# VEGETATION ANALYSIS OF NORTH AND SOUTH EDGES IN A MATURE OAK-HICKORY FOREST[1]

BRUCE A. WALES[2]
*Department of Botany, Rutgers—The State University, New Brunswick, New Jersey*

TABLE OF CONTENTS

## ABSTRACT

The north and south edges of a mature oak-hickory forest on the New Jersey Piedmont are characterized by local-scale vegetation gradients. These gradients are determined by both exposure-induced microclimatic influences and historical factors. The north edge has been relatively undisturbed since establishment. A narrow vegetative transition is associated with the relatively narrow microclimatic transition within the edge. A low thicket of tree growth (*Cornus florida, Prunus avium, Viburnum prunifolium*) mingled with woody vines and herbs is found exterior to the original edge. The old edge ends about 10 m within the forest and is characterized by increased densities and basal areas (compared to center) for *Quercus* spp. and *Prunus avium*.

The original south edge is found about 20 m within the present forest. It is characterized by increased densities and basal areas of *Quercus* spp. and *Viburnum prunifolium*. Agricultural abandonment about 1900 accounts for reforestation in front of the old edge. The area immediately in front of the original edge is an open stand in which both *Prunus avium* and *Viburnum prunifolium* have increased densities. Exterior to this is a dense strip of medium-sized trees which is characterized by increased densities of *Quercus* spp. and *Prunus avium*. The remaining area is composed of small trees (*Quercus velutina, Prunus avium*) with clumps of woody vines between and upon them. The wide microclimatic transition at one time within the original south edge was transferred to the present edge with the development of a closed canopy within the reforested strip. Few edge effects are found now beyond 20 m within the stand.

The segregation of species within and between the edges is more subtle than that between north and south slopes in the region. Species characterized by shade intolerance or good vegetative reproduction, or both, are prevalent at the edges. Many of these species also are associated with secondary succession in forest gaps, but edge responses are stronger than gap responses for most species. These include *Fraxinus americana, Prunus avium, P. serotina, Sassafras albidum*, and *Viburnum prunifolium*. Among canopy dominants *Quercus velutina* shows a stronger edge response than *Q. alba* or *Q. rubra*. *Carya ovalis* shows no significant edge response, whereas *C. ovata* displays a strong one. Relatively tolerant species such as *Fagus grandifolia, Acer saccharum*, and *A. platanoides* display no edge response. Most tree distributions are more localized than those of their reproductive size classes, presumably as a result of environmental selection acting upon seedlings and saplings within different forest microhabitats such as edges, gaps, and well-stratified areas of the stand.

Although the techniques are different, this study represents a local-scale example of direct gradient analysis in that plots (amenable to analysis of variance) are used as microlocational indices of the environmental complex and are matched to known microclimatic gradients.

---

[1] Received February 12, 1971; accepted January 10, 1972.

[2] Present address: Department of Biological Sciences, University of California, Santa Barbara, Calif. 93106.

## INTRODUCTION

In forested regions a border between a forest stand and an adjacent field, cleared by man and maintained by his agriculture, is both a microclimatic and a vegetational transition zone. Since the edge of the forest acts as an escarpment, the direction of exposure is paramount in determining the nature of the microclimatic transition (Geiger 1965). On north and south forest edges the effective width of the transition is different for each microclimatic element at a given boundary. The effective transition width for any one element is different at the two boundaries and, at a given boundary, varies with the seasons (Wales 1967).

Given this complexity of environmental variation, the objective of this study was to examine the variation in the plant distributions in a forest center and on its north and south edges and to describe and interpret the vegetational transitions. The variation in the distribution of each of several plant species was partitioned into components attributable to various sources, each source representing a different type of distribution into or along the edges of the stand, or both. Individual species distributions and vegetation gradients are interpreted in the light of the known physiology of the species and their responses within forests on level terrain and on north and south slopes, which represent exposure-induced microenvironments similar to the ones dealt with here.

Most of the literature dealing with forest edges is concerned with the prairie-forest margin in the United States or elsewhere. Both the regional pattern in the prairie-forest margin and the old field-forest border in the eastern United States are problems involving variation in the distributions of plants and their associated environments. The two situations differ primarily with respect to scale. For example, mappers of continental vegetation types (Shantz and Zon 1924, Küchler 1964) drew lines representing the first-order ecotones (Carpenter 1935) or intergradations (Allee et al. 1949) between great bodies of vegetation such as deciduous forest and grassland. Several workers studied the individual stands within such broad-scale transitions (Daubenmire 1936, Buell and Cantlon 1951). Other investigators, notably Weaver and his associates (and others reviewed extensively in Weaver 1954), examined the border zones between the individual stands of forest and grassland.

Microclimatic and ecological studies of old field-forest margins are difficult to find. Only scattered microclimatic observations are reported in Geiger's (1965) treatise on microclimatology. Ecological studies of edge vegetation include those of Oosting and Kramer (1946), who investigated the establishment of pine in the edges of mixed pine-hardwood forests in the Southeast, and Trimble and Tryon (1966), who documented canopy changes in old growth adjacent to gaps cut in Appalachian hardwood stands.

## STUDY AREA

### *Forest history*

The study was conducted in Hutcheson Memorial Forest, known also as Mettler's Woods. The 26.3-ha mature oak forest (Buell 1957) is situated about 1.6 km east of East Millstone (40°30′N, 74°34′W) on the Piedmont in New Jersey. It was subjected to periodic burning before 1711 by the Lenape Indians, but has not been burned over since that time (Day 1953, Buell, Buell, and Small 1954). The land was settled in 1701 by Europeans and was acquired as a natural area by Rutgers University in 1955. Much of the forest, particularly the eastern part, never has been cut and cleared, although prior to 1950 fallen trees often were salvaged for firewood (Buell 1957).

In November 1950 a severe storm toppled or broke more than 300 canopy trees (Monk 1957). This catastrophic natural event (Buell 1957) can be thought of as a "natural harvest" (Reiners and Reiners 1965), but the activity of loggers associated with the removal of the damaged trees represents man's greatest disruptive influence in recent time. Since 1950, management has been designed to minimize man's influence.

### *Forest structure and function*

In the upland portion, where the edge study was carried out, the forest shows a distinct vertical stratification into four layers (Monk 1961*a*). White oak (*Quercus alba*), black oak (*Q. velutina*), red oak (*Q. rubra*), and red hickory (*Carya ovalis*) make up the main canopy, which reaches heights of 29 m. A pronounced understory of flowering dogwood (*Cornus florida*) reaches heights of 11 m. The shrub layer, averaging 1 m in height, is dominated by maple-leaved viburnum (*Viburnum acerifolium*). The herb layer is best developed in spring when May-apple (*Podophyllum peltatum*) is abundant.

Gaps associated with windthrows and other disturbances represent areas of localized secondary succession within the stand. Although old-field species and woody adventives play a temporary role in the reestablishment of typical forest structure, gap closure itself is a function of forest trees. Red maple (*Acer rubrum*) and white ash (*Fraxinus americana*) fill the gaps more often than the oaks and hickories (Monk 1961*a*).

Several woody alien species in the upland part of the stand were investigated by Ambler (1965). Norway maple (*Acer platanoides*) and sweet cherry (*Prunus avium*) have members in the canopy, but tree-of-heaven (*Ailanthus altissima*) is present only in the sapling size class. Japanese honeysuckle (*Lonicera japonica*) has a wide distribution (Ambler 1965) and has spread extensively since 1950 (M.F. Buell, *personal communication*). All of these species except Norway maple are associated with the forest margins, with windthrows, or with other openings in the stand.

In a taxonomic study of the forest and its edges, Frei and Fairbrothers (1963) reported 312 species of vascular plants: 77% in the forest, 57% along the edges, and 34% in both places. Thirteen per cent of the species were trees, 12% were shrubs, and the remaining 75% were herbaceous plants.

Bard (1952) concluded that Hutcheson Memorial Forest could be considered as a climax community because the low oak reproduction might well represent an amount sufficient to restock the stand. Monk (1961*a*) classed the forest as a variant of the oak-hickory forest type common to the Piedmont, but stated that it did not have the climax status which this community exhibits on the Piedmont in the southeastern United States. A trend toward more maple was suggested because of the low survival of oak saplings and the successful introduction of Norway maple and sugar maple (*Acer saccharum*).

The interrelated factors of wind, drought, and disease have influenced the stand significantly. A 1963 survey of all dead trees in the eastern section showed that on the well-drained portion 69.5 trees per hectare with a basal area of 972 sq dm (47% of living basal area) were harvested naturally in recent years (Reiners and Reiners 1965). Over 80% were oaks and hickories. Windthrows and windsnaps accounted for over half of the trees. Disease accounted for about one-third, and the remainder were cut. The drought of 1957 caused dramatic changes in the seasonal radial growth curves of trees in Hutcheson Memorial Forest (Buell et al. 1961). The 1957 and 1958 surveys by Small (1961) indicated that many trees of many species were damaged or killed. He suggested that the interacting factors of root-system injury by the root-rot fungus *Armillaria melea* and stress caused by drought accounted for the increased injury and kill observed during his second survey.

### *Habitat variation*

The gently rolling Piedmont is underlain by Triassic red shale of the Brunswick Formation (Kümmel 1940). The Wisconsin glacial terminal moraine is located a few kilometers north of the forest, and Salisbury (1902) postulates that gravel scattered over the area represents fluvial material deposited by a river flowing south from the glacier. The soil in the upland section of the forest is classed as a deep, well-drained silt loam. Although gravel is occasionally observed throughout the profile, the major influence is that of the shale (Ugolini 1964).

The advective climate of New Jersey is controlled largely by continental polar air masses with northwest and north winds in winter, and by maritime tropical air masses with southwest and south winds in summer. At New Brunswick, 13 km east of the forest, the mean daily maximum and minimum temperatures for July and January are 29°C and 17°C, and 4°C and −6°C respectively. Absolute extremes are 41°C and −27°C. The length of the growing season is 240 days (Biel 1958). At New Brunswick the average July precipitation is 115 mm, and the corresponding value in January is 85 mm (Dunlap 1959). The period between September 1961 and September 1966 was the longest and most severe drought to occur in the last 100 years (D. V. Dunlap, state climatologist, *personal communication*). Droughts of this type might be expected to occur only once every 200 years (Horowitz, Dunlap, and Shulman 1965).

In a microclimatic study Sparkes and Buell (1955) found that air and soil temperatures within the stand showed a smaller annual range than those in an adjacent 40-year-old field. The annual temperature extremes in the forest ranged from 32°C to −19°C at 5 cm above the litter, and from 23°C to −2°C at 4 cm in the soil below.

## METHODS

### *Rationale of experiment*

Within the environmental complex, relief, parent material, and microclimate represent three interacting groups of factors which have the potential to act differently upon vegetation in different places, such as the north and south boundaries and within the stand. The rationale of this experiment is to minimize the effects of the first two groups and to examine the effects of the third.

Within the upland maple-leaved viburnum shrub-type forest (Fig. 1), areas found on level or at most gently rolling, deep well-drained or at least moderately well-drained soils, derived from Brunswick shale, were identified. This was accomplished by superimposing Ugolini's (1964) soils map on Monk's (1957) vegetation map of the forest. By taking samples only in the identified area, dissimilar influences of relief and parent material were minimized.

