FORESTS OF SMALL STREAM BOTTOMS IN THE COASTAL PLAIN OF SOUTHWESTERN ALABAMA

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Abstract. Overstory and understory data were collected from 49 forest stands in 27 small stream bottoms in the Gulf Coastal Plain region of southwestern Alabama. The stands were arranged in a single-dimensioned ordination on the basis of the importance values of the persistent species in the overstories. Leading dominant species, from the “dry” end to the “wet” end of the ordination gradient, were Cornus florida, Pinus palustris, Quercus nigra, Liquidambar styraciflua, Nyssa sylvatica v. sylvatica, Magnolia virginiana, and N. sylvatica v. biflora.

Two important seral species, most prominent at the middle of the ordination gradient and of relatively little importance at either end, were Pinus elliottii and Liriodendron tulipifera. The stand position on the ordination gradient, referred to as the moisture-regime index, was significantly related to water-table depth, soil-surface gradient, and soil pH at 63.5 cm. Failure to obtain significant relationship with other soil variables was attributed to the high frequency of fresh soil deposition in the small stream bottoms. As a check on the ordination analysis, species-presence data were used to construct a species-correlation diagram. When species moisture-regime numbers from the ordination analysis were inserted in this diagram, good agreement was revealed in the results of the two independent analyses.

INTRODUCTION

In southern Alabama, “branch-bottoms” are recognized as consisting of the wet alluvial and colluvial areas along small intermittent or perennial streams. The vegetation and the habitat of these areas differ from those of both the uplands and the larger flood plains. Although individual branch-bottoms are narrow, irregular, and small, Croker (1963) estimates that they cover about one-fifth of the total longleaf pine area in southern Alabama and probably account for a third of its total productive capacity. In spite of the high frequency and large total area of the southern branch-bottoms, scientists have neglected them in the past. Increased markets for the trees in these areas, resulting primarily from increased utilization of hardwoods for pulpwood, have caused more attention to be focused on them. In addition, branch-bottom areas offer possibilities of almost ideal habitat conditions for deer, wild turkey, squirrel, and other game species. In the interest of sound ecological management in the branch-bottoms, a better knowledge of the specific plant communities and habitats is needed.

The major objectives of this study were (1) to sample quantitatively the branch-bottom forests of southwestern Alabama for the purpose of describing the community structures, and (2) to study the relationships of the community structures to certain habitat factors.

LITERATURE REVIEW

Of the several discussions in the literature on vegetation and habitats similar to those of the branch-bottoms of southwestern Alabama, only one is based essentially on quantitative data. In a study of wetter hardwood sites in north-central Florida, Monk (1966) described “mixed swamps” and “bayheads” as occurring along creeks, rivers, sloughs, and depressions where seasonal flooding is common. Mixed swamps, he found, may be dominated by Fraxinus caroliniana, Acer rubrum, Nyssa sylvatica (includes var. biflora), Liquidambar styraciflua, Taxodium distichum, and Sabal palmetto; Ulmus floridana, Quercus nigra, Q. laurifolia, Carya aquatica, and Magnolia virginiana are important locally. Bayheads are dominated by Gordonia lasianthus, Magnolia virginiana, and Persea palustris, and Liquidambar styraciflua, Nyssa sylvatica, Acer rubrum, Quercus nigra, Pinus elliottii, and Taxodium distichum are important locally.

Essentially qualitative studies have been re-
ported by Wells (1928, 1942), Pessin (1933), Harper (1943), Braun (1950), Penfound (1952), and Putnam, Furnival, and McKnight (1960). Wells' (1942) climax vegetation of "meso-hydric" sites of the Southeast might well encompass the branch-bottom vegetation of this report. Putnam et al. (1960) recognized a category of "other lowland hardwood sites" for the Southeast that would definitely include the branch-bottoms. In her classification of the deciduous forests of eastern North America, Braun (1950) apparently included the branch-bottoms of the southeastern coastal plain in her statement that "pine and sweet bay flats, with their dense tangle of shrubs and lianas, interrupt the longleaf pine woods."

THE STUDY AREA

The study area, approximately 600 square miles in extent (Fig. 1), is within the physiographic region known as the Lower Coastal Plain (Adams et al. 1926) or the Undulating Coastal Plain Province (Hodgkins 1965). The area is characterized by flat to rolling topography. The climate of the study area is characterized by abundant precipitation in all seasons and moderate to high temperatures throughout the year (U.S. Department of Agriculture Weather Bureau 1930, Long 1964). Average annual precipitation is between 60 and 65 inches (152 and 165 cm). The average "frost-free" season at Brewton is 231 days (U.S. Department of Agriculture 1941).

The recent alluvial and colluvial material in the branch-bottoms is most commonly classified in the Baldwin County soil survey as "wet loamy alluvial lands" (McBride and Burgess 1964). Soils are described as saturated most of the time and gray to black in the upper part, depending on the amount of organic matter, and gray, black, or mottled in the lower part. The exposed geologic material outside the branch-bottoms is mainly of Pliocene origin and consists predominantly of marine sands and gravels (Adams et al. 1926). The soils developed from these are, of course, generally sandy in texture. In addition, older Miocene material, consisting predominantly of marine clays, is exposed along the lower sides of the deeper valleys where the soils tend to be "heavy" or clayey in texture.

