Hardwood Forest Vegetation of the North Carolina Piedmont

by

Robert K. PEET and Norman L. CHRISTENSEN

Contents

1. Introduction

Historically, considerable attention has been given to the woody vegetation of the North Carolina piedmont, particularly with respect to forest development. Indeed, revegetation following cropland abandonment on the piedmont has served as a model for studies of secondary seccession in general (see ODUM 1969, CONNELL and SLATYER 1977). Research on herbaceous vegetation in this region has also primarily been related to succession (CRAFTON and WELLS 1934, BILLINGS 1938, OOSTING 1942, KEEVER 1950). Relatively little attention has been given to the herb understory or field layer composition of late succession and climax forests. Whereas the floristics of particular sites

have been described (BATSON 1952, EBERT 1957, BEARD 1959, KORNAS 1965, DAYTON 1966, GIBBON 1966, NEMETH 1968, SECHREST and COOPER 1970, WHIGHAM 1971, BORN-KAMM 1975), no studies have examined floristic variation over a wide range of site conditions for the southeastern piedmont.

In this report we outline the results of a study of hardwood forest vegetation of the North Carolina piedmont. A more comprehensive monograph including floristic tables and details of woody plant composition will be published elsewhere. Our goals here are (1) to characterize patterns of understory (< 1 m tall) composition of mature hardwood forests, (2) to demonstrate the relationships of these patterns to environmental factors, and (3) to show the relationships of these patterns to variation in dominant woody vegetation.

Acknowledgements

2. Environment

The climate of the North Carolina piedmont is warm temperate (Figure 1; moist mesothermal, Cfa, KöPPEN 1936). Rainfall varies between 1000 and 1250 mm per year while mean annual potential evapotranspiration is approximately 750 mm per year (NELSON and ZILLGITT 1958). Although rain may occur year-round, July and August are wettest months owing to convectional storms. The frost-free period averages 210 days and winters are comparatively mild (KOPEC and CLAY 1975) with temperatures rarely dropping below -15°C.

The piedmont varies in elevation from 500 m near the Blue Ridge Escarpment to less than 75 m in stream valleys near the Coastal Plain Fall Zone. Within our study area elevation ranged from 75 m to 230 m.

As we shall show, the nature of the parent material influences soil characteristics (LEE 1955, STUCKEY 1965, PERKINS et al. 1973) and, consequently, vegetation patterns. The piedmont is underlain by a variety of igneous, metasedimentary, and metaigneous rocks ranging in age from late Precambrian to

Figure 1. Climate diagram for Raleigh, North Carolina (modified from WALTER and LIETH 1967).

Ordovician (HATCHER 1972). During the Triassic, faulting along the eastern piedmont created grabens and rift valleys which collected considerable quantities of sediment. A system of such Triassic basins containing clastic sediments, primarily clays, sands, and silts, extends for 2500 km along the eastern piedmont. Late Triassic and early Jurassic dikes and intrusions of acidic and basic maffic rocks are common throughout the piedmont. Because the acidic (high quartz) rocks are resistant to weathering, they often form or at least cap the higher hills (200-250 m) in this area. Otherwise, owing to the antiquity of the piedmont landscape the underlying rocks have weathered to a thick saprolite, often over 6 m deep (CADY 1950).

Piedmont soils are predominantly Ultisols (SOIL SURVEY STAFF 1975, DUNN 1977), or, alternatively, red-yellow podsols (LEE 1955), reflecting the age of the

16

landscape. Such soils are characterized by conspicuous profile development with considerable clay accumulation in the B horizon. However, despite long periods of weathering under similar environmental conditions, striking soil differences can be traced to subtle differences in lithology. For example, a slightly higher magnesium content can result in a montmorillonite clay layer with impeded drainage rather than a well-drained soil with kaolinite (CADY 1950). In addition, soils developing from acidic crystalline rocks or Triassic sediments generally have low concentrations of divalent cations (exchangeable Ca<1 ME/100g soil) whereas soils weathering from more basic rocks have higher concentrations of such cations (exchangeable Ca≈4-8 ME/100 g soil).

There is considerable variation among soils developing from one parent rock type, largely as a consequence of variation in drainage and weathering. For example, on well-drained slopes over Carolina "slate" (predominantly volcanic rocks) soils typically have a well developed A horizon underlain by a comparatively permeable kaolinite clay subsoil. In contrast, just as increased magnesium content can lead to increased formation of montmorillonite clays, the reduced drainage on flat sites retards clay weathering resulting in a preponderance of montmorillonite clays and a shallow A horizon. The montmorillonite gives the subsoil a plastic, impermeable character which further impedes water movement and root growth. Similar soil catenas occur over other parent rocks.

3. History of human influence

Woodland and Paleoindian peoples inhabited the North Carolina piedmont from at least 10,000 BP up to 500-1000 AD (HUDSON 1976). From this period until European colonization (ca. 1700 AD) several Indian nations including the Sioux, Tuscororas, and Cherokees, occupied the piedmont. While little is known of the specific impact these people had on the vegetation, many tribes practiced a form of shifting agriculture, which over the period of a millenium undoubtedly altered the vegetation of the alluvial bottomlands they farmed (HUDSON 1976, HATLEY 1977). Perhaps more important was the Indian's use of fire. Nearly all commentaries of early explorers in this region mention the use of fire by Indians, a practice which discouraged woody growth, encouraged herbaceous

production and thereby increased carrying capacity for game animals (HATLEY 1977). The result of this practice was that forest understories were open, perhaps even savanna-like, and fire-resistant tree species such as *Quercus alba* increased in importance (KOMAREK 1974, CHRISTENSEN 1979).

Soon after European colonization land clearing began on the piedmont on a grand scale. By the mid-nineteenth century nearly all arable land on the piedmont was under cultivation (POWELL 1975). Economic factors and poor land management forced abandonment of much farmland during the latter half of the nineteenth and early part of the twentieth century. Today, much of the piedmont landscape is in some stage of recovery from this abandonment.

While land too rocky or otherwise unfavorable for cultivation has remained in hardwood forest, this land has not been spared   disturbance. Up to and through the early twentieth century, wood was the primary energy source in the Carolinas and many hardwood forests show the effects of long periods of selective cutting. During the late nineteenth century such selective cutting was intensified to provide wood for a growing furniture industry and for railroad ties (PINCHOT and ASHE 1897). The result is that today no old-growth forests remain on the piedmont although scattered large oaks, often in excess of 300 years of age, persist in many of the woods which were selectively cut. In addition to cutting, grazing of both cattle and hogs has until recently been a chronic source of forest disturbance.

4. Study area and methods

In our discussion we shall use data collected from 105 forest stands with minimal evidence of recent disturbance and in which hardwoods account for over 80 % of the total cover and basal area. Most of the samples were located in various parts of the Duke University Forest in Orange and Durham Counties, North Carolina. In order to assure adequate coverage of all site conditions, additional stands were sampled in neighboring forests belonging to the University of North Carolina and in Umstead State Park. Nearly all piedmont soil series and parent materials were represented.

Within each stand, a permanent 0.1 ha (20 x 50 m) sampling unit was established. All trees (<1.25 cm dbh) were tallied within this area. Sapling and shrub

Table 1. Average soil characteristics of recognized forest types.

Forest Group	pH	Organic (%)	Ca (ppm)	Mg (ppm)	K (ppm)	Σ Ca Mg K (me/100g)	P (ppm)	Water Storage (1-15 bar)
Alluvial	5.3	5.1	1036	195	57	6.92	4.0	6.7
Swamp	4.8	8.1	489	165	68	3.97	0.9	12.3
Montmorillonite	4.1	5.7	136	32	42	1.05	3.5	5.9
Mesic Eutrophic	5.2	7.7	782	177	84	5.58	5.4	7.2
Bluff	4.0	8.2	100	23	58	0.84	3.2	11.0
Monadnock	4.3	6.6	59	20	49	0.59	2.4	11.5
Oligotrophic	4.1	6.3	128	27	52	0.99	2.6	13.8
Dry Eutrophic	4.8	8.0	655	121	64	4.42	4.7	6.7
Dry-mesic Eutrophic	5.3	6.0	533	139	65	3.97	3.1	6.5
Mesic Mesotrophic	4.8	6.4	314	70	64	2.31	2.7	10.0
Dry Mesotrophic	4.5	6.7	154	44	55	1.27	2.6	11.0

stems (<1 m tall, <1.25 cm dbh) were recorded within a 4 m wide transect traversing the length of the plot down the center (a 20 % subsample). Species specific cover of leaf area below 1 m in height was recorded for twenty-five 0.5 x 2 m contiguous quadrats running the length of the center transect. We shall refer to all plant leaf area below one meter in height as understory. All species present in the 0.1 ha sample but absent from the 0.5 x 2 m subquadrats were recorded. Importance values (0-100) for understory species were calculated as the average of relative cover and relative frequency. Species present but not occurring in the subquadrats were assigned importance values of 0.01.