Nothing could be found in the history of the forest to cast doubt upon the assumption that all the forest edges were established shortly after the

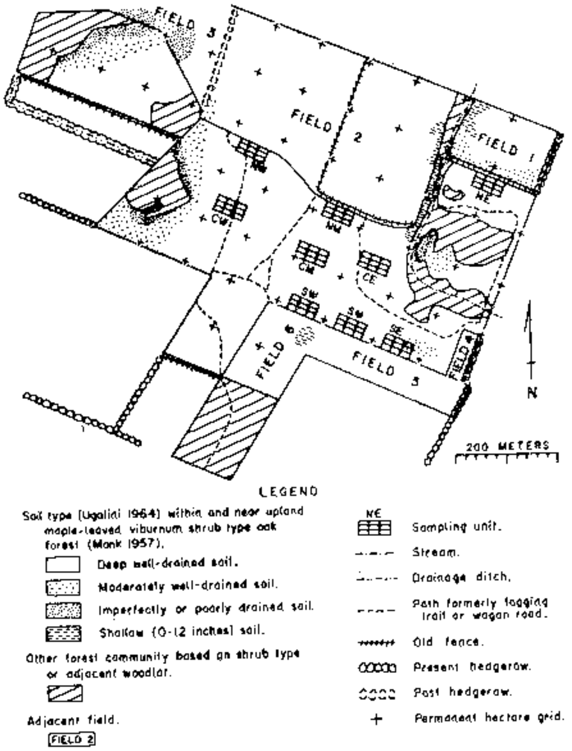

FIG. 1. Map of Hutcheson Memorial Forest showing positions of the sampling units.

arrival of the European settlers in 1701 or perhaps even before that time. The edges can be traced definitely to the early 1800's on an old map in the possession of a former owner. Although it can be established safely that all of the margins are very old, the age of forest gaps is uncontrollable in a natural stand.

The degree of recent man-made disturbance was taken into account in the selection of sampling sites. Areas of severe disturbance associated with the logging activity, especially areas in the center part of the stand now dominated by Japanese honeysuckle, were avoided. Also, old logging trails and an old wagon road, both now paths, were avoided to some extent. Otherwise, the sampling units were selected arbitrarily with respect to the vegetation (usually in some convenient relationship to permanent hectare stakes), so that gaps were sampled along with well-stratified sections of the stand.

In a forest climax region, old forest edges are maintained by man's continued use of adjacent fields. At the time of the study all fields adjacent to sampling sites were in early stages of secondary succession. Previous use of the fields along each edge was fairly uniform, but evidence indicates that land-use history cannot be eliminated as a dissimilar influence between north and south sides. Unavoidably, land-use history joins microclimate as an independent variable in this study.

### *Experimental design*

Nine 60- by 30-m sampling areas, referred to hereafter as units, were established in the forest (Fig. 1). At the forest margins the edge of each unit was placed at the end of the tree branches, which represents an arbitrary but fairly easily recognized position within most field-forest transitions (Fig. 2). Each unit is comprised of three columns ($r_1$, $r_2$, $r_3$) perpendicular to the forest boundary and six rows ($R_1$, $R_2$, ... $R_6$) running parallel with the boundary from the edge toward the interior of the stand. At the forest center (FC) the rows were arbitrarily numbered 1 to 6 from north to south, the direction of numbering presumed to be meaningless there. The three columns are considered as replicates in each unit. Thus, each unit is comprised of eighteen 5- by 20-m quadrats which form the six rows and three columns in the unit.

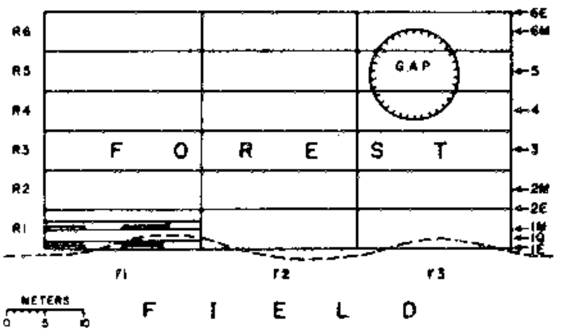

FIG. 2. Typical unit. R, row; r, column; ←, shrub line transect; - - - -, end of tree branches. *Seedling quadrats in same row combined prior to ANOVA.

This arrangement of quadrats represents a design for a three-factor analysis of variance (ANOVA) with replication. In this design there are three levels (north, center, south) of the first factor, position ($P$); six levels of the second factor, row ($R$); and three levels (west, middle, east) of the third factor, unit ($U$). Trees were sampled on the 5- by 20-m quadrats which follow this $3 \times 6 \times 3$ design. The same design was employed for sapling and seedling quadrats and shrub line transects, except that for the saplings and seedlings there are 12 rows and for the shrubs there are 10 (Fig. 2).

The ANOVA was used to partition the total variation in each of many data sets into mean squares which are associated with the three factors (main effects) and the interactions between them. The $F$-ratio was employed to determine the relative importance of these sources of variation by determining which main effects, or interactions, or both, have significantly greater variation (mean squares) than the random variation inherent in the error term (within replicates mean square). A 5% probability level has been used throughout.

A nonsignificant main effect or interaction is taken as evidence supporting the null hypothesis that no variation, other than that due to chance, exists for that source of variation. On the other hand, a significant main effect or interaction supports the belief that variation greater than chance variation exists. For example, a significant position main effect (response to position) indicates that at least one mean is significantly different from the means for the other two positions. In similar fashion, significant main effects of row or unit indicate that at least one mean is significantly different from the others among the six or three means, respectively. When their interactions are significant, main effects have little meaning as such.

A significant interaction shows that the factors fail to act independently. Thus, the interpretation of a significant $P \times R$ interaction is that the row-to-row variation is different, depending upon whether one starts at the center or the north or south sides of the stand. This can be seen in Fig. 3 and 4 where the rows for each position are shown for several species. The interpretation of a significant $P \times U$ interaction is that the unit-to-unit variation is different along the north and south edges and down the center of the stand, from west to east in each case (Fig. 6). The $R \times U$ interaction has no biologically meaningful interpretation in this design.

A significant three-factor interaction is the most difficult to interpret. It is interpreted as a failure of position and row to act independently of unit. The row-to-row variation is different on the north, center, and south depending upon where, in terms of units, one starts in the stand (Fig. 5).

Because the objective of this experiment is to evaluate variation within and along the edges compared to that within the stand, the strategy employed has been (a) to accept the center mean and its 95% confidence interval (CI) as representative of the population within the forest center, and (b) to use this mean with appropriate interactions to determine which row or unit means, or both, are significantly different than that for the population in the center. Thus, failure of a point to fall within the 95% CI of the center mean is taken as evidence that the point is representative of a population different than that in the center with a 5% significance level.

Because of known microclimatic and historical differences between the north and south margins and the forest center, significant $P \times R$ and $P \times R \times U$ interactions, taken to mean significant variation of one sort or another into the different edges, were anticipated. A significant $P \times U$ interaction, taken to mean significant variation along the edges or within the stand, or both, is not mutually exclusive of a $P \times R$ interaction. However, either a $P \times U$ interaction or a $P \times R$ interaction may be further elucidated by a $P \times R \times U$ interaction. For example, the high densities of sweet cherry in certain units on the north and south in Fig. 6 are accounted for by the high amounts (clumps) of sweet cherry in rows near the edge in those units (Fig. 5).

Analyses of variance were performed on the following categories of data: tree, sapling, and seedling densities, tree basal areas, shrub cover, and vegetative traits relating to reproduction (stump sprouts) and structure. The analyses were performed in all cases where an individual vegetational characteristic showed a frequency of at least 10%.

When data consist of small numbers, and especially when zeros are present, they often follow the Poisson distribution in which the mean and variance are equal (Steel and Torrie 1960). Because this violates assumptions underlying the ANOVA, transformations recommended by Bartlett (1947) were evaluated. On computer runs with tree densities, basal areas, and shrub cover, neither $\sqrt{X + 0.0001}$ nor $\sqrt{X + 0.5}$ gave results at the 5% significance level which would lead to different conclusions than those with the original data. Since this was the case, the transformations were discarded and all data were used in their original form.

### *Sampling techniques*

Size-class definitions similar to those used by many investigators (Buell and Cantlon 1950, Cantlon 1953, Monk 1961*b*) in the Middle Atlantic States were employed. This method avoids splitting data for *Cornus florida* into two meaningless categories.

Trees were defined as stems equal to or greater than 2.5 cm (1 inch) dbh. On each of the 162 5- by 20-m quadrats the number of stems of each species, their diameter at breast height, and origin were determined. Diameter at breast height was measured to the nearest one-tenth inch with a diameter tape, for later conversion to basal area. Origin refers to the presence of tree-sized stump sprouts. A count by species was made of standing dead trees. A tree with numerous suckers forming a pseudo-canopy was taken as alive. Dead trees were characterized by a few suckers, more commonly none at all, and peeled bark or broken limbs, or both.

Saplings were defined as stems less than 2.5 cm dbh and equal to or greater than 30 cm (1 ft) in height (to terminal bud). On each 1- by 20-m sapling quadrat, two per tree quadrat (Fig. 2), the number of stems of each species and the origin of the stems were determined. Two types of sapling-sized stump sprouts were observed and tabulated separately: (a) those obviously originating from the roots of a living or dead standing tree, and (b) those not so associated which were usually of about equal size suggesting that they originated as the result of damage to a single young stem.

Seedlings were defined as stems less than 30 cm in height (to terminal bud) and more than 1 year old as evidenced by the presence of a terminal bud scar. On each ½- by 5-m seedling quadrat, four per tree quadrat (Fig. 2), the number of stems of each species and the origin of the stems were determined. Origin was defined by the same criteria described for saplings. In addition, root sprouts and stems originating from occasional rhizomes were noted.

Shrub cover was measured on 20-m line transects (Fig. 2). The cover measured includes that contributed by the following: shrub species such as maple-leaved viburnum regardless of height, high-growing woody vines such as poison ivy (*Rhus radicans*) equal to or greater than 30 cm in height and all Japanese honeysuckle, tree saplings which were all considered to be in the shrub layer, branches of trees where the foliage was equal to or less than 1.5 m above the ground, and unoccupied space.

The cover contributed by Japanese honeysuckle was placed into two classes based on density. In class 1 runners are relatively few, and the ground is visible over at least half or usually more of the total area influenced by the plant. Individual runners climb saplings and seedlings. In class 2, a dense mat obscures more than half of the ground, or usually all of the area influenced by the plant. Numerous runners climb saplings and seedlings. Often, the litter layer is not well defined under class 2 honeysuckle.

Cover contributed by May-apple was measured on the same 20-m line transects used for shrubs. The first and third 5-m segments of these transects were used later to sample the cover contributed by the following categories of vegetation: summer- and early fall-flowering herbs regardless of height, low-growing woody vines such as poison ivy less than 30 cm in height and all Virginia creeper (*Parthenocissus quinquefolia*), tree seedlings, which were all considered to be in the herb layer, and unoccupied space.

Because the presence of canopy gaps and associated vegetation (Monk 1961*a*, Ambler 1965) represented a potential source of variation superimposed upon the forest center and the edge pattern, gap areas were located in several units and delimited in advance in order to carry out subsampling of the vegetation within them. Old logging trails and a wagon road, now paths, which represent "noise" in the stand similar to gaps, were delimited also. From measurements in the forest, gap maps were constructed for six of the nine units. During the growing season transects were sampled in 1967 and quadrats in 1968 on a permanent grid system. Nomenclature follows Fernald (1950).

## ANALYSIS OF EDGES

### *Individual species distributions*

*Tree species.*—The means and confidence intervals for structural properties of the major tree species (Table 1) represent the yardstick by which variation in the distribution of each species or vegetative trait is measured. The species referred to as transgressives are potential canopy species presently represented by small trees with heights ranging from below the understory to within the canopy. Present canopy species are seldom found as small trees.