A longleaf pine forest predominates on the uplands between the branch-bottoms. Some of its species, notably longleaf pine (Pinus palustris Mill.), flowering dogwood (Cornus florida L.), southern red oak (Quercus falcata Michx. v. falcata), and hickory (Carya spp. Nutt.), impinge on the drier edges of the branch-bottoms. The longleaf forest is looked upon as a fire-stable association maintained since prehistoric times or earlier through frequent man-caused and lightning-caused burnings (Wahlenberg 1946; E. V. Komarek, personal communication). Heavy commercial exploitation over the past 60 years has brought about the present prevalent second-growth and third-growth stands, but does not seem to have caused any appreciable alteration in floristic composition. The major tree species of the branch-bottoms, other than the above species, are slash pine (Pinus elliottii Engelm. v. elliottii), yellow-poplar (Liriodendron tulipifera L.), sweetgum (Liquidambar styraciflua L.), water oak (Quercus nigra L.), black tupelo (Nyssa sylvatica Marsh v. sylvatica), swamp tupelo (N. sylvatica Marsh. v. biflora (Walt.) Sarg.), sweetbay magnolia (Magnolia virginiana L.), and red maple (Acer rubrum L.).

Except for the minor proportion of its area in the longleaf pine type, the branch-bottom forest has been subjected to fire disturbance only infrequently; the wetter areas often have no signs or history of any previous fire disturbance. Until the recent development of a market for pulpwood of the hardwood species, commercial exploitation consisted almost solely of culling out of the more valuable pines and yellow-poplar. This exploita-

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* Nomenclature used for scientific names is that of Little (1953), except that Fernald (1950) is used for non-tree species not listed in Little.
tion has produced a conspicuous decrease in the floriastic representation of slash pine and yellow-poplar, and in many areas rotting stumps of these species are the only evidence that they were ever present.

**Methods**

*Field and laboratory methods*

To obtain a well-distributed group of sample branch-bottoms, a grid was superimposed over topographic maps of the study area. Bottoms nearest the intersections of the grid lines were studied (1) if the bottom was of sufficient size to accommodate a 0.5- by 2.0-chain (0.1-acre) or 10.06- by 40.20-m (0.04-ha) plot oriented parallel to the drainage of the bottom; (2) if the bottom was not located in a sphere of disturbance from nearby roads; and (3) if the bottom showed no signs of excessive or recent disturbance from logging, agricultural operations, or other factors. As the field work progressed and the number of accessible grid-located bottoms was exhausted, the distributional requirement had to be relaxed. In all, 27 branch-bottoms were sampled (Fig. 1).

In each bottom, a transect line was oriented perpendicular to the drainage and surveyed with compass and tape. This line was extended approximately 1 chain (20.11 m) up the toe-slope on at least one side of the bottom, thus insuring the sampling at each transect line of the transitional zone between the branch-bottom forest and the upland longleaf forest. At 0.5-chain (10.06-m) intervals along this transect, the elevation above the lowest point in the bottom was determined with an Abney level. The length of the transect line was then divided subjectively into segments of relatively homogeneous vegetation and physical environment. A 0.1-acre (0.04-ha) sample plot was located in the center of each segment with its long axis perpendicular to the transect line and half of the plot on either side of the line. As stated previously, the plot was 0.5 by 2.0 chains (10.06 by 40.20 m) in dimension. Forty-nine plots were established in this manner.

Within each plot, all stems larger than 1.5 inches (3.81 cm) dbh were recorded by species to the nearest 1 inch in diameter. Hereafter, these species are called overstory species. Any stumps present were measured to the nearest 1 inch at the cut surface and recorded by species if identification was possible. Sprout production by the cut stumps was recorded when observed. Woody stems less than 1.5 inches dbh but greater than 1 ft (30.48 cm) tall were counted and recorded by species in each 10 adjoining milacre (6.6 by 6.6 ft, 2.01 by 2.01 m, 0.004 hectare) quadrats placed in a linear arrangement in the center of the 0.1-acre plot. Hereafter, these species are called understory species. Some species, *Acer rubrum* for example, occurred in both the overstory and understory. *Arundinaria tecta* (Walt.) Chapm., non-woody but classed in the understory for simplicity, was not enumerated, but simply noted if present in a quadrat. In addition, general notes were made for each 0.1-acre plot. These included presence of mosses, history of fire, evidence of grazing, extent of logging, amount and type of litter, and apparent drainage condition of the plot.

The soil was sampled with a 3.25-inch (8.26-cm) diameter bucket auger in each half of the 0.1-acre plot. Thickness, matrix color, and color and extent of mottling were noted in all well-defined horizons. Colors were recorded according to the Munsell notation (Munsell Color Co. 1954). Pint samples of these horizons were collected and dried at room temperature prior to preparation for laboratory analysis. Samples were not collected for depths of more than 72 inches (183 cm), nor was digging continued upon reaching a dense, impermeable stratum at a depth less than 72 inches. If a water table was encountered, its depth below the soil surface was noted.

Soil samples were air-dried at room temperature and then passed through a 2-mm sieve to remove gravel and large roots. The weight of the gravel-sized particles was recorded for each sample. Particle-size distribution was determined by the hydrometer method (Day 1965). Because of the high content of organic matter in many of the soils, it was necessary to digest the material with 30% H₂O₂ to prevent interference with the particle-size determination. Soil pH values were determined in a 1:1 soil:water mixture with a glass electrode pH meter (Peech 1965). Organic carbon was determined by the Walkley-Black chromic acid procedure (Allison 1965).

*Methods of classifying the vegetation and the habitat*

Two procedures were used in the synthesis of vegetation and habitat data. In the first, here-called the leading dominant analysis, the importance values of species were used to construct an ordination of the plots. Variation of vegetation and habitat factors were then studied in relation to this ordination. This procedure has been widely used by the Curtis school in the United States which, like Gleason (1926), holds that vegetation is a continuum and cannot be classified into discrete entities (Kershaw 1964). The continuum concept was developed by Cottam (1949), Curtis and McIntosh (1950, 1951), and Brown and Cur-
The procedure used in the present study, as outlined below, follows that developed by these workers.

