

A Comparison of Piedmont and Coastal Plain Upland Hardwood Forests in Virginia

Stewart Ware

Department of Biology, College of William and Mary
Williamsburg, VA 23185

ABSTRACT

Both the Piedmont and Coastal Plain of Virginia have traditionally been treated as part of the Oak-(Hickory)-Pine Forest Region. To assess the similarity of hardwood forests of these two physiographic provinces, a detrended correspondence analysis ordination (using DECORANA software) was constructed using 51 Piedmont and 22 central Coastal Plain upland hardwood forest stands. *Quercus alba* was a usual dominant in both physiographic provinces; its Importance Value (IV) exceeded 10% in 88% of the stands. On the basis of other important species, however, the stands fell into three distinct groups: (a) 15 northern Piedmont stands on Triassic substrates, with *Carya* spp. IV > 18% and little *Q. prinus* or *Q. coccinea*; (b) non-Triassic Piedmont stands from the southern, central, and northern Piedmont, with one or both of *Q. prinus* and *Q. coccinea* with IV > 10%; and (c) 22 Coastal Plain stands usually with high IV of *Fagus grandifolia* or *Q. falcata*. The Coastal Plain forests had more in common with the *Fagus*-rich Southern Mixed Hardwood Forest of the southeastern Coastal Plain than with the much nearer forests of the Virginia Piedmont.

INTRODUCTION

Both the Piedmont and central Coastal Plain of Virginia have traditionally been treated as part of the Oak-(Hickory)-Pine Forest Region, with oak-hickory forest regarded as the potential upland climax which would develop with the demise of the successional shortleaf (*Pinus echinata*), Virginia (*P. virginiana*), and loblolly (*P. taeda*) pines (Braun, 1950; Oosting, 1956; Kuchler, 1964). Braun's (1950) grouping of these two physiographic provinces into the same forest region was not based on much quantitative data, but largely on visual observation of the vegetation. The first modern quantitative vegetational study of the upland oak-hickory forests of the Piedmont was carried out by Gemborys (1974) in Prince Edward Co., Virginia (Fig. 1), and this inspired a similar study of upland hardwood forest stands in six central Coastal Plain counties (Fig. 1) by DeWitt and Ware (1979).

Though the differences in sampling methods and data analysis made direct quantitative comparison between the two studies impractical, DeWitt and Ware (1979) did compare a list of the most important species in the central Coastal Plain with a list of the most important species found in the upland stands among those in Gemborys' (1974) Piedmont study. This comparison revealed that white oak (*Quercus alba*) was the most important species in both areas, but the abundant Piedmont oak species chestnut (*Q. prinus*), scarlet (*Q. coccinea*), and northern red oak (*Q. rubra*) were unimportant in the Coastal Plain. On the other hand, beech (*Fagus grandifolia*) had high importance in the Coastal Plain but was rare in the Piedmont. DeWitt and Ware (1979) thus concluded that their Coastal Plain forest stands had