The pattern of significant interactions and main effects (Table 2) shows that the distribution of transgressives is different from that of the canopy trees, understory trees, and vegetative traits in the forest center and edges. Two of the three transgressives show significant $P \times R \times U$ interactions for density, and all three species lack the predominance of $P \times R$ interactions or $R$ main effects so apparent for the other groups. Thus, transgressives generally show significant variation both into and along the edges or within the stand, or both, whereas the canopy and understory trees and vegetative traits generally show significant variation into the edges of the stand. The precise nature of the distribution for each species can be elucidated further only by inspection of the appropriate significant interactions and main effects.

The $P \times R$ interactions of density and basal area for all species upon which the ANOVA was performed (Fig. 3 and 4) show which of the six rows at each of the three positions have means significantly greater or less than the center means given in Table 1. The predominance of significantly different values near the edges on both sides of the forest clearly demonstrates edge responses for most species. As a result, the community composition at the edges is different from that in the center.

Compared to the $F$-ratio, the confidence interval is slightly more liberal in declaring values significantly different from the center mean. For example, neither red hickory nor red maple show biologically meaningful, significant interactions or main effects involving rows (Table 2), yet the confidence interval declares means near the edges significantly different from the center mean for both species (Fig. 3 and 4). Similarly, the $F$-ratio indicates merely a re-

TABLE 1. Structure of tree layer in forest center

| Species or vegetative trait | Density | | Basal area | | Percentage of basal area |
|---|---|---|---|---|---|
| | Number/100 m² | Upper and lower CL[a] | Cm²/100 m² | Upper and lower CL[a] | |
| Total tree | 14.85 | 17.68<br>12.02 | 2,415 | 3,763<br>1,068 | 100.0 |
| Understory | | | | | |
| *Cornus florida* | 12.22 | 14.65<br>9.79 | 569 | 689<br>454 | 23.5 |
| *Amelanchier arborea* | 0.02 | | 2 | | 0.1 |
| Canopy | | | | | |
| Total oak | 0.96 | 1.66<br>0.27 | 1,607 | 2,908<br>316 | 66.6 |
| *Quercus alba* | 0.59 | 1.19<br>0.00 | 1,059 | 2,062<br>56 | 43.9 |
| *Q. velutina* | 0.26 | 0.66<br>−0.00 | 399 | 1,171<br>−0 | 16.5 |
| *Q. rubra* and *coccinea* | 0.11 | 0.53<br>−0.00 | 149 | 548<br>−0 | 6.2 |
| *Carya ovalis* | 0.11 | 0.40<br>−0.00 | 139 | 427<br>−0 | 5.8 |
| *Fagus grandifolia* | 0.06 | | 39 | | 1.6 |
| Transgressive[b] | | | | | |
| *Acer rubrum* | 0.35 | 0.81<br>−0.00 | 36 | 112<br>−0 | 1.5 |
| *Fraxinus americana* | 0.78 | 1.29<br>0.27 | 13 | 179<br>−0 | 0.5 |
| *Acer platanoides* | 0.19 | | 4 | | 0.2 |
| *Acer saccharum* | 0.11 | | 2 | | 0.1 |
| *Sassafras albidum* | 0.04 | | 1 | | <0.1 |
| *Prunus avium* | 0.02 | 0.54<br>−0.00 | <1 | 197<br>−0 | <0.1 |
| Vegetative traits | | | | | |
| Number of branches ≤ breast height | 0.54 | 1.42<br>−0.00 | — | | — |
| Tree-sized *Cornus florida* stump sprouts | 1.65 | 2.99<br>0.31 | — | | — |

[a] Confidence limits (CL) are applicable to PxR interactions in Fig. 3 and 4 only.
[b] Potential canopy species with heights ranging from below understory to within canopy.

sponse to row rather than row by position for both red oak and white oak density. Since both the $F$-ratio and confidence interval are based on probabilities, such inconsistencies occasionally arise.

Since black oak and the two vegetative traits are characterized solely by $P \times R$ interactions among the interactions (Table 2), their distributions are described completely, within the capabilities of this design, by Fig. 3 and 4. The description is essentially one of row variation by position uniformly in (independently of) the various units.

For species characterized by $P \times R \times U$ interactions, Fig. 3 and 4 give an incomplete picture in that the variation associated with units is ignored. The row means are derived from all three units as a whole, and it is impossible to determine where (which units) along the row the known significant variation in density or basal area occurs. This type of variation is seen best by considering the transgressives.

The significant $P \times R \times U$ interaction for sweet cherry density shows that significantly greater densities occur only in the edge rows of certain units on both sides of the forest (Fig. 5). These clumps of

TABLE 2. Summary of interactions and main effects for density and basal area, by species or vegetative trait, in the tree layer of forest center and edges (X = significant)

| Density | | | | | | | | Basal area | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P | R | U | PxR | PxU | RxU | PxRxU | Species or vegetative trait | P | R | U | PxR | PxU | RxU | PxRxU |
| X | X | X | X | X | | | Total tree | | X | | X | | | |
| | | | | | | | Understory | | | | | | | |
| X | | X | X | X | | | *Cornus florida* | X | X | X | X | X | X | X |
| | | | | | | | Canopy | | | | | | | |
| | X | X | X | | X | X | Total oak | | X | | X | | | |
| | X | | | | | | *Quercus alba* | | | | X | | | |
| | | | X | | | | *Q. velutina* | | X | | X | | | |
| X | X | X | | X | | | *Q. rubra* and *coccinea* | | X | X | X | X | X | X |
| | | | | | | | *Carya ovalis* | | | | | | X | |
| | | | | | | | Transgressive | | | | | | | |
| X | X | X | | X | | X | *Prunus avium* | X | X | | | X | | |
| X | | X | | X | | X | *Fraxinus americana* | | X | | | X | | X |
| X | | X | | X | | | *Acer rubrum* | X | | X | | X | | |
| | | | | | | | Vegetative traits | | | | | | | |
| | | | | | | | Number of branches | | | | | | | |
| | X | X | X | | | | ≤ breast height | Not applicable | | | | | | |
| | | | | | | | Tree-sized *Cornus florida* | | | | | | | |
| | | | X | | | | stump sprouts | Not applicable | | | | | | |

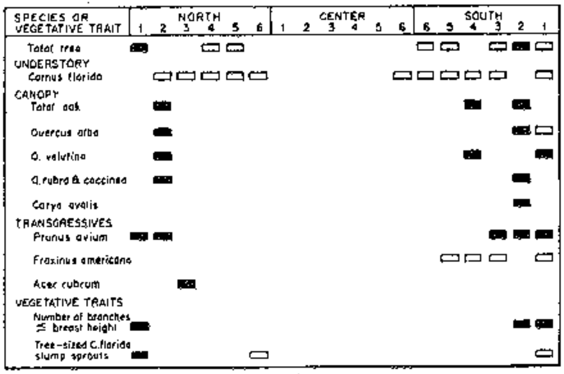

FIG. 3. Density per quadrat (100 m²) in the tree layer by rows at the three positions ($P \times R$ interaction) compared to the center mean. Shaded and open bars indicate values significantly greater and less than center mean (as shown in Table 1), respectively.

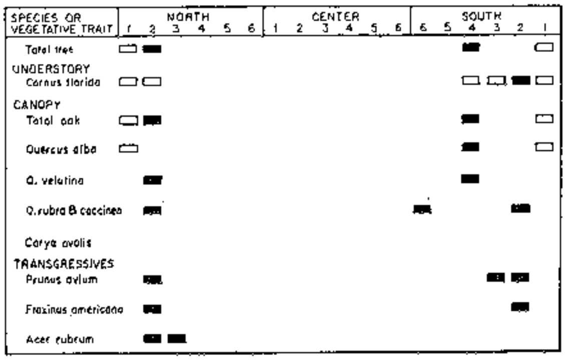

FIG. 4. Basal area (cm²) per quadrat (100 m²) in the tree layer by rows at the three positions ($P \times R$ interaction) compared to the center mean. Shaded and open bars indicate values significantly greater and less than center mean (as shown in Table 1), respectively.

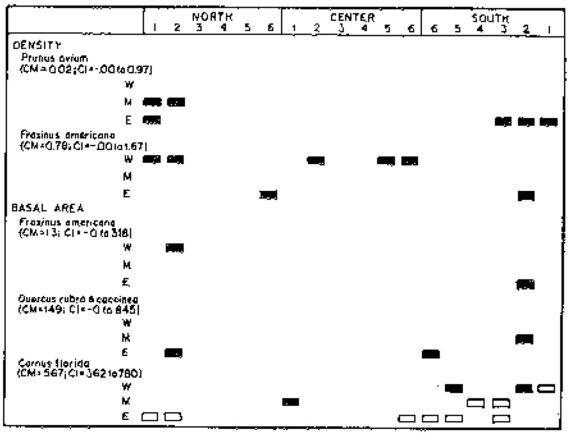

FIG. 5. Density and basal area per 100-m² quadrat of selected species in the tree layer by position, row, and unit ($P \times R \times U$ interaction) compared to the center mean. Shaded and open bars indicate values significantly greater and less than center mean, respectively. W, west; M, middle; E, east. CM, center mean; CI, confidence interval.

trees at the edges account for the significantly greater number of trees in the units where they occur (Fig. 6). For sweet cherry basal area, the nonsignificant $P \times R \times U$ interaction (Table 2) indicates that there is less unit-to-unit variation in the response to $P \times R$ than is observed for density. Furthermore, as is the case with density, the variation between replicates is so great that the $F$-ratio distinguishes merely an $R$ main effect rather than a $P \times R$ interaction.

Red maple shows a tendency to clump in the edge units, but in contrast to sweet cherry, the

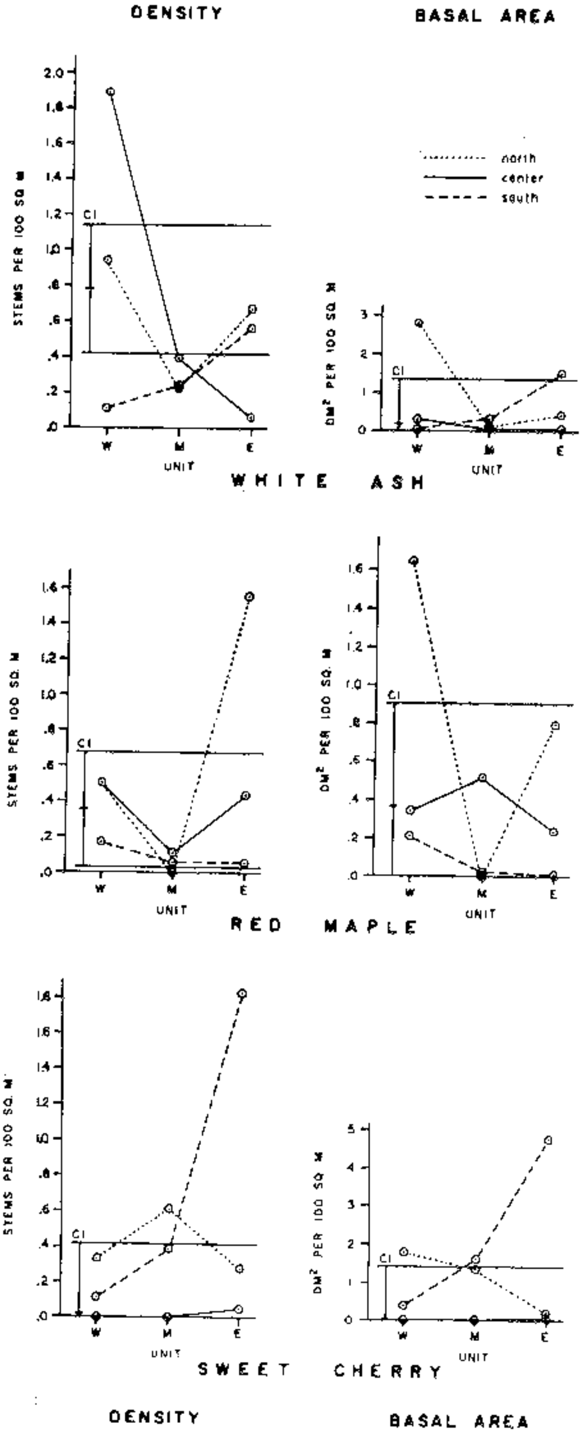

FIG. 6. Significant $P \times U$ interactions of density and basal area for trees of transgressive species. W, west; M, middle; E, east. CI, confidence interval.

clumping is independent of row (Table 2 and Fig. 6).

