

Is the Fall Line a Vegetational Boundary? Forest Succession in Pocahontas State Park, Virginia

Elizabeth Ann Wolff and Stewart Ware,
Department of Biology, College of William and Mary
Williamsburg, VA 23187-8795

ABSTRACT

Forest vegetation studies in the Coastal Plain and Piedmont of Virginia have revealed that the dominant tree species are different in those two physiographic provinces. We asked whether this difference was caused by geological differences, or by other, perhaps climatic influences. In other words, is the physiographic boundary between the two provinces (the Fall Line) also the vegetational boundary? We sampled overstory, understory, sapling, and seedling layers of 30 old but second growth hardwood sites in the Piedmont 14 km west of the Fall Line. *Quercus alba* L. was the most abundant overstory tree, as is usual for both Piedmont and Coastal Plain. Typically Coastal Plain *Q. falcata* Michx. was important in more sites than typically Piedmont species like *Q. prinus* Willd., *Q. velutina* Lam., and *Q. coccinea* Muehchh., but *Q. rubra* L., sometimes regarded as Piedmont-related, was more important than *Q. falcata*. In the understory, sapling, and seedling layers, none of the oaks were important. *Cornus florida* L., *Acer rubrum* L., *Nyssa sylvatica* Marshall, and *Ilex opaca* Aiton were important in these lower layers; the first three are widespread in both physiographic provinces and the last is a typically Coastal Plain species. Among species likely to become overstory dominants in the area, only the typically Coastal Plain *Fagus grandifolia* Ehrh. was well represented in the three lower strata, with *Liquidambar styraciflua* L. a distant second. The absence or low importance of several Piedmont oak species in the overstory and the high importance of *F. grandifolia* and *I. opaca* in the lower strata means this Piedmont site is (or will be as succession proceeds) more like the Coastal Plain than like the rest of the Piedmont. Thus, the vegetational boundary is not at the physiographic boundary (the Fall Line), but is further west.

INTRODUCTION

Virginia's Coastal Plain and Piedmont physiographic provinces have both traditionally been treated as a part of an oak-(hickory)-pine forest region. Braun (1950) put forward this assumption for the areas north of the James River, and concluded that since pine was merely a successional species, oak and hickory would ultimately dominate in the climax communities of both these physiographic provinces. Braun (1950) believed that the Virginia Coastal Plain south of the James was part of a Southern Evergreen Forest Region, and she used the Fall Line as the boundary between that region and her Oak-Hickory-Pine Forest Region to the west. Oosting (1956) asserted that Braun (1950) actually had described not the climax vegetation of this region but its "fire, flood and edaphic 'subclimaxes'." He

thus concluded that neither the Fall Line nor the James River were vegetation boundaries, and that the entire Virginia Coastal Plain would develop oak-hickory climax vegetation. Küchler (1964) likewise included all the Virginia Coastal Plain in his oak-hickory-pine forest region along with the Piedmont, and this treatment was continued by Vankat (1979) and Greller (1988).

More recently DeWitt and Ware (1979), Clark and Ware (1980), and Monette and Ware (1983) all concluded that the maturing upland hardwood forest vegetation of the Coastal Plain and Piedmont of Virginia are different from one another. Both areas have much white oak (*Quercus alba* L.) but the Piedmont forests also have much scarlet (*Q. coccinea* Muenchh.), black (*Q. velutina* Lam.), and chestnut (*Q. prinus* L.) oak, while the Coastal Plain forests have relatively little of these and instead have much beech (*Fagus grandifolia* Ehrh.) and southern red oak (*Q. falcata* Michx.).

While none of these last three works said so explicitly, at least by implication they re-erected the physiographic boundary between the Piedmont and Coastal Plain (the Fall Line) as a vegetational boundary. However, Ware (1991) pointed out that Piedmont studies have been done mostly in the western half of the Piedmont (Gemborys 1974, Clark and Ware 1980, Farrell and Ware 1991), rather than the eastern part near the Fall Line, and that the vegetational boundary might not coincide with the Fall Line, but rather might be west of there, and that it might be a broad transition instead of a narrow zone like the Fall Line.

It is unknown whether the differences between the vegetation of these physiographic provinces in Virginia arise because of the geological and associated edaphic differences between the Coastal Plain and Piedmont provinces, or because of climatic differences between the western Piedmont and the more maritime-influenced Coastal Plain. The Swift Creek Natural Area of Pocahontas State Park in Chesterfield Co., VA, is 15 km west of the Fall Line, and geologically is clearly in the Piedmont, complete with the above-ground boulders and small rock exposures that characterize many Piedmont woods. However, it is geographically very close to the Coastal Plain and might be expected to be climatically much like the inner Coastal Plain. We undertook this quantitative study of vegetation and soil characteristics of the area to determine whether Coastal Plain-like or Piedmont-like vegetation is present in this area, as a step toward answering the question of whether physiography and geology are the deciding factors in determining the vegetational differences, or whether some other factors, perhaps climate, might play that role. We examined the overstory (large tree), understory (small tree), sapling and seedling layers to determine how the present composition of these old but second growth woods is changing (succeeding) in comparison to adjacent regions. We also examined how species distribution and abundance in all vegetation strata are affected by direction and degree of slope and by several edaphic factors.

METHODS

Sample sites were in the Swift Creek Natural Area in Pocahontas State Park, along the hiking trails that encircle Beaver Lake (an artificial impoundment on Swift Creek) and extend southward along Park Road (VA Rt. 780). Sites were chosen by walking along the trail and placing a sample plot upslope or downslope

from the trail each time there was a major change in the direction of slope (provided the site was sufficiently undisturbed). To be judged suitable for sampling, sites had to be dominated by large old hardwood trees and lack obvious signs of recent disturbance, such as saw-cut stumps, large canopy openings, or scorched bark (indicating recent ground fires). Areas dominated by tuliptree (*Liriodendron tulipifera* L.) were avoided, since it, like loblolly pine (*Pinus taeda* L.), is a successional species with broad ecological tolerances, and tends to obscure vegetational responses to environmental variables.