Importance values were determined separately for overstory and understory by different methods, in accordance with the kinds of data taken. The importance value for each overstory species in a plot was the sum of its relative density in per cent and its relative dominance in per cent. Hence the sum of all importance values of overstory species in any one plot was 200. That species in the overstory having the highest importance value was designated the "leading dominant" for the plot. The importance value for each understory species in a plot was the sum of its relative density in per cent and its relative frequency in per cent. Hence the sum of all importance values for understory species in any one plot was 200. Overstory and understory importance values are obviously not comparable since they were derived partially from different kinds of measurements. For this reason the two sets of values could not be combined for the leading dominant analysis, and only the overstory importance values were used for this purpose.

Overstory importance values were determined without slash pine and yellow-poplar. Only by omitting their contributions to density and basal area could the influence of culling out of these species on the subsequent ordination of the plots be reduced or possibly eliminated. The longleaf pine was of course as heavily utilized as the slash pine, but in this case, there was no obvious reduction in the representation of the species being exploited. The longleaf was located primarily on the drier edges of the bottoms and on the toe-slopes above the bottoms. In these situations it is a major component of the essentially upland longleaf forest which has maintained itself in the face of commercial exploitation and frequent burning.

The second synthesis procedure, hereafter referred to as the correlation analysis, was designed to develop a three-dimensional diagram depicting inter-species relationships (Goodall 1953, Agnew 1961, Kershaw 1964). The data from each plot consisted only of the presence or the absence of each species and of the presence or absence of each noted item such as fire evidence and grazing evidence. Both overstory and understory data were used. All possible combinations of species and noted items were tested for degree of association by means of the chi-square test (Snedecor 1956, Steele and Torrie 1960).

Data derived from the soil analyses were taken to E. A. Perry, State soil scientist (Alabama), U. S. Soil Conservation Service, who correlated the observed profiles with standardized soil series descriptions. Thus it was possible to name and classify the soils in the branch-bottoms.

**RESULTS**

**Leading dominant analysis**

Of the 65 woody species encountered in the plots, 27 were observed in the overstory and 62 in the understory. *Arundinaria tecta*, a non-woody species, was also listed in the understory. Plots having the same leading dominant species were combined. For each leading dominant group of plots, mean importance values were computed for all the major overstory species. These data are presented in Table 1, except that six plots are not included which had leading dominant species which were not leading dominants in at least one other plot. The species order in Table 1, identical for rows and columns, has been made such that the values in each row and in each column most nearly approach a smoothed curve. The entire procedure used in Table 1 closely follows Curtis and McIntosh (1951) and Brown and Curtis (1952), who have set forth in some detail both the philosophy and the procedures for the entire leading dominant analysis. In the Table 1 analysis, slash pine and yellow-poplar were completely ig-

**Table 1.** Average importance values* of overstory species in plots with given species as leading dominants. Calculated for those species that were leading dominants in two or more plots

| Number of plots | Leading dominant       | Cornus florida | Pinus palustris | Quercus nigra | Liquidambar styraciflua | Nyssa sylvatica v. sylvatica | Magnolia virginiana | Nyssa sylvatica v. biflora |
|-----------------|-----------------------|----------------|----------------|----------------|-------------------------|--------------------------|---------------------|--------------------------|
| 2               | Cornus florida        | 71             | 44             | 24            | 14                      | -                        | -                   | -                        |
| 6               | Pinus palustris       | 18             | 129            | 6             | 14                      | 9                       | 3                   | 1                        |
| 4               | Quercus nigra        | 12             | -              | 139           | 6                       | -                       | 1                   | -                        |
| 6               | Liquidambar styraciflua | -              | 7              | 22            | 144                     | 7                       | 13                  | -                        |
| 9               | Nyssa sylvatica v. sylvatica | 3       | 4              | 2             | 12                      | 112                      | 32                  | 2                        |
| 6               | Magnolia virginiana  | -              | -              | -             | 10                      | 2                       | 24                  | 99                       |
| 10              | Nyssa sylvatica v. biflora | -        | -              | -             | 6                       | 5                       | 31                  | 119                      |

*Importance value for an overstory species is the summation of the species' relative density and relative dominance. The total of all importance values for any one plot is 200. *Liriodendron tulipifera* and *Pinus elliottii* were ignored in the computations of relative density and relative dominance.
The term moisture-regime number was chosen because it relates to the climax adaptation number of Curtis (1952) in association with one or more of the major species and ranged from 1 for high constancy and low importance values in the plots studied. The final list of moisture-regime numbers for all 25 tree species is given in Table 2.

Two points should be made. The first is that on the basis of the order shown in Table 1, a moisture-regime number (see below), similar in concept to the climax adaptation number of Curtis and McIntosh (1951), was assigned to each of the 25 tree species. Values were assigned arbitrarily and ranged from 1 for Cornus florida to 9 for Nyssa sylvatica v. biflora. The moisture-regime numbers of the tree species not shown in Table 2, except for Pinus elliottii and Liriodendron tulipifera, were assigned on the basis of their close association with one or more of the major species in that table. The final list of moisture-regime numbers for all 25 tree species is given in Table 2.

The moisture-regime number was multiplied by the importance value of each overstory species in each plot. The sum of these products for a plot gave a weighted figure which was called the moisture-regime index of the plot. This final index can vary between 200 and 1,800. The moisture-regime index of the plot can be looked upon as a measure of the total habitat as expressed by the total tree composition. Its main use was in ranking the plots along a gradient or scale, such that those plots which were most similar from the standpoint of their overstory composition were placed close together, whereas those dissimilar in composition were placed more remotely from each other (Table 3). This arrangement is a phytosociological ordination on one dimension.