In addition to vegetation samples, several environmental factors were measured. Information on slope, aspect and topographic position was gathered at the time of sampling. Five soil samples were collected from each stand (upper 10 cm of mineral soil) and analyzed for exchangeable calcium, magnesium, potassium, and phosphate. Organic matter content (loss on ignition), pH and water retention at 1 and 15 bars were also determined for each sample (see Table 1).

To determine relationships between vegetational trends and site conditions, understory importance values were transformed ($\log_{10} x+1$), double standardized (BRAY and CURTIS 1957) and ordinated using Reciprocal Averaging (RA; HILL 1973, 1974). Because it does not assume monotonic linear responses of species along environmental gradients, this technique is preferable to most other ordination procedures, such as Principal Components Analysis. GAUCH et al. (1970)

have shown RA to be equally as effective as nonlinear multidimensional scaling (FASHAM 1977, PRENTICE 1977) but computationally more efficient. An additional advantage of Reciprocal Averaging technique is that it simultaneously creates an ordination of species and stands. By comparing axis scores for particular species, it is possible to identify diagnostic species or combinations of species for particular parts of the stand ordination. Analyses were done by progressive fragmentation of the data set; that is, after initial ordination in 2 or 3 dimensions, distinctive groups of stands, based on environmental correlations and canopy dominants, were removed and the residual stands reordinated. In this way, the impact of the initially observed factor on subsequent analysis was greatly reduced. The specifics of this approach are described in PEET (1979).

5. Results

5.1. *First ordination*

Stand scores for the first and second axes of an ordination of all 105 stands are displayed graphically in Figure 2. Although most stands are aggregated in the upper right corner of this ordination, several stand groupings can be identified as corresponding to particular site conditions. Those stands with low to intermediate second axis scores (bottom half of the graph) occur on sites where the soil is periodically saturated with water. The first axis scores for these stands correspond to site hydrologic features. Stands with low first axis scores are primarily alluvial or riparian forests, characterized by well defined drainage and abundant moisture and nutrients. Stands with intermediate first axis scores are more swamp-like; that is often with saturated soils, but with less clearly defined drainage patterns. The right side of this continuum contains stands which occur on upland sites but which have shallow, montmorillonitic subsoils that impede drainage. These are soils of alternating, but extreme moisture conditions. Following wet weather the soil is saturated and roots must endure anaerobic conditions. Because the clay layer severely restricts water and root penetration, once the shallow surface horizon dries out, drought conditions prevail.

The dominant trees in stands in alluvial forests include *Liquidambar styraci-flua*, *Liriodendron tulipifera*, *Platanus occidentalis**, *Carpinus caroliniana**, *Fagus grandifolia*, *Ulmus rubra**, *Acer rubrum*, and *Fraxinus pennsylvanica*. Broader floodplains adjacent to the study area and transitional to coastal plain vegetation contain a number of codominating oaks including *Quercus lyrata*, *Q. michauxii*, and *Q. falcata* var. *pogodaefolia*. The narrow forest fringe along most stream edges of the region is dominated by such light-demanding species as *Acer negundo**, *Betula nigra**, *Platanus occidentalis**, and *Alnus serrulata*. Shrubs and lianas are a significant component in the understory of these alluvial communities comprising in excess of 40 % of the ground cover (plants <1m tall). Among the lianas, the introduced *Lonicera japonica** is most important, occurring with high cover values at each site, thereby greatly re-ducing the cover of many native species. Other important shrubs and vines in-clude *Rhus radicans*, *Parthenocissus quinquefolia*, *Sambucus canadensis**, *Lin-dera benzoin**, *Aesculus sylvatica**, *Viburnum rafinesquianum*, and *Euonymus americana*.

The alluvial forests are among the most diverse studied here, with an average of 17 tree, 17 shrub and 42 herbaceous species per 0.1 ha. Among the herbs *Boehmeria cylindrica**, *Clematis virginiana**, *Polystichum acrostichoides**, and *Botrichium virginianum** occurred in all stands, while *Microstegium virmineum** and *Uvularia sessilifolia** had the highest cover values. The rich flora and high productivity is not only a consequence of favorable hydrologic condi-tions, but also high levels of available soil nutrients. For example, exchange-able cations (Ca + Mg + K) averaged 6.9 ME/100 g soil, nearly three times the average for the other forest types (Table 1).

Species diversity in the more poorly drained swamp forests is somewhat lower than in the alluvial forests with an average of 15 tree, 13 shrub, and 31 herb species. Among the dominant trees *Liquidambar styraciflua**, *Liriodendron tulipifera*, *Fraxinus pennsylvanica**, *Ulmus rubra*, and several species of *Carya* and *Quercus* are shared with the alluvial forests. In addition, species such as *Quercus phellos**, *Ulmus alata*, *Ilex decidua*, and *Ilex ambigua* are common. Vines and trailing plants such as *Lonicera japonica*, *Rhus radicans**,

---

Asterisks (*) designate species whose distributions are modal indicating they attain their highest constancy in this type.

Parthenocissus quinquefolia*, Campsis radicans*, and *Smilax rotundifolia**
account for nearly 50 % of the understory cover. Herb diversity is reduced one
third from alluvial woods, and herbs account for only 8 - 9 % of the total
understory cover compared to 35 % in alluvial forests. Levels of exchangeable
cations are equivalent to those of more fertile, upland forests, but lower
than in alluvial forest soils. The water holding capacity of these soils is,
however, higher than that of alluvial soils, thus reflecting higher clay con-
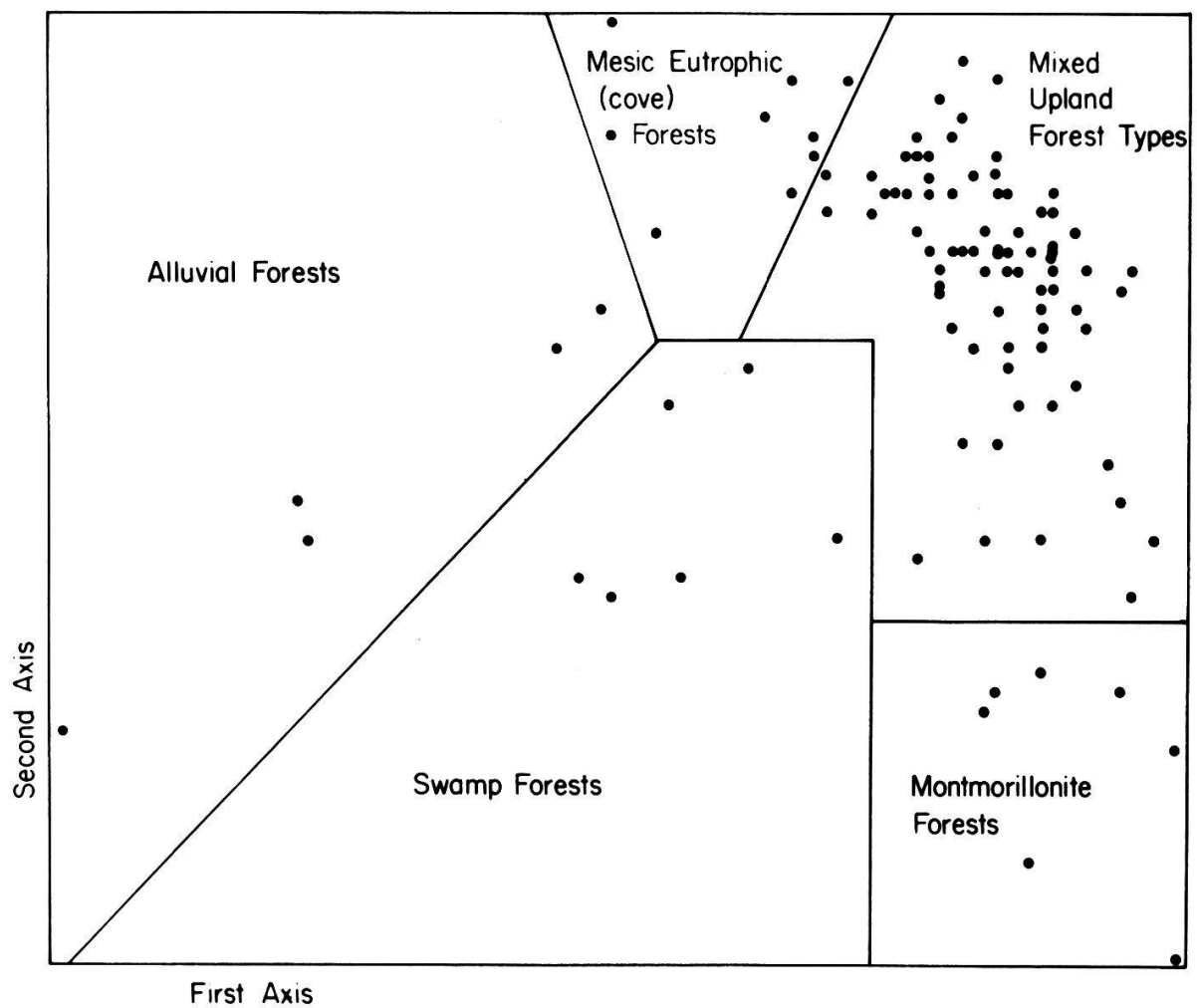tent. These forests show considerable similarity to the forests of broad