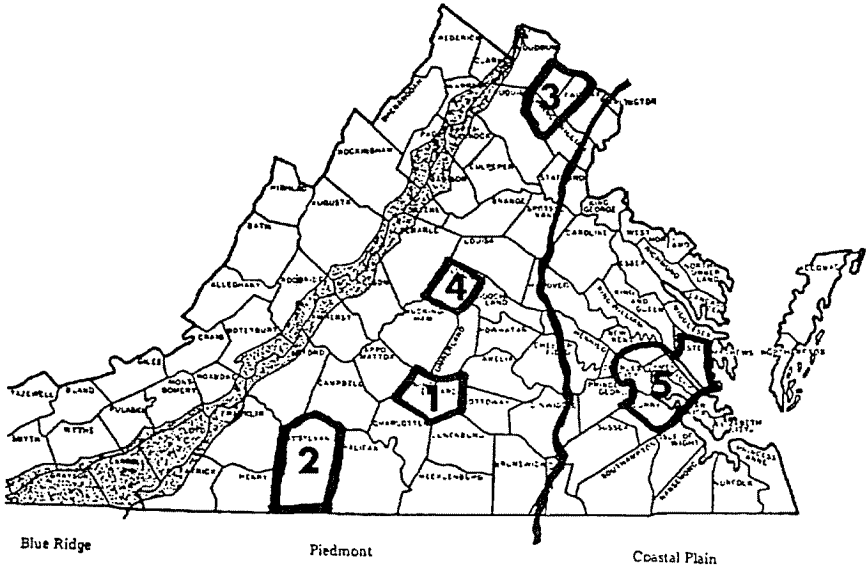


FIGURE 1. Location of the study areas in the Piedmont and Coastal Plain of Virginia. 1 = Gemborys (1974); 2 = Clark and Ware (1980); 3 = Farrell and Ware (1991); 4 = Diggs and Hall (1981); and 5 = DeWitt and Ware (1979) and Monette and Ware (1983). Base map modified from Harvill (1970).

a closer relationship to the beech-rich stands of the Coastal Plain to the south (Quarterman and Keever, 1962) than to the oak-hickory forests of the Piedmont. Despite these conclusions and a later reiteration (Monette and Ware, 1983) of the similarity of Virginia Coastal Plain upland forests to those farther south, most workers have continued to treat both the Piedmont and Coastal Plain of Virginia as part of the same forest region--the Oak-(Hickory)-Pine Region (Vankat, 1979; Greller, 1988).

In the last decade three additional studies (Fig. 1) of upland forest vegetation have been carried out in the Piedmont of Virginia using the same combined Bitterlich-circular quadrat method (Levy and Walker, 1971) employed by DeWitt and Ware, (1979). This similarity of method allows direct quantitative comparisons of DeWitt and Ware's (1979) Coastal Plain data with that from the more recent Piedmont studies. The present paper makes that comparison of 22 central Coastal Plain forests with those from the Piedmont. The Piedmont forests include 22 upland hardwood stands in the southern Virginia Piedmont (Clark and Ware, 1980), four upland hardwood stands in Fluvanna Co. in the central Piedmont (Diggs and Hall, 1981), and 25 upland hardwood stands in the Piedmont portions of Fairfax, Loudoun, and Prince William counties in northern Virginia (Farrell and Ware, 1991).

METHODS

In all four studies (DeWitt and Ware, 1979; Clark and Ware, 1980, Diggs and Hall, 1981, and Farrell and Ware, 1991) stands were chosen which were

predominantly hardwood, without saw-cut stumps or other obvious signs of recent (> 20-30 yr) disturbance, and were large enough to allow at least three combined Bitterlich-circular quadrat sample points (Levy and Walker, 1971). At each point basal area of each species was measured by the Bitterlich method using either a Bitterlich stick or a Spiegel Relaskop (sighting prism). Density of each species was measured by counting all tree stems ≥ 10.16 cm (4 in) in diameter at breast height (dbh). In each stand relative basal area and relative density of trees were calculated for each species, and then the relative values were averaged to yield importance value (IV; base of 100) for that species in that stand. Both the statistical tests (Sokal and Rohlf, 1981) of the tabular data and the detrended correspondence analysis (DCA) ordinations (using DECORANA software; Hill and Gaugh, 1980) were based on IV's. Because of the great difficulty of reliably distinguishing the hickories *Carya glabra* and *C. ovalis* in the field in summer when nuts are not available (Johnson and Ware, 1982), these two taxa were combined in this analysis, regardless of which name was applied by the original workers. There were 22 southern Piedmont stands, 25 northern Piedmont stands, and four central Piedmont stands, for a total of 51 Piedmont stands, and 22 Coastal Plain stands, for a grand total of 73 stands.

