Mohler 1984).

TWINSPAN analysis of the 76 plots sampled in 1984 identified three subtypes in the chestnut oak forest, but these clusters showed some instability when the larger sample of 134 plots was analyzed (i.e., 14 of 41 plots were reclassified), and the subtypes will not be explicitly discussed here. In general, however, there was a gradient in composition from plots with hemlock as a codominant, in which sugar maple was missing, to plots codominated by sugar maple or pignut hickory, in which hemlock was absent (Table 1). Plots with hemlock as a major codominant verge on Braun's (1950) hemlock-hardwood type.

Canopy structure in the chestnut oak forests was distinctly vertically stratified, with chestnut and red oaks occupying the larger tree size classes and hemlocks and maples primarily restricted to subcanopy or understory positions. Sugar maple was the most abundant canopy tree in the sapling layer, except under a hemlock overstory, where hemlock saplings were abundant. Understory tree species such as ironwood (*Ostrya virginiana* (Mill.) K. Koch), shadbush (*Amelanchier* spp. Medic.) and striped maple (*Acer pensylvanicum* L.) were also relatively abundant, the latter species reaching its greatest relative abundance in stands co-dominated by hemlock. Prior to 1984, flowering dogwood (*Cornus florida* L.) was one of the dominant understory tree species throughout the region. However, it has been almost eliminated from the forests of the Arboretum by a fungal pathogen. Maple-leaved viburnum (*Viburnum acerifolium* L.) was the overwhelmingly dominant shrub, regardless of canopy composition (Table 2). The seedling layer in chestnut oak forests was dominated by sugar maple, red maple and shadbush, with striped maple important in hemlock co-dominated stands.

As in the other forest types (see pp. 113–114), coverage values for individual herbaceous species were generally so low as to be relatively uninformative (usually less than 3%, on average). Herbaceous cover in the chestnut oak type was especially sparse, averaging only 12.8% for all herbs together, much lower than in the other forest types. Hemlock dominated stands were

Table 1. Two-way table of tree species importance values (based on stems >10 cm DBH) in the upland forests of the Mary Flagler Cary Arboretum. Each column represents one plot. The scale indicates a doubling of species importance values, i.e., 0 = present as standing dead only, 1 < 2.5%, 2 < 5.0%, 3 < 10.0%, 4 < 20.0%, 5 < 40.0%, 6 < 80.0%, 7 > 80.0%. All species which occurred in at least two plots are listed.

	Chestnut oak forests	Oak–hickory forests	Red maple forests
Tsuga canadensis	5656030442-3445-61-----0-------0-------4-2	-----------------5---	-------------
Fagus grandifolia	----------------------------------2---445-	---------------------	-------------
Acer saccharum	---------2-2444234525355453-75635443554553	-------2--4-1-4-1-2--	11-1-65333---
Ostrya virginiana	---------0-------3-1--322------13---------	----------------02---	-----3-------
Quercus prinus	--55665656655556554-343452343655-636-65455	----3--405-3523--1---	-6-----------
Quercus rubra	-463555243545553-4-556344467-445646452-325	---4--5025---3-43----	223---2------
Carya glabra	--------22343343335533534------------33--4	44653-0-22--3-53533--	4-1----22----
Carya tomentosa	------------------5-------3---------------	------32-------------	-------------
Betula lenta	53-----3-2---------3----------34-1-23-42--	----------54454453-5-	-------34---2
Fraxinus americana	---------------125-3333-4-2------12-4--2-2	----053-4--0-44-4-0-4	3-30-3-5-----
Quercus alba	----------234-----244445454----1--------3-	3242154--4-45345-4-55	-------------
Carya ovata	-----------------2----2----13-------------	-45232-3--23-----1---	2------------
Cornus florida	---------0-0--------------------------3--2	-221----0-----2------	-0--------2--
Quercus velutina	----2-0---322----3---3-------3-20----3----	6642344544655-243-654	301-3--------
Liriodendron tulipifera	--	---------------------	-----------34
Pinus rigida	--	---------------------	4-3----------
Pinus resinosa	--	---------------------	---6---------
Quercus bicolor	--	------------------3--	----4--5-----
Prunus avium	--	----1----------------	-0-------1---
Prunus serotina	--	----2------------1---	--1-0-3------
Juniperus virginiana	--	0-----------------534	----2--------
Ulmus americana	--	-2---3------------2--	------0-30---
Acer rubrum	-1--32443-11212-2--2----341--332--32-44343	5024655564454632-42-5	4444655567776
Amelanchier spp.	--------2--------------------112----------	---------22----------	---13-4------
Pinus strobus	6--2344243-4---30--3----0---------2320----	0--55-033------434--2	1463-45------

Table 2. Relative cover (average percent of total shrub cover in stand) of shrub species in the major upland forest types. Species occurring in more than 5 stands in any forest type are listed. Total cover is the average percent of ground covered by shrubs in a stand.

