Hardwood Forest in the Coastal Plain of Virginia East of the Suffolk Scarp

Penelope Williams Cazier
College of William & Mary - Arts & Sciences

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HARDWOOD FORESTS IN THE COASTAL PLAIN
OF VIRGINIA EAST OF THE SUFFOLK SCARP

A Thesis
Presented to
The Faculty of the Department of Biology
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Arts

by
Penelope Williams Cazier
1992
APPROVAL SHEET

This thesis is submitted in partial fulfillment of the requirements for the degree of Master of Arts

[Signature]
Author

Approved, July 1990

Stewart A. Ware
Stewart A. Ware, Ph. D.

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Gustav W. Hall, Ph. D.
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For his loving support and encouragement I thank my husband, Bill. He encouraged me to take time from teaching to go back to school, and never complained about the long hours of study. He's been my partner and mainstay.

Many thanks are extended to my thesis committee and especially to the Wares, who have taken me under their wings. I thank them both for introducing me to native orchids, granite rock outcrops, biology field work, and professional meetings. Stewart Warehas spent many hours teaching me how to do research and guiding me through each step of the process. I am most grateful for his patience, guidance, and friendship.
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</tr>
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</table>
ABSTRACT

Twenty-three stands of older second growth hardwoods on level, low elevation uplands in the eastern Coastal Plain of Virginia were sampled and analyzed for correlation of vegetation with edaphic factors. Unlike the highly dissected, well-drained upland hardwood forests of the upper Coastal Plain which are dominated by white oak, southern red oak, beech, and tuliptree, the forests of the lower Coastal Plain were dominated by red maple, sweetgum, white oak, cherrybark oak, beech, tuliptree, basket oak, and loblolly pine. Sweetgum was the leading dominant in five stands, and red maple led in four stands. American holly, red maple, and sweetgum were the leading dominants in the understory. Both detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) ordinations separated the sites into two groups: a more mesophytic Group I with high importance values of beech, white oak, and pine, and a more hydrophytic Group II with high values of high importance values of tuliptree, basket oak, cherrybark oak, willow oak, or swamp laurel oak.

Relatively few environmental variables showed significant correlation with the composition of the vegetation in the lower Peninsula. The soils of this area were generally acidic and low in nutrients, and are often hydric. Surprisingly, there was no significant correlation coefficient relating levels of pH to vegetation. The highest correlation coefficient related levels of zinc to vegetation to all ordinations of canopy species. More importantly, vegetation was correlated with elevation and related to soil types and physiographic divisions. Despite the presence of hydric soils, the high values of southern swamp species, and the relationship of elevation and vegetation, there was no correlation between vegetational pattern and moisture variables. This lack of correlation between vegetation and moisture is probably due to the unusual amount of subsurface drainage and the resulting site alteration. The hardwood forests on the flat, low land east of the Suffolk Scarp represent a transition between the dissected uplands and stream bottomlands of the eastern Coastal Plain of Virginia.
HARDWOOD FORESTS IN THE COASTAL PLAIN OF VIRGINIA
EAST OF THE SUFFOLK SCARP
INTRODUCTION

The Coastal Plain of Virginia was once considered to be an area of oak-hickory climax vegetation (Braun 1950, Vankat 1979), but in recent years has been judged to be more like the Southern Mixed Hardwood Forest (Quarterman and Keever 1962) of the more southern Atlantic and Gulf Coastal Plain (Dewitt and Ware 1979, Monette and Ware 1983). These last two studies included the dissected, well-drained uplands on the Peninsula of Virginia between the York and James Rivers. *Quercus alba, Q. falcata, Fagus grandifolia, and Liriodendron tulipifera* were found to be the dominant hardwood species in this upper portion of the Peninsula. In the lower portion of the Peninsula, adjacent to and east of the Suffolk Scarp, the land is not well dissected, but is low and level. Since dissection greatly influences prevailing vegetation (Nesom and Treiber 1977), there was a need to compare the hardwood forests of the flat, low land of the Peninsula adjacent to and east of the Suffolk Scarp with other hardwood sites in Virginia's Coastal Plain. This study was conducted to determine the composition of hardwood forests on the undissected eastern portion of the Peninsula of Virginia, to compare these to other Coastal Plain hardwood forests, and to determine whether any differences can be correlated with topography, elevation, moisture, or edaphic factors.
Figure 1. Map of eastern Virginia with study sites indicated by solid circles. (base map from DeWitt and Ware 1979)
Figure 2. Map of the study area on the lower Peninsula of Virginia. Scarps are indicated by toothed lines, with teeth pointing uphill. The three segments of the Suffolk Scarp (one north of the York River) are labeled "S"; the two segments of the Big Bethel Scarp are labeled "B"; and the Kingsmill Scarp is labeled "K". The two stands west of the Suffolk Scarp and north of the Kingsmill Scarp are on the Grafton Plain (GP); the two stands south of the Kingsmill Scarp are on the Huntington Flat (HuF). The four stands between the Suffolk and Big Bethel Scarps are on the narrow, north-south trending Hornsbyville Flat (HF), and the fifteen stands east of the Big Bethel Scarp are on the Hampton Flat (HaF). (Base map from Johnson et al.)
PHYSIOGRAPHY AND GEOLOGY