RESULTS

Because the northern and southern Piedmont studies are farther from one another geographically than either is from the central Coastal Plain, it was necessary first to ask whether these two Piedmont areas were sufficiently similar that they might be combined for comparison with the Coastal Plain. Table 1 compares the frequency of an IV > 10% and the presence for each major species in the northern versus the southern Piedmont. White oak was the overwhelming dominant in both areas. The remaining species in the upper part of Table 1 were more important in the south, and those in the lower half of the table (*Q. velutina* downward) were more important in the north. Based on this comparison, the southern and northern Piedmont appear to be quite different ($P < 0.05$, G test for goodness of fit). However, fifteen of the stands in northern Virginia are on Triassic substrates of the Leesburg Basin, while the other ten stands, like those of the rest of the Piedmont, are on Paleozoic or pre-Cambrian substrates (Fig. 2). A comparison of the composition of the Triassic and non-Triassic northern Virginia stands (Table 2; significantly different at the $P < 0.05$ level, G test for goodness of fit) revealed that the species which were more abundant in the north were generally those species which reached high importance in the Triassic, and those species more important in the south were mostly ones which were less abundant on Triassic substrates. The exceptions were sourwood (*Oxydendron arboreum*), which does not range into the northern Piedmont study area (Harvill et al., 1986), blackgum (*Nyssa sylvatica*), which was more important in the north but mostly on non-Triassic substrates there, and northern red oak, which was more important in the north but apparently not substrate specific. The ten non-Triassic stands in the northern Piedmont (Table 2) had a fairly similar composition (NS, G test for goodness of fit) to the southern Piedmont (Table 1) and central Piedmont (Fluvanna Co.) stands (Diggs and Hall, 1981). Therefore, these ten northern Virginia stands and the four central Virginia stands were combined with the 22 southern Virginia stands to produce a 37-stand

TABLE 1. Presence and importance of major overstory species in upland hardwood forests of the southern and northern Virginia Piedmont. All hardwood species are listed which had an IV > 10 in at least one stand in either area, or were present in at least half the stands in either area.

	Southern (n = 22)		Northern (n = 25)	
	With IV > 10	Present	With IV > 10	Present
	% (n)	% (n)	% (n)	% (n)
<i>Quercus alba</i>	86.4(19)	100.0(22)	80.0(20)	100.0(25)
<i>Q. prinus</i>	54.5(12)	72.7(16)	16.0(4)	24.0(6)
<i>Q. coccinea</i>	45.5(10)	95.5(21)	20.0(5)	52.0(13)
<i>Liriodendron tulipifera</i>	31.8(7)	59.1(13)	4.0(1)	52.0(13)
<i>Acer rubrum</i>	27.3(6)	86.4(19)	16.0(4)	44.0(11)
<i>Oxydendron arboreum</i>	9.1(2)	81.1(18)	--(0)	--(0)
<i>Q. falcata</i>	9.1(2)	59.1(13)	--(0)	36.0(9)
<i>Liquidambar styraciflua</i>	4.5(1)	13.6(3)	--(0)	--(0)
<i>Q. stellata</i>	--(0)	50.0(11)	--(0)	20.0(5)
<i>Q. velutina</i>	18.2(4)	86.4(19)	48.0(12)	96.0(24)
<i>Carya tomentosa</i>	4.5(1)	68.2(15)	40.0(10)	72.0(18)
<i>C. glabra/ovalis</i>	4.5(1)	68.2(15)	36.0(9)	84.0(21)
<i>Nyssa sylvatica</i>	9.1(2)	95.5(21)	28.0(7)	64.0(16)
<i>Q. rubra</i>	--(0)	4.5(1)	24.0(6)	76.0(18)
<i>Fraxinus americana</i>	--(0)	9.1(2)	16.0(4)	44.0(11)
<i>Ulmus rubra</i>	--(0)	--(0)	8.0(2)	40.0(10)

Piedmont composite, and then compared with the 22 Coastal Plain stands (Table 3). The two groups are significantly different at the $P < 0.01$ level (G test for goodness of fit).