At each site a ten-meter radius circular plot was placed, and species and diameters of all trees at least 2.5 cm dbh (= diameter at breast height [1.37 m]) were recorded. Large trees were defined as woody stems ≥ 10 cm dbh, and small trees as stems ≥ 2.5 cm but < 10 cm dbh. For each species at each site in the large tree layer, percent of total basal area (= relative dominance) and percent of total density (= relative density) were calculated, and averaged to yield the relative importance value (I.V.) for a given species at that site. Species were considered important at a site if their I.V. ≥ 10 . These same procedures were used for stems in the small tree layer. Woody stems having a dbh < 2.5 cm and that were at least 1.5 m tall were considered saplings; woody plants with heights ≥ 0.5 m and < 1.5 m were classified as seedlings. Saplings and seedlings were counted but not measured. For these strata, relative density (R.D.) was calculated for each species for each site. Species were considered important at a site if their R.D. was ≥ 10 . Herbaceous species, which were very rare in these woods during our August to November sampling period, were not counted.

At the center of each plot we measured the direction of slope exposure (aspect) and degree of slope (an average of the degree of slope upslope and downslope). For correlation analysis, aspect in degrees was transformed by the cosine transformation of Beers, Dress, and Wensel (1966) (hereafter BDW aspect), with SW = lowest value and NE = highest value, and also by the asymmetric transformation of aspect of E. Crone and S. Ware (Crone 1991; hereafter C&W aspect). In the latter transformation, when aspect in degrees is 0 to 225 (N to SW), then $A' = \cos(A/1.25) + 1$, where A = aspect in degrees and A' = transformed value. When aspect is 225 - 360 (SW to N) then $A' = \cos[(A - 360)/0.75] + 1$. This transformation also assigns the lowest transformed value to SW, but the highest value in the C&W transformation is N, while it is NE in the BDW transformation. Both of these formulas were used because even though northeast slopes are considered the most favorable for total plant growth (Beers, et al. 1966), north-facing slopes are the coolest and moistest (Geiger 1965), which may affect distribution. At each sample site soil samples to 10 cm depth were extracted from three or four spots within the plot. Soil samples were sent to the VPI & SU soil laboratory for pH, Ca, Mg, P, K, Zn and Mn analysis. Soil texture analyses were performed using the LaMotte timed sedimentation method. As a rough approximation of soil organic matter, soils were grouped into six categories based on color, with the lightest colored soils given a value of one, and the darkest a value of six. Vegetation data were subjected to detrended correspondence analysis (DCA) ordination using CANOCO software (Ter Braak 1988). Tests for Pearson product-moment correlation of the various measured environmental variables with the ordination axes were used to detect vegetation-environment relationships.

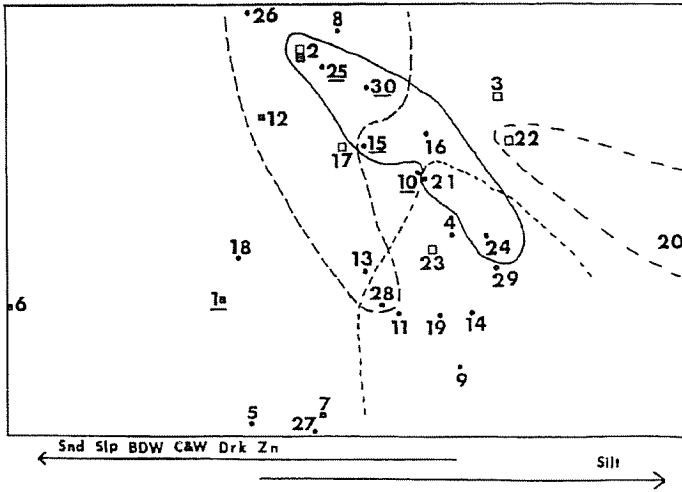


FIGURE 1a. ADCA ordination of the overstory layer of the 30 sampled sites. Arrows indicate direction of correlation of environmental variables with the axis. Snd = % sand; Silt = % silt; Slp = degree of slope; BDW = aspect transformed by the Beers et al. (1966) formula; C&W = aspect transformed by the asymmetrical formula of Crone and Ware (Crone 1991); Drk = darkness of A horizon (organic matter); Zn = soil zinc. The lower right short-dash line encloses sites with very high I.V. ($\geq 50\%$) of *Quercus alba*, which was important all across the ordination. The solid line encloses sites with *Q. falcata* I.V. ≥ 10 ; the upper center long-dash line encloses sites with *Q. rubra* I.V. ≥ 10 ; the right dashed line encloses sites with *Q. coccinea* I.V. ≥ 10 . The five sites with underlined numbers had *Q. velutina* I.V. ≥ 10 . The five sites represented by a solid square had *Fagus grandifolia* I.V. ≥ 10 ; the sites represented by an open square had *Liquidambar styraciflua* I.V. ≥ 10 .