As indicated by significant $P \times R \times U$ interactions for both density and basal area and a significant row main effect for basal area (Table 2), white ash is intermediate between sweet cherry and red maple in its response at the edge. In Fig. 5 several rows both in the center and at the edges have densities significantly greater than the center mean, but basal area is significantly greater than the center mean on only two rows near the edge where the density is high. Thus, there are clumps of trees both in the stand and along the edges, but only at the edges are there large trees. The heterogeneity of the white ash distribution both in the center and at the edges is indicated further in Fig. 6. Only the units which have the clumps fall within or above the confidence interval of the center mean.

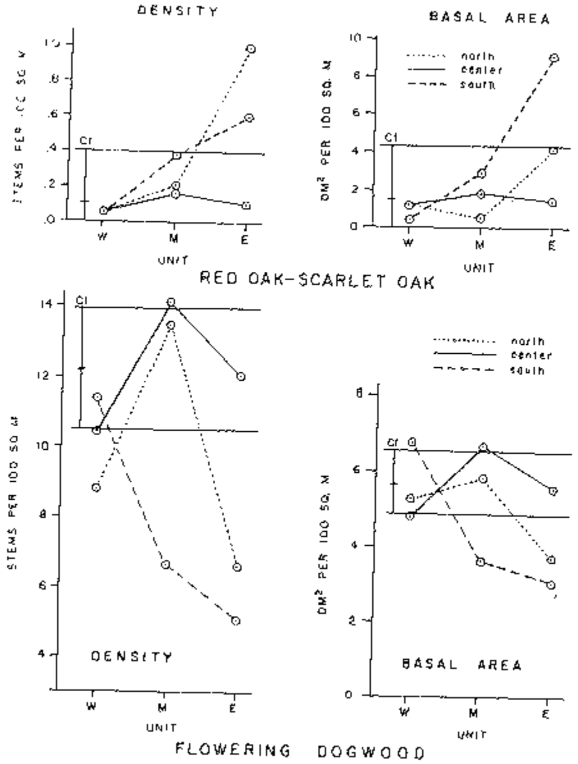

FIG. 7. Significant $P \times U$ interactions of density and basal area for canopy and understory trees. W, west; M, middle; E, east. CI, confidence interval.

Among canopy species, red oak is the only oak which shows significant variation along as well as into the edge (Table 2, Fig. 7). For basal area, the response to $P \times R$ from unit to unit is variable enough so that the $P \times R \times U$ interaction is significant. Clumping in rows at both edges (Fig. 5) accounts for this significance and also the high basal area in the SE unit (Fig. 7).

Flowering dogwood has perhaps the most complex distribution. In the center, one of the six row values in the significant $P \times R$ interaction for density falls outside the confidence interval of the center mean (Fig. 3). Moreover, the same is true of two of the three center values in the significant $P \times U$

interactions for both density and basal area (Fig. 7). This is taken as evidence that the flowering dogwood distribution lacks homogeneity, such as that demonstrated by the oak distributions in the center. As seen in Fig. 7, the variation along the edges is as great or greater than that within the stand. For basal area, the response to $P \times R$ from unit to unit is variable enough so that the $P \times R \times U$ interaction is significant (Table 2). Clumping near the edge on the south primarily accounts for this significance (Fig. 5) and primarily accounts for the high basal area on the SW unit (Fig. 7).

The density of tree-sized flowering dogwood stump sprouts is significantly greater than in the forest center (FC) on N1 and significantly less than in the forest center on S1 and N6 (Fig. 3). Since the number of stump sprouts is a function of the number of past or present trees, or both, it is also meaningful to determine what proportion of the total number of existing stems is of sprout origin. For the center mean, N1, S1, and N6 the values are 13%, 55%, 0%, and 24%, respectively.

*Reproductive size classes.*—The species found as seedling- and sapling-sized stems in the forest center are shown in Table 3. The paucity of oak reproduction noted by Monk (1961*a*) is readily apparent; white ash and flowering dogwood account for over 80% of both the seedling- and sapling-sized stems.

The stems tabulated in Table 3 include those of seedling- and sapling-sized stump sprouts not associated with tree-sized stems and occasional root sprouts for a few species. For seedlings, the sprout categories are comparatively unimportant (average approximately 10% of the stems). Among saplings for the most numerous transgressives, and especially for flowering dogwood, stump sprouts account for one-third to two-thirds of the total stems in each case. Furthermore, for flowering dogwood, seedling- and sapling-sized sprouts from the bases of living and dead trees account for an additional 30 stems per quadrat.

The sparse oak reproduction made an ANOVA of their distributions inappropriate. However, meaningful trends are seen by plotting diagrams of the scattered reproduction which was found. Although total oak seedlings bear no particular relationship to row or unit and the number is comparatively small (1.85 seedlings per quadrat), over three times as many were found at the south position as in the center or north edge. White oak, black oak (not found in the center), and red oak account for 40%, 20%, and 40% of the total seedlings, respectively. For total oak saplings, both position and row appear important. Although only one sapling (white oak) was recorded in the center, three saplings (red oak) were found all in row 2 on the north, and seven saplings (six black oak and one red oak) were encountered all in row 1 on the south.

TABLE 3. Density per quadrat (100 m²) in the forest center of stems in the seedling and sapling size classes (density per hectare = value per quadrat × $10^2$)

| Species or species group | Seedling | Sapling |
|---|---|---|
| Total stem | 98.15 | 34.58 |
| Understory | | |
| *Cornus florida* | 23.34 | 15.96 |
| Canopy | | |
| Total oak | 0.56 | 0.05 |
| *Quercus alba* | 0.19 | 0.05 |
| *Q. rubra* and *coccinea* | 0.37 | |
| *Carya ovalis* | 1.85[a] | 0.23 |
| *Fagus grandifolia* | | 0.14 |
| Transgressive | | |
| *Fraxinus americana* | 58.70 | 13.80 |
| *Acer rubrum* | 1.85 | 1.44 |
| *Acer platanoides* | | 0.19 |
| *Acer saccharum* | | 0.09 |
| *Sassafras albidum* | 0.37 | 0.05 |
| *Prunus avium* | 4.82 | 0.37 |
| *Viburnum purnifolium* | 4.63 | 1.57 |
| *Prunus serotina* | 1.48 | 0.23 |
| *Celtis occidentalis* | 0.37 | 0.19 |
| *Carya ovata* | [a] | 0.09 |
| *Ulmus americana* | | 0.09 |
| *Morus alba* | | 0.09 |
| *Crataegus* spp. | | 0.05 |
| *Juniperus virginiana* | 0.19 | |

[a] *Carya ovalis* seedlings contain some *C. ovata*.

Significant interactions and main effects for the densities of both seedling- and sapling-sized stems of species abundant enough to perform a meaningful ANOVA are summarized in Table 4. For seedlings, all species except black haw show only significant $P \times U$ interactions among the interaction terms. For saplings, all species except red maple show significant $P \times U$ interactions. However, in this case, sweet cherry and the composite total show significant $P \times R \times U$ interactions, and sweet cherry and black haw show significant $P \times R$ interactions.

The interaction pattern increases in complexity from seedlings to trees for flowering dogwood, sweet cherry, and white ash (Tables 2 and 4). These species are characterized by only $P \times U$ interactions as seedlings. This type of variation is also significant for saplings and trees, but additional sources of variation also are significant in the older size classes. For sweet cherry, interactions involving rows are significant for both saplings ($P \times R \times U$, $P \times R$) and trees ($P \times R \times U$). For white ash and flowering dogwood, significant row interactions occur for trees.

Trends described earlier for the oaks show a similar increased complexity of interaction pattern

TABLE 4. Summary of interactions and main effects for density, by species or species group, for seedling and sapling size classes (X = significant)

| Seedlings | | | | | | | | Saplings | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P | R | U | PxR | PxU | RxU | PxRxU | Species or species group | P | R | U | PxR | PxU | RxU | PxRxU |
| | | | | X | | | Total stem | | X | | | X | | X |
| | | | | | | | Understory | | | | | | | |
| X | | X | | X | | | *Cornus florida* | X | | | | X | | |
| | | | | | | | Transgressive | | | | | | | |
| X | | | | | | | *Viburnum prunifolium*[a] | X | | X | X | X | | |
| X | | | | X | | | *Prunus avium* | X | X | X | X | X | X | X |
| X | | | | X | | | *Fraxinus americana* | X | | X | | X | | |
| X | | X | | X | | | *Acer rubrum* | X | | X | | | | |
| X | | X | | X | | | *Sassafras albidum*[a] | X | | X | | X | | |

[a] Sassafras and black haw analyzed for seedlings and saplings although tree samples were too small for meaningful ANOVA.

by size class. For seedlings a position effect is noteworthy. For saplings, both position and row are important. As trees (Table 2), all three species show interactions or main effects involving rows. Thus, increased complexity of interaction by size class from seedlings to trees appears to be characteristic of canopy trees as well as flowering dogwood and the transgressives.

The nature of this increased complexity is illustrated best by sweet cherry. Figure 8 describes completely, within the capabilities of this design, the comparatively simple seedling distribution. This interaction changes little by size class (Fig. 8 and Fig. 6). However, the significant $P \times R \times U$ interaction (Fig. 9) is needed to describe the more complex distribution of saplings. Clumps of saplings are found in rows near the edges only in certain units on both sides of the stand. Comparison of the sweet cherry sapling and tree $P \times R \times U$ interactions (Fig. 9 and Fig. 5) reveals that the clumps of sweet cherry extend farther into the stand as saplings than as trees. Not only different types of interactions, but also the different nature of the same types for different size classes are effective in describing the changes in distributions by size class.

Several species not abundant enough to study by ANOVA were investigated by merely plotting their distributions by size class on quadrat maps. Three species found only as seedlings and saplings in the center were found in all three size classes at both stand edges. These include black cherry (*Prunus serotina*), shagbark hickory (*Carya ovata*), and black haw. In the tree size class black cherry was found more often on the north and shagbark hickory more often on the south. Tree-sized black haw was found in abundance in row 1 of all northern units and in rows 3–6 of the SM and SE units. As in the case of sweet cherry (Fig. 9 and Fig. 5), black haw extends farther into the stand at the edges as saplings than as trees. It displays the same trend of increased complexity of interaction by size class demonstrated by several other species.