Excluding white oak, the species in Table 3 can be placed into three groups: six species noticeably more important in the Piedmont; five species more or less equally important in both Coastal Plain and Piedmont; and six species more important in the Coastal Plain. In the first group, chestnut oak and scarlet oak were not only much less likely to have high IV in the Coastal Plain, but they were also less likely to be present, while in the next three species the difference in structural importance was more pronounced than the difference in presence. In the second group, both *Carya glabra/ovalis* and *C. tomentosa* as well as the Table 2 species American ash (*Fraxinus americana*) and slippery elm (*Ulmus rubra*) would seem to be more important in the Piedmont if Triassic sites had been included, but were actually no more important in the Piedmont than in the Coastal Plain when only the far more extensive Paleozoic and pre-Cambrian Piedmont sites were considered. In the third group, the greater importance of beech and southern red oak (*Quercus falcata*) is based on both IV and presence, while that of holly (*Ilex opaca*), basket oak (*Q. michauxii*) and sand hickory (*C. pallida*) is based on presence only. The latter two species do not range as far west into the Piedmont as the sampled sites are located (Harvill et al., 1986), so those species would not be expected in the sampled stands from that physiographic province.

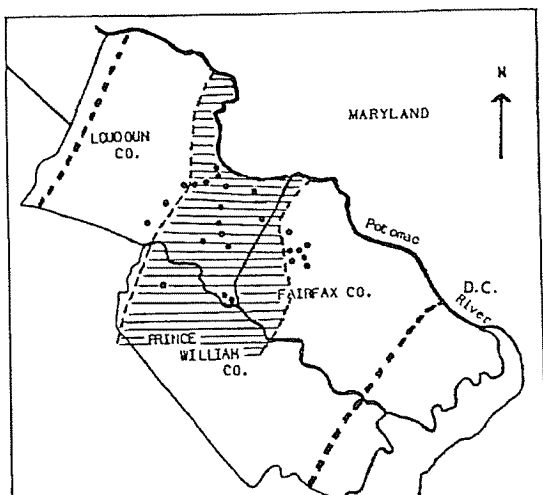


FIGURE 2. Location of Triassic and non-Triassic sites in the northern Piedmont area studied by Farrell and Ware (1991). The Triassic belt (Leesburg Basin) lies in western Fairfax and eastern Loudoun counties, separated by dashed lines from the non-Triassic areas to the east and west of it.

These tabular comparisons were all based on arranging stands by geographic, physiographic, or geological categories, a kind of direct environmental analysis, as opposed to an *indirect* environmental or vegetational arrangement of stands, such as in a detrended correspondence analysis (DCA) ordination. When all 73 stands were plotted on the first two axes of such an ordination, they fell into three identifiable groups based on their geological and physiographic origins (Fig. 3). The group of 17 stands on the lower right of the ordination is designated TR because 14 of them are in the Triassic basin of northern Virginia. The remaining three are from non-Triassic northern Piedmont sites (2 stands) or Fluvanna County (one stand). The group of 21 stands in the upper center of Fig. 3 are designated CP because all except two of them are Coastal Plain stands. The two added stands are one southern Piedmont and one central Piedmont stand. Each of these has southern red oak $IV > 10$, a species which was often important in Coastal Plain stands. The third group of 34 stands, consisting of 21 southern Piedmont stands, 11 northern Piedmont stands, two central Piedmont stands, and two Coastal Plain stands, constitutes a representative sample of what present day upland hardwood forests of the non-Triassic Piedmont are like, and are designated PD. The two Coastal Plain stands in this group had red maple (*Acer rubrum*) $IV > 10$, like many Piedmont but unlike most other Coastal Plain stands, and did not have much beech or southern red oak. In a second DCA ordination in which the 17 TR stands were omitted and only the typical Piedmont and the Coastal Plain stands were included (Fig. 4), the stands from the two different physiographic provinces again fell in different portions of the ordination, and this time the two Coastal Plain stands mentioned above did not fall with the PD stands, but lie between them and the CP stands (Fig. 4). Thus, indirect (vegetational) analysis and direct physiographic and geological analyses produced very similar groupings of stands, with only two stands falling in the wrong physiographic province on the second ordination (Fig. 4).

TABLE 2. Comparison of presence and importance of major overstory species on Triassic and non-Triassic substrates in northern Virginia. All hardwood species which had an IV 10 on either substrate are included.