Species	Chestnut oak forests	Oak-hickory forests	Red maple forests
Berberis thunbergii		0.8	
Cornus racemosa	0.6	22.9	12.1
Corylus cornuta	3.2		
Gaylussacia baccata	1.6	2.4	6.6
Lindera benzoin	0.1	6.0	1.0
Lonicera tatarica	0.2	0.2	0.4
Parthenocissus quinquefolia	5.1	24.0	17.9
Rhododendron nudiflorum	0.5		
Rosa multiflora		0.2	
Rubus spp.	0.2	3.7	27.5
Vaccinium angustifolium	12.8	0.6	1.6
Vaccinium vacillans	1.0	5.5	
Viburnum acerifolium	69.9	25.4	21.3
Viburnum prunifolium		3.0	
Viburnum rafinesquianum	3.0	0.7	0.7
Vitis spp.	0.3	2.2	2.5
Total cover	10.5	12.8	16.0

notably species poor (only 8.8 species per $\frac{1}{20}$ ha plot in ten plots grouped by TWINSPAN on the basis of hemlock dominance), but greater herbaceous diversity occurred under other canopy trees (22.1 herbaceous species per $\frac{1}{20}$ ha plot for the remaining 32 stands). The most frequently occurring herbs (Table 3) included several species (e.g., *Dryopteris marginalis* (L.) Gray, *Aralia nudicaulis* L., *Uvularia perfoliata* L. and *Mitchella repens* L.) which were much less common in the other forest types.

Oak-Hickory Forests. Chestnut oak and red oak occurred only sporadically in the other primary cluster of the classification (Table 1). That cluster was further divided by TWINSPAN into two relatively homogeneous groups. The first one, with 21 plots, was dominated by black oak and red maple, with pignut hickory and white oak as codominants. This group is similar in composition to the oak-hickory forests described by Braun (1950) in the glaciated section of the Oak-Chestnut Region and will be called the oak-hickory type in this study.

The oak-hickory plots differed substantially in structure from the chestnut oak forests. Stratification of species was not as pronounced as it was in the chestnut oak plots, though the oaks were still concentrated in the canopy stratum while red maple was more abundant in sub-canopy and understory strata. Total tree basal area in the oak-hickory forests was the lowest of any of the groups (Table 4). This was coupled with a high percentage of sky visible through the canopy, reflecting the relatively open canopy that appears to be characteristic of these stands (Table 4). The sapling layer was relatively dense, and dominated by witch hazel, flowering dogwood, sugar maple, hornbeam and red maple. The seedling layer was intermediate in density and not strikingly different from the chestnut oak forest

Table 3. Frequency of occurrence (%) of herbaceous species grouped by the forest type in which they are most commonly found. All species with greater than 20% frequency in at least one forest type are listed.

	Chestnut oak	Oak-hickory	Red maple
Chestnut oak forests			
Aquilegia canadensis	23.8	4.8	0.0
Aralia nudicaulis	45.2	14.3	7.7
Asplenium platyneuron	35.7	19.0	7.7
Carex platyphylla	38.1	4.8	7.7
Dryopteris marginalis	59.5	23.8	7.7
Eupatorium rugosum	31.0	28.6	7.7
Galium lanceolatum	23.8	14.3	15.4
Hepatica americana	21.4	4.8	0.0
Mitchella repens	31.0	19.0	7.7
Monotropa uniflora	64.3	52.4	23.1
Polypodium vulgare	35.7	14.3	7.7
Uvularia perfoliata	21.4	4.8	7.7
Viola palmata	21.4	9.5	0.0
Oak-hickory forests			
Antennaria plantaginifolia	28.6	42.9	15.4
Arisaema triphyllum	35.7	38.1	7.7
Chimaphila maculata	16.7	33.3	23.1
Geranium maculatum	4.8	28.6	0.0
Hypericum punctatum	2.4	23.8	0.0
Maianthemum canadense	16.7	38.1	30.8
Smilacina racemosa	9.5	28.6	7.7
Uvularia sessilifolia	14.3	23.8	0.0
Red maple forests			
Achillea millefolium	2.4	9.5	23.1
Aster divaricatus	42.9	47.6	69.2
Galium triflorum	11.9	33.3	38.5
Hieracium pratense	7.1	19.0	30.8
Polygonatum pubescens	38.1	23.8	46.2
Potentilla simplex	26.2	42.9	69.2
Veronica officinalis	31.0	42.9	61.5
Ubiquitous			
Aster macrophyllus	28.6	9.5	15.4
Dryopteris spinulosa	21.4	23.8	23.1
Galium circaezans	21.4	23.8	23.1
Polygala paucifolia	33.3	28.6	30.8
Solidago spp.	57.1	47.6	84.6
Solidago caesia	50.0	38.1	53.8
Sedge spp.	81.0	81.0	75.0
Grass spp.	42.9	52.4	58.3

Table 4. Structural characteristics (mean and range) of the major upland forest types. *P* values are for one-way ANOVA F tests for differences among the means for the three forest types.