By means of the smoothing technique of Brown and Curtis (1952), Fig. 2 was constructed for those overstory species that were the leading dominants in two or more plots. It shows for each species the relationship of importance value to moisture-regime index. Figure 3 shows the relationships for those species which were not leading dominants on two or more plots, but had a sufficient number of occurrences to permit the plotting of representative curves. Figure 4 is a plotting of importance values for Pinus elliottii and Liriodendron tulipifera over moisture-regime index values of the plots. For this figure, all importance values of the overstory species were re-computed with slash pine and yellow-poplar included instead of excluded. The moisture-regime index values of the plots, however, are the same as those in soil pH, percentage of carbon in the soil, soil texture, or any number of others, may not have some controlling influences over the vegetation arrangement as presented. The second point is that the ranking of a species with a certain moisture-regime number is valid only for the range of conditions encountered and for the population of the plots studied.
### Table 3. Moisture-regime indices and species importance values (ignoring Pinus elliottii and Liriodendron tulipifera) in plots or stands. Maximum importance values in stands, revealing the leading dominant species, are italicized.

| Stand number | Moisture-regime index | Quercus falcata | Quercus hirta | Populus deltoids | Pinus palustris | Betula occidentalis | Symphoricarpos occidentalis | Malus amphidromus | Lonicera maackiana | Vitis riparia | Salix nigra | Salix repens | Magnolia grandiflora |
|--------------|-----------------------|-----------------|---------------|-----------------|-----------------|-------------------|---------------------------|-----------------|-----------------|-------------|-------------|-------------|-----------------------|
| 25:3         | 332                   | 52 60           | 51            | 26              | 10              |                   |                           |                 |                 |             |             |             |                       |
| 1:3          | 336                   | 35 7            | 81            | 38              |                 |                   |                           |                 |                 |             |             |             |                       |
| 6:3          | 365                   | 34 17           | 30            | 79              | 24              | 11                |                           |                 |                 |             |             |             |                       |
| 5:1          | 358                   | 12 16           | 151           | 37              |                 |                   |                           |                 |                 |             |             |             |                       |
| 14:4         | 418                   | 16 18           | 186           | 51              |                 |                   |                           |                 |                 |             |             |             |                       |
| 6:1          | 464                   | 2 50            | 187           |                 |                 |                   |                           |                 | 187             | 23           |             |             |                       |
| 20:1         | 520                   | 20 25           | 41            |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 21:1         | 525                   | 41 11           | 188           | 23              |                 |                   |                           |                 |                 |             |             |             |                       |
| 19:2         | 527                   | 157            | 14           | 5               |                 |                   |                           |                 |                 |             |             |             |                       |
| 11:1         | 547                   | 16 9            | 3             | 5               | 178             |                   |                           |                 |                 |             |             |             |                       |
| 5:3          | 669                   | 138            | 17            |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 25:1         | 712                   | 29 48           | 183           |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 7:1          | 719                   | 4 58            | 111           |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 12:1         | 763                   | 23 12           | 71            |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 19:1         | 1075                  | 2 13            | 180           |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 22:1         | 876                   |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 22:2         | 878                   |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 19:1         | 935                   | 49             | 220           |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 24:1         | 1027                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 23:1         | 1035                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 15:1         | 1072                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 14:2         | 1093                  | 26             | 17            |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 3:1          | 1105                  | 38             | 14            |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 2:4          | 1124                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 2:1          | 1128                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 6:2          | 1206                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 4:1          | 1358                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 22:5         | 1314                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 10:1         | 1314                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 14:1         | 1317                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 6:2          | 1353                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 10:3         | 1354                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 8:2          | 1361                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 27:1         | 1553                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 22:2         | 1521                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 13:1         | 1546                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 17:1         | 1546                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 10:1         | 1553                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 20:2         | 1572                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 13:4         | 1582                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 16:18        | 1618                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 9:3          | 1619                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 13:3         | 1669                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 20:1         | 1691                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 19:2         | 1750                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
| 20:1         | 1796                  |                 |               |                 |                 |                   |                           |                 |                 |             |             |             |                       |
cies that were not leading dominants in two or more different species to each other.
and taking the sum of products of the importance value that species in all plots. The mean weighted plots. I,
preferences on the moisture-regime-index scale, species enumerated in the quadrats, mean mois­
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values of these against moisture-regime index were
moisture-regime-index values are shown for the
understory species in Table 4.

Fig. 2 and 3. These curves present graphically a composite picture of the relationships of the dif­
ferent species to each other.
Species of the understory also exhibited marked preferences on the moisture-regime-index scale, and the curves obtained by plotting the importance values of these against moisture-regime index were similar to the curves obtained for the overstory species. However, since there were 62 understory species enumerated in the quadrats, mean moisture­regime-index values are presented in the in­
terest of saving space. A mean weighted moisture­regime index was calculated for each species by taking the sum of products of the importance value times moisture regime index per plot and then dividing by the sum of the importance values of that species in all plots. The mean weighted moisture­regime-index values are shown for the understory species in Table 4.

Several given species occupy widely different relative positions along the moisture­regime index in the understory as compared to the overstory. This is largely a result of variability caused by low numbers of occurrences of the species in either of the two layers. With high numbers of occurrences for a species in both layers, and assuming that species are similarly distributed in both layers, a

Fig. 3. Importance value curves for six overstory spe­
cies that were not leading dominants in two or more
plots. 1, Quercus falcata; 2, Carya spp.; 3, Sym­
polocos tinctoria; 4, Ilex opaca; 5, Acer rubrum; 6, Cyrilla racemiflora.