Figure 2. First reciprocal averaging ordination indicating Alluvial, Swamp,
and Montmorillonite Forest Types.

22

floodplains along slow moving streams to the east of the study area. Among
the more distinctive herb species with high constancy are *Galium obtusum**,
Arisaema triphyllum*, *Carex rosea**, *C. blanda**, *C. complanata**, *Solidago
caesia**, and *Festuca obtusa**.

At sites with montmorillonitic subsoil, species diversity is further reduced,
particularly in the shrub-liana category (only 9 per 0.1 ha). Among the do-
minant tree species shared with the swamp forests are *Quercus phellos*, *Ulmus
alata*, *Fraxinus* spp., *Carya ovata*, and *Quercus stellata**. Other dominants in-
clude *Quercus marilandica**, *Diospyros virginiana**, *Juniperus virginiana*, *Pinus
taeda*, and *P. echinata*. *Vaccinium stamineum*, *V. vacillans*, and *Viburnum rafin-
esquianum* account for most of the shrub cover. Patches of *Smilax rotundifolia*,
Rhus radicans, and *Vitis rotundifolia* are associated with swales. Although
herb diversity is not much reduced from the swamp forests (27.4 per 0.1 ha),
there are relatively few shared species. Among the more common and diagnostic
herbs are *Andropogon* spp.*, *Aster solidagineus**, *Danthonia spicata**, *Hieraceum
venosum**, and *Hypericum hypericoides**.

In addition to shallow soils and variable moisture conditions, the montmoril-
lonite soils are generally infertile. Exchangeable cations total only 1.0 ME/
100 g and the mean pH is 4.1. Consequently, these areas are rather unproduc-
tive and even mature forests on such soils have a characteristic low stature.

5.2. *Second ordination*

Figure 3 represents a reordination of the stand data after deletion of the
alluvial, swamp and montmorillonite stands. On this graph, stands with both
low first and second axis scores are those which occur in low, moist canyons
and coves. In addition to favorable moisture conditions, these sites contain
ample nutrients for plant growth which derive from upslope leaching. We shall
refer to these sites as mesic eutrophic forests, or alternatively cove fo-
rests because of their similarity to the cove forests described from the
southern Appalachians (c.f. WHITTAKER 1956). Cove forests are also apparent
on the first ordination, albeit somewhat less distinctively, where they can
be seen to be intermediate in composition between the wet, nutrient rich
alluvial forests and the mixed upland *Quercus* forests.
The cove forests match the alluvial forests in total species per 0.1 ha (75)

and, as might be expected, share many species with these communities. The dominant trees characteristic of cove forests include *Fagus grandifolia**, *Liriodendron, Quercus alba, Q. rubra, Fraxinus americana,* and *Acer saccharum* var. *floridanum** in the overstory, and *Cornus florida, Acer rubrum, Cercis canadensis, Prunus serotina, Ostrya virginiana**, and *Carpinus caroliniana* in the understory tree layer. Shrubs account for 29 % while herbaceous species comprise 25 % of the understory (<1 m tall) cover. Shrub species include four species of *Viburnum, Euonymus americana, Aesculus sylvatica,* and *Sambucus*
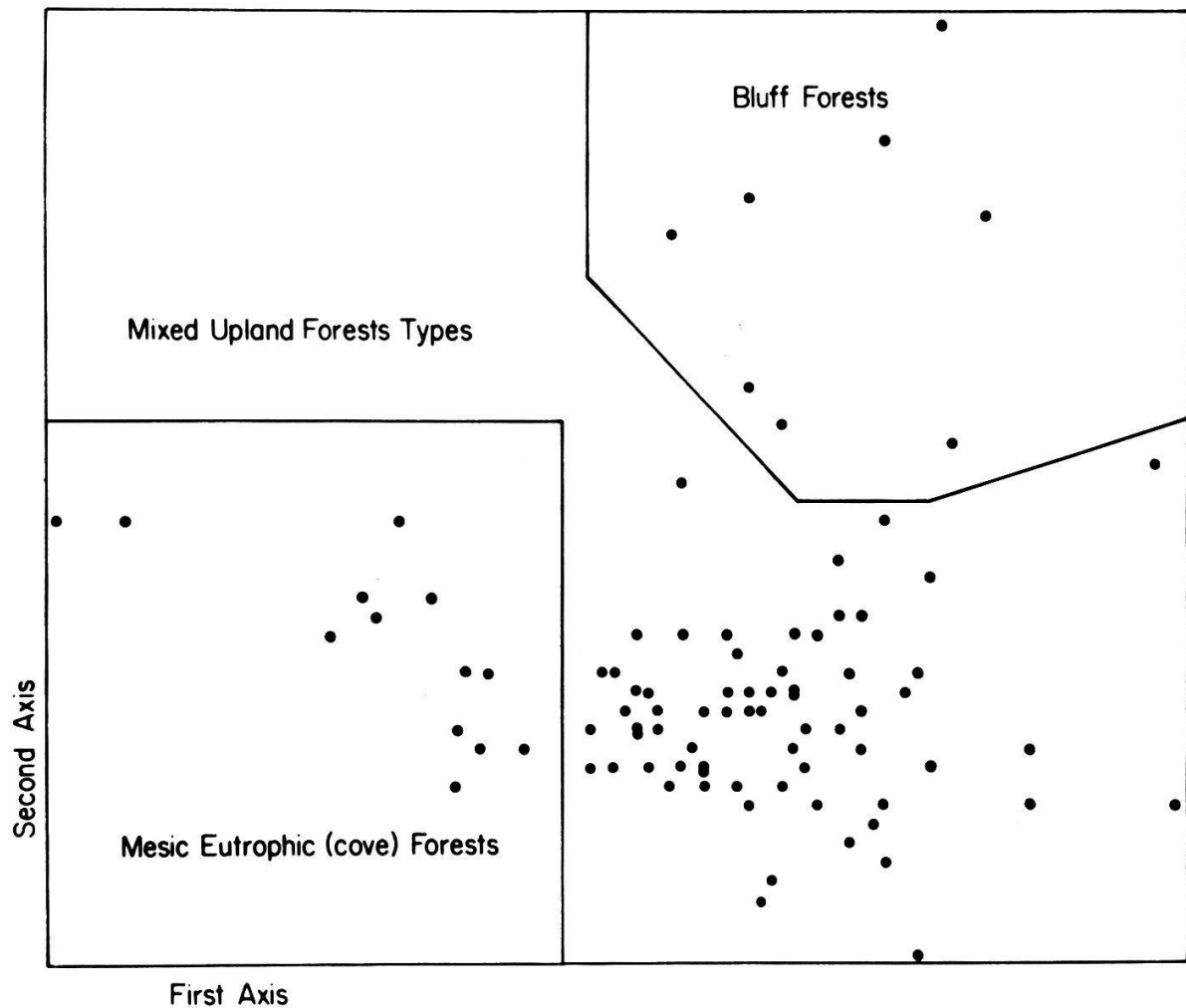

Figure 3. Second reciprocal averaging ordination indicating Mesic Eutrophic and Bluff Forest Types.