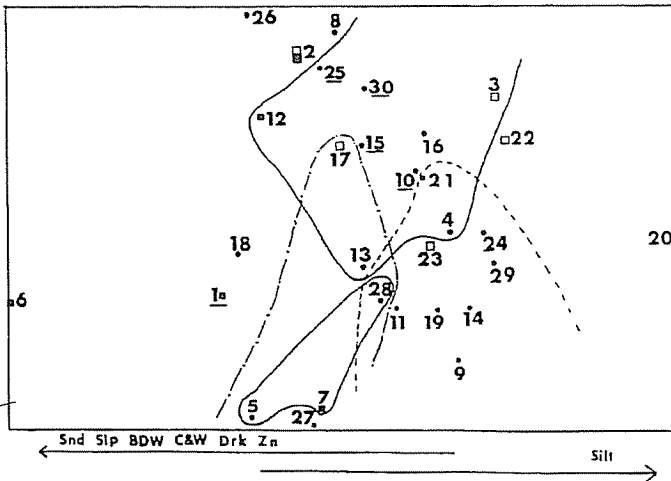


FIGURE 1b. DCA ordination as in Fig. 1a. The upper solid line encloses sites with *Liriodendron tulipifera* I.V. ≥ 10 ; the dash-dot line encloses all sites with *Carya glabra* I.V. ≥ 10 ; and the lower solid line encloses sites with *Acer rubrum* I.V. ≥ 10 . The short-dash contour enclosure with *Q. alba* I.V. ≥ 50 is repeated from Fig. 1a for ease of comparison.

TABLE 1. Mean (standard error), median, and range of environmental variables for 30 sites.

Variable	Mean (S.E.)	Median	Range
C&W aspect	1.01 (0.69)	1.03	0 - 2.00
BDW aspect	1.06 (0.73)	1.26	0 - 2.00
Slope (°)	13.15 (7.73)	10.5	2 - 34
% Sand	58.00 (8.24)	57	40 - 80
% Silt	29.92 (7.05)	30	20 - 40
% Clay	13.30 (6.96)	13	3 - 37
Soil Color	3.34 (1.27)	3	1 - 7
pH	4.72 (0.33)	4.8	4.1 - 5.4
Minerals (ppm):			
Zn	1.47 (0.47)	1.4	0.9 - 2.5
Mn	14.47 (3.47)	16.1	3.6 - 16.1
P	2.57 (1.67)	2	1 - 9
Ca	178.11 (131.42)	144	60 - 624
Mg	33.73 (18.60)	30	14 - 107
K	50.57 (11.43)	51	29 - 82

The taxonomic nomenclature of Harvill et al. (1992) is followed. Most individuals of *Carya* spp. did not have mature fruit during the period of sampling. Since the vegetative characteristics are not always reliable in separating (*C. ovalis* (Wang.) Sarg.) from *C. glabra* (Miller) Sweet (Johnson and Ware 1982), sterile plants with one or more of the vegetative characteristics of *C. ovalis* were lumped with *C. glabra*. In the sapling and seedling layers no attempt was made to separate sterile *Vaccinium* and *Gaylussacia*. Previous experience of the second author with flowering or fruiting specimens in similar woods has shown that *V. stamineum* L. and *G. baccata* (Wang.) K. Koch (and in the Coastal Plain, *G. frondosa* (L.) T. and G.) are likely to be the predominant low ericads, and *V. corymbosum* L. the predominant tall species (sapling layer).

RESULTS

Large tree layer.

The DCA ordination for large trees is shown in Figs. 1a and 1b, and environmental variables are summarized in Table 1. Significant correlations ($P < 0.05$) of environmental variables with the axis of this and later ordinations are presented in Table 2 and shown on each ordination diagram. In the large tree ordination no environmental variables were significantly correlated with the second DCA axis. Site 6, heavily dominated by mockernut hickory (*Carya tomentosa* (Poir.) Nutt) and American ash (*Fraxinus americana* L.), and site 20, heavily dominated by scarlet oak, were isolated at either end of the first axis. A second ordination omitting these two sites did not yield an improved ordination; that is, it did not spread the sites out any more broadly across the ordination, and even fewer environmental factors were correlated with the axes, so only the original ordination is presented here.

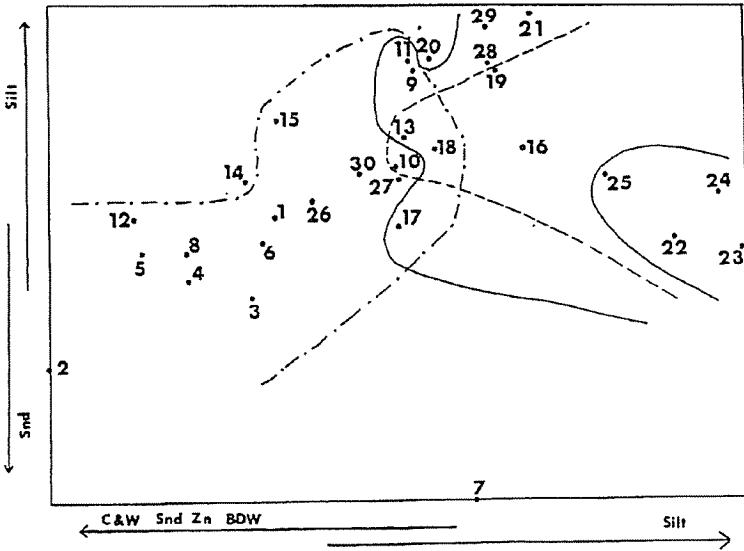


FIGURE 2a. DCA ordination as in Fig. 1a, but of the small tree layer. Sites with *Cornus florida* I.V. > 10 were spread broadly across the ordination. The upper center solid line encloses to the right sites with *Nyssa sylvatica* I.V. ≥ 10 ; the right solid line encloses sites with either *Carya glabra* or *C. tomentosa* I.V. ≥ 10 ; the dashed line encloses sites with *Liquidambar styraciflua* I.V. ≥ 10 ; the dash-dot line encloses sites with *Fagus grandifolia* I.V. ≥ 10 .