Fig. 4. Importance value curves for Pinus elliottii (1) and Liriodendron tulipifera (2).

Table 4. Mean weighted moisture­regime indices for understory species (less than 1.5 inches dbh but greater than 1 ft tall) based on importance values.*

| Understory species              | Mean weighted moisture­regime indexb |
|---------------------------------|--------------------------------------|
| Crataegus ovata                 | 360                                  |
| Rhus toxica                      | 365                                  |
| Rhus copallina                  | 368                                  |
| Osmundthus americanus           | 361                                  |
| Lyonia mariana                  | 464                                  |
| Symphoia tinctoria              | 559                                  |
| Quercus falcata                 | 613                                  |
| Gelsemium sempervirens          | 652                                  |
| Aesculus flava  grungeoflavia   | 662                                  |
| Lonicera japonica               | 685                                  |
| Cornus florida                  | 691                                  |
| Quercus nigra                   | 750                                  |
| Diospyrrys virginiana           | 801                                  |
| Ilex glabra                     | 873                                  |
| Halesia spp.                    | 878                                  |
| Smilax pumila                   | 878                                  |
| Pothergilla gardeni             | 882                                  |
| Hamamelis surnalia              | 917                                  |
| Vitis rotundifolia              | 925                                  |
| Illicium floridanum             | 931                                  |
| Liquidambar styraciflua         | 933                                  |
| Smilax laurifolia               | 942                                  |
| Carya spp.                      | 978                                  |
| Nyssa sylvatica v. sylvatica    | 1019                                 |
| Salix nigra                     | 1027                                 |
| Rhus spp.                       | 1041                                 |
| Callicarpa americana            | 1014                                 |
| Vaceinium spp.                  | 1264                                 |
| Clethra alnifolia               | 1100                                 |
| Hypericum spp.                  | 1105                                 |
| Ilex opaca                      | 1111                                 |
| Ilex coriacea                   | 1146                                 |
| Ilex glabra                     | 1206                                 |
| Rhus radicans                   | 1194                                 |
| Styrax americana                | 1201                                 |
| Liriodendron tulipifera         | 1205                                 |
| Magnolia grandiflora            | 1206                                 |
| Carya spp.                      | 1206                                 |
| Cyrilla racemiflora             | 1267                                 |
| Decumaria barbara               | 1274                                 |
| Acer rubrum                     | 1276                                 |
| Crataegus ovata                 | 1286                                 |
| Cliftonia monophylla            | 1300                                 |
| Kerria japonica                 | 1323                                 |
| Magnolia virginiana             | 1329                                 |
| Lindera melissaefolium          | 1335                                 |
| Arundinario tecta               | 1358                                 |
| Rhododendron spp. (B)           | 1380                                 |
| Itea virginica                  | 1392                                 |
| Rhododendron spp. (A)           | 1403                                 |
| Morus cerasifera                | 1424                                 |
| Ceanothus ovatus                | 1425                                 |
| Atius serrulata                 | 1494                                 |
| Viburum nudum                   | 1527                                 |
| Rhus glabra                     | 1544                                 |
| Nyssa sylvatica v. bifora       | 1547                                 |
| Pyrus arbutifolia               | 1553                                 |
| Lyonia lucida                   | 1618                                 |
| Persea spp.                     | 1618                                 |
| Leucothoe catesbaei             | 1619                                 |
| Praxinus quadranulata           | 1796                                 |

*Importance value = per cent relative density + per cent relative frequency.
$\sum$ (importance value of species in each plot) (moisture regime index of plot)
\(|\sum\) (all importance values of the species)

*Mean weighted moisture­regime index of these species is unreliable, due to their low numbers of occurrences and low importance values in the plots studied.
species should occupy the same moisture-regime-index position in both layers. Of course, seral species, such as Pinus elliottii, Liriodendron tulipifera, Populus heterophylla, or Salix nigra, normally have relatively low numbers in the understory in comparison with the overstory.

Soils and topography as related to the leading dominant analysis

In general, plots with moisture-regime indices between 300 and 800 are typically of the relatively well-drained Ochlockonee, Congaree, and Ducker soils. From 800 to 1,100, the moderately well-drained Iuka and the somewhat poorly drained Mantachie are most common. Poorly drained Bibb is most common between 1,100 and 1,500. Above 1,500, the poorly drained Bibb, Chastain, and Johnston prevail. Thus, the drainage classification of the soil types follows the moisture-regime index quite well.

Soil pH at 25 inches (63.5 cm), a depth chosen to remove variability resulting from recent deposits of alluvial material, decreased at high moisture-regime index values (Fig. 5). The correlation coefficient of -0.412 is significant at the 1% level. According to Buckman and Brady (1960), soil pH is closely related to the drainage condition of the soil, poorly drained soils generally having lower pH values than better drained soils.

Another indicator of the drainage condition of a plot is the position of the free water table beneath the soil surface. In Fig. 6 this depth is plotted for each of the two soil borings in each plot against the moisture-regime index of the plot.

The correlation coefficient of -0.621 is significant at the 1% level, the water table tending to be closer to the surface as the moisture-regime index increases. However, the possible effects of arbitrarily using 50 inches (127 cm) for the depths of all water tables deeper than 50 inches should be noted.

Other soil variables were tested against moisture-regime indices, but none showed a significant relationship. Variables tested included depth of the organic topsoil layer, percentage of organic matter in the top soil, and soil texture at various positions in the soil profile. It was concluded that these variables reflected the kinds of materials recently deposited by flood waters rather than moisture regimes in situ.