	Chestnut oak forests	Oak-hickory forests	Red maple forests	*P* value
Canopy height (m)	24.3	22.9	21.8	n.s.
	(16–34)	(15–33)	(10–31)	
Percent sky visible	8.1	11.8	8.9	n.s.
	(0–30)	(1–56)	(2–16)	
Tree density (stems/ha)	510.5	494.3	647.7	0.09
	(220–1040)	(320–1100)	(360–1640)	
Tree basal area (m^2/ha)	24.8	20.0	24.8	0.09
	(12–54)	(8–45)	(7–46)	
Sapling density (stems/ha)	2075	2400	2431	n.s.
	(200–5440)	(560–6520)	(720–4920)	
Seedling density (#/m^2)	3.2	4.1	6.8	<0.01
	(0–8)	(0–9)	(2–18)	

type. In contrast, the shrub layer within the oak-hickory plots was relatively distinctive. Although maple-leaved viburnum was still the most abundant shrub species, dominance was shared almost equally with virginia creeper (*Parthenocissus quinquefolia* (L.) Planch. and gray dogwood (*Cornus racemosa* Lam.) (Table 2). Neither of the latter two species was common in the chestnut oak stands. Total shrub cover was relatively high in the oak-hickory plots, averaging 12.8% (Table 2).

The oak-hickory group had the highest diversity of herbaceous species of the three major forest types. One hundred and nine vascular plant species were found in the 21 oak-hickory plots. The oak-hickory group also had the greatest number of introduced herb species (15 of 19 introduced species present within the upland forests). Grass species occurred more frequently than in the chestnut oak type, and occurred in over half the oak-hickory plots (Table 3). Sedges, which occurred frequently in all three forest types (Table 3), were distinguished in the oak-hickory type by a much greater average cover (9.2%, as compared to 4.3% in chestnut oak and 3.2% in red maple). *Hypericum punctatum* Lam., *Geranium maculatum* L. and *Smilacina racemosa* (L.) Desf. were common herbs in the oak-hickory plots, but were rarely found in the other forest types (Table 3).

Red Maple Forests. The third main group of plots identified by TWINSPAN was distinguished by the very low relative abundance of oaks and the high relative abundance of red maple (Table 1). Sugar maple and white pine are the major codominants in this red maple forest type. Structurally, these plots were distinguished by very high densities of saplings and seedlings and by a high shrub cover relative to the other forest types (Tables 2, 4). The sapling layer was dominated by red maple, ironwood, and sugar maple. Red maple seedlings made up 38% of total seedling density. The most distinctive shrubs were species of *Rubus*; otherwise the shrub layer was very similar to the oak-hickory communities (Table 2). Total herbaceous cover was the highest of the three forest types (39.9% average cover, compared to 29.4% for oak-hickory and 12.8% for chestnut oak), but herb species diversity was lower than in the oak-hickory plots. *Aster divaricatus* L., *Veronica officinalis* L. and *Potentilla simplex* Michx. occurred with high frequency in this forest type, but were also relatively common in the other forest types. *Achillea millefolium* L. was encountered commonly in the red maple plots, but occurred rarely in the other forest types (Table 3).

Environmental Characteristics of the Major Forest Types. Overall, the three major forest types showed few significant differences in mean environmental conditions, in part because of the wide range of conditions found within each group (Table 5). Observed differences were related primarily to site topography. Chestnut oak forests tended to occur at higher elevations on the steepest, rockiest sites (Table 5). The importance value of chestnut oak, the dominant tree species in these stands, was significantly higher on upper and mid-slope topographic positions than on lower slopes and in local depressions (Tukey's Studentized Range Test, $P < 0.05$). Chestnut oak stands codominated by hemlock tended to occur on particularly steep (mean slope of 14%) east facing slopes (6 of 8 stands in the random sample). Several of these stands, including those with the largest (>50 cm DBH) and

Table 5. Environmental conditions (means and ranges) for the three upland forest types. *P* values are for one-way ANOVA F tests for differences among the means for the three forest types.