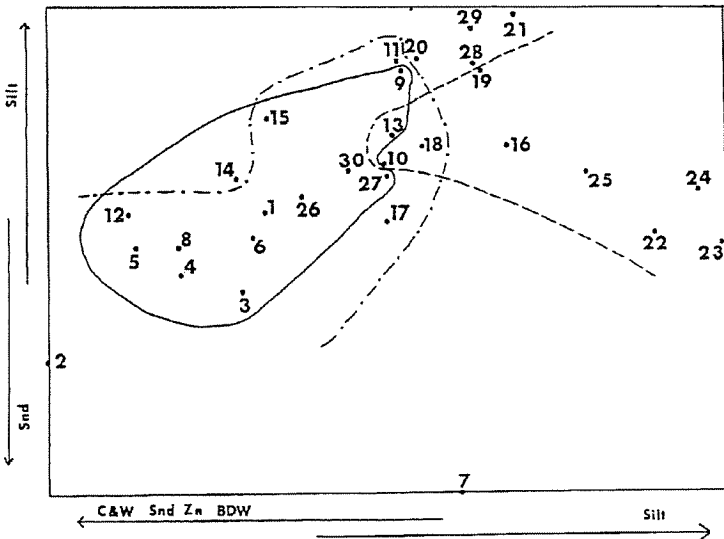


FIGURE 2b. DCA ordination as in Fig. 2a. The left solid line encloses sites with *Acer rubrum* I.V. ≥ 10 ; the right dashed line and the left dash-dot line repeat the enclosure contours for *Liquidambar styraciflua* and *Fagus grandifolia* from Fig. 2a for ease of comparison.

White oak was overwhelmingly the most important species in the overstory, with an I.V. ≥ 10 at all but two (#5 and #17) of the 30 sites, and I.V. > 25 at 21 sites. Sites in which white oak had the highest I.V.'s (≥ 50) were concentrated in the lower right center portion of the ordination (Fig 1a).

Though tuliptree-dominated sites were not sampled, this widespread species was nonetheless a component at many sample sites dominated by other species, reaching I.V. ≥ 10 at eleven sites. It was most abundant in the upper center portion of the ordination (Fig 1b), often at the same sites where southern red oak and black oak were important (Fig. 1a), and overlapping the area of high importance of northern red oak (*Q. rubra* L.). In contrast with tuliptree, sites with high pignut hickory (*Carya glabra*) I.V. were concentrated at the lower end of the second ordination axis (Fig. 1b), as were the three sites with red maple (*Acer rubrum* L.) I.V. ≥ 10 . Though there was a concentration of the red and black oaks and tuliptree at the upper end of the second ordination axis (Fig. 1a), and a concentration of pignut hickory, red maple, and highest I.V. of white oak at the lower end, none of the measured environmental variables were correlated with the second axis. The five sites with mockernut hickory I.V. ≥ 10 were scattered widely over the ordination.

Beech had an I.V. ≥ 10 in the overstory in only five of the 30 sites, with all five on the left half of the first axis of the ordination, with higher aspect values, higher sand, and darker soil (higher soil organic matter). Black oak, typically a Piedmont species, was important largely within the enclosure contour of southern red oak, a typically Coastal Plain species (Ware 1991), and the other typically Piedmont species, scarlet oak, reached I.V. ≥ 10 only at two sites. Other species that had I.V. ≥ 10 at least two sites in the overstory were sweetgum (*Liquidambar styraciflua* L.), 5 sites; and blackgum (*Nyssa sylvatica* Marshall), loblolly pine, and post oak (*Quercus stellata* Wang.), each with two sites. Chestnut oak was not encountered at all in this study.

Small tree layer.

The ordination of the small tree layer is presented in Figs. 2a and 2b. Site #7 (strongly dominated by *Carpinus caroliniana* Walt.) is isolated because though *C. caroliniana* occurred at 13 sites, it was usually of low I.V., reaching an I.V. ≥ 10 at only two other sites. Omission of site #7 did not yield an improved ordination, however. Flowering dogwood (*Cornus florida* L.), beech, red maple, black gum, holly (*Ilex opaca* Ait.), and sweet gum were important species in the small tree layer. Dogwood, an understory tree, was the most important species in this layer, with an I.V. ≥ 10 at 24 of the 30 sites. Its lowest I.V.'s were in the 5 left-most sites. Beech was the most important potential overstory species in the small tree layer. It reached I.V. ≥ 10 at 19 sites, 15 of which did not have high beech I.V. in the large tree layer. High red maple I.V. was strongly associated with high beech I.V. (Fig. 2b), while high I.V. of both blackgum and sweetgum were concentrated at the opposite end of the first axis of the ordination, where aspects were lower and soil was finer-textured. Four of the five sites with *Carya* spp. I.V. ≥ 10 were also found there. The 12 sites with high I.V. of holly were spread across the upper center of the ordination, overlapping broadly the concentration of high beech-high red