The topographic gradient across a plot and across the 0.5-chain (10-m) section immediately upslope along the transect line appeared to be related to moisture-regime-index values. Slope gradient across the plot and that of the 0.5-chain section upslope were plotted against moisture-regime index in Fig. 7 and 8, respectively. The correlation coefficients of -0.433 and -0.372 are significant at the 1% level. Those plots with high gradients tend to have lower moisture-regime indices, and most of those with lower gradients have high indices (Fig. 7). This is probably due to better surface and subsurface drainage of the plots with steeper gradients. Gradients of the upslope sections of the transect (Fig. 8) show the same general relationship, i.e., the greater the slope, the lower the moisture-regime index of the plot, but
Correlation analysis

Because the understory data could not be used in the leading dominant analysis, a direct analysis of species interrelationships was made based solely upon the presence or absence of species in plots, whether in the overstory or the understory. The procedure used in this analysis follows that described by Agnew (1961).

As a first step, a list showing the understory and overstory species enumerated in each plot was prepared. Those species found in three or fewer plots were eliminated from the analysis. In addition to treating species on a presence or absence basis, certain habitat factors were also treated in the same manner. For example, if grass were present in a plot, as indicated in the field notes, this information was treated in the same manner as the presence of a plant species. Recent history of fire in a plot, presence of mosses, recent logging in the areas, presence of stream channels, and evidence of grazing by cattle or deer were also considered. In all, a total of 46 species and six habitat factors was utilized in the analysis.

A two-by-two contingency table was constructed for each possible pair of the 52 species and habitat factors, and chi-square values, with probability levels, were determined for each table. On a chance basis, 66 of the 1,362 possible pairs would show significant correlations, either positive or negative, at the 5% level of probability. Of positive correlations, the observed number (125) exceeded the expected (33) greatly, but the negative correlations (46) were not much greater than 33.

Agnew (1961) says that "the explanation of the paucity of negative correlations is that the low total number of occurrences of many species precludes any negative correlation between them."

Several factors seem to cause exception to the general rule that the steeper the slope, the lower the moisture-regime index of a plot. A plot located at the base of a slope often has a higher moisture-regime index than expected from the gradient across the plot itself. This situation results from high amounts of runoff and subsurface flow from the adjoining slope. Plots located in the center of wide bottoms often are drier than those at the edges because of the absence of this extra water. In other cases, plots have low gradients along the transect but have lower moisture-regime indices (are drier) than expected. This is often the result of greater downstream gradients.

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Pairs having significant positive correlations were arranged on a two-dimensional network (constellation) for easy visualization (Fig. 9) (see below for explanation). In the first approximation of the arrangement, significant pairs with species or habitat factors closely related to disturbance were not utilized. These pairs were those including logging, fire, stream channels, grazing, grass, Pinus elliottii, Liriodendron tulipifera, Rubus spp., Smilax laurifolia, or Lonicera japonica. This omission facilitated construction of the constellation by allowing the writers to better visualize often complex interrelationships demonstrated by undisturbed communities. These species and habitat factors, not shown in Fig. 9, were added to the constellation (Fig. 10) according to their proper relationships after the positions of the other species or habitat factors had been determined in Fig. 9. Significant negative correlations were used to confirm or deny the proposed position of any species or habitat factor in the constellation.

In placing the pairs on the constellation, the
distance between each member was governed by the reciprocal of the chi-square value of the two-way table. That is, the greater the chi-square value, the closer the members of the pair were placed. Agnew (1961) says that "the main rule followed . . . (is to) . . . obtain an arrangement in which the total length of lines indicating positive correlation is as small as possible." In actual practice, the construction of the constellation was an evolutionary process, with each successive attempt a better approximation of a "correct" diagrammatic representation of community composition. In other words, as the approximation improved, the total line length decreased.

The final constellation, neglecting disturbance-related factors, is shown in Fig. 9. Three main groups of species can be and have been conveniently segregated in Fig. 9. The group 1 species
are typical of the best drained sites, the group 2 species of the intermediate sites, and the group 3 species are typical of the sites of poorest drainage.

Among the disturbance species and habitat factors in Fig. 10, those directly related to logging operations (Lonicera japonica, Rubus spp., and of course logging itself) are found only in groups 1 and 2. Pinus elliottii and Liriodendron tulipifera, species whose presence is largely due to an absence of logging, are found in group 3. Fire-related species or habitat factors (Smilax laurifolia, grasses, and fire itself) are positioned in group 2. The habitat factor of grazing is found in group 1. The presence of stream channels, a feature directly related to water abundance, is positioned in group 3.

Comparison of results obtained by the two methods

In Fig. 11 those species common to the leading dominant analysis and the correlation analysis are retained in the constellation, and the species moisture-regime numbers (Table 2) have been added. The moisture-regime numbers follow a reasonable progression from the upper left to the lower right of the constellation. Thus agreement is good between the results of these two analyses, even though they were based on two entirely different methods that use different kinds of data.

DISCUSSION

Continuum vs. discrete classification

Daubenmire (1966) maintains that demonstration of a continuum is inherent in continuum methodology, just as demonstration of discrete units is inherent in classification methodology. We believe that the leading dominant analysis used in this study has proven the continuum in an abstract sense. That is to say, the concrete forest communities involved in this study do indeed exist on an abstract continuum scale of species composition.

In the field, however, it is equally clear that any given concrete community may be either discrete

* From Hansen (1962, “continuum” is defined as “The occurrence of populations of organisms along a gradient, forming a distribution pattern of intergrading populations. “Population” is “A group of interacting individuals of the same species or smaller Taxa in a common spatial arrangement.”
A word should be said about the deliberate use in this study of a one-dimension ordination instead of a multi-dimension technique (Goodall 1954, Bray and Curtis 1957). The writers were certain, from previous exploratory work, that soil drainage or aeration was an overriding habitat variable that would exert primary influence along one dimension. Effects of other habitat variables on the vegetation were in no way evident, leaving the impression that an enormous amount of sampling would be necessary to demonstrate such effects if they existed. The only other source of additional dimensions was succession. This source was eliminated, it was felt, when slash pine and yellow-poplar were omitted from the analysis, an omission which was necessitated in any case because of past culling practices.