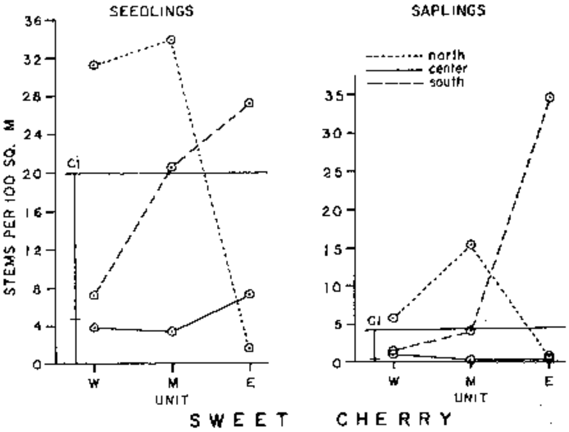

FIG. 8. Significant $P \times U$ interaction of density for sweet cherry seedlings and saplings. W, west; M, middle; E, east. CI, confidence interval.

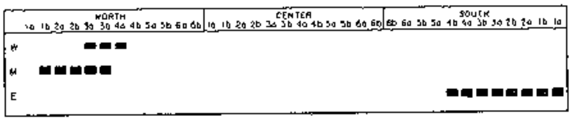

FIG. 9. Sweet cherry sapling density per quadrat by position, row, and unit ($P \times R \times U$ interaction) compared to the center mean. Shaded bars indicate values significantly greater than center mean. Center mean, 0.37; upper CL, 13.88; lower CL, –0. W, west; M, middle; E, east.

*Shrubs and herbs.*—Although this study emphasizes tree species, analyses of the distributions of the principal shrubs and herbs are included to provide additional evidence for delimiting and characterizing the edges of the stand. On an average 20-m shrub transect in the center, there are 13 m (66%) of plant cover (Table 5). Unoccupied space extends 9 m, or 45%. Thus, there are approximately 2 m (11%) of overlap between species. Most of the plant cover is almost equally divided among maple-

TABLE 5. Cover (expressed as meters per 20-m transect and as percentage) for the shrub and herb layers in the forest center

| Species or species group | Mean (m) | Upper and lower CL[a] | Percentage |
|---|---|---|---|
| Shrub | | | |
| Total plant cover | 13.2 | | 65.8 |
| Overlap | 2.2 | | 11.2 |
| *Viburnum acerifolium* | 4.8 | 6.3<br>3.3 | 24.1 |
| *Lonicera japonica* | | | |
| (1) less dense | 3.2 | 4.9<br>1.5 | 15.9 |
| (2) dense mat | 0.6 | 1.7<br>−0.0 | 3.2 |
| *Cornus florida* | | | |
| Sapling | 2.0 | | 9.8 |
| Sprout | 0.8 | | 3.9 |
| *Fraxinus americana* | 0.6 | | 2.8 |
| Branches ≤ 1.5 m high | 0.3 | 1.0<br>−0.0 | 1.4 |
| *Acer rubrum* | 0.2 | | 1.0 |
| *Rubus allegheniensis* | 0.2 | 0.5<br>−0.0 | 1.0 |
| *Viburnum prunifolium* | 0.1 | | 0.6 |
| *Lindera benzoin* | 0.1 | | 0.5 |
| *Viburnum dentatum* | T[b] | | 0.2 |
| Twelve other species | 0.3 | | 1.4 |
| Unoccupied space | 9.0 | | 45.4 |
| Herb | | | |
| *Podophyllum peltatum* | 7.5 | 9.8<br>5.2 | 37.6 |

[a] Confidence limits (CL) are applicable to PxR interactions in Fig. 10 only.
[b] T = Trace.

TABLE 6. Summary of interactions and main effects for cover of principal components of shrub layer (exclusive of tree reproduction) and herb layer (X = significant)

| Species or species group | Cover | | | | | | |
|---|---|---|---|---|---|---|---|
| | P | R | U | PxR | PxU | RxU | PxRxU |
| Shrub | | | | | | | |
| *Viburnum acerifolium* | X | X | X | X | X | X | X |
| *Lonicera japonica* | | | | | | | |
| (1) less dense | X | X | X | X | X | | X |
| (2) dense mat | X | X | X | X | X | X | X |
| *Rhus radicans* | X | X | X | X | X | X | X |
| Branches ≤ 1.5 m high | X | X | X | X | | X | X |
| *Rubus allegheniensis* | X | X | | X | X | | |
| Herb | | | | | | | |
| *Podophyllum peltatum* | X | X | X | X | | X | |

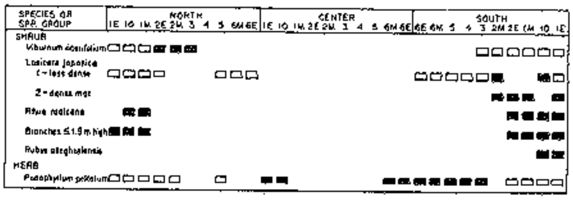

FIG. 10. Cover per 20-m transect of principal components in the shrub and herb layers by rows at the three positions ($P \times R$ interaction) compared to the center mean. Shaded and open bars indicate values significantly greater and less than center mean (as shown in Table 5), respectively.

leaved viburnum, Japanese honeysuckle (mostly less dense class 1), and sapling-sized stems of three tree species: flowering dogwood, white ash, and red maple.

All the shrub categories listed in Table 6 show significant $P \times R \times U$ interactions except *Rubus allegheniensis*. More interactions, especially $P \times R \times U$ interactions, are significant for the shrubs than for the trees or their reproductive size classes (Tables 2, 4, and 6). Thus, the shrub distributions are quite complex, more complex than most of the tree distributions. In contrast, the distribution of May-apple shows a meaningful response only to $P \times R$ among the interaction terms.

The significant $P \times R$ interactions for the various shrub categories and May-apple are summarized in Fig. 10. It should be realized from the figure headings that the first five shrub transects represent a distance of only two tree rows, while the second five represent the remaining four rows. Forest species (maple-leaved viburnum, May-apple) show significantly less cover at the immediate edge on both sides in comparison to the forest center. Conversely, poison ivy and tree branches show significantly more cover at the immediate edge on both sides, but *Rubus allegheniensis* and class 2 Japanese honeysuckle show this condition only on the south. In terms of forest composition, it is evident that tree branches and shade-intolerant shrubs with excellent capabilities of vegetative reproduction are more important than typical forest-center shrubs and herbs at both stand edges.

Figure 10 is limited, of course, in its depiction of the variation within the distributions of the various categories. It shows the overall contribution of each category by row at each position, but it gives no indication of how or where along the row the contribution is made. The existence of significant $P \times R \times U$ or $P \times U$ interactions, or both, indicates that considerable variation within rows and between units is to be expected, except in the distribution of May-apple (Table 6). Detailed analysis of this variation is beyond the scope of this work.

### *Community structure at the edges*

The total number of values significantly different from the center mean by position and row ($P \times R$ interaction) in the tree, shrub, and herb layers is summarized in Table 7 (Fig. 3, 4, and 10). The high

TABLE 7. Total number of values significantly different from the center mean in the tree, shrub, and herb layers by position and row (P × R interaction) (summary of vertical additions by row in Fig. 3, 4, and 10)

| | North | | | | | | Center | | | | | | South | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Layer | 1 | 2 | 3 | 4 | 5 | 6 | 1 | 2 | 3 | 4 | 5 | 6 | 6 | 5 | 4 | 3 | 2 | 1 |
| Tree density (Fig. 3) | 4 | 6 | 2 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 3 | 4 | 4 | 7 | 8 |
| Tree basal area (Fig. 4) | 4 | 8 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 5 | 2 | 4 | 4 |
| Shrub-herb cover (Fig. 10) | 5 | 2 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 2 | 3 | 3 | 5 |
| Total | 13 | 16 | 4 | 2 | 4 | 3 | 0 | 0 | 0 | 0 | 0 | 2 | 5 | 5 | 11 | 9 | 14 | 17 |

values characteristic of N1, N2, and S1 through S4 show the magnitude and inward extent of the combined edge response of all species at each boundary. They also show that the north edge is narrower than the south.

At this scale of variation, the problem of deriving an actual compositional gradient from the individual species distributions or patterns is not solved easily. Arranging the species together, such as in Fig. 3, 4, and 10, represents a middle ground between the more illustrative means of presentation available for each individual species (Pidgeon and Ashby 1942, Ashby 1948) and the further investigation of species assemblages through association measures. A subjective assessment of the significant interactions of the various species in the figures, supplemented by reconnaissance notes and other data not easily subjected to ANOVA, is used below to describe the structure of the edges.

The rows N2 and S4 mark the inner limits of the high numbers of significantly different values (Table 7). These two rows display many similarities in both horizontal and vertical structure. On both rows, the presence of large trees is indicated by a total tree density typical of the center paired with a significantly larger basal area. The distinguishing feature is the high basal area, contributed by the oaks on the south and by the oaks, sweet cherry, and white ash on the north. The bottom branches of the canopy trees occur at low levels on the boles and extend over and into the lowered understory of the rows exterior to both N2 and S4.

The areas exterior to N2 and S4 are different in both structure and extent. The north edge is not only narrower, but also less complex than the south edge.

N1 is essentially a low thicket of arborescent growth mingled in places with clumps of poison ivy from the shrub layer. The most distinguishing feature is the low canopy of the understory and transgressives. This is represented by significant increases (compared to center) in both the number of low branches and their cover. Most of the branches are contributed by flowering dogwood which is represented by a significantly higher number of stump sprouts than in the center. These sprouts comprise 55% of the total *Cornus florida* stems on N1. The higher number of small trees compared to the center is contributed not only by flowering dogwood, but also by higher densities of black haw and sweet cherry, the latter occurring in clumps. Scattered black cherry and an occasional shagbark hickory, not found in the center, are observed also. In the shrub layer poison ivy and tree branches dominate rather than maple-leaved viburnum and class 1 Japanese honeysuckle. Sapling-sized stems of sweet cherry in the vicinity of the tree clumps and black haw extend from N1 toward the interior. Herb-sized poison ivy, Virginia creeper, and various grasses characteristic of abandoned fields are found in the herb layer rather than May-apple.

Important features of N2 include significantly higher (than in the center) densities for each oak species and sweet cherry. These species (except white oak) and white ash also contribute significantly higher basal areas. The sweet cherry and white ash occur in clumps along the edge, and red oak shows a tendency to clump also. As on N1, scattered black cherry and shagbark hickory are observed. May-apple cover is significantly lower than the center.

On S1 scattered, small trees contribute total density and basal area significantly less than in the center. After flowering dogwood, less important because of significantly lower values of both density and basal area, sweet cherry (in clumps) and black oak, both showing density values significantly greater than the center, are most important. Clumps of poison ivy and class 2 Japanese honeysuckle in addition to *Rubus allegheniensis*, all contributing significantly higher cover values than in the center, form a dense growth between and upon the trees. Class 2 Japanese honeysuckle is replaced by the less dense class 1 immediately under the lowered canopy of the understory and transgressives. The low canopy is represented by significantly higher values than the center for both the number of low branches and their cover. Sapling-sized stems of sweet cherry associated with the tree clumps extend from S1 toward the interior. May-apple cover is significantly less than in the center. The herb layer is composed of poison ivy and grasses characteristic of old fields. It is spotty because of the dense shrub layer.