	Chestnut oak forests	Oak-hickory forests	Red maple forests	*P* value
Slope (°)	10.8 (0–35)	10.2 (0–37)	7.0 (0–17)	n.s.
Exposed bedrock (% of stands)	67	38	23	<0.01*[1]
Litter depth (cm)	3.40 (0.8–10.3)	2.33 (0.3–5.4)	3.03 (1.8–4.9)	0.04*
Mineral soil pH	4.65 (4.2–5.3)	4.58 (4.0–5.4)	4.53 (4.1–5.5)	n.s.
% organic matter	11.6 (6.6–18.3)	12.0 (5.6–20.1)	13.6 (8.1–21.4)	0.11
Ca (mg/kg)	540.3 (21–2462)	390.6 (70–2865)	635.1 (54–3867)	n.s.
K (mg/kg)	117.2 (50–214)	117.6 (43–206)	122.0 (59–273)	n.s.
Mg (mg/kg)	59.1 (9–207)	47.9 (11–323)	69.3 (9–378)	n.s.
Mn (mg/kg)	42.8 (5–130)	37.6 (16–113)	37.4 (12–63)	n.s.
Fe (mg/kg)	5.6 (2–12)	6.7 (2–25)	7.6 (3–16)	n.s.
Soil moisture (%)	31.0 (20–37)	28.4 (24–31)	28.4 (24–32)	n.s.
Soil texture				
% sand	42.9 (31–62)	41.2 (36–47)	38.6 (35–42)	n.s.
% silt	34.3 (21–43)	34.3 (32–37)	34.8 (28–40)	n.s.
% clay	22.8 (17–29)	24.5 (21–28)	26.6 (22–30)	0.11
Rock (% cover of bare ground)	5.28 (0–27)	2.90 (0–9)	0.85 (0–7)	0.023*
Elevation (meters)	156.1 (109.7–204.2)	145.6 (125.0–181.4)	152.3 (123.4–205.7)	n.s.

[1] Variance test for homogeneity of the binomial distribution, Snedecor and Cochran 1967: 240–242.

oldest (>200 years) hemlock trees, occurred on the steep lower slope of the southernmost Canoo Hill, bordering on the east branch of Wappingers Creek.

Oak-hickory plots also tended to occur on steep slopes, but with less exposed rock and at significantly lower elevations than chestnut oak stands ($t = 2.0$, $N = 63$, $P < 0.05$). Red maple stands occurred over a wide range of elevations, but were limited mostly to sites with shallow slopes and a minimum of exposed bedrock (Table 5).

Soil texture showed only slight differences among the forest types, with red maple plots having slightly finer textured soils than the other two forest types. There was no significant difference among the three types in average soil moisture during the 1985 growing season (Table 5). There had been a major drought during the previous year, but precipitation was slightly above normal during the period of measurement.

The wide range of concentrations of major cations in the soil of each forest type (Table 5) is presumably due to fine scale heterogeneity in the composition of the glacial till from which the soils are derived. As a result, there were no significant differences among the forest types in cation concentrations, although the red maple stands were generally found on the richest soils and the oak-hickory stands were generally found on the poorest soils.

LAND-USE HISTORY RECONSTRUCTION. Of the total acreage of the more than one dozen farms that included portions of the current forests of the Arboretum, 43% (319 ha) is currently forested, in contrast to 20% (150 ha) in 1875 and 22% (161 ha) in 1865 (Table 6). Given land use patterns in the area in the last century, it is reasonable to assume that all of the land forested in 1875 is still forested. Thus, approximately 54% of the current forests were in cleared agricultural land in 1875.

Table 6. Changes in forest area over time for all parcels currently including some of the Cary Forest (see Fig. 2). Percentages forested are based on U.S. (1865) and N.Y.S. (1875) census data and a recent (1980) aerial photo, except for "woodlots," which were areas repeatedly and specifically mentioned as forest in the 18th and 19th century land records. In the 19th century, "woodlots" were in all cases but one not part of farms (i.e., areas of land largely used for agriculture) listed in part A. "Inferred old woods" are areas of original forest within each farm inferred from field evidence (see text, pp. 110–111). For parcel locations and distribution of inferred areas of old woods, see Fig. 2.

	Inferred old woods (ha)	1865		1875		1980	
		Total area	% forest	Total area	% forest	Total area	% forest
A. Farms							
Bacon	10.3	61.9	15.0	61.5	16.4	61.5	45.0
Badgley	0.0	49.8[a]	0.0	49.8[a]	0.0	49.8	51.2
Conover	7.8	40.1	24.2	42.5	15.3	42.5	18.4
Crear	6.8	30.4	46.7	30.4	26.6	31.7	100.0
Gifford	13.5	80.9	20.0	80.9	12.5	82.0	21.1
Hall	3.6	43.3	12.2	44.1	11.3	45.0	43.6
Henry	6.7	78.1	14.0	75.7	12.3	76.2	12.6
Humphrey	5.5	7.3	72.8	7.3[b]	72.8	7.3	100.0
Knapp	14.9	74.9	24.3	72.0	16.8	69.6	43.4
Lovelace	3.2	34.8	9.2	34.8[b]	9.2	34.8	9.2
Petit	12.7	66.8	21.3	66.8[b]	21.3	66.8	46.9
Saccomanda							
West	17.5	46.5	26.0	54.6	26.0	54.6	88.1
East	7.8	80.9	4.9	80.9	10.0	79.7	28.9
B. Woodlots		38.7	100.0	38.7	100.0	38.7	100.0
C. Total		734.4	22.0	740.0	20.3	740.2	43.2

[a] Area given in census did not match known land records; the latter were used; see text.
[b] 1875 statistics not found; assumed same as 1865.