	Triassic (n = 15)		Non-Triassic (n = 10)	
	With IV > 10 % (n)	Present % (n)	With IV > 10 % (n)	Present % (n)
<i>Quercus alba</i>	86.7(13)	100.0 (15)	70.0 (7)	100.0 (10)
<i>Nyssa sylvatica</i>	6.7 (1)	46.7 (7)	60.0 (6)	90.0 (9)
<i>Q. prinus</i>	-- (0)	6.7 (1)	40.0 (4)	50.0 (5)
<i>Q. coccinea</i>	-- (0)	53.3 (8)	40.0 (4)	50.0 (5)
<i>Acer rubrum</i>	6.7 (1)	26.7 (4)	30.0 (3)	70.0 (7)
<i>Liriodendron tulipifera</i>	-- (0)	20.0 (3)	10.0 (1)	100.0 (10)
<i>Q. rubra</i>	26.7 (4)	80.0 (12)	20.0 (2)	70.0 (7)
<i>Q. velutina</i>	53.3 (8)	93.3 (14)	40.0 (4)	100.0 (10)
<i>Carya glabra / ovalis</i>	46.7 (7)	93.3 (14)	20.0 (2)	70.0 (7)
<i>C. tomentosa</i>	60.0 (9)	93.3 (14)	10.0 (1)	40.0 (4)
<i>Fraxinus americana</i>	26.7 (4)	66.7 (12)	-- (0)	10.0 (1)
<i>Ulmus rubra</i>	13.2 (2)	60.0 (9)	-- (0)	10.0 (1)

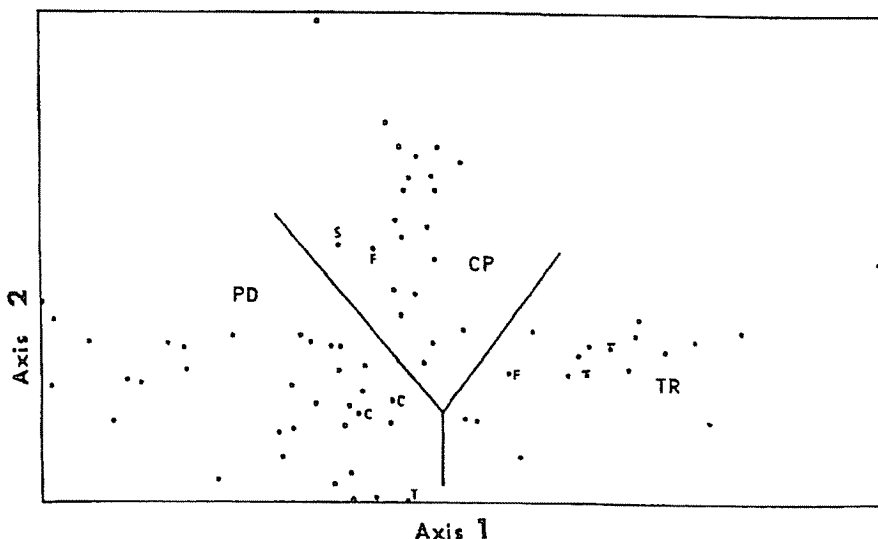


FIGURE 3. DCA ordination of 73 Piedmont and Coastal Plain stands. Group TR contains 14 northern Triassic stands, along with one central Virginia (F) stand and two non-Triassic northern Virginia stands (bar above the dot). The upper center group CP contains 19 Coastal Plain stands and one southern (S) and one central (F) Piedmont stand (both with high *Quercus falcata* IV). The remaining group (PD) consists of 31 non-Triassic Piedmont stands and three *Acer rubrum*-rich stands from the Triassic (T) or Coastal Plain (C). Only four stands fail to group with others from their physiographic province.

TABLE 3. Comparison of importance and presence of major overstory species of the central Coastal Plain and the Piedmont (non-Triassic). All species with IV > 10 in at least one stand are included.