On S2 a total tree basal area typical of the center is contributed by a significantly higher density of trees. The high density is associated with significantly higher values of white oak, red oak, and sweet cherry (in clumps), in addition to flowering dogwood which shows a value higher than the other edge rows, but not significantly different from the center. Scattered shagbark hickory and an occasional black cherry, not found in the center, are observed. Basal areas significantly greater than the center are contributed in a clumped fashion by flowering dogwood, red oak, and white ash in addition to sweet cherry. In the shrub layer a significantly lower value of maple-leaved viburnum is associated with significantly higher values of poison ivy and class 1 or class 2 Japanese honeysuckle, or both, all contributed in clumps at various locations along the row. In the herb layer a significantly lower value of May-apple is associated with high values of the shrubs above or of herb-sized poison ivy.

On both S1 and S2 the intermingling of tree branches and woody vines in the shrub zone, all represented by values significantly higher than in the center, gives a thicket-like appearance to the two rows. This is especially true in S2 because of the high density of trees.

On S3 a total tree basal area typical of the center is contributed by a significantly lower number of trees. The low density is associated with significantly lower values for both white ash and flowering dogwood. Despite its low density, flowering dogwood is still the most numerous tree. It is followed by equal numbers of sweet cherry (in clumps) and black haw, both represented by values higher than the center for both density and basal area. The black haw is found only in the SM and SE units. In contrast, more flowering dogwood occurs in the SW unit. The lack of poison ivy, class 2 Japanese honeysuckle, and tree branches near the ground gives S3 a forest-like appearance. However, both maple-leaved viburnum and class 1 Japanese honeysuckle are characterized by cover values significantly lower than in the center. May-apple, with a cover value significantly greater than the center, covers approximately three-fourths of the row.

On S4 black oak and black haw (in the SM and SE units) have densities higher than the center. These species and white oak possess significantly higher basal areas than the center. Both flowering dogwood and white ash are represented by densities significantly less than in the center. In the shrub layer maple-leaved viburnum exhibits cover values typical of the center. Sapling-sized stems of sweet cherry in the vicinity of the tree clumps noted earlier terminate their inward extension.

The areas interior to both N2 and S4 are similar in that they are characterized by comparatively few values significantly different than the center. Vertical structure appears similar to that within the stand. Values of flowering dogwood are consistently lower than in the center on these rows as they are on most others at both edges. On N3 through N6 sapling-sized stems of sweet cherry in the vicinity of tree clumps extend through row 4. On the south, higher densities of both tree- and sapling-sized black haw extend from row 4 through row 6. Also, the significantly higher cover of May-apple and the significantly lower cover value of class 1 Japanese honeysuckle noted in S3 both extend through S6.

Phenological observations conducted during several periods between 1963 and 1968 indicate that differences in the timing of vegetative processes between the two edges and between the edges and the center are not very striking. The differences which do occur are found primarily during spring and fall in the herb layer, the vegetative layer closest to the climatologically active surface at those times of year (Wales 1967). During fall, defoliation tends to occur slightly earlier for all tree species at the edges than at the center.

The tree layer at the edges is distinct from the center in spring not because of differences in the timing of vegetative processes of the same species, but because many species characteristic of the edges as opposed to the center flower or leaf out, or both, earlier in spring. These indicator species include sweet cherry, black cherry, and black haw.

## DISCUSSION

### *Role of land history at the edges*

When the woods adjacent to the present forest were clear-cut and the land converted to agricultural use, the north and south edges undoubtedly were well defined. This study attempts to evaluate the changes which have occurred over the years in vegetation within these two exposure-induced microenvironments established by man. However, in a forest-climax region edges are maintained in their original positions only by continued use of the adjacent land. An edge maintained at its original position may be thought of as a stabilized edge. In contrast, abandonment leads to reforestation in front of an established edge. In this situation the edge may be thought of as an unstabilized one because both the original position of the edge and its microclimate have changed gradually. Thus, the nature and width of established forest edges are determined not only by microclimatic gradients within the edges, but also by man's continued use or disuse of the adjacent land.

Several converging lines of evidence lead to the belief that N2 and S4 are the original edges of the stand. The evidence is gathered from the vegetation itself, from scars in the vegetation left by man's activity, and from the history of the land as found in documents and the memories of both past and present owners.

In terms of present vegetation, the total number of significant differences for all layers is high and variable exterior to both N2 and S4, and relatively low and constant to the interior (Table 7). As described above, the three oak species contribute heavily to the high number of significant differences in the two rows, both in terms of density and especially basal area. Except for red oak, diameters at breast height for oaks are smaller than the center exterior to the two rows but equal to or greater than the center within these rows (*unpublished data*). Perhaps the most striking similarities are the lowness of the branches on the boles, their predominance on the field sides of the trees, and the lean of the boles toward the adjacent field. These characteristics are especially pronounced on the south.

The actual cutting date which established N2 and S4 as the original edges appears to be lost, but evidence indicates that the date was during or before settlement by Europeans. Many of the present oaks, concentrated around the 38-cm-dbh size class, were established during Colonial times when the open conditions in the lower layers, caused by frequent pre-Colonial fires, probably were still in existence (Monk 1961*b*). Growing under these conditions when the original edges were established, oaks in the vicinity of the edges and their progeny were influenced by the microclimatic transition zones created there.

Literature concerning the nature of vegetation within edges is difficult to find. However, the similarities between the oaks found in N2 and S4 are the same as characteristics noted by foresters in recent time for oaks released from competition by various thinning and cutting practices. For example, the vertical structure of the two edges is similar to, but more pronounced than, that described for red oak (and yellow-poplar) at edges of hole cuttings in poletimber stands of Appalachian hardwoods (Trimble and Tryon 1966). The increased diameter growth of white oak at the south edge is typical of that observed for over-topped trees once released (Minckler 1956 and others) and trees with unobstructed crowns. Since black oak fails under dense canopies (Fowells 1965), its presence and increased density and diameter growth at both N2 and S4 are difficult to explain in terms other than an edge effect. If N2 and S4 are the original edges, surely the origin of rows exterior to them can be found in the history of the edges.

Since European settlement, the fields adjacent to the north edge have been under the same ownership as the forest. A slight mound in row 1 under the branches of the understory trees, but in front of their boles, represents an old furrow slice which commonly accumulates along the sides of agricultural fields. This, plus barbed wire embedded in trees positioned in row 2 in two of the three units (Fig. 1), establishes that the north boundary has remained stabilized through the years. The significantly higher number of tree-sized flowering dogwood stump sprouts in row 1 indicates that the edge was trimmed from time to time, a rational act of a farmer owning both forest and field and seeking maximum use of the field.

In 1905 the Mettler family sold the field south of fields 5 and 6 to John Schnidt (Fig. 1), but permitted the new owner to farm fields 5 and 6 while working his newly acquired land. This arrangement was never changed even after Rutgers University acquired the land. Thus, although the forest and adjacent fields on the south have remained under the same ownership, the fields have not been farmed by the owner of the forest. According to a member of the Schnidt family in residence since 1912, it was a family policy not to farm close to the forest (Mrs. Frank Finch, *personal communication*). Partial abandonment, then, accounts for the advancement of the forest beyond S4. Growth-ring counts of several of the larger trees in S1 and S2 showed them to be approximately 50 years old. This coincides rather well with the initiation of the management policy described above and also the introduction of tractors, which would place a man higher and provide inducement to remain away from the low branches near the edge of the stand.

Comparison of the south edge studied here with another part of the south boundary to the west (Fig. 1) yields additional evidence indicating that forest advancement on the south is due to land use. On the south boundary to the west, the property line and forest edge coincide, and the owner of the field has plowed to his line for over 40 years (F. Rogozinski, *personal communication*). The similarities and differences between this area and the north boundary are documented elsewhere (Wales 1967). The width of the south boundary on the west is more similar to the north boundary than to the adjacent boundary on the south. The southwest boundary differs from the north in composition rather than in width and shows similarities to the adjacent boundary on the south.

From land history one learns that a low thicket (N1) has grown up in front of the relatively stabilized north edge, but that approximately 15 m of forest (S1-S3) have become established in front of the south edge which became relatively unstabilized shortly after 1900. The most interesting feature of the newly established forest strip is the structure of S2. The formation of a new edge is evidenced by oak densities significantly higher than those in the center. Although typical of values in the center, the basal area of these trees is low compared to the original edges because the trees are still young.

### *Role of microclimate*

Two analogies concerning the microclimatic and vegetational transitions are evident from the study of the variation within both the edges and center of the stand. Just as the transition zone for each microclimatic element at a single, given boundary is different, the vegetative transition for each species at that boundary is different. For several species the presence or absence of an edge response at all (white ash) or the width of the edge (sweet cherry, black haw) varies by size class for the species. Just as the transition for any one microclimatic element is different at the north and south boundaries, the vegetative transition for each species differs at the two boundaries. One would hardly expect otherwise, since the various species, each possessing a given genetic potential, interact with other species within the microclimatic transitions.

Interpretation of the segregation of species within the edges and in the center is dependent upon the recognition of four different, exposure-induced microhabitats: (1) north edge, (2) south edge, (3) well-stratified areas, and (4) gaps associated with windthrows or other disturbances within the stand.

*Edge versus gap effects.*—Reconnaissance and a pilot study verified that many of the shade-intolerant species (sassafras, sweet cherry, white ash) known to occur within forest gaps were also prevalent at the edges of the stand. Gaps, varying in size, shape, age, and hence vegetative composition, are found both in the center and at the edges, thus representing, to a greater or lesser degree, noise superimposed upon the edge gradient into an otherwise well-stratified stand. Since the relative importance of the gaps and edges was unknown, it was thought initially that so much variation might be introduced between replicates by the gaps that few significant differences would be found at the edges of the stand. (Since the replicates contain both gap and non-gap areas, variation associated with gaps is incorporated in the error mean square, against which all other sources of variation are compared.) Presumably, this would apply to the dominant oaks and especially to the shade-intolerant transgressives, since elimination of one or two oak trees is followed by establishment of several individuals of the transgressive species.

Gaps were identified and subsampled for analysis in the event that gap influences masked the edge effect. As the number of significant differences in Table 7 clearly shows, this did not occur. Gap influences are evident in the results to some extent, and it is best that they be described briefly before proceeding.

One interesting feature of the data is the relatively wide 95% confidence intervals leading to a —0.00 lower confidence limit for many species. This is in part a consequence of the increased variation within the error mean square associated with gap influence. Thus, the absence of a given species in a given quadrat is expected.

A number of cases (sweet cherry and others) have been noted where an edge effect in certain units, indicated by a significant $P \times R \times U$ interaction, also is reflected in a significant $P \times U$ interaction because of the large contribution of the edge rows in those units. For a species represented by large numbers of individuals in gaps, such as white ash, significantly higher densities than in the center are noted not only in edge rows in certain units at the boundaries, but also in one row at the interior of a boundary unit and in several rows within one unit in the center (Fig. 5). These rows all were shown to be high in gap area on the gap maps.

*Species segregation at the edges.*—A comparison of the distributions of the various species and their reproductive size classes clearly shows a segregation among species and between size classes at the edges and within the stand. These findings are especially interesting when interpreted in the light of findings concerning the physiological capabilities of the various species when available and their responses within forests on level terrain and on north and south slopes, exposure-induced microhabitats similar to the ones examined in this study.

Evidence has been presented to show that despite the elimination of numerous individuals by windthrow and disease (Reiners and Reiners 1965), each species of the nonreproducing (Table 3 and Monk 1961*b*), dominant oaks is characterized by a homogeneous distribution in the forest center (Table 2 and Fig. 7). Black oak shows the strongest response at the edges. It is described as more drought resistant and less shade tolerant than the other two species (Fowells 1965) and is especially prevalent on the south. Not only are its values for both density and basal area significantly higher than the center in the original edge (S4), but also it is the dominant oak at the leading edge of the forest strip (Fig. 3, 4).