24

canadensis. Among the herb species are many which typify cove forests in the Appalachians including *Smilacina racemosa**, *Tiarella cordifolia**, *Carex blanda*, *Adiantum pedatum*, *Phryma leptostachya**, *Trillium catesbaei*, *Chamaelirium luteum**, and *Cimicifuga racemosa** as well as such uncommon species as *Cypripedium calceolus** and *Panax quinquefolium**. Floristically, the mesic eutrophic or cove forests are intermediate between the Appalachian cove forests and the Beech-Magnolia forests of the southeastern coastal plain described by QUARTERMAN and KEEVER (1962). The unity of these geographically distinct types is doubtless to be found in the abundance of moisture and nutrients of the sites they occupy.

Bluff forests delimited in the upper left of the second ordination are distinctive in several respects. The dominant life forms are low trees and shrubs, the herbaceous flora being rather depauperate (only 18 species per average 0.1 ha). Dominant trees include *Oxydendrum arboreum*, *Acer rubrum*, *Quercus alba*, *Q. coccinea*, *Q. prinus*, and *Fagus grandifolia*. *Amelanchier arborea** and *Sassafras albidum* have their modal abundances in these forests. More distinctive is the well developed shrub stratum which includes *Vaccinium vacillans**, *V. stamineum*, *Rhododendron nudiflorum**, *R. catawbiense**, *Hamamelis virginiana**, *Kalmia latifolia**, *Viburnum acerifolium*, and *V. rafinesquianum*. In rockier places *Kalmia* and *Rhododendron* may form dense thickets 3 m high. Among the herbs, a group with typically little cover in these forests, *Hexastylis minor**, *Chimaphila maculata*, *Polygonatum biflorum*, and *Epigaea repens** are the most common.

The bluff forests are characterized by shallow, acidic (pH = 3.9), nutrient poor soils, but a cool, mesic microclimate owing to their northern exposures and proximity to streams. Together, these conditions provide an environmental setting less characteristic of the piedmont than of the mountains 200 km to the west. Consequently, a number of typically mountain plants not found elsewhere on the piedmont occur in the bluff forests. These include *Asplenium montanum**, *Cornus alternifolia**, *Galax aphylla**, *Gillenia trifoliata**, *Iris cristata**, *Kalmia latifolia**, and *Rhododendron catawbiense**. These forests are also home to surviving sprouts of the American chestnut, *Castanea dentata**, which was generally uncommon in the piedmont. Outside the study area but in neighboring counties disjunct populations of *Pinus strobus* (BEARD 1959) and *Tsuga canadensis* (OOSTING and HESS 1956) exist in bluff habitats, perhaps

as relicts from the last glacial period (HARDIN and COOPER 1967).

5.3. Third ordination

The result of reordination of the residual stands after removal of mesic eutrophic and bluff forests is presented graphically in Figure 4. Included are upland stands classified by OOSTING (1942) as oak-hickory forest, the putative climax type for this area. At the top of this graph (high second axis scores) are segregated hardwood stands occurring typically on monadnocks or isolated high hills, characterized by nutrient poor, acid crystalline rocks (andesite, pyrophyllite, quartz, quartzite). These were the most nutrient poor sites sampled with exchangeable cations averaging 0.5 ME/100 g soil. Because the parent rock is resistant to weathering, these sites often typify ridges and hill tops with shallow soils and more xeric microclimates. The higher elevation of these hills could also help account for the dominance of *Quercus prinus*, a predominantly mountain species in North Carolina. In both soil characteristics and species composition these forests appear similar to and continuous with the bluff forests of more sheltered sites.

All of the above factors probably contribute to the low diversity characteristic of monadnock sites (34.0 species per 0.1 ha average). Among the trees occurring on these sites *Quercus prinus**, *Oxydendrum arboreum*, *Quercus alba*, *Q. coccinea**, *Acer rubrum*, and *Carya tomentosa* are most common with the first two clearly dominating all except the most isolated stands. This is the only forest type where tree species contribute over half (66.5 %) of the understory cover (<1 m tall). Shrubs, particularly *Vaccinium stamineum**, *V. vacillans*, *V. tenellum**, and *Viburnum rafinesquianum*, comprise just over 30 % of the cover with herbs accounting for less than 4 %. Average herb diversity was only 10 species per 0.1 ha. Although a few herbs have their modes abundance in these forests, there appear to be no herbs which are truly diagnostic of this type.

Stands with high first axis and intermediate second axis scores (Figure 4) also occur on nutrient-poor sites and are designated oligotrophic forests. Soils on these sites have weathered from either acid igneous rocks or Triassic Basin sediments and are somewhat more fertile (average exchangeable cations = 1.0 ME/100 g) than the monadnock forests. Unlike the monadnock forests, these

26

forests typically occur on flat or only gently sloping uplands. This type corresponds most closely with OOSTING's (1942) White Oak type.

The dominant tree in the oligotrophic forests is *Quercus alba* which is associated with *Carya ovata, C. ovalis, C. glabra*, Quercus stellata,* and *Q. velutina**. Understory trees include *Oxydendrum arboreum, Cornus florida, Acer rubrum*. Tree seedlings again are an important component of the understory (<1 m tall). Shrubs, including *Viburnum rafinesquianum, Vaccinium stamineum,* and *V. vacillans,* are also important. The herbaceous flora is relatively
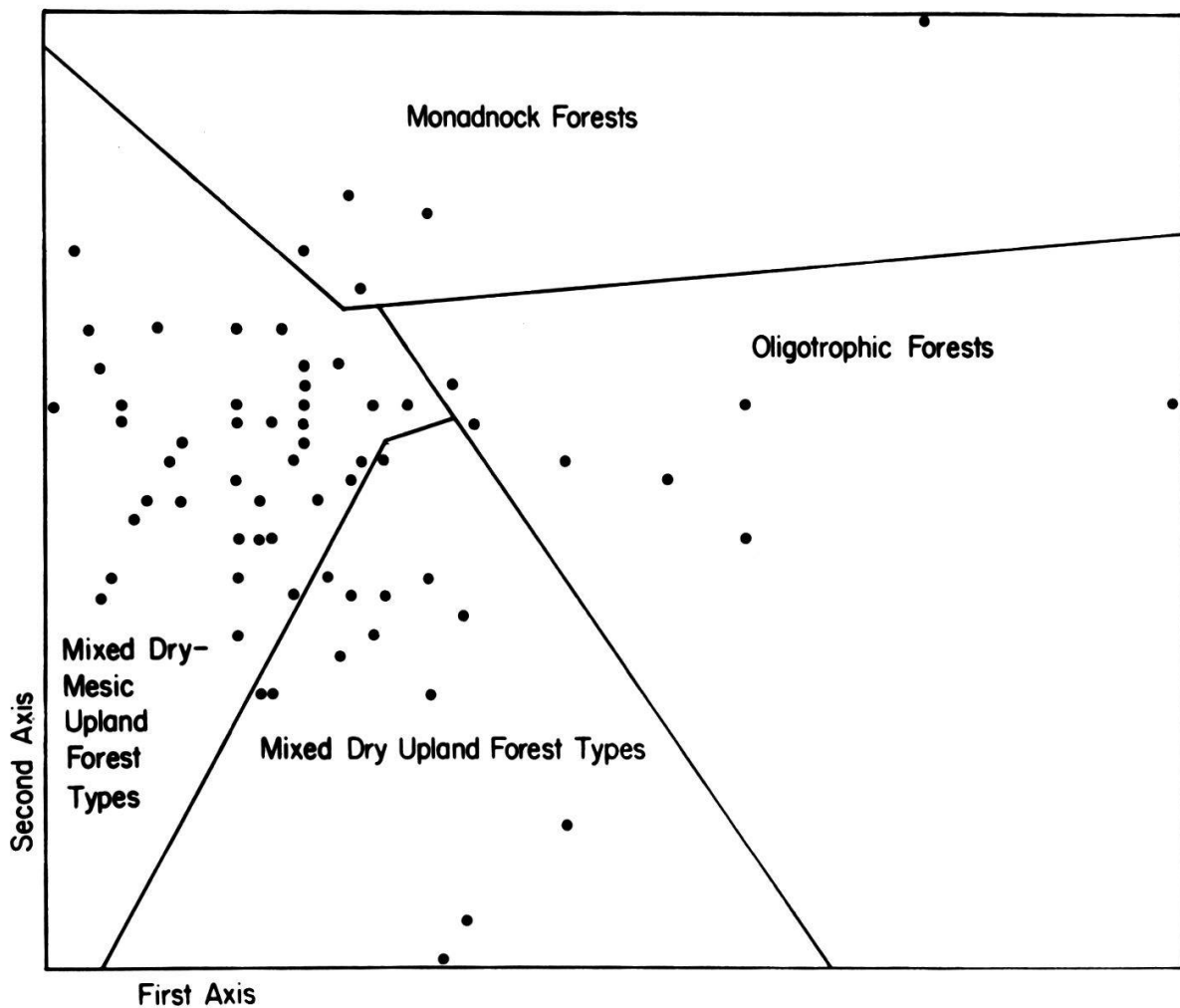

Figure 4. Third reciprocal averaging ordination indicating Monadnock and Oligotrophic Forest Types.

depauperate (13 species per 0.1 ha) and monotonous, a few species such as
Chimaphila maculata*, *Hieraceum venosum*, *Tephrosia virginiana**, and *Stipa
avenacea** occurring in most of the stands but with low abundance. Except for
the absolute dominance of *Quercus alba* and *Oxydendrum,* the woody flora of
these sites is quite similar to that of other upland sites, but the low herb
diversity results in total species diversity nearly as low as in monadnock
forests.