The lower eastern Peninsula of Virginia is part of the Coastal Plain bordered by the York River to the northwest, James River to the southeast, and Chesapeake Bay to the east as shown in Figure 1. The land appears as a level plain gently sloping seaward, interrupted only by low terraces called escarpments. During the Pleistocene epoch as the sea levels rose and fell with the melting and regrowth of glaciers, the coastline moved alternately eastward and westward. These Pleistocene coastlines remain today as low, gradually rising, generally north-south trending escarpments or scarps (Bevin 1957). These escarpments are shown along with other topographic features on the map in Fig. 2. The easternmost portion of the lower Peninsula, lying between Big Bethel Scarp (B) to the west and the Chesapeake Bay to the east, is the Hampton Flat (HaF in Fig. 2), 0-4.6 m above sea level. Hampton Flat lies on the Lynnhaven Formation, which is 75-80,000 years old. West of Hampton Flat is Hornsbyville Flat (HF), a long, narrow strip of land 6.1-10.7 meters in elevation, located between the Big Bethel and Suffolk Scarps (S). Hornsbyville Flat lies on the Sedgefield Formation, which is 120,000 years old. West of the Suffolk Scarp and south of the Kingsmill (K) Scarp is the Huntington Flat (HuF) about 9 m in elevation and about 200,000 years old. West of the Suffolk Scarp and north of the Kingsmill Scarp, is the Grafton Plain (GP) which is 16.8 or more meters in elevation. The Grafton Plain lies on the 700,000 year-old Chuckatuck Formation (Gerald Johnson, personal communication).
The soils on the low lying flats of the lower Peninsula are fine sandy loam, loam, or silt loam and range from poorly drained to moderately well-drained. There are seven soil series, four of them are classified as hydric soils (Bethera, Chickahominy, Nimmo, and Tomotley), though none of them experience regular flooding. Most of the soils found on the Hampton Flat are Tomotley, a fine sandy loam series. This soil is deep, poorly drained, strongly acidic, low in organic matter and in fertility. From December to March the water table level is at the soil surface to 0.3 meters below the surface. Other soil types on the Hampton Flat include Dragston and Nimmo, both fine sandy loam soils. From November to April the water table depth is 0.3-0.8 meters below the surface in Dragston soil; in Nimmo soil the water table level is 0-0.2 meters below the surface from December to April. The soil series on the Hornsbyville Flat include Bethera, Tomotley, and Tetotum. Bethera and Tetotum are silt loam soils whose water table level from December to April is 0-0.5 and 0.5-0.8 meters below the surface, respectively. Two soils were present on stands on the Huntington Flat: Tomotley and Chickahominy, a silt loam soil (Mike Newhouse, personal communication). Chickahominy soil is poorly drained with the water table level 0-0.2 meters below the surface from November to April. On the Grafton Plain the Izagora series is a deep, moderately well-drained, upland, loamy soil that is low in organic matter and in soil fertility. The water table level of Izagora is the lowest in this area, remaining 0.7-0.9 meters below the surface from December to March. All the soils in this study are generally low in pH, in fertility, and in organic matter. They are poorly drained and slow in run-off because of the level or nearly level slope, low elevation, and high water table (Hodges et al. 1985).
METHODS

On the low, level, upland (non-floodplain) flats of the lower Peninsula, stands were chosen for sampling if they were predominantly hardwood, relatively homogeneous, showed no obvious signs of recent (>20 yr) timbering or other major disturbances, and were large enough (+1 ha) for placement of a minimum of three, but preferably four, sampling points 40 m apart. A total of 23 stands were sampled by the combined Bitterlich/circular plot method (Levy and Walker 1971). For each sampling point, dominance of each species was calculated by measuring cross-sectional area at breast height (m^2/ha) by the Bitterlich variable radius method using the Spiegel Relaskop. Density for overstory species was determined by counting all stems ≥ 10.16 cm in diameter at breast height (dbh) within a 10 meter radius circular plot. The relative dominance and density for each overstory species in each stand were calculated separately as a percent of total dominance (m^2/ha) or total density (stems/ha) respectively. These two relative percentages were averaged together to yield the importance value (I.V.) for that canopy species in the stand.

The understory species were also sampled. Density of understory species was determined by counting all stems between 1 cm and 10.16 cm dbh in a 10 meter radius circle. Relative density alone was calculated for the understory layer, since no separate basal area (dominance) measurements were made.