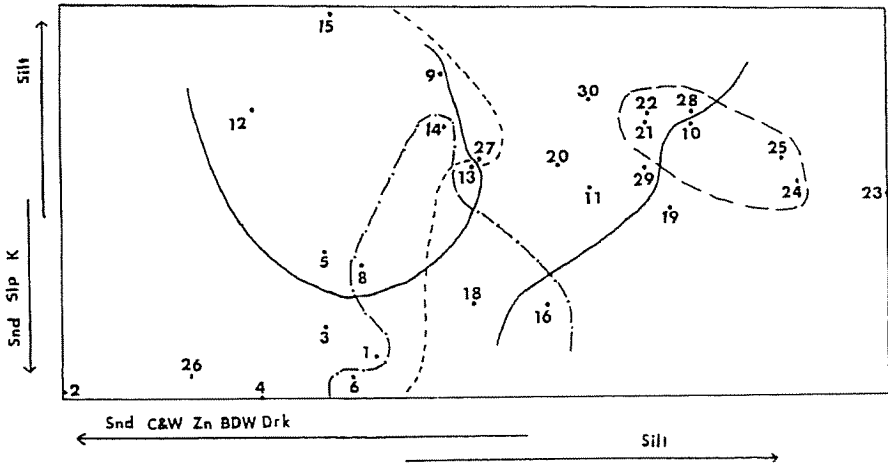


FIGURE 3. DCA ordination as in Fig. 1a, but of the sapling layer. K = soil potassium. High relative density (R.D.) of *Cornus florida* and *Ilex opaca* are spread broadly across the ordination. The short-dash line in the center encloses to the left sites with *Fagus grandifolia* R.D. ≥ 10 . The upper left solid line encloses sites with high (>25) *Acer rubrum* R.D.; the lower center dot-dash line encloses sites with *Carpinus caroliniana* R.D. ≥ 10 ; the right solid line encloses to the right sites with *Liquidambar styraciflua* R.D. ≥ 9 ; the right long-dash line encloses sites with high (>25) R.D. of *Nyssa sylvatica*.

maple and high black gum-high sweet gum sites. However, holly was absent from the six left-most and the three right-most sites.

Despite their importance in the overstory, northern red, southern red, black, and scarlet oaks and tuliptree failed to reach I.V. ≥ 10 in the small tree layer, and white oak did so in only one site.

Sapling layer.

An ordination of this layer is presented in Fig. 3. In the original ordination of the sapling layer, site 7 (heavily dominated by *Corylus americana* Walt., which occurred nowhere else) and site 17 (heavily dominated by *Asimina triloba* (L) Dunal) were isolated at the ends of the first and second DCA axes, respectively. Omission of those two anomalous sites from a second ordination produced a better spread of sites and significant correlation of several environmental variables with the first and second DCA axes, so the ordination presented here has the two anomalous sites omitted.

Dogwood was the most abundant species in the sapling layer, with relative density (R.D.) $\geq 10\%$ in 24 of the 30 sites, and R.D. $\geq 25\%$ in 15 of these sites. Three sites with no dogwood (#2, #4, #12) are on the far left of the first DCA axis. Red maple was the second most important species, with R.D. ≥ 10 at 17 sites all across the ordination, but the 7 sites with R.D. >25 were concentrated in the upper left portion of the ordination (Fig. 3). The nine sites with holly R.D. ≥ 10 were spread broadly across the ordination, co-occurring with high R.D. of every other important species in one or more sites, while sites with high *Carpinus caroliniana* were concentrated in the lower center portion of the ordination. Beech was the most important potential overstory species in the sapling layer, reaching R.D. ≥ 10

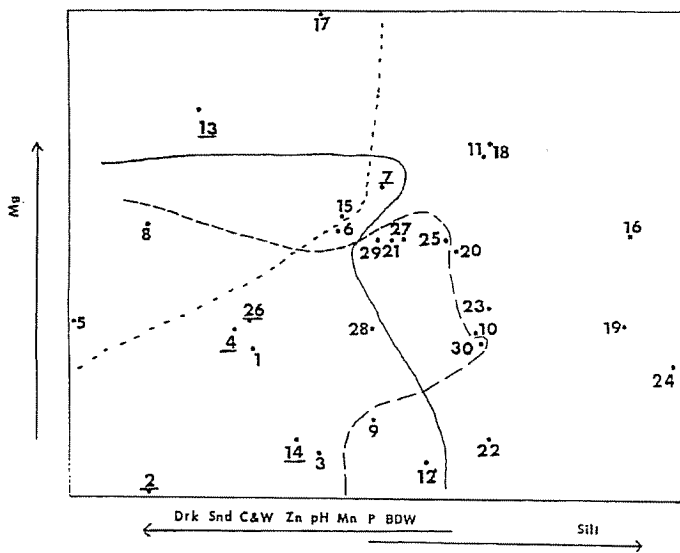


FIGURE 4a. DCA ordination as in Fig. 1a, but of the seedling layer. Additional environmental variables not given in Fig. 1a are Mg, Mn, P, and pH, referring to soil minerals and acidity. The solid line encloses sites with *Fagus grandifolia* relative density (R.D.) ≥ 10 ; the long-dash line encloses sites with *Ilex opaca* R.D. ≥ 10 ; the short-dash line encloses sites with *Asimina triloba* R.D. ≥ 10 . The six sites with their numbers underlined have *Fraxinus americana* R.D. ≥ 10 .