5.4. Fourth ordination

An ordination of the residual stands from ordination 3 is illustrated in
Figure 5. The first axis scores in this ordination correspond to a moisture
gradient from xeric (low scores) to mesic (high scores); moisture status here
is primarily a consequence of slope, aspect and soil texture. Second axis
scores have a high correlation with exchangeable cations (R^2 = 0.7), low fer-
tility sites having the highest scores. All of the stands with low second
axis scores occur on soils derived from basic igneous rocks. We have divided
the fourth ordination into 4 parts based on these environmental correlates
and on dominant trees.

Stands with low first and second axis scores are on ridges and dry slopes
with high soil nutrient content. These stands which we refer to as dry eutro-
phic forests are dominated by *Quercus stellata* and *Q. alba*. Although herb
cover is comparatively sparse, herb diversity is not depressed, averaging 25
species per 0.1 ha. Among the more common herbs are *Carex* spp. (primarily
artitecta* and *nigromarginata**), *Polygonatum biflorum*, *Galium circaezans*,
Uvularia perfoliata, *Scleria oligantha**, *Aristolochia serpentaria**, and
Euphorbia corollata*.

Stands with high first axis scores but low second axis scores occur on fer-
tile soils with more mesic exposures. These dry-mesic eutrophic forests sup-
port a greater mixture of canopy tree species but have fewer herb species
(20 per 0.1 ha) than are found in the dry eutrophic forests. Dominant trees
include *Quercus alba*, *Q. rubra**, *Fraxinus americana*, *Liriodendron*, and *Carya*
spp., while *Cercis canadensis**, *Cornus florida**, *Acer rubrum*, and *Chionanthus
virginicus** predominate in the understory. A well developed shrub layer is
present with *Viburnum rafinesquianum*, *Lonicera japonica*, and *Euonymus ameri-*

canus having the greatest cover. The most important herbaceous species are *Desmodium nudiflorum**, *Uvularia perfoliata**, *Polygonatum biflorum**, *Hexastylis arifolia**, and *Galium circaezans*.

Stands with high second but low first axis scores, generally mixed *Quercus-Carya* stands, are designated dry mesotrophic forests. The grouping corresponds most closely to OOSTING's White Oak-Black Oak-Red Oak Forest and is characteristic of moderately infertile, comparatively dry slopes. These stands average only 43 species per 0.1 ha. Several species of *Quercus* and
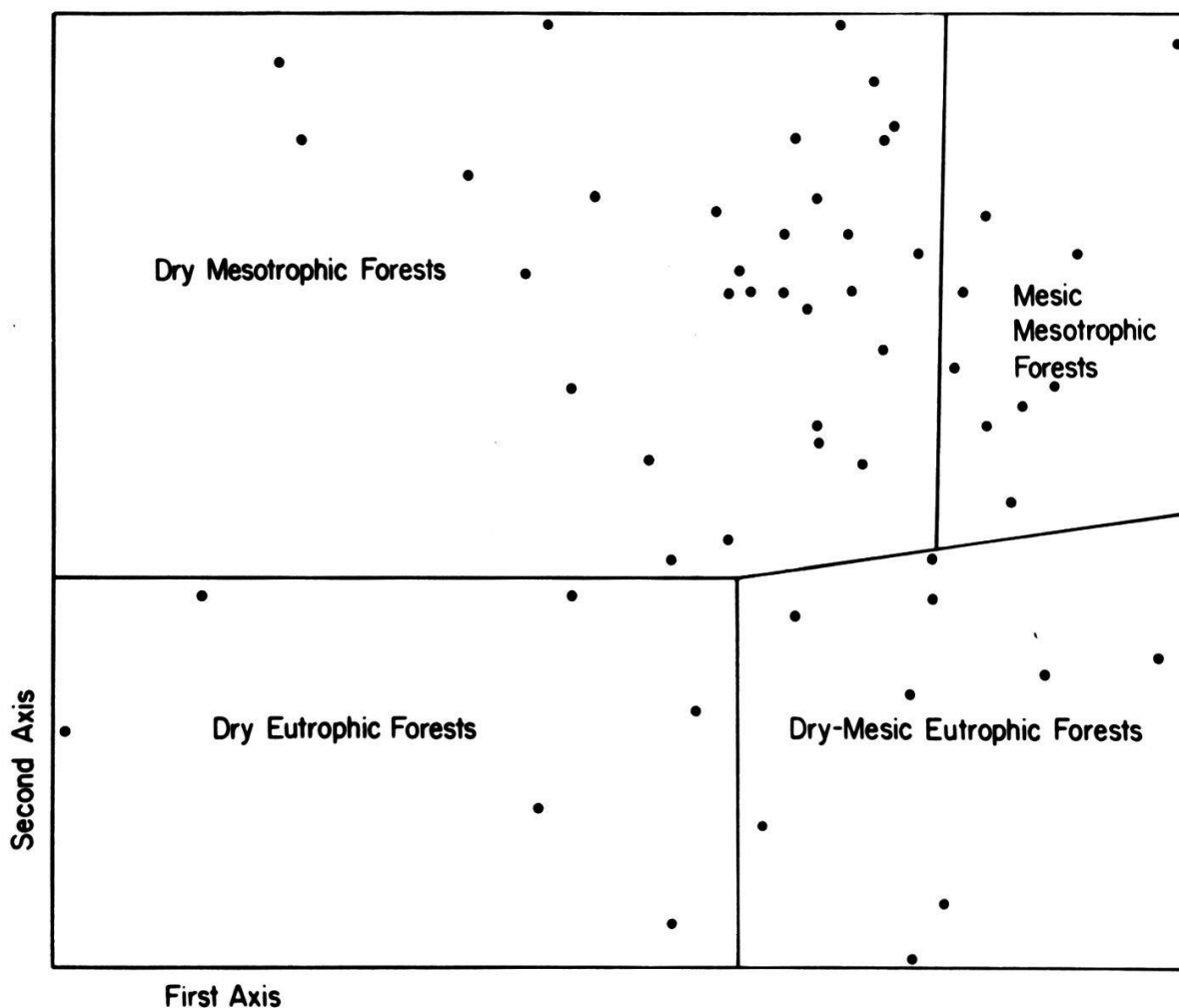

Figure 5. Fourth reciprocal averaging ordination indicating Dry Eutrophic, Dry-mesic Eutrophic, Dry Mesotrophic, and Mesic Mesotrophic Types.

29

Carya share dominance including *Quercus alba, Q. velutina, Q. rubra, Carya tomentosa, C. glabra, C. ovata,* and *C. ovalis. Cornus florida, Acer rubrum, Prunus serotina, Nyssa sylvatica,* and *Juniperus virginiana* regularly occur in the understory. Again, *Viburnum rafinesquianum* is the dominant shrub with *Vaccinium stamineum* and *Vitis rotundifolia* also being important. Average constancy for prevalent species is only 24.8 % compared to 39 - 42 % for all other identified community types. The low constancy suggests that this grouping is rather heterogeneous and perhaps should be further divided.