Of the land listed as forest in 1875, about 26% (38.7 ha) was in small parcels mentioned repeatedly in land records since the early 1800's as permanent woodlots (Table 6). Approximately another 16% (24 ha) was mentioned once as forest in the early 1800's and is at present occupied by stands established prior to 1890. Thus, about 42% of the 1875 forest area (i.e., approximately 19% of current forests) can be considered with reasonable certainty to have never been cleared for agriculture. In all probability, the remainder of the 1875 forests also fall into this category, since agricultural activity in Dutchess County was then at an all time high, and virtually all land which could be cleared for agriculture was in improved farmland (Roberts and Reynolds 1938; see Study Area: Local Agricultural History).

In addition to documenting the history of land clearing within the Cary Forest as a whole, the land records and agricultural statistics provide considerable information about the distribution within the forest of original and secondary forest areas. Original forest areas which can be located with confidence include the following: (1) entire parcels repeatedly and specifically designated as woodlots in the land records (Table 6; Fig. 2); (2) parts of old farms mentioned as woods in the early 1800's and presently containing old trees (Fig. 2); and (3) wooded areas in old farms where the area in closed forest accords more or less precisely with the area mentioned as woods in 1875 (e.g., Conover and Lovelace parcels; Table 6; Fig. 2). These original forest areas tended to be located in the higher and steeper parts of the forest, mostly around the Canoo Hills and on the steep slopes adjoining the east branch of Wappingers Creek (compare Figs. 1, 2).

Except for the Badgley Farm (Fig. 2) for which the agricultural census records show a complete absence of woods in 1875 (Table 6), the historical data are of less direct use in locating areas formerly cleared for agriculture. However, it is clear that the amount of woodland has increased substantially in several parcels since 1875 (e.g., the Hall, Bacon, Knapp and Petit parcels) and some areas which were largely cleared land at that time are now almost entirely covered with trees (e.g., the Crear and Saccomanda-west parcels) (Table 6; Fig. 2).

Field evidence from stone fences and stand ages largely corroborated land-use history determinations based on historical records. Areas identified primarily as abandoned farmland are bounded and subdivided by stone fences and generally contain stands established since 1890, while the reverse is true for areas identified as former woodlots (Fig. 2). In addition, stone fence and stand age data, along with the 1930's aerial photo, helped to distinguish locations of secondary and original forests within old farms where historical data were insufficient to do so. For example, older original forest on the north side of the Bacon parcel (Fig. 2) is clearly divided by a stone fence from younger secondary forests to the south (Figs. 1, 2). Similarly, two small areas of old forest on the northern side of the Crear parcel (Fig. 2) are separated by stone fences from the younger secondary forests which occupy the remainder of the parcel (Figs. 1, 2). The old aerial photo confirmed that areas of young forest in the southern part of the Badgley Farm, and on the west side of the Canoo Hills tract, (parts of the Knapp and Hall parcels) (Fig. 2) could clearly be identified as old fields as late as the middle 1930's. Using field evidence and the aerial photo, similar distinctions were possible for the other old farms.

Based largely on such evidence from the several sources discussed above, we constructed a map showing the most probable distribution of original forests and secondary forests in the study area (Fig. 2). In constructing the map, an appropriately situated stone fence was used in most cases as the most likely demarcation line between areas of young and old forest. Where stone fences were not available, wire fences or rock piles were used when these artifacts appeared, on the basis of field observations, to mark the boundaries of old fields. Undrained swampy areas supporting trees were also mapped as old forest and sometimes appeared to separate former agricultural land on one side from original forest on the other (e.g., in the Saccomanda-west parcel, Fig. 2). In the few cases where there were no obvious anthropogenic boundaries between land use types, we used boundaries inferred from aerial photos and soils maps. Based on soils evidence, a small area of young forest in the southern part of the Saccomanda-east parcel was mapped as woodlot.

A test of the accuracy of the map was provided by the agricultural census data. For virtually all farms providing land use statistics, the amount of land mapped as original forest was reasonably close (i.e., within 4 ha) to the area reported as woodland in 1875 (Table 6).

LAND-USE HISTORY RELATIONSHIPS TO CURRENT VEGETATION. The spatial distribution of the three main forest types was clearly related to the pattern in land-use history described above (Fig. 2). Chestnut oak stands, including those codominated by hemlock, were restricted almost entirely to original forests that were never cleared for agriculture, while oak-hickory and red maple stands were largely restricted to abandoned agricultural land. A few old oak-hickory stands occurred at low elevations, usually just outside of old-fields currently dominated by oak-hickory vegetation. The one old red maple stand was associated with a swamp in the Saccomanda-west farm.