For convenience in use, either the ordination gradient or the correlation constellation can be broken arbitrarily into seemingly discrete community classes. The division of the constellation in Fig. 9 is an example, but divisions should be tailored to suit specific needs. In dividing the ordination gradient, each class should be assigned a specific portion of the moisture-regime-index scale. Major and minor overstory species, ignoring slash pine and yellow-poplar, can be assigned for each class from Fig. 2 and Table 3. Slash pine and yellow-poplar might occur as seral species, of more or less importance, at any moisture-regime index above 600. Understory species can be assigned from Fig. 3 and Table 4. Actual moisture-regime index can be computed for any stand through applying the moisture-regime numbers in
Table 2 to the species importance values, as was done in this study.

Liriodendron tulipifera as a wet-site species

Yellow-poplar is generally looked upon as a site-sensitive species attaining good development only in moist but well-drained situations. According to McCarthy (1933), it rarely grows well in very dry or very wet situations. Fowells (1965) states, "Toward the southern limit of the range, where high temperatures and soil moisture probably become limiting, the species is usually confined to well-drained stream bottoms" (italics added). In the first bottoms of major flood plains, the species is notable for its absence, even from the relatively well-drained ridges.

In view of the above, the occurrence and good development of yellow-poplar in very wet branch-bottoms is very surprising. What seems to be involved is a tolerance of the species, heretofore unrecognized, for "wetness" in the form of prolonged soil saturation. The kind of "wetness" for which the species is intolerant is prolonged flooding, which is a normal occurrence in first bottoms of major flood plains. Flooding in the branch-bottoms is normally very brief, probably because of the relatively high stream gradients as well as the smallness of the watersheds involved.

Magnolia virginiana may be similar to yellow-poplar with respect to tolerance for wetness. Widely recognized in the South as a common wet-site species, it is yet notable for its almost complete absence from the first bottoms of major flood plains.

Conclusions and Applications

Perhaps the major contribution of this study is its delineation and description of a portion of the distinctive plant world of the branch-bottoms in the southeastern coastal plain. Unquestionably, a study of much broader geographic range would have correspondingly broader utility for practical application. Pending such a study, tentative applications and recommendations can be drawn from this one.

The stable vegetation offers the most perceptible and the most measurable basis for classifying the branch-bottom ecosystems. The usual soil variables which might serve the same purpose (depth of topsoil, organic matter in the topsoil, depth to mottling, and the like) are unreliable here because of the frequency of new soil depositions. The physical habitat is relatively stable, but it appears to be dependent almost solely upon the relative rates between subsurface flow of water into the branch-bottoms and subsurface drainage out of them.

The phytosociological ordination can be used as the basis for evaluating branch-bottom habitats for different purposes. Productivity is of course of prime concern, whether it be total productivity or productivity for commercial wood products or for game species. Also important are evaluations of trafficability and of various treatment effects related to management.

Productivity of the branch-bottoms for wood products is generally considered to be high (Croker 1963). It seems likely, however, that productivity will be lowest at the swamp tupelo end of the ordination gradient as developed in this study. From observation, trafficability can be said to be at least a minor problem throughout the gradient, but at moisture-regime indexes of 1,000–1,200 and above, trafficability for tractors and similar vehicles would seem to be prohibitive virtually the year around.

In the management of the branch-bottoms for wood production, the forester may be interested simply in maximum fiber production for paper pulp, or he may be interested primarily in the more valuable wood products attainable for the most part from the pines and the yellow-poplar. If maximum fiber production is his goal, he need only apply the simple coppice method in regenerating stands, assuming that he can solve his trafficability problems. The major hardwood species are prolific in their ability to sprout from the stump.

If maximum production of the more valuable pines and yellow-poplar is sought, the longleaf pine can best be treated as an extension of the adjoining upland forest while some guidance for maintaining or increasing the slash pine and the yellow-poplar can be obtained from Figure 4. Culling out of slash pine and yellow-poplar in the lower moisture-regime indices has resulted in their decline, whereas at the higher indices they are evidently limited by the habitat. Heavy cutting and logging, the provision for seed sources (or planting), and perhaps the supplementary use of herbicides on the competing species are indicated for the drier and medium moisture-regime indices; it will be difficult and costly to do much of anything on the wettest sites of the highest indices. However, if the slash pine is already the dominant species on one of these wet sites, it may be feasible to reduce the hardwoods with cutting and herbicides to the point where they can be further controlled and excluded through periodic burning, utilizing the pine litter as the major fuel. The junior author has observed the successful use of fire in this way in slash pine on Myatt soil, at about the Magnolia virginiana portion of the ordination gradient, in northern Baldwin County.
The presence of seed-bearing yellow-poplar in any branch-bottom stand scheduled for harvest would seem to present an opportunity for easily increasing the representation of that species in the regeneration stand. Clark and Boyce (1964) found in Indiana that viable yellow-poplar seed remains stored for several years in the litter and duff of undisturbed stands, ready to germinate under conditions normally associated with cutting and logging. In line with this finding, Merz and Boyce (1958), Sander (1966), and others have found that the more complete the cutting and logging, the more prolific and vigorous the yellow-poplar seedling reproduction. Although the branch-bottoms of southern Alabama are far removed from the locales of the studies cited, it seems reasonable nevertheless to at least hypothesize similar habits of the native yellow-poplar. This would indicate the desirability of thorough clear-cutting to maximize reproduction of the species. Follow-up cultural work might be necessary to ensure that the yellow-poplar seedlings are not submerged by the growth of neighboring sprouts.