Between the dry mesotrophic forests and the dry-mesic eutrophic forests is a group of stands which we refer to as mesic mesotrophic forests. This forest type and the dry mesic eutrophic type merge, with increasing soil moisture, into the cove and alluvial forests. Like the dry mesotrophic stands, the mesic mesotrophic forests have relatively low species diversity (45 per 0.1 ha) but are dominated by a mixture of hardwoods more characteristic of mesic sites such as coves. These include *Liriodendron tulipifera*, Fagus grandifolia,* and *Quercus rubra.* Other important tree species include *Acer rubrum, Cornus florida,* and *Quercus alba.* Herb diversity is rather low with only 14 species per 0.1 ha. Dominant herbs include *Polygonatum biflorum, Chimaphila maculata,* and *Desmodium nudiflorum.*

6. Discussion and conclusions

6.1. *Environmental correlations*

Although the four ordinations shown in Figures 2-5 have been used primarily to identify community types, they can be used to illustrate the major forms of environmental variation correlated with community composition. Table 2 presents Spearman rank correlation coefficients of selected soil characteristics compared with the ordination axes.

The first axis of the first ordination, in addition to being strongly related to soil moisture, shows a strong negative correlation with all soil cations. Similarly, the second axis is strongly related to soil cation levels. The most favorable sites are thus the cove and alluvial forests which have both abundant moisture (without anaerobic conditions) and nutrients. The

Table 2. Spearman rank correlations of soil variables with ordination axes.

	pH	Total[1] Cations	Ca	Mg	K	Organic Matter	PO_4	AWI[2]	PWP[3]
Ordination 1									
Axis 1	-0.717*	-0.768*	-0.743*	-0.792*	-0.285*	0.031	-0.091	0.353*	0.111
Axis 2	0.380*	0.275*	0.255*	0.267*	0.346*	0.185	0.201	-0.129	-0.092
Ordination 2									
Axis 1	-0.744*	-0.763*	-0.734*	-0.753*	-0.425*	-0.103	-0.300	0.540*	0.193
Axis 2	-0.095	-0.215	-0.196	-0.241	0.041	0.055	0.023	-0.012	0.036
Ordination 3									
Axis 1	-0.628*	-0.509*	-0.472*	-0.549*	-0.231	-0.093	-0.132	0.440*	-0.250
Axis 2	-0.074	-0.378*	-0.353*	-0.374*	-0.072	0.034	-0.258	0.208	-0.254
Ordination 4									
Axis 1	0.418*	0.140	0.124	0.176	0.137	0.019	-0.181	-0.111	-0.088
Axis 2	-0.493*	-0.599*	-0.581*	-0.542*	-0.093	0.013	-0.336	0.603*	0.123

1 Total cations = sum of Ca, K and Mg in milli-equivalents
2 AWI = Available water index = -1 bar water retention minus -15 bar water retention
3 PWP = Permanent wilting point = -15 bar water retention
* indicates significant at 0.01 level

montmorillonite forests of the lower right have the least favorable soils among the stands sampled, being low in cations and periodically water saturated (anaerobic).

The first axis of the second ordination is one of decreasing soil fertility, being negatively correlated with pH, calcium, magnesium, potassium, and phosphate. This axis clearly delimits the nutrient rich cover forests. The bluff forests, at the opposite end of the nutrient gradient, are similar to cove forests in their occurrence on cool, moist sites.

In the third ordination, both axes are again correlated with soil cations, the upper right portion of the ordination containing the most oligotrophic sites. The perpendicular gradient from upper left to lower right represents variation in site moisture, primarily as related to slope and aspect. The monadnock forests usually occur on north or east slopes at our highest elevations, whereas the dry upland types tend to be on flat or slightly south-facing slopes. The final ordination is similar to the third in being strongly correlated with both soil fertility and moisture gradients.

Examination of the four ordinations shows the overriding importance of soil,

pH, nutrient content, and the interaction of various moisture and exposure factors. Even after all the extreme forest types have been removed, highly significant correlations are obtained between soil nutrient characteristics and the ordination axes. The result is in direct contrast to the earlier work of COILE (1933) who found insufficient variation in soil reaction to account for the distribution of forest types.

In upland soils most of the variation in soil nutrients is a direct result of the parent material from which the soil developed. The sterile monadnock soils have weathered from quartz and aluminium rich rocks such as andesite, pyrophyllite, and quartzite. The dry mesotrophic and oligotrophic forests develop on soils derived from highly weathered granites, volcanics, and sedimentary rocks with varying amounts of non-quartz minerals. At the other extreme are the eutrophic forests which are typically found on soils derived from diorites, gabbros, and other rocks high in ferromagnesian minerals.

6.2. *Species richness*

Among the eleven communities we recognize, average species richness of vascular plants (species per 0.1 ha) varies from a high of 76 in the alluvial forests to a low of 34 in the monadnock forests. Most of this variation occurs in the herbaceous component. Tree species number varies only between 15 (swamp forests) and 21 (dry-mesic eutrophic forests) species. Similarly shrub species richness varies only between 7 (oligotrophic forests) and 17 (alluvial forests). In contrast, herbaceous species richness varies from a low of 10 in the monadnock forests to a high of 42 in the alluvial forests. The stand with the highest richness contained 29 tree species, 19 shrubs and 69 herbs for a total of 119 species.

While PEET (1978) has warned of the danger inherent in a unidimensional interpretation of species richness, Figure 6 suggests a gradient in exchangeable soil cations to be of major importance in controlling species richness. A regression using the sum of exchangeable calcium, magnesium, and potassium (ME/100 g soil) to predict the average richness of each of the eleven recognized communities yielded an R^2 of 0.85. While species richness has previously been reported to be correlated with soil fertility and pH (see WHITTAKER 1972), no previous studies have shown such strong correlations. Our results

are consistent with those of MONK (1965, 1967) who, although working prima-
rily with trees, reported soil fertility to be the major factor influencing
richness in related coastal plain communities in northcentral Florida.
Species richness of piedmont forests also appears to be related to soil
moisture conditions. The three communities with the most abundant soil mois-
ture are included in the four communities with highest richness. Among those
communities with low soil cations, the drier sites are less rich. The impor-
tance of soil moisture as a second factor influencing richness is also con-
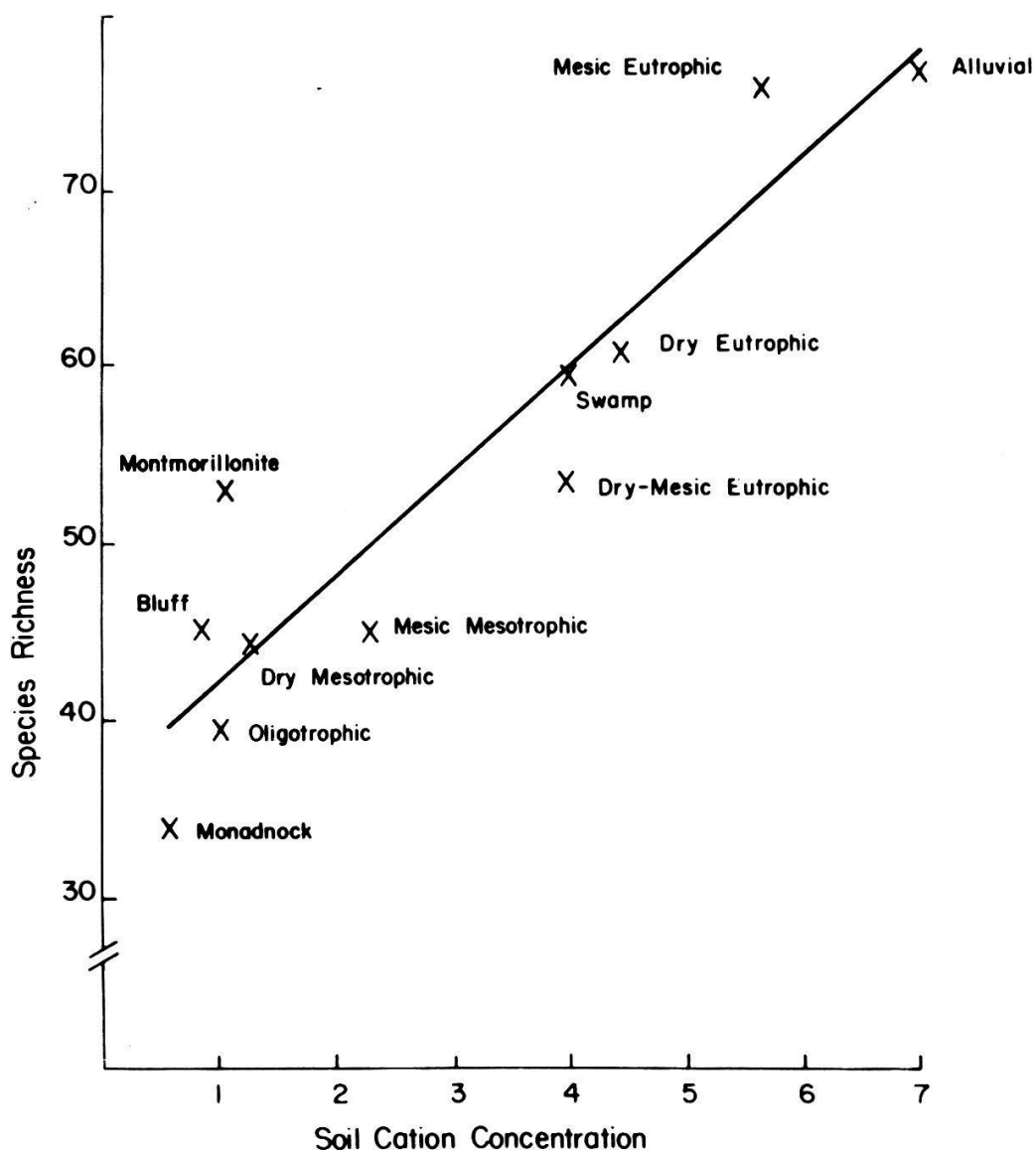sistent with the findings of MONK.