	Piedmont (n = 36)		Coastal Plain (n = 22)	
	With IV > 10 % (n)	Present % (n)	With IV > 10 % (n)	Present % (n)
<i>Quercus alba</i>	83.3(30)	100.0(36)	90.9 (20)	100.0 (22)
<i>Q. prinus</i>	50.0(18)	63.9(23)	-- (0)	4.5 (1)
<i>Q. coccinea</i>	41.6(15)	75.0(27)	-- (0)	31.8 (7)
<i>Q. velutina</i>	27.8(10)	91.6(33)	4.5 (1)	68.1 (15)
<i>Acer rubrum</i>	27.8(10)	83.3(30)	9.1 (2)	81.8 (18)
<i>Nyssa sylvatica</i>	22.2 (8)	91.6(33)	-- (0)	68.1 (15)
<i>Oxydendron arboreum</i>	5.5 (2)	50.0(18)	-- (0)	31.8 (7)
<i>Q. stellata</i>	2.7 (1)	50.0(18)	-- (0)	36.3 (8)
<i>Carya glabra/ovalis</i>	8.3 (3)	69.4(25)	-- (0)	68.1 (15)
<i>C. tomentosa</i>	5.5 (2)	63.9(23)	4.5 (1)	72.7 (16)
<i>Q. rubra</i>	5.5 (2)	27.7(10)	9.0 (2)	68.1 (15)
<i>Liriodendron tulipifera</i>	22.2 (8)	66.7(24)	22.7 (5)	86.3 (19)
<i>Liquidambar styraciflua</i>	2.7 (1)	13.8 (5)	4.5 (1)	86.3 (19)
<i>Q. falcata</i>	8.3 (3)	55.4(20)	27.3 (6)	90.9 (20)
<i>Fagus grandifolia</i>	-- (0)	2.7 (1)	54.4 (12)	81.8 (18)
<i>Ilex opaca</i>	-- (0)	2.7 (1)	4.5 (1)	86.3 (19)
<i>Q. michauxii</i>	-- (0)	-- (0)	4.5 (1)	36.6 (8)
<i>C. pallida</i>	-- (0)	-- (0)	4.5 (1)	22.7 (5)

DISCUSSION

In the tabular comparison of groups of stands it is important to remember that all stands were second growth, and that all data presented here are based on overstory trees (≥ 10.16 cm dbh). Some of the differences between stands may be products of differential disturbance histories, and some differences may be because species were present in the understory but not picked up in the overstory sample. Red maple and blackgum are quite commonly present in upland forests of the Coastal Plain, but usually as understory trees, so that they are often too small to be recorded in sampling data based on larger trees. (However, both regularly reach the canopy in bottomland forests of the Coastal Plain; see Glascock and Ware [1979]). Sourwood is also a common understory species in the Coastal Plain, so it likewise may have been present in the understory in many of the sampled stands but not recorded in the overstory. In the Coastal Plain both red maple and sourwood may experience an increase in growth after selective timbering has opened up the canopy, and under those conditions may reach a dbh of > 10 cm. If this is also true in the Piedmont, the high importance of these two species in upland stands there might be a product of past selective timbering which took place so long ago that it is no longer detectible by saw-cut stumps or other signs of such disturbance. However, why such a result would have occurred more often in the southern, central, and northern Piedmont and in Gemborys' (1974) study area than