LITERATURE CITED

Adams, G. L., C. Butts, L. W. Stephenson, and W. Cooke. 1926. Geology of Alabama. Geol. Surv. Alabama, Spec. Rep. 14. 321 p.

Agnew, A. D. O. 1961. The ecology of Pinus effusus L. in North Wales. J. Ecol. 49: 83-102.

Allison, L. E. 1965. Organic carbon, p. 1367-1378. In C. A. Black [ed.] Methods of soil analysis. Amer. Soc. Agron., Inc., Madison, Wisc.

Braun, E. L. 1950. Deciduous forests of eastern North America. The Blakiston Co., Philadelphia, Pa. 596 p.

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

Brown, R. T., and J. T. Curtis. 1952. The upland conifer-hardwood forests of northern Wisconsin. Ecol. Monogr. 22: 217-234.

Buckman, H. O., and N. C. Brady. 1960. The nature and properties of soils. Macmillan Co., New York. 567 p.

Clark, B. F., and S. G. Boyce. 1964. Yellow-poplar seed remains viable in the forest litter. J. Forest. 62: 564-567.

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

Crocker, T. C., Jr. 1963. Challenge of the branch-bottoms in the longleaf forests of south Alabama. J. Alabama Acad. Sci. 34: 138-139.

Curtis, J. T., and R. P. McIntosh. 1950. The interrelations of certain analytic and synthetic phytosociological characters. Ecology 31: 434-455.

Day, P. R. 1965. Particle fractionation and particle-size analysis, p. 545-567. In C. A. Black [ed.] Methods of soil analysis. Amer. Soc. Agron., Inc., Madison, Wisc.

Fernald, M. L. 1950. Gray's manual of botany. American Book Co., New York. 1632 p.

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

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

Goodall, D. W. 1953. Objective methods for the classification of vegetation. I. The use of positive interspecific correlation. Austral. J. Bot. 1: 39-63.

—. 1954. Objective methods for the classification of vegetation. III. An essay in the use of factor analysis. Austral. J. Bot. 2: 304-324.

Hansen, H. C. 1962. Dictionary of ecology. Philosophical Library, Inc., New York. 382 p.

Harper, R. M. 1943. Forests of Alabama. Geol. Surv. Alabama, Monogr. 10. 230 p.

Hodgkinis, E. J. [ed.] 1965. Southeastern forest habitat regions based on physiography. Auburn Univ. Exp. Sta. Forest Dep. Ser. No. 2. 10 p.

Kershaw, R. A. 1964. Quantitative and dynamic ecology. American Elsevier Publishing Co., Inc., New York. 183 p.

Karr, E. L. 1953. Check list of native and naturalized trees of the United States. U. S. Dep. Agr. Handb. 41. 472 p.

Long, A. R. 1964. Monthly rainfall pattern in Alabama. J. Alabama Acad. Sci. 35: 45-49.

McBridge, E. H., and L. H. Burgess. 1964. Soil survey of Baldwin County, Alabama. U. S. Dep. Agr. Soil Cons. Serv., Soil Surv. Rep., series 1960, No. 12. 110 p.

McCarthy, E. F. 1933. Yellow-poplar characteristics, growth and management. U. S. Dep. Agr. Tech. Bull. 356. 58 p.

Merz, R. W., and S. G. Boyce. 1958. Reproduction of upland hardwoods in southeastern Ohio. U. S. Dep. Agr., Cent. States For. Exp. Sta., Tech. Pap. 155. 24 p.

Monk, C. D. 1966. An ecological study of hardwood swamps in north-central Florida. Ecology 47: 649-654.

Munsell Color Co., Inc. 1954. Munsell soil color charts. Baltimore, Md. 9 charts.

Peech, M. 1965. Hydrogen-ion activity, p. 914-926. In C. A. Black [ed.] Methods of soil analysis. Amer. Soc. Agron., Inc., Madison, Wisc.

Penfound, W. T. 1952. Southern swamps and marshes. Bot. Rev. 18: 413-446.

Pessin, L. J. 1933. Forest associations on the uplands of the lower Gulf coastal plain. Ecology 14: 1-13.

Putnam, J. A., G. M. Furnival, and J. S. McKnight. 1960. Management and inventory of southern hardwoods. U. S. Dep. Agr. Handb. 181. 102 p.

Sander, I. L. 1966. Composition and distribution of hardwood reproduction after harvest cutting, p. 30-33. In Proceedings, Symposium on hardwoods of the Piedmont and coastal plain. Georgia For. Research Coun., Macon, Ga.

Snedecor, G. W. 1956. Statistical methods. Iowa State Univ. Press, Ames, Iowa. 534 p.

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

U. S. Department of Agriculture. 1941. Climate and man. Agr. Yearbook 1941. 288 p.

U. S. Department of Agriculture, Weather Bureau. 1930. Summaries of climatological data by sections. Revised ed. Section 101—Eastern, Central and South-
ern Alabama. Washington, D. C. p. 101–1 to 101–31.

Wahlenberg, W. G. 1946. Longleaf pine: its use, ecology, regeneration, protection, growth, and management. Charles Lathrop Pack Forestry Foundation, Washington, D. C. 429 p.

Wells, B. W. 1928. Plant communities of the coastal plain of North Carolina and their successional relations. Ecology 9: 230–242.

———. 1942. Ecological problems of the southeastern United States coastal plain. Bot. Rev. 8: 533–561.