Figure 6. Relationship between species richness (average species number per
0.1 ha sample) for a forest type and average exchangeable cations
(ME Ca, Mg, K/100 g).

GLENN-LEWIN (1977) and WHITTAKER (1977) have suggested that while species richness (species per 0.1 ha) may be interpretable at a local level, few consistent patterns emerge in large-scale comparative studies. However, the convergent results of PEET (1978) and AUCLAIR and GOFF (1971) for the fire-influenced northern hardwood and boreal forests, and our results and those of MONK (1965, 1967) for the hardwood forests of the southeastern piedmont and coastal plain suggest that broad regional generalizations may be possible.

6.3. Comparison with other studies

Several authors have previously reported on selected forest types found in or near our present study area (see Table 3). The most comprehensive investigation was that of OOSTING (1942). Following the Clementsian terminology of his day, OOSTING referred to the upland oak-hickory forests as the climatic climax, the mesic cove forests as postclimax and the montmorillonite sites as preclimax. He also recognized alluvial or bottomland forests. OOSTING further divided the upland oak-hickory complex into three forest types. The white oak, red oak, black oak type was the most common and corresponds most closely to our dry-mesic mesotrophic forest. His white oak type is very similar to our oligotrophic forest in the striking dominance of *Quercus alba*, though OOSTING did not report the low soil nutrient levels we found. On dry ridges OOSTING found a white oak, post oak type essentially equivalent to our dry eutrophic forest.

KORNAS (1965) and BORNKAMM (1975) have attempted to apply the nomenclature of the southern European phytosociological school to single stands within our study area. Both studies were limited in scope, with only 29 releves between them. Our interpretation of the community names they recognize is shown in Table 3.

NEMETH (1968), working in the Hill Experimental Forest approximately 30 km north of the study area, recognized five forest types on the basis of topographic position. His study differs from those preceding only in that he recognized a *Quercus prinus* type on high hills, the equivalent of our monadnock forest.

Particularly striking in the preceding discussion is the consistent failure of previous workers to recognize the importance of edaphic factors, and espe-

Table 3. Forest type equivalents of various authors.

Present study	OOSTING (1942)	NEMETH (1968)	KORNAS (1965)	BORNKAMM (1975)
Alluvial	Bottomland	I	Bottomland[4]	Bottomland[3a]
Swamp				Bottomland[3b]
Montmorillonite	Preclimax			
Mesic eutrophic	Postclimax	II	Mesophytic beech-oak-maple[1]	Beech-maple[1b]
Mesic mesotrophic	White oak, red oak black-oak			Beech-maple[1a]
Dry-mesic mesotrophic		III	Oak-hickory upland[2] (heavy soils form)	
Oligotrophic	White oak	IV	Oak-hickory upland[2] (light soils form)	
Dry eutrophic				
Dry-mesic eutrophic	White oak, post oak			
Bluff				
Monadnock		V		

1 = *Aceri-Fagetum carolinianae*
1a = *Aceri-Fagetum typicum*
1b = *Aceri Fagetum trillietosum*

2 = *Caryo-Quercetum falcatae*

3 = *Carici roseae-Liquidambaretum*
3a = *Carici-Liquidambaretum typicum*
3b = *Carici-Liquidambaretum caricetosum crinitae*

4 = *Platano-Ulmetum americanae*

cially soil nutrient status, in the determination of forest composition. Our
work supports the idea that the very old and highly weathered soils of the
piedmont of the southeastern United States vary considerably with respect to
several ecologically important factors. These soil variations reflect the
underlying parent material and the nature of the weathering process. Addi-
tional studies are now needed to examine the variation in community response
to substrate with geography, as well as the physiological mechanisms respon-
sible for this variation in forest composition.

Summary

The piedmont of North Carolina is characterized by a warm temperate climate
with year-round rainfall. Soils in this region are ultisols derived from a
variety of parent rocks. The predominant natural vegetation is broadleaved
deciduous hardwood forest. Vegetation and soils of 105 hardwood stands were
quantitatively sampled. Vegetation data were subjected to repeated Reciprocal
Averaging ordination (RA), with progressive fragmentation of the data set in-
to distinctive groups based on environmental correlations and canopy domi-
nants. Eleven community types are recognized: 1) Alluvial Forests; 2) Swamp
Forests; 3) Mesic Eutrophic Forests; 4) Dry-Mesic Eutrophic Forests; 5) Dry
Eutrophic Forests; 6) Mesic Mesotrophic Forests; 7) Dry Mesotrophic Forests;
8) Oligotrophic Forests; 9) Montmorillonite Forests; 10) Bluff Forests; and
11) Monadnock Forests. Ordination axes were often highly correlated with
availability of soil exchangeable bases and site moisture conditions. Species
richness, which varied from an average of 34 species per 0.1 ha in Monadnock
Forests to 76 species per 0.1 ha in Alluvial Forests, was highly correlated
with total soil cation availability (R^2 = 0.85). The relationships of these
results to previous studies are discussed.

Zusammenfassung

Das Gebiet des Piedmont in North Carolina ist durch ein warmes Klima mit über
das ganze Jahr verteilten Niederschlägen ausgezeichnet. Unter diesen Bedin-
gungen entstehen über den verschiedensten Muttergesteinen Ultisol-Böden. Als
natürliche Vegetation herrschen breitblättrige sommergrüne Hartholz-Wälder
vor. Die Vegetation und die Böden von 105 Hartholz-Beständen wurden quantita-
tiv analysiert. Die Vegetationsdaten wurden mehrfach nach dem Reciprocal
Averaging (RA) ordiniert und auf Grund von Umweltbeziehungen und dominanten
Bäumen zunehmend in deutliche Gruppen aufgeteilt. Es werden elf Gesellschafts-
typen unterschieden: 1. Auenwälder, 2. Sumpfwälder, 3. Wälder auf mittelfeuch-
ten, nährstoffreichen Böden, 4. Wälder auf halbtrockenen, nährstoffreichen
Böden, 5. Wälder auf trockenen, nährstoffreichen Böden, 6. Wälder auf mittel-
feuchten, mässig nährstoffreichen Böden, 7. Wälder auf trockenen, mässig
nährstoffreichen Böden, 8. Wälder auf nährstoffarmen Böden, 9. Wälder über

Montmorillonit, 10. Steilhangwälder, 11. Wälder über Monadnock-Böden. Die Ordinationsachsen waren oft streng korreliert mit dem Gehalt an austauschbaren Basen und mit den Bodenfeuchtigkeitsverhältnissen. Der Artenreichtum, der zwischen einem Mittel von 34 pro 0.1 ha in den Wäldern über Monadnock-Böden bis zu 76 pro 0.1 ha in den Auenwäldern variierte, war streng korreliert mit dem Gehalt verfügbarer Kationen im Boden (R^2 = 0.85). Die Resultate werden mit den Ergebnissen früherer Arbeiten verglichen.

References

AUCLAIR, A.N. and GOFF, F.G., 1971: Diversity relations of upland forests in the western Great Lakes area. Amer. Nat. *105*, 499-528.

BATSON, W.T., 1952: The floristics of the Iredell soil series in the central piedmont of North Carolina. Ph.D. thesis, Duke University, Durham N.C.