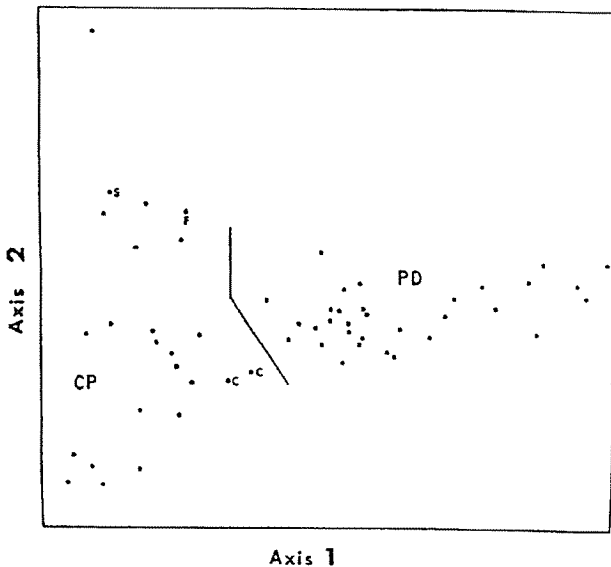


FIGURE 4. DCA ordination of PD and CP stands from Figure 3. The two (C) stands from Figure 3 now fall closer to the other Coastal Plain (CP) stands than to the PD stands, while F and S from the Piedmont again fall with *Quercus falcata*-rich Coastal Plain stands. Stands in the lower left have high IV of *Fagus grandifolia*.

in the Coastal Plain is unclear. It may well be that in general blackgum, red maple, and sourwood are simply more successful in the Piedmont than in the Coastal Plain. Such greater success in the Piedmont seems to be the case with black oak, often present in Coastal Plain stands but usually represented there by relatively few individuals.

The apparent greater importance of the pignut hickory complex (*Carya glabra/ovalis*) in the Piedmont was because of two northern Virginia stands which (according to county soil maps) are on non-Triassic soils but which had the higher soil Ca, Mg, and pH which usually characterizes Triassic soils (Farrell and Ware 1991). On the ordination these two stands fell with the Triassic sites in the group TR, and thus are anomalous as members of the non-Triassic grouping in Table 2. If they were excluded from the comparison, the pignut hickory complex would be of similar importance in both the PD and CP groupings.

Tuliptree (*Liriodendron tulipifera*) is extremely abundant in the Coastal Plain, perhaps second only to loblolly pine in abundance. Its lower IV in the Coastal Plain (Table 3) is related to stand selection criteria used in this study. Stands with abundant tuliptree usually have either much loblolly pine (younger stands) or relatively little white oak (older stands), both of which are signs of past selective cutting, and such stands were excluded. In the Piedmont the proportion of stands with tuliptree present was lower than in the Coastal Plain, but the proportion of stands with abundant tuliptree which were without clear evidence of past selective timbering (and thus suitable for sampling) was about the same.

The low importance of northern red oak in non-Triassic sites in the three recent Piedmont studies is in contrast to the high importance of that oak in Gemborys' (1974) study, a point first noted by Clark and Ware (1980). The three more recent

Piedmont studies have all reported the presence of both scarlet oak and northern red oak (with the former not infrequently having a high IV). However, Gemborys (1974) reported only the presence of northern red oak; therefore it seems probable that the name *Quercus rubra* as used by Gemborys (1974) is inclusive, and encompasses individual trees which other workers may have separated out as scarlet oak.

The contrast in the importance of southern red oak in the Piedmont and Coastal Plain seems clear based on these data. However, it should be noted that in Gemborys' (1974) study, southern red oak had a relative importance among potential canopy species greater than 10% in six of 24 upland stands (25%), and it was present in either overstory or understory in 20 of the 24 stands (83.3%). These values are quite comparable in importance to what DeWitt and Ware (1979) found in the Coastal Plain.

While one should not forget the caveat noted above about interpreting comparisons of hardwood stands which may have different disturbance histories, the fact is that the indirect gradient analysis (DCA ordination) produced a grouping of stands which deviates only in minor ways from the *a priori* grouping by physiographic and geologic categories. Thus, the recent data on Piedmont hardwood forests support the notion advanced by DeWitt and Ware (1979) that the Piedmont and the central Coastal Plain of Virginia are different vegetationally. Despite the masking dominance of white oak in many stands, the difference manifests itself largely in the higher importance of chestnut, scarlet, and black oak in the Piedmont versus the higher importance of beech and southern red oak in the central Coastal Plain. To treat these as parts of a single forest region, especially of a region for which beech is not listed as one of the common canopy dominants, is not consistent with the available quantitative data.