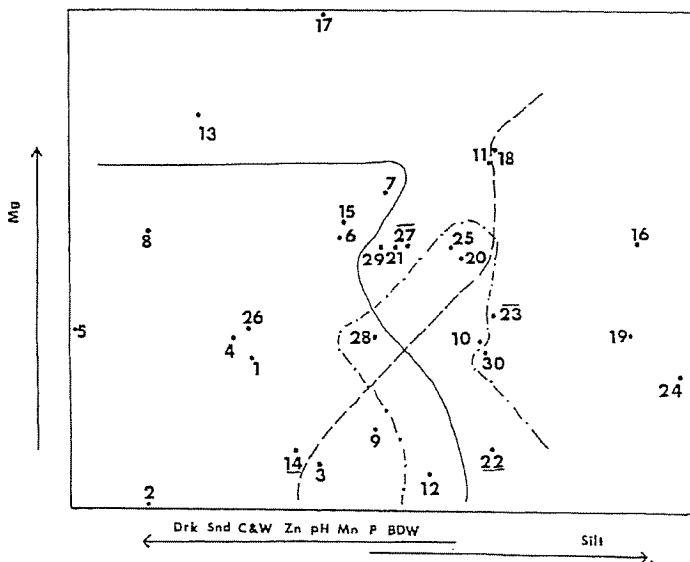


FIGURE 4b. DCA ordination as in Fig. 4a. The dashed line encloses to the right sites with *Liquidambar styraciflua* R.D. ≥ 10 ; the dot-dash line encloses sites with *Vaccinium/Gaylussacia* spp. R.D. ≥ 10 ; the solid line repeats the *Fagus grandifolia* contour from Fig. 4a for ease of comparison. The two sites with bars over the numbers had *Carya glabra* R.D. > 10 ; the two sites with bars under the numbers had *Carya tomentosa* R.D. > 10 .

in 14 sites. It was important in the left side of the ordination, in the same sites where it was important in the small tree layer. Though blackgum and sweetgum were most important in sites on the right side of the ordination where soils are silty and slope is less steep and of lower aspect, both species also reached R.D. ≥ 10 in some sites on the left side of the ordination. American ash reached R.D. ≥ 10 in two sites and was present in seven other sites, all on the left half of the ordination. Of other species important in the large tree (overstory) layer, northern red oak, mockernut hickory, pignut hickory and tuliptree reached R.D. ≥ 10 in only one site each in the sapling layer.

Seedling layer.

The ordination of the seedling layer is presented in Figs. 4a and 4b. More measured variables were significantly associated with this ordination than with any of the other layers. Dogwood was abundant as a seedling all across the ordination, reaching I.V. ≥ 10 at 21 sites. The areas of high concentration of holly, beech, white ash, and *Asimina triloba* (Fig. 4a) were on the left half of the first axis. Sweetgum was concentrated on the right and lower center portion of the ordination (Fig. 4b), and *Vaccinium/Gaylussacia* spp. were concentrated in the lower right center of the ordination. Red maple reached R.D. ≥ 10 in only two sites. Other species with R.D. ≥ 10 in at least two sites were *Carpinus caroliniana* (four widely scattered sites), pignut hickory, mockernut hickory, white oak, and *Diospyros virginiana* L. (persimmon).

DISCUSSION

Though white oak was the overwhelming dominant in the overstory, it was not reproducing itself, for it was important at only one site of the small tree layer and at only two sites of the seedling layer; the species did not reach R.D. ≥ 10 in the sapling layer. Our study area was like the Coastal Plain study area of Monette and Ware (1983), in that white oak was not reproducing well at those sites where it was a overstory dominant. In our study as in Monette and Ware's (1983), white oak is apparently successional, for it is not reproducing, while beech, sweetgum, blackgum and red maple are important in the lower strata at those sites where white oak is a overstory dominant.

Northern red oak was another important component of the overstory in some sites (Fig. 1a). It often was important at the same sites as tuliptree, unlike Kasmer et al.'s (1984) finding that the two strongly dissociated from one another in the Pennsylvania Piedmont. However, northern red oak was not reproducing, since it was rarely present in the lower layers of vegetation; the same holds true for tuliptree, southern red oak, black oak and scarlet oak.

Pignut hickory and mockernut hickory had an I.V. ≥ 10 in the overstory at six and four sites respectively, and though they were better represented in lower layers than oak, the sites where they were most abundant in the lower layers were not necessarily the same ones where they were important in the overstory. Therefore, like the oaks, the hickories appear to be reproducing poorly under shade.

In contrast to the species above, beech and sweetgum were well represented in the reproductive layers. While exceeding I.V. of 10 at only 5 sites in the overstory, beech reached an I.V. of 10 in an additional 14 sites in the small tree layer, and R.D.

≥ 10 in an additional 3 sites in the remaining two layers. In all layers we found the most beech on northerly and easterly facing slopes, which are generally moister than other exposures (Geiger 1965). However, beech also had higher importance in sandy soil, which is regarded to be drier than silty soil (Marks and Harcombe 1981). The greater abundance of beech on northerly and easterly slopes vs. its lower importance on southerly and westerly slopes might be interpreted as the result of a moisture gradient. However, the gradient of higher beech importance at sandier sites and lower importance at less sandy sites would suggest an opposing moisture gradient, and thus would at least partially nullify a solely moisture-based interpretation. The effects of direction of exposure and of sandiness may cancel each other; further studies should be carried out to determine how these two variables interact and the degree to which each affects soil moisture individually. In any case, unless there is a severe disturbance in the understory, beech will surely be the species of highest importance in the future overstory at a large majority of our sites, given its abundance in the small tree, sapling, and seedling layers.

Sweetgum reached I.V. ≥ 10 in the overstory in only five sites, reached that level in six additional sites in the small tree layer, and R.D. ≥ 10 in an additional four sites in the remaining two layers. Only one of the sites where the species was important in the overstory lacked high sweetgum importance in one or more of the lower layers. Thus, while sweetgum does seem to be recruiting into the lower strata, it is less likely to be present in all three of the lower layers than is beech, and sweetgum's greatest importance is reached in lower aspect, high silt sites where beech isn't very important. Given that the presence of sweetgum in lower layers in upland sites doesn't always presage its ultimate entry into the overstory (Oosting 1942; Monette and Ware 1983), it is hard to predict whether sweetgum will actually increase or decrease in importance as succession proceeds.