BEARD, L.S., 1959: Notes on the vascular flora along the lower Deep River of North Carolina. J. Elisha Mitchell Sci. Soc. *75*, 132-134.

BILLINGS, W.D., 1938: The structure and development of old field shortleaf pine stands and certain associated physical properties of the soil. Ecol. Monogr. *8*, 437-499.

BORNKAMM, R., 1975: A vegetation map of the Henry J. Oosting Natural Area, Orange County, North Carolina. Duke University School of Env. Stud., Tech. Pap. 3.

BRAY, J.R. and CURTIS, J.T., 1957: An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27, 325-349.

CADY, J.G., 1950: Rock weathering and soil formation in the North Carolina piedmont region. Soil. Sci. Soc. Amer., Proc. *5*, 337-342.

CHRISTENSEN, N.L., 1979: Fire regimes in southeastern ecosystems. In: MOONEY, H.A., BONNICKSEN, L., CHRISTENSEN, N.L., LOTAN, J., and REINERS, W.A. (eds.), Fire Regimes and Ecosystem Properties. U.S.F.S. (in press).

COILE, T.S., 1933: Soil reaction and forest types in the Duke forest. Ecology *14*, 323-333.

CONNELL, J.H. and SLATYER, R.O., 1977: Mechanisms of succession in natural communities and their role in community stability and organization. Amer. Natur. *111*, 1119-1144.

CRAFTON, W.M. and WELLS, B.W., 1934: The old field prisere: an ecological study. J. Elisha Mitchell Sci. Soc. *49*, 225-246.

DAYTON, B.R., 1966: The relationship of vegetation to Iredell and other piedmont soils in Granville County, North Carolina. J. Elisha Mitchell Sci. Soc. *82*, 108-118.

DUNN, J., 1977: Soil survey of Orange County, North Carolina. USDA, Soil Cons. Serv.

EBERT, J.B., 1957: Bluff vegetation in lower piedmont of North Carolina. Master's thesis, Duke University, Durham, N.C.

FASHAM, M.J.R., 1977: A comparison of nonmetric multidimensional scaling, principal components and reciprocal averaging for the ordination of simulated coenoclines, and coenoplanes. Ecology *58*, 551-561.

GAUCH, H.G., WHITTAKER, R.H., and SINGER, S.B., 1980: A comparative study of nonmetric ordinations. J. Ecol. (in press).

GIBBON, E.L., 1966: The vegetation of three monadnocks in the eastern pied-
        mont of North Carolina. Master's thesis, North Carolina State Univ.,
        Raleigh, N.C.
GLENN-LEWIN, D.C., 1977: Species diversity in North American temperate forests.
        Vegetatio *33*, 153-162.
HARDIN, J.T. and COOPER, A.W., 1967: Mountain disjuncts in the eastern pied-
        mont of North Carolina. J. Elisha Mitchell Sci. Soc. *83*, 139-150.
HATCHER, R.D., Jr., 1972: Developmental model for the southern Appalachians.
        Geol. Soc. Amer. Bull. *83*, 2735-2760.
HATLEY, M.T., 1977: The dividing path: the direction of Cherokee life in the
        eighteenth century. Master's thesis, Univ. North Caroliny, Chapel
        Hill, N.C.
HILL, M.O., 1973: Reciprocal averaging: an eigenvector method of ordination.
        J. Ecol. *61*, 237-249.
–   1974: Correspondence analysis: a neglected multivariate method. J.
        Royal Stat.Soc. Ser. C *23*, 340-354.
HUDSON, C.M., 1976: The southeastern Indians. Univ. Tennessee Press, Knox-
        ville. 573 pp.
KEEVER, C., 1950: Causes of succession on old fields of the piedmont, North
        Carolina. Ecol. Monogr. *20*, 229-250.
KOMAREK, E.V., 1974: Effects of fire on temperate forests and related eco-
        systems: southeastern United States. In: KOZLOWSKI, T.T. and AHLGREN
        C.E. (eds.), Fire and Ecosystems. Academic Press, 251-278.
KOPEC, R.J. and CLAY, J.W., 1975: Climate and air quality. In: CLAY, J.W.,
        ORR, D.M., and STUART, A.W. (eds.), North Carolina Atlas. Univ. North
        Carolina Press, Chapel Hill, N.C. 92-111.
KöPPEN, W., 1936: Das geographische System der Klimate. In: Handbuch der Kli-
        matologie. Vol. 1, P.C.
KORNAS, J., 1965: Phytosociological observations on plant communities of the
        Duke Forest near Durham, North Carolina, U.S.A. Frag. Flor. Geobot.
        11, 307-338.
LEE, W.D., 1956: The soils of North Carolina: their formation, identification
        and use. North Carolina Agr. Exp. Stat. Tech. Bull. *115*.
MONK, C.D., 1965: Southern mixed hardwood forest of northcentral Florida.
        Ecol. Monogr. *35*, 335-354.
–   1967: Tree species diversity in the eastern deciduous forest with
        particular reference to northcentral Florida. Amer. Nat. *101*, 173-187.
NELSON, T.C. and ZILLGITT, W.M., 1969: A forest atlas of the South. USDA
        Forest Service, Southern For. Exp. Sta. Pub. 27 pp.
NEMETH, J.C., 1968: The hardwood vegetation and soils of Hill Demonstration
        Forest, Durham County, North Carolina. J. Elisha Mitchell Sci. Soc.
        84, 482-491.
ODUM, E.P., 1969: The strategy of ecosystem development. Science *164*, 262-270.
OOSTING, H.J., 1942: An ecological analysis of the plant communities of pied-
        mont North Carolina. Amer. Midl. Nat. *28*, 1-126.
–   and HESS, D.W.,1956:Microclimate and a relic stand of *Tsuga canadensis*
        in the lower piedmont of North Carolina. Ecology *37*, 28-39.
PEET, R.K., 1978: Forest vegetation of the Colorado Front Range: patterns of
        species diversity. Vegetatio *37*, 65-78.
–   1979: Ordination as a tool for analyzing complex data sets. Vegetatio
        (in press).

PERKINS, H.F., BYRD, H.J., and RICHIE Jr., F.T., 1973: Ultisols--Light-
colored soils of humid temperate areas. In: BUOL, S.W. (ed.), Soils
of the Southern States and Puerto Rico. Southern Coop. Ser. Bull.
174, 73-86.

PINCHOT, G. and ASHE, W.W., 1897: Timber trees and forests of North Carolina.
North Carolina Geol. Surv. Bull. *6*.

POWELL, W.S., 1975: History. In: CLAY, J.W., ORR, D.M., and STUART, A.W.
(eds.), North Carolina Atlas. Univ. North Carolina Press, Chapel Hill,
N.C. 12-31.

PRENTICE, I.C., 1977: Non-metric ordination models in ecology. J. Ecol. *65*,
85-94.

QUARTERMAN, E. and KEEVER, C., 1962: Southern mixed hardwood forest: climax
in the southeastern coastal plain, U.S.A. Ecol. Monogr. *32*, 167-185.

RADFORD, A.E., AHLES, H.E., and BELL, C.R., 1968: Manual of vascular flora
of the Carolinas. Univ. North Carolina Press, Chapel Hill, N.C.

SECHREST, C.G. and COOPER, A.W., 1970: An analysis of the vegetation and soils
of upland hardwood stands in the piedmont and coastal plain of Moore
County, N.C. Castanea *35*, 26-57.

SOIL SURVEY STAFF, 1975: Soil Taxonomy. USDA Agr. Handbk. 436.

STUCKEY, J.L., 1965: North Carolina: its geology and mineral resources. North
Carolina Dept. Cons. Dev., Raleigh, N.C.

WALTER, H. and LIETH, H., 1967: Klimadiagramm-Weltatlas. Gustav Fischer Ver-
lag, Jena.

WHIGHAM, D.F., 1971: An ecological study of *Uvularia perfoliata* in the
Blackwood Division of Duke Forest, North Carolina. Ph.D. thesis,
Univ. North Carolina, Chapel Hill, N.C.

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

– 1972: Evolution and measurement of species diversity. Taxon *21*,
213-251.

– 1977: Evolution of species diversity in land communities. Evol. Biol.
10, 1-67.

Address of the authors: Dr. Robert K. PEET
Department of Botany
Coker Hall 010 A
University of North Carolina
Chapel Hill, N.C. 27514, U.S.A.

Dr. Norman L. CHRISTENSEN
Department of Botany
Duke University
Durham, N.C. 27706, U.S.A.