PRESETTLEMENT AND EARLY SETTLEMENT VEGETATION. The land survey records suggest that the forests in the vicinity of the present day Arboretum were dominated by white oak, black oak and hickories throughout the period 1730–1800 (Table 7). These species occur now largely as important components of the oak-hickory forest type. Dominants of the other forest types, including chestnut oak, sugar maple, red maple, white pine, and hemlock, are of conspicuously low importance in the early survey records. By 1780–1800, many of the trees listed in the surveys were described as saplings (Table 7), suggesting that at this time, much of the land being surveyed was already second growth forest.

Discussion. Most modern vegetation studies, based on increasingly sophisticated statistical correlations, emphasize environmental gradients as the major cause of vegetation patterns. The effects of history, less easily quantified and utilized in statistical analyses, are often ignored or assumed to represent a secondary, independent source of variation in vegetation data (Hamburg and Sanford 1986). In contrast, our data provide some quantitative support for earlier, mostly qualitative, studies of northeastern forests which emphasized complicated interactions between land-use history and environment in descriptions of vegetation patterns (e.g., Bromley 1935; Raup and Carlson 1941; Winer 1956; McIntosh 1972).

In broad outline, environmental relationships of plant communities in the Cary Forest are similar to those documented elsewhere in the glaciated section of the oak-chestnut forest region (sensu Braun 1950). As in our study, chestnut oak forests tend to occur on steep, rocky, upper slopes or ridgetops (Raup 1938; Braun 1950; Niering 1953; Spurr 1956). Forests dominated or codominated by hemlock are typically found

Table 7. Percent occurrence of tree species in presettlement and early settlement forests based on a tabulation of witness trees listed in all land records (65 deeds and mortgages) of Great Lots 6, 7, 12 and 13 of the Great Nine Partners Patent prior to 1800. Also given are current percentages of canopy tree species in the present study.

Species	<1760	1761–1780	1781–1800	Entire period (<1800)	Current (1984)
White oak	47.4	30.0	32.0	36.3	4.0
Black oak	15.8	10.0	16.5	15.3	4.1
Red oak	1.8	3.3	4.9	3.7	10.4
Chestnut oak	4.0	—	1.9	2.1	13.7
Pin oak	—	—	0.9	0.5	0.0
Swamp white oak	—	—	0.9	0.5	0.3
Unidentified oaks	15.8	6.7	1.0	3.7	—
All oaks	73.7	50.0	59.2	62.1	32.5
Hickory[a]	12.3	10.0	8.8	10.0	8.9[b]
Elm	1.8	20.0	3.9	5.8	6.6
Maple	3.5	10.0	2.9	4.2	29.6[c]
Willow	—	—	5.8	3.2	0.0
Ash	1.8	3.3	2.9	2.6	3.4
Hemlock	—	3.3	2.9	2.1	7.2
Poplar	1.8	—	2.9	2.1	0.1
Pine	3.5	—	1.9	2.1	9.2[d]
Chestnut	1.8	—	1.9	1.6	0.0
Others	—	3.3	6.8	4.2	2.5
Total # of witness trees	57	30	103	190	
% saplings	28.1	26.6	47.5		

[a] Usually given as walnut, but probably hickory (e.g., Winer 1956, Whitney and Davis 1986).
[b] *Carya glabra, C. ovata, C. tomentosa* (Poir.) Nutt.
[c] *Acer rubrum, A. saccharum.*
[d] *Pinus strobus, P. resinosa* Ait.

on mesic north or east facing slopes, often near streams (Braun 1950; Niering 1953; Niering and Goodwin 1962). Hemlock may be confined to such habitats by a requirement for high levels of soil moisture or by the greater incidence of past fires in drier habitats (Winer 1956; Hemond *et al.* 1983). Forests dominated by white oak were apparently prevalent at lower elevations prior to European settlement (Bromley 1935; McIntosh 1962, 1972; Russell 1981) and occur presently, as in our study, in somewhat less rocky midslope or lower slope habitats (e.g., Niering 1953; Goodlett 1954; though see Raup 1938). Finally, our data also showed some tendency for red maple stands to occur on finer textured soils on shallow slopes; this is consistent with the general observation that red maple is most important in swamps (Bromley 1935) or in other areas of impeded drainage (e.g., Hicock *et al.* 1931; Goodlett 1960; Lorimer 1984).