Unlike most of the overstory species, the important species of the small tree layer were represented in the sapling and/or seedling layers. Dogwood was abundant all across the small tree, sapling, and seedling layer ordinations. Its highest dominance in the small tree layer was associated with silty soils, though this may be an artifact of the reduced abundance of beech and red maple in these soils (Fig. 2b), since dogwood was abundant without respect to edaphic factors in the sapling and seedling layers.

Holly, an important understory species, reached highest importance at the high silt end of the ordination in the small tree layer, but in the sapling and seedling layers the species reached highest importance at the high sand end of the ordination. This anomaly may possibly be explained by the sandier sites being older forest (further along in succession) with the holly having already gotten large enough to count in the small tree layer, but not reproducing well under heavy shade. Siltier sites may be younger forests, with holly still in the younger age classes, but not yet large enough to count in the small tree layer. In contrast, blackgum may not have this broad tolerance of soil texture that holly does, since blackgum was associated with silty soil in both small tree and sapling layers (the only two strata where blackgum was important; it did not reach R.D. ≥ 10 in the seedling layer).

Red maple was important in only three sites in the overstory (Fig. 1b), but it was one of the most abundant species in the small tree and sapling layers, important at 14 and 17 sites, respectively. In the small tree layer red maple was strongly

TABLE 2. Significant correlations ($P < 0.05$) between DCA vegetational axes and environmental variables. See text for explanation of the two aspect variables.

Size stratum:	Large Trees		Small Trees		Saplings		Seedlings	
	I	II	I	II	I	II	I	II
DCA Axis:								
Eigen value:	0.44	0.28	0.44	0.17	0.50	0.27	0.42	0.28
Environmental variables:								
C&W aspect	-0.393	ns	-0.509*	ns	-0.449	ns	-0.547*	ns
BDW aspect	-0.444	ns	-0.375	ns	ns	ns	-0.387	ns
Slope ($^{\circ}$)	-0.468*	ns	ns	ns	ns	ns	ns	0.417
% Sand	-0.471*	ns	-0.502*	-0.420	-0.501*	-0.447	-0.547*	ns
% Silt	0.376	ns	0.379	ns	0.417	0.431	0.521*	ns
Soil Color	-0.428	ns	ns	ns	ns	ns	0.554*	ns
Zn	-0.408	ns	-0.400	ns	ns	-0.381	-0.524*	ns
Mn	ns	ns	ns	ns	ns	ns	-0.469*	ns
P	ns	ns	ns	ns	ns	ns	-0.431	ns
pH	ns	ns	ns	ns	ns	ns	-0.495*	ns

* $P < 0.01$. Clay (%), Ca, Mg, and K were not significantly correlated with any axis.

associated with beech in sandier soils on northerly and easterly aspects. In the sapling layer this association broke down, and red maple occurred much more broadly, with no association with any measured environmental variable. This may, as with holly, suggest a successional differential, with red maple not yet large enough to be important in the small tree layer at younger sites. Despite its importance in the small tree and sapling layers, red maple, like blackgum, was poorly represented in the seedling layer of all but two sites.

The present overstory, then, is in a state of succession. Neither oaks nor tuliptree are reproducing. Farrell and Ware (1991) also found that the important species in the overstory of their Piedmont sites were not reproducing, except for hickory, but in our study area not even hickory was reproducing well. American beech, red maple, sweetgum, blackgum, and white ash are the important species of the lower strata with the theoretical potential to enter the overstory. However, it was noted above that sweetgum may not successfully enter the canopy layer, and it is also the case that in both the Piedmont and Coastal Plain red maple and blackgum usually remain understory species in upland sites (Christensen 1977, Clark and Ware 1980, Monette and Ware 1983, Ware 1991). It is also uncertain that white ash, important in the seedling layer of some sites, will successfully reach the overstory in a closed canopy forest. Beech will probably come to dominate the overstory in the future, and if it continues to reproduce as at present, beech will remain a dominant in all strata until a disturbance occurs.

The environmental factors that show correlation in the distribution and importance of the various species within the various strata have been discussed above with each of the respective species. Overall, soil texture was the environmental factor that was correlated most often with the patterns of distribution (Table 2).

Sand and silt were significant factors in all four vegetation layers. Aspect was also a significantly correlated variable (C&W aspect all four strata; BDW aspect in two strata).

Other significant environmental factors that were correlated in at least two of the layers in this area were degree of slope, soil color (organic matter), and Zn. Zn is an unusual mineral to be correlated with vegetational distribution and abundance, in that few studies have found such an association.

The seedling layer was most strongly associated with the measured environmental factors, since ten factors were significantly correlated with the first and second axes of the seedling ordination (Table 2). Mn and P were significant only in the seedling layer. Fewer significant correlations between environmental factors and ordination axes were found the other layers: seven in the overstory, five in the small trees, and four in the saplings.

It might be argued in theory that the overstory layer of older second growth forests might be expected to show the greatest effect of past disturbance, and thus the least correlation with measured environmental variables, while the seedling layer of these forests, especially older ones, should show the least effect of disturbance, and thus the greatest correlation with environmental variables. However, in our study area the overstory showed significant correlations with more environmental variables than the intermediate layers. As mentioned earlier, dogwood, holly, red maple, and blackgum remain in lower strata long after their initial invasion, so the initial establishment of individuals of these species at a site may have taken place nearly the same time as the establishment of other species that are now in the overstory. The distribution of the understory species among sites in the small tree and sapling layers thus may be as likely as that of the overstory trees to reflect past disturbance. Given that understory species often are abundant at a much larger proportion of sites than potential canopy species, these understory species may also have broader environmental tolerances than the species of the overstory. Thus, correlation with measured environmental variables will not necessarily be higher in the small tree and sapling layers than in the overstory layer.