Oak seedlings were sparse, and most of them were encountered throughout the southern units where direct light penetrates through the side of the stand, where the understory is poorly developed (Fig. 7), and where the litter layer is fairly thin over much of the area (*unpublished data*). Over 90% of the small number of saplings were found in N2 and S1 where their crowns are exposed to the more favorable light regime. Both black oak and red oak are more numerous at the edges than white oak, and black oak dominates on the south.

Scattered individuals of shagbark hickory were encountered only at the immediate edge on both sides, especially on the south. Although evidence indicating an edge response for red hickory was inconclusive, this species is found throughout the stand. Therefore, it may be inferred that red hickory is more shade tolerant than shagbark. This inference is supported by Monk's (1961*b*) sapling-height growth data which show more height growth for red hickory than shagbark hickory in dense and intermediate shade (5-35% full sunlight).

American beech (*Fagus grandifolia*) was encountered in areas peripheral to its main distribution described by Haines' (1965) map. As shown by the map, the distribution of American beech displays no edge effect. The species possesses a low compensation point (Burns 1923) and is classed as very tolerant (Baker 1949). Its presence in the forest is correlated with an increase in the clay fraction of the soil (Haines 1965) rather than the exposure-induced microclimatic effects associated with edges and gaps studied here.

Several features of the complicated distribution of flowering dogwood are of interest. On N1 the high number of small trees, which is the only density on the north not significantly lower than the center, is explained by the fact that over one-half of the stems are of stump-sprout origin. The low density of trees in S1 is a result not unexpected in a situation where a new forest is becoming established within an abandoned strip. The real problems to account for are the high density on S2, which is not significantly different from the center, and the significantly lower densities found in rows interior to both S2 and N1. Also, interior to S4 and N2, the original edges, these trees are larger in diameter than those observed in the center. Thus, somewhere beyond row 6 on both sides of the stand, flowering dogwood grades to a more dense population of smaller trees.

As a common understory component in both the southern and northern Piedmont (Oosting 1942, Monk 1961*a*), flowering dogwood is considered to be very shade tolerant (Baker 1949). It sprouts abundantly, and taller, more numerous sprouts have been observed after winter cuttings than after midsummer cuttings in North Carolina (Buell 1940). Also, in North Carolina, soil moisture was the most important factor in seedling survival (Ferrell 1953). Flowering dogwood is susceptible to drought (May 1952).

Low reproduction in the edges compared to the center and large numbers of damaged and dead standing trees, observed especially on the south, are factors influencing the flowering dogwood distribution which appears to be related to the recent severe and prolonged drought. Its ability to sprout prolifically and the fact that flowering dogwood is a prominent member in gap closure are additional factors influencing the present distribution. A full interpretation of this distribution is dependent upon future evaluation of these various factors.

In virgin stands black cherry is associated with disturbance, usually windthrow (Fowells 1965). Within Hutcheson Memorial Forest naturalized sweet cherry is more numerous within such areas than the native black cherry. In the center both species are represented as seedlings, but there are fewer black cherry saplings and only sweet cherry is represented by trees. These trees are invariably associated with disturbance, usually windthrow.

Just as the more mesic north and east slopes are more favorable for black cherry than south and west slopes in the Middle Atlantic States (Hough 1953), the north boundary is more favorable for black cherry than the south boundary. Although scattered trees occur at the immediate edges on both sides, there is five times more black cherry on the north.

Sweet cherry is represented by clumps of trees along both edges. It is found within both the thicket-like N1 and original edge N2 on the north and the full width of the forest strip (S1-S3) on the south. Scattered larger trees are found interior to the clumps in both edges. Thus, sweet cherry extends farther into the edges than black cherry on both sides. From their responses both within the forest and at its edges, one may infer that sweet cherry is slightly more shade tolerant than the native species.

Sweet cherry seed dissemination by gravity from seed trees mostly occurring in clumps and successful seedling establishment are the logical factors accounting for the similarity of the $P \times U$ interactions for seedlings and trees. Since in the center the trees found in gaps usually are not large enough to produce seed, bird dissemination must account for most of the seedlings established within the stand. Presumably, limited dissemination as well as competitive interactions among species prominent in gap closure account for the limited number of sweet cherry trees in gaps in the stand.

As factors such as low light intensity and root competition for moisture take their toll among the larger seedling populations near tree clumps in both edges, a sapling distribution develops which indicates that sweet cherry penetrates both edges farther as saplings than as trees. Most of the sapling-sized stems interior to the trees are multiple-stemmed sapling sprouts. Apparently adverse factors are limiting the advance of sweet cherry farther into the stand, since the sapling sprouts leaf out early and show growth in the spring, but are leafless and often die back by summer. In contrast, sapling populations not significantly different from the center produce significantly higher tree populations under the higher light regime near the edge, as shown on NE1 (Fig. 5, 9).

White ash, shade tolerant in youth but increasingly intolerant with age (Guenther 1951), is a major component of second-growth forests in the Northeast and is consistently found in small numbers in virgin stands, where it owes its existence to disturbance, usually windthrow (Cope 1948). The heterogeneity shown in the density distribution in this study is related to a tendency to clump in rows both at the edges and within the center in certain units. However, clumping of basal area occurs only at the edges.

Further investigation is needed to ascertain to what extent the increased basal area in the edges is due to increased diameter growth at the edges compared to the center per se, and to what extent it is due merely to the uneven age of the white ash trees. Several obviously older trees contribute greatly to the increased basal areas in N2 and S2. In contrast, the population within the stand is comprised primarily of young trees, established since the canopy was opened considerably in 1950.

Sugar maple has a low compensation point (Burns 1923) and is classed as very tolerant (Baker 1949). It shows a strong response to release after several years of suppression (Conover and Ralston 1959). Height growth of sugar maple saplings in dense shade (1–6% full sunlight) was greater than that of other species studied in Hutcheson Memorial Forest (Monk 1961*b*). Growth of Norway maple, which was studied only in intermediate shade (30% full sunlight), approached that of sugar maple. Increased importance with time of sugar maple and possibly Norway maple in the stand was suggested by Monk (1961*b*) because of the low survival of oak saplings and the successful introduction of both maples. Cessation of Indian fires and the subsequent development of a dense shrub layer were seen as the causative factors presently favoring the more fire-sensitive, shade-tolerant maples over the less fire-sensitive, shade-intolerant oaks.

Although the data are not directly comparable, it is evident that 10 years after Monk's (1961*b*) sampling, both sugar maple and Norway maple are important components of the stand. Seedling and sapling populations of both species are associated primarily with the local presence of young seed trees. Norway maple in all size classes was found in the plots of all three positions, except that no seedlings were found in the center plots. Trees and saplings of sugar maple were found throughout center and north units, but seedlings were found only on the north. No sugar maple was encountered in southern plots. The distributions of both species show no relationship to rows at either edge of the stand.

Red maple is considered as a major component in gap closure by Monk (1961*a*). In this study its distribution shows clumping along the north edge (Fig. 6), but no significant variation into either edge (Tables 2, 4, and 6). It is classed as tolerant by Baker (1949) and showed less sapling height growth than sugar maple in dense (about 8% full sunlight) shade, and less growth than either sugar maple or Norway maple in intermediate (about 35% full sunlight) shade (Monk 1961*b*).

Sassafras was found infrequently in gaps as small trees in the forest center, but it is locally important in the SW unit where several trees measuring over 20 cm dbh were observed in rows 2, 3, and 4. Tree-sized sassafras also occur in other southern units, but not in northern ones. The local concentration in the SW forest strip probably represents a remnant of the secondary succession within the area, since Bard (1952) reports this species as prominent in 60-year fields. A number of dead, overtopped trees indicates that suppression leads to elimination.

Monk (1957) saw such a strong relationship between open canopy conditions and the presence of black haw that he used the species as an indicator for disturbance and classed one narrow section of the forest characterized by much side light and many blowdowns as the black haw shrub type. Similar results were obtained in this study. Although encountered only as seedling- and sapling-sized stems in the center, tree-sized black haw is a consistent component of the thicket-like N1 where individuals with their crowns exposed to the more favorable light intensity are quite vigorous.

A number of features noted interior to row 3 in the SM unit and especially in the SE unit are the same as features described for Monk's (1957) black haw shrub type, and it may be that this area was overlooked in his study. These features include the increased densities compared to the center of black haw and sweet cherry in both the tree and sapling size classes, the significantly decreased density compared to the center of flowering dogwood, and the increased number of white ash compared to the other unit on the south.

A general relationship which applies to most species is an increasing complexity in their distributions from seedlings to trees. Seed dispersal, germination, and seedling establishment and survival all influence the seedling distributions, usually represented only by significant $P \times U$ interactions. As time passes, the seedlings of the various species interact with other species within the different microhabitats, including gaps and well-stratified areas in the stand and the north and south edges. Certain species are favored over others in the different areas, resulting in local concentrations and hence more complex distributions for many species, represented by larger numbers of significant interactions. As the process continues among saplings, tree distributions are developed, characterized by a still greater complexity as indicated by still higher numbers of significant interactions, especially $P \times R \times U$ interactions. When the significant interactions are investigated, it is apparent that no two species are distributed and thus segregated in exactly the same way.

The ANOVA has identified the shrub distributions as opposed to those of the trees or their reproductive size classes as the most complex distributions, by virtue of their high number of significant interactions, especially $P \times R \times U$ interactions. The fact that shrubs are sensitive indicators of habitat conditions has been used by a number of investigators to classify different forest types (Oosting and Billings 1939, Daubenmire 1952, Monk 1957). The great value of shrubs as indicators of edge effect within a single forest type is shown in Fig. 10.

Future studies should be devoted to the determination of the physiological bases for the segregations of species described above. Partly as a result of the soil moisture vs. light controversy, there is considerable literature concerning competitive interactions between pines and hardwoods involving such factors as light, water, and minerals. However, literature concerning similar interactions between the hardwoods themselves or the hardwoods and various shrub components is found much less easily. Moreover, the possible roles of chemical interactions (auto-intoxication, synergism, allelopathy) and of animals during establishment of dominance and pattern have been investigated very little thus far in eastern deciduous forests.

A pronounced segregation of species is observed on the relatively steep north-south slopes of the central Appalachian Mountains (Smith 1966 and others). A more subtle segregation of species occurs on the north and south slopes of hills on the New Jersey Piedmont. For example, Cantlon (1953), working on a hill 180 m high near my study area, described an oak-hickory forest in which northern hardwood members are more important on the north slope. Among oaks and hickories, red oak is more important on the north slope, and black oak and hickories are more important on the south. My analysis shows a similar, yet even more subtle segregation of species over short distances within edges of forests on level terrain.

The edges share with forest gaps both a vertical and a horizontal structure intermediate between that of the well-stratified forest and adjacent old fields. Species prevalent in the later stages of secondary succession, especially shade-intolerant species and species characterized by good vegetative reproduction, are the ones prevalent within the edges and gaps of the stand.

Although the species composition varies somewhat with latitude, the border zones between individual stands of forest and grassland within the prairie-forest margin bear a resemblance to those examined in this study. There is usually a thicket-like low tree zone or a shrub thicket, or both, between forest and grassland proper (Weaver 1954). As within old field-forest edges, shade-intolerant species and species characterized by good vegetative reproduction are prominent among the species found in these zones. For example, species of *Rhus*, *Rubus*, *Prunus*, *Amelanchier*, and others are listed as representative members.