Despite tendencies toward similar relationships between vegetation and environment as have been observed in other northeastern forests, quantitative environmental differences among the vegetation types in the Cary Forest were notably minor. It is possible that environmental variables which we did not measure (e.g., other soil nutrients or soil depth) are more important determinants of vegetation pattern than the variables we did measure. However, two factors associated with land-use history may also have contributed to variability in vegetation-environment relationships: (1) Post-agricultural landscapes are largely devoid of competition from established trees. Also, stochasticity in seed dispersal and establishment is enhanced by a scarcity of seed trees and reduced opportunities for bird dispersal of seeds (McDonnell and Stiles 1983). Together, these factors may allow some plants to establish in environments where they would otherwise be unable to do so, thus blurring environmental distinctions among species and communities. This effect may have been important in reducing environmental differences between oak-hickory and red maple, the two communities now found on abandoned agricultural lands; and (2) different kinds of land use may have selected for different kinds of plant communities, regardless of the environment. This possibility is distinctly suggested by the strong spatial association of chestnut oak stands with original forests, and oak-hickory and red maple stands with abandoned agricultural lands. Differences between oak-hickory and red maple may also be due to cultural selection.

Of the three major community types, the current importance of the red maple type is most likely due to past effects of agricultural land-use history. The general absence of oaks and hickories and the codominance of maples and pines which distinguishes this forest type is very different from any upland forest type existing prior to European settlement either locally, or in the oak-chestnut forest region as a whole (Bromley 1935; Deevey 1939, 1943; Braun 1950; Russell 1981; Whitney and Davis 1986). On the other hand, red maple and white pine are well known as prolific invaders of abandoned agricultural land and often dominate first-generation forests developing on old fields (Bromley 1935; Raup and Carlson 1941; Winer 1956; Hemond *et al.* 1983; Whitney and Davis 1986). *Achillea millefolium,* a common herb in this forest type, is a well known old-field species in northern New Jersey (Bard 1952). Species of *Rubus,* also common in the understory of the red maple forests, are also largely associated with secondary forests (Whitney and Foster 1988), and with the latter stages of old-field succession (Bard 1952), and occur rarely in primary woodland (Whitney and Foster 1988).

Because of the relatively high abundance of white pine in this forest type, the red maple forests in the Cary Arboretum strongly resemble old-field white pine forests described in detail at the Harvard Forest (Raup and Carlson 1941; Spurr 1956; Goodlett 1960 and references therein) and common throughout central New England (Raup 1940). In contrast to the typical situation described at the Harvard Forest, where red maple and other hardwoods succeeded pine following cutting of the latter (or destruction of original old-field stands by the 1938 hurricane), red maple and pine appear to have originated contemporaneously at the Cary Arboretum following abandonment of farmland at the end of the last century (J. S. Glitzenstein, unpublished tree age data). Enhanced dominance of red maple and other light-seeded hardwoods in first-generation old-field pine stands has been attributed to the combination of a limited seed source for pine (Spurr 1956; Winer 1956) and the exposure of bare ground just prior to field abandonment, which provides a suitable seed bed for the light seeds of these hardwoods (Spurr 1956). In the Cary Arboretum, stands dominated by pine and red maple may have originated on formerly cultivated fields, where the availability of a mineral soil seedbed and reduced competition from perennial grasses and forbs (Beckwith 1954) may have favored red maple establishment. Cultivation would also have prevented the accumulation of hardwood sprout regeneration, possibly explaining the virtual absence of the less prolific and more poorly dispersed oaks and hickories from the red maple forest type. In the Cary Forest, cultivated fields most likely occurred on moister, less rocky sites were maple would have been most favored in any case. Thus, a combination of environmental and historical factors may explain the current abundance and distribution of the red maple type in the old-field forests of the Cary Arboretum.

Red maple forests resemble the old-field white pine forests of central New England and show little resemblance to original forest vegetation in the oak-chestnut forest region. In contrast, oak-hickory forests, although also presently confined to old fields at the Cary Arboretum, are similar in tree species composition to examples of old growth forests in this forest region (Nichols 1913; Bromley 1935) and to data on presettlement vegetation from this (Table 7) and other studies (Winer 1956, especially in the southern part of his study area; Russell 1981; Lorimer 1984; Whitney and Davis 1986). In the Cary Arboretum, original oak-hickory forests probably occurred on lower elevation sites which were cleared for agriculture at an early date. Following agricultural abandonment, these sites apparently followed the typical successional pathway in southern New England (Lutz 1928) and northern New Jersey (Bard 1952), in which early successional dominants red cedar (note the occasional occurrence of this species in the understory of the oak-hickory forests; Table 1) and gray birch (decomposing examples of which were occasionally encountered on the forest floor; J. S. Glitzenstein personal observation) were "gradually replaced by other hardwoods, notably white, black and red oak, hickory, red maple and black birch" (Raup 1940: 267). In the Cary Forest, this type of succession, leading back toward the original forest dominants, may have occurred mostly on drier old-field sites naturally more favorable for regeneration of white oak, black oak and hickories. These "poorer" sites were also more likely to have been pastured than cultivated, thus allowing for the development of considerable sprout regeneration of oaks and hickories which may have been released as the cattle were finally removed (Den Uyl 1938, 1961).