All of the study sites discussed in this paper are well within the Piedmont or well within the Coastal Plain, so it cannot be discerned from the data presented here whether the usual boundary (the Fall Line) between these two physiographic provinces is also a vegetational boundary. The vegetational boundary is likely to be a transition zone much less discrete than the physiographic boundary, and may well be west of the Fall Line. A study of the shrub/herb layers in 30 hardwood forests along a 116 km east-west transect across the Fall Line through New Kent, Hanover, and Louisa counties VA (Binns 1980) revealed no sharp vegetational changes, and my comparison of that study with shrub data from Monette and Ware's (1983 and unpublished) central Coastal Plain study revealed no significant differences in shrub layer composition between the Piedmont and Coastal Plain stands. Further work is needed to determine the location and width of the boundary area between the two vegetational areas, and whether the shrub and herb layers respond in the same way that the overstory layer does. Given the putative southern relationship of the central Coastal Plain studies, more work also needs to be done in the northern Coastal Plain of Virginia to determine whether that region is more like the central Coastal Plain to the south or the Piedmont to the west.

LITERATURE CITED

- 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. 595 p.
- Clark, D., and S. Ware. 1980. Upland hardwood forests of Pittsylvania Co., Virginia. *Virginia J. Sci.* 31: 28-32.
- DeWitt, R., and S. Ware 1979. Upland hardwood forests of the central Coastal Plain of Virginia. *Castanea* 44: 163-174.
- Diggs, G. M., Jr., and G. W. Hall. 1981. Vascular flora and vegetation of the Kent Branch watershed, Fluvanna Co., Virginia. *Virginia J. Sci.* 32: 23-33.
- Farrell, J. D., Jr., and S. Ware. 1991. Edaphic factors and forest vegetation in the Piedmont of Virginia. *Bull. Torrey Bot. Club* 118: 161-169.
- Gemborys, S. R. 1974. The structure of hardwood forest ecosystems of Prince Edward County, Virginia. *Ecology* 55: 614-621.
- Glascock, S, and S. Ware. 1979. Forests of small stream bottoms in the Peninsula of Virginia. *Virginia J. Sci.* 30: 17-21.
- Greller, A. M. 1988. *Deciduous Forests*. Chapter 10 (p.285-316) in Barbour, M. G., and W. D. Billings, eds., *North American Terrestrial Vegetation*. Cambridge University Press. 434 p.
- Harvill, A. M., Jr. 1970. *Spring Flora of Virginia*. McClain Printing Co., Parsons, WV. 240 p.
- Harvill, A. M., Jr., T. R. Bradley, C. E. Stevens, T. F. Wieboldt, D. M. E. Ware, and D. W. Ogle. 1986. *Atlas of the Virginia Flora*. 2nd ed. Virginia Botanical Associates, Farmville, VA. 135 p.
- Hill, M. O., and H. G. Gauch, Jr. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47-58.
- Johnson, G. G., and S. Ware. 1982. Post-chestnut forests in the central Blue Ridge of Virginia. *Castanea* 47: 329-343.
- Kuchler, A. W. 1964. *Potential Natural Vegetation of the Conterminous United States*. Special Publication 36, American Geographical Society, New York. 116 p. and map.
- Levy, G. F., and S. Walker. 1971. The combined Bitterlich rangefinder-circular quadrat method in phytosociological studies. *Jeffersonia* 5: 37-39.
- Monette, R., and S. Ware. 1983. Early forest succession in the Virginia Coastal Plain. *Bull. Torrey Bot. Club* 110: 80-86.
- Oosting, H. J. 1956. *The Study of Plant Communities*. 2nd ed. W. H. Freeman and Co., San Francisco, CA. 440 p.
- Quarterman, E., and C. Keever. 1962. *Southern Mixed Hardwood Forest: climax in the southeastern Coastal Plain, U.S.A.* *Ecol. Monogr.* 32: 167-185.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. W. H. Freeman and Co., New York. 859 p.
- Vankat, J. L. 1979. *The Natural Vegetation of North America*. John Wiley and Sons, New York. 261 p.