*Interrelationships between history, microclimate, and vegetation.*—As the thicket-like N1 grew up over the years, it gradually modified the microclimate to which it was responding at the original edge. The effective width of the microclimatic transition zone is narrower on the north boundary than on the south. The light regime of the north edge is dominated by diffuse light except for short periods each day during summer when direct light is incident upon the edge. Thus, the penetration of light into the north side is negligible. The advective influences of wind and precipitation, most active on the north during the dormant season, have the greatest penetration into the stand. The thermal regime during the growing season is not dissimilar from that in the center of the stand (Wales 1967).

In view of its history of stabilization and narrow microclimatic transition, especially during the growing season, it is not surprising to find that the north boundary is characterized by a narrow vegetational transition, the inner limit of which, for practical purposes, is found in the original edge N2. Only an increased density of depauperate sweet cherry sapling sprouts and a decreased density of flowering dogwood trees represent edge influences beyond N2.

Reforestation of the abandoned strip in front of the original south boundary complicates the situation in terms of the width of microclimatic and vegetative transition zones. As the forest grew up within the original field periphery, the microclimate and vegetation within the original edge and field periphery were changed.

Direct light dominates the light regime of the present south edge. Not only the duration of sunshine and the total amount of solar energy, but also the depth of light penetration into the side of the stand, are greater on the south than on the north. Prevailing winds during the growing season are incident upon and penetrate into the south edge. The south is usually the warmest margin of the stand. Daily maximum temperatures 11°C warmer than the north have been observed at 5 cm above the litter during every season of the year. For most elements the microclimatic transition zone is wider on the south than on the north, especially during the growing season (Wales 1967).

Microclimatic conditions similar to those described above probably existed within the original forest edge. As the new forest grew up within the abandoned strip, the associated microclimate must have had similarities to that described for old fields (Sparkes and Buell 1955). With the coalescence of individual crowns to form a closed canopy and associated forest microclimate, many properties of the microclimate at the original edge were transferred to the new edge in the forest strip.

The general sequence of vegetation development in the forest strip may have been similar to that described in old fields (Bard 1952). After the crowns coalesced to form a canopy and a forest microclimate developed, many properties of the vegetation in the original edge were lost in the lower layers of the stand.

In view of its recent history of instability and its wide microclimatic transition, especially during the growing season, it is not surprising to find that the south boundary is characterized by a wide vegetational transition. The present inner limits, for practical purposes, are less well defined than on the north. The decreased density of flowering dogwood and increased density of both tree- and sapling-sized black haw (on two units) may be remnants related to microclimatic conditions once existent within the original edge.

The use of the ANOVA is subject to the same statistical disadvantages as most measures of pattern. In this case, I had the opportunity to match my plots to known microclimatic gradients, thereby making biological interpretations more meaningful. In quantifying the species distributions and assessing vegetation gradients along, into, and along and into the edges and inside the stand, the positions, units, and rows of the ANOVA were used as locational indices of the environmental complex. Although the actual techniques and the scale of variation are different, the similarity of approach between this work and Whittaker's (1967) direct gradient analysis has led him (*personal communication*) to term individual forest edges "microecoclines."

## ACKNOWLEDGMENTS

I wish to express my sincere appreciation to M. A. Wales, M. F. Buell, D. E. Fairbrothers, A. V. Havens, and B. B. Stout for their helpful discussions and for their critical review of early drafts of the manuscript. B. B. Stout and M. A. Wales aided greatly with the statistical and computer-processing aspects of the work. I am indebted to C. H. Muller for many rewarding discussions of community concepts.

Financial support was provided in part by the National Science Foundation (GB 3343) and the William L. Hutcheson Memorial Forest Committee. The manuscript was written while in residence at the University of California, Santa Barbara, and I am indebted to that institution for the use of its facilities.

## LITERATURE CITED

Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. Principles of animal ecology. W. B. Saunders Co., Philadelphia. 837 p.

Ambler, M. A. 1965. Seven alien plant species. William L. Hutcheson Mem. Forest Bull. **2**(2):1–8.

Ashby, E. 1948. Statistical ecology. II. A reassessment. Bot. Rev. **14**:222–234.

Baker, F. S. 1949. A revised tolerance table. J. For. **47**:179–181.

Bard, G. E. 1952. Secondary succession on the Piedmont of New Jersey. Ecol. Monogr. **22**:195–215.

Bartlett, M. S. 1947. The use of transformations. Biometrics **3**:39–52.

Biel, E. R. 1958. The climate of New Jersey, p. 53–98. *In* S. J. Flink [ed.] Economy of New Jersey. Rutgers Univ. Press, New Brunswick, N. J.

Billings, W. D. 1952. The environmental complex in relation to plant growth and distribution. Q. Rev. Biol. **27**:251–265.

Buell, J. H. 1940. Effect of season of cutting on sprouting of dogwood. J. For. **38**:649–650.

Buell, M. F. 1957. The mature oak forest of Mettler's Woods. William L. Hutcheson Mem. Forest Bull. **1**:16–19.

Buell, M. F., H. F. Buell, and J. A. Small. 1954. Fire in the history of Mettler's Woods. Bull. Torrey Bot. Club **81**:253–255.

Buell, M. F., H. F. Buell, J. A. Small, and C. D. Monk. 1961. Drought effect on radial growth of trees in the William L. Hutcheson Memorial Forest. Bull. Torrey Bot. Club **88**:176–180.

Buell, M. F., and J. E. Cantlon. 1950. A study of two communities of the New Jersey Pine Barrens and a comparison of methods. Ecology **31**:567–586.

———. 1951. A study of two forest stands in Minnesota with an interpretation of the prairie-forest margin. Ecology **32**:294–316.

Burns, G. F. 1923. Studies in tolerance of New England forest trees. IV. Minimum light requirement referred to a definite standard. Univ. Vermont Agr. Exp. Sta. Bull. **225**:3–30.

Cantlon, J. E. 1953. Vegetation and microclimates on north and south slopes of Cushetunk Mountain, New Jersey. Ecol. Monogr. **23**:241–270.

Carpenter, J. R. 1935. Fluctuations in biotic communities. I. Prairie-forest ecotone of central Illinois. Ecology **16**:203–212.

Conover, D. F., and R. A. Ralston. 1959. Results of crop-tree thinning and pruning in northern hardwood saplings after nineteen years. J. For. **57**:551–557.

Cope, J. A. 1948. White ash management possibilities in the Northeast. J. For. **46**:744–749.

Daubenmire, R. F. 1936. The "Big Woods" of Minnesota: its structure, and relation to climate, fire and soils. Ecol. Monogr. **6**:233–268.

———. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. Ecol. Monogr. **22**:301–330.

Day, G. M. 1953. The Indian as an ecological factor in the northeastern forest. Ecology **34**:329–346.

Dunlap, D. V. 1959. Climates of the states: New Jersey. (Climatography of the U.S. No. 60–28) U.S. Gov. Printing Office, Washington, D. C.

Fernald, M. L. 1950. Gray's manual of botany. 8th ed. American Book Co., New York. 926 p.

Ferrell, W. K. 1953. Effect of environmental conditions on survival and growth of forest tree seedlings under field conditions in the Piedmont region of North Carolina. Ecology **34**: 667–688.

Fowells, H. A. [ed.] 1965. Silvics of forest trees of the United States. Forest Service, U.S. Dep. Agr., Agr. Handb. 271. 762 p.

Frei, K. R., and D. E. Fairbrothers. 1963. Floristic study of the William L. Hutcheson Memorial Forest, New Jersey. Bull. Torrey Bot. Club **90**: 338-355.

Geiger, R. 1965. The climate near the ground. (Transl. from German by Scripta Technica, Inc.) Harvard Univ. Press, Cambridge, Mass. 611 p.

Guenther, K. W. 1951. An investigation of the tolerance of white ash reproduction. J. For. **49**:576–577.

Haines, E. M. 1965. The distribution of *Fagus grandifolia* in Hutcheson Memorial Forest, New Jersey. Bull. N. J. Acad. Sci. **10**:12–21.

Horowitz, J. L., D. V. Dunlap, and M. D. Shulman. 1965. Drought in North Jersey is worst in thirty-six years. N. J. Agr. **47**:14–15.

Hough, A. F. 1953. Preliminary recommendations for the management of black cherry on the northern Allegheny Plateau. J. For. **51**:184–188.

Küchler, A. W. 1964. Potential natural vegetation of the conterminous United States. Am. Geogr. Soc. Spec. Publ. 36.

Kümmel, H. B. 1940. The geology of New Jersey. N. J. Dep. Conserv. Econ. Dev., Bull. 50. 1–203 p.

May, C. 1952. Dogwood diseases in the east. U.S. Dep. Agr. Bur. Plant Indus. Soils and Agr. Engin., 4 p.

Minckler, L. S. 1956. Response of pole-sized white oak trees to release. J. For. **55**:814–815.

Monk, C. D. 1957. Plant communities of Hutcheson Memorial Forest based on shrub distribution. Bull. Torrey Bot. Club **84**:198–206.

———. 1961*a*. The vegetation of the William L. Hutcheson Memorial Forest, New Jersey. Bull. Torrey Bot. Club **88**:156–166.

———. 1961*b*. Past and present influences on reproduction in the William L. Hutcheson Memorial Forest, New Jersey. Bull. Torrey Bot. Club **88**:167–175.

Oosting, H. J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. Am. Midl. Nat. **28**:1–126.

Oosting, H. J., and W. D. Billings. 1939. Edapho-vegetational relations in Ravenel's Woods, a virgin hemlock forest near Highlands, N. C. Am. Midl. Nat. **22**:333–350.

Oosting, H. J., and P. J. Kramer. 1946. Water and light in relation to pine reproduction. Ecology **27**: 47–53.

Pidgeon, I. M., and E. Ashby. 1942. A new quantitative method of analysis of plant communities. Aust. J. Sci. **5**:19–21.

Reiners, N. M., and W. A. Reiners. 1965. Natural harvesting of trees. William L. Hutcheson Mem. Forest Bull. **2**(2): 9–17.

Salisbury, R. D. 1902. The glacial geology of New Jersey. Vol. V. Trenton, N. J.

Shantz, H. L., and R. Zon. 1924. Natural vegetation of the United States (Part IV), 29 p. *In* O. E. Baker [ed.] Atlas of American Agriculture. U.S. Gov. Printing Office, Washington, D.C.

Small, J. A. 1961. Drought response in William L. Hutcheson Memorial Forest, 1957. Bull. Torrey Bot. Club **88**:180–183.

Smith, R. L. 1966. Ecology and field biology. Harper and Row, New York. 686 p.

Sparkes, C. H., and M. F. Buell. 1955. Microclimatological features of an old field and an oak-hickory forest in New Jersey. Ecology **36**:363–364.

Steel, R. G. D., and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., Inc., New York. 481 p.

Trimble, G. R., Jr., and E. H. Tryon. 1966. Crown encroachment into openings cut in Appalachian hardwood stands. J. For. **64**:104–108.

Ugolini, F. C. 1964. Soil development on the red beds of New Jersey. William L. Hutcheson Mem. Forest Bull. **2**(1):1–34.

Wales, B. A. 1967. Climate, microclimate and vegetation relationships on north and south forest boundaries in New Jersey. William L. Hutcheson Mem. Forest Bull. **2**(3):1–60.

Weaver, J. E. 1954. North American prairie. Johnsen Publ. Co., Lincoln, Neb. 348 p.

Whittaker, R. H. 1967. Gradient analysis of vegetation. Biol. Rev. **49**:207-264.