The previous discussion suggests that the present occurrence of oak-hickory vegetation on old fields at the Cary Arboretum may reflect coincidence between past land-use patterns and natural habitat boundaries rather than a direct effect of land-use history in selecting for certain species of trees. Similarly, the association of chestnut oak forests with former woodlots is probably also due more to historical coincidence than to direct effects of land use on vegetation. Steep, rocky, upper slope sites where these forests occurred were of little use in agriculture and would have been used primarily for production of fuelwood, tanbark, and charcoal (Winer 1956; Cronon 1983). Though chestnut oak probably always predominated in these areas (Bromley 1935; Spurr 1956; Robichaud and Buell 1973), frequent cutting would have maintained or even enhanced the dominance of this species because of its superior ability to sprout from cut stumps (Ross *et al.* 1986). McIntosh (1972), for example, found that chestnut oak became more important after logging on the lower slopes of the Catskill Mountains than it had been in the presettlement land survey data for the area. Such trends may also help explain increased chestnut oak abundance in the current forests as compared to the presettlement land surveys of the Cary Arboretum area. Another explanation may be that early surveyors did not distinguish chestnut oak from white oak in witness tree data (e.g., Russell 1981), though this did not seem to be the case in surveys of nearby tracts in Dutchess County (JSG personal observation). Also, sites dominated by chestnut oak and chestnut may have been underrepresented in early land survey records because these sites typically occurred on poor soils in inaccessible areas, and were therefore avoided by early farmers (Russell 1981).

Although the major tree species of the oak-hickory and chestnut oak forests may be the same as in the presettlement forests, a number of differences between these two forest types in understory species composition do appear to reflect the direct effects of land-use history. In the chestnut oak type, major understory species such as striped maple, maple-leaved viburnum and the herbs *Aralia nudicaulis* and *Mitchella repens* are typically associated with primary woodlands (Whitney and Foster 1988). In contrast the composition of understory vegetation in the oak-hickory type strongly reflects an old-field history. Gray dogwood, a dominant shrub in oak-hickory stands, is a common old-field shrub in northern New Jersey (Bard 1952), and is the most common shrub of extant old fields in the Cary Arboretum (C.D. Canham, unpublished data). Red cedar, a dominant old-field tree (Lutz 1928, Bard 1952) occurs occasionally in the understory of the oak-hickory stands, but is entirely absent from the chestnut oak forests. *Hypericum punctatum,* one of the distinctive forbs in the oak-hickory forests, is typically quite abundant in the intermediate stages of old-field succession in New Jersey but is absent from mature original woodland (Bard 1952). The high frequency of exotic agricultural weeds, and the abundance and diversity of the herbaceous component in general, also clearly reflect the old-field origins of the oak-hickory forests (Bard 1952).

In addition to explaining some of the compositional differences between the oak-hickory and chestnut oak forest types, land-use history differences may also help to explain some of the structural and environmental differences associated with these vegetation types. Thus, the stratified canopy structure of the chestnut oak stands is very typical of the development of largely even-aged stands after logging (Oliver 1978), and is consistent with the prevailing mode of forest regeneration in heavily used woodlot stands (Winer 1956). In contrast, less distinct stratification in the oak-hickory stands suggests a very protracted period of stand filling consistent with the presumed origin of these stands as old pastures, in which woody plant establishment would have been retarded by cattle herbivory and strong competition from established grasses and perennial forbs (Den Uyl 1938, 1961; Beckwith 1954; Buell *et al.* 1971). Reductions in soil nutrients and litter associated with severe erosion in these old pastures (Secor *et al.* 1955) may also have retarded the rate of succession and contributed to the lower basal area and more open canopies of these stands (Tilman 1988). Limited overstory competition may, in turn, help to explain the persistence of many typical old-field species in the understory of the oak-hickory forests.

In conclusion, we suggest that the result of land-use history in the forests of the Cary Arboretum has been to weaken "the broader control of the forests by climate and soils" (Whitney and Davis 1986: 70), but not to obscure it entirely. The association of the major forest types with different land-use practices appears to reflect both the direct effects of land use on current vegetation and a close tracking by farmers of environmentally determined boundaries between the major forest types. Probably the most notable effect of agricultural history has been to favor regeneration of pine and maple. These species, which currently contribute almost 40 percent of canopy trees, made up only 6 percent of the witness trees for surveys done prior to 1800 (Table 7). Relative importance of white pine should decline with time, as old-field trees die and are replaced by hardwoods (Raup and Carlson 1941; Spurr 1956; Goodlett 1960). However, the relatively greater shade tolerance of red maple than "climax" oaks suggests that enhanced importance of red maple, due in part to land-use history, is likely to remain a long-term feature of Hudson Valley forests (Lorimer 1984).

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