Ware (1991) described the Coastal Plain's maturing vegetation to be dominated by white oak, beech, and southern red oak, whereas white oak, chestnut oak, scarlet oak and black oak characterize the Piedmont. Some (Gemborys 1974, Farrell and Ware 1991) have reported northern red oak to be important in parts of the Piedmont, and it might be argued that it is also a Piedmont species. Though the characteristically Piedmont chestnut oak is absent, 50% of the sites (15 of 30) had northern red oak, black oak, or scarlet oak as important species, and beech was important at only five sites, so the present overstory seems to have more Piedmont-like vegetation. In contrast, beech is important at many sites of the understory, and holly is also important in the small tree and other layers. Neither beech nor holly are very important in the understory of typical Piedmont forests (Ware 1991).

The abundance of these typically Coastal Plain species in the lower layers supports the notion that the Swift Creek Natural Area of Pocahontas State Park contains (or will ultimately contain) Coastal Plain-like vegetation. The finding of Coastal Plain type vegetation west of the Fall Line refutes any assumption that the Fall Line *per se* is the vegetation boundary between Coastal Plain and Piedmont vegetation. This is concordant with the findings of Binns (1980), who, looking only

at the herb and shrub layers of the forest, found no sharp change in vegetation along a 116 km transect in Virginia that crossed the Fall Line.

As noted earlier, Ware (1991) suggested that the vegetational boundary between the Coastal Plain and Piedmont need not be coincident with the physiographic boundary, and suggested that the vegetational boundary might be a transitional zone west of the Fall Line. Although the physiographic characteristics west of the Fall Line are different from these of the Coastal Plain, it seems that these geologic and edaphic factors are not sufficient to cause a great change in the mature vegetation just west of the Fall Line. Further studies need to be done farther west in the Piedmont to determine the nature and location of the boundary or transitional zone between the Piedmont-like and Coastal Plain-like vegetation provinces of Virginia.

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LITERATURE CITED

- Beers, T.W., P.E. Dress, and L.C. Wensel. 1966. Aspect transformation in site productivity research. *J. Forestry* 64: 691-692.
- Binns, S.J. 1980. An interphysiographic analysis of herb and shrub vegetation of Virginia forests. Unpublished Master's Thesis. Virginia Commonwealth University, Richmond, VA.
- Braun, E. L. 1950. *Deciduous Forests of Eastern North America*. The Blakiston Co., Philadelphia, PA. 596 pp.
- Christensen, N. 1977. Changes in structure, pattern and diversity associated with climax forest maturation in Piedmont, N.C. *Amer. Midl. Natur.* 97: 176-188.
- Clark, D. A., and S. Ware. 1980. Upland hardwood forests of Pittsylvania County, Virginia. *Virginia J. Sci.* 31: 28-32.
- Crone, E. 1991. Forest composition and environmental variables and land use in the Northern Neck of Virginia. Unpublished Undergraduate Honors Thesis. College of William and Mary, VA.
- DeWitt, R., and S. Ware. 1979. Upland hardwood forests of the central Coastal Plain of Virginia. *Castanea* 44: 163-174.
- Farrell, J., and S. Ware. 1991. Edaphic factors and forest vegetation in the Piedmont of Virginia. *Bull. Torrey Bot. Club* 118: 161-169.
- Geiger, R. 1965. *The Climate Near the Ground*. Translated by Scripta Technica, Inc. Harvard University Press, Cambridge, MA. 611 p.
- Gemborys, S. R. 1974. The structure of hardwood forest ecosystems of Prince Edward County, VA. *Ecology* 55: 614-621.
- Greller, A. M. 1988. Deciduous Forest, pp. 287-316. In: Barbour, M. G., and W. D. Billings (eds.), *North American Terrestrial Vegetation*. Cambridge Univ. Press, New York.
- Harvill, A. M., Jr., T. R. Bradley, C. E. Stevens, T. F. Wieboldt, D. M. E. Ware, D. W. Ogle, G. W. Ramsey, and G. P. Fleming. 1992. *Atlas of the Virginia Flora*. III. Virginia Botanical Associates, Burkville, VA.

- Johnson, G. G., and S. Ware. 1982. Post-chestnut forests in the central Blue Ridge of Virginia. *Castanea* 47: 329-343.
- Kasmer, J., P. Kasmer, and S. Ware. 1984. Edaphic factors and vegetation in the Piedmont lowland of southeastern Pennsylvania. *Castanea* 49: 147-157.
- Küchler, A. W. 1964. Potential Natural Vegetation of the Coterminous United States. Special Publ. #36. The American Geographical Society, New York. 116 p.
- Marks, P. L., and P. A. Harcombe. 1981. Forest vegetation of the Big Thicket, southeast Texas. *Ecolog. Monogr.* 51: 287-305.
- Monette, R., and S. Ware. 1983. Early forest succession in the Virginia Coastal Plain. *Bull. Torrey Bot. Club* 110: 80-86.
- Oosting, H. J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. *Amer. Midl. Nat.* 28: 1-126.
- Oosting, H. J. 1956. *The Study of Plant Communities*. 2nd ed. W.H. Freeman and Co., San Francisco. 440 pp.
- Ter Braak, C.J.F. 1988. CANOCO--a FORTRAN program for canonical community ordination by correspondence analysis, principal components analysis and redundancy analysis. Agricultural Mathematics Group, Wageningen, The Netherlands. 95 pp.
- Vankat, J. L. 1979 *The Natural Vegetation of North America*. John Wiley and Sons, New York, 261 pp.
- Ware, S. 1991. A comparison of Piedmont and Coastal Plain hardwood forests in Virginia. *Virginia J. Sci.* 41:401-410.