Taxonomic nomenclature follows Harvill et al. (1986), except that for Nyssa sylvatica var. biflora (swamp blackgum), Nyssa biflora Walter is used following Brown and Kirkman (1990), and for Quercus falcata var. pagodifolia (cherrybark...
oak), *Quercus pagoda* Raf. is used. Harvill *et al*. (1986) used *Quercus laurifolia* for both *Q. laurifolia* Michaux (swamp laurel oak) and *Quercus hemisphaerica* Bartram (upland laurel oak). In this study *Quercus laurifolia* is applied only to swamp laurel oak.

Soil samples were collected from each stand and forwarded to the Virginia Polytechnic Institute and State University Soil Testing Laboratory to determine pH and concentrations (ppm of oxides) of potassium, phosphorus, calcium, magnesium, zinc, and manganese. Soil texture was determined using a Lamott timed sedimentation test. Since the contour of the land is level or nearly so, the degree of slope was usually zero and aspect was not a consideration. At each site one or two Bouyoucos gypsum blocks were buried at a depth of approximately 25 cm. Every two weeks from May 1990 through December 1990, each stand was visited to record available soil moisture from the blocks with a Bouyoucos moisture meter.

The soil series for stands in York County were obtained from the Soil Survey of James City and York Counties and the City of Williamsburg, Virginia (Hodges *et al*. 1985). Soil types for stands in Hampton, Newport News, and Poquoson were provided by Dr. Michael Newhouse of the Soil Conservation office in Williamsburg.

The moisture readings were treated in three ways. First, an average was taken of all moisture readings from each site. Second, an average was taken of the three driest readings, and finally, an average was made from the four driest readings. These three moisture averages were treated as separate environmental factors.

Species I.V.'s of the overstories of the 23 study sites were used in detrended correspondence analysis (DCA) and, along with environmental data, in canonical correspondence analysis (CCA) using the computer program
CANOCO, written by Cajo J.F. Ter Braak (1988). CANOCO is an extension of the Cornell Ecology program DECORANA (Hill 1979). A DCA ordination was run omitting Acer rubrum and Liquidambar styraciflua data. To examine the relationship between the stands sampled in the current study and other nearby studies, a grand ordination was constructed using vegetation data from the 23 hardwood stands of the current study, plus three additional sampled stands for which no environmental data was available; the 27 upland stands (DeWitt and Ware 1979), plus one poorly drained willow oak site sampled by DeWitt and Ware (unpublished); 18 stream bottomlands of Parsons and Ware (1982), and four additional bottomlands stands from Glascock and Ware (1979). A total of 72 stands from the Coastal Plain of Virginia were used in the grand ordination. For the understory, both DCA and CCA were run using relative densities. Statistical analyses, including product-moment correlation and the Chi square association test, followed Scheffler (1979).
### TABLE 1. RANK IN DOMINANCE OF OVERSTORY SPECIES

<table>
<thead>
<tr>
<th>Species</th>
<th>I.V.&gt;10</th>
<th>Times Ranked</th>
<th>Times Present</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer rubrum</td>
<td>18</td>
<td>4 6 2</td>
<td>23</td>
</tr>
<tr>
<td>Liquidambar styraciflua</td>
<td>11</td>
<td>5 5 4</td>
<td>23</td>
</tr>
<tr>
<td>Quercus alba</td>
<td>9</td>
<td>5 3 1</td>
<td>19</td>
</tr>
<tr>
<td>Pinus taeda</td>
<td>7</td>
<td>2 1 3</td>
<td>18</td>
</tr>
<tr>
<td>Quercus pagoda</td>
<td>6</td>
<td>2 2 3</td>
<td>19</td>
</tr>
<tr>
<td>Liriodendron tulipifera</td>
<td>6</td>
<td>1 2 2</td>
<td>12</td>
</tr>
<tr>
<td>Quercus michauxii</td>
<td>4</td>
<td>1 1 1</td>
<td>18</td>
</tr>
<tr>
<td>Fagus grandifolia</td>
<td>3</td>
<td>2 1 1</td>
<td>5</td>
</tr>
<tr>
<td>Quercus phellos</td>
<td>2</td>
<td>0 0 2</td>
<td>15</td>
</tr>
<tr>
<td>Quercus nigra</td>
<td>2</td>
<td>1 1 0</td>
<td>10</td>
</tr>
<tr>
<td>Quercus laurifolia</td>
<td>2</td>
<td>0 0 2</td>
<td>4</td>
</tr>
<tr>
<td>Nyssa biflora</td>
<td>2</td>
<td>0 1 0</td>
<td>3</td>
</tr>
<tr>
<td>Quercus palustris</td>
<td>1</td>
<td>0 1 0</td>
<td>8</td>
</tr>
</tbody>
</table>
### TABLE II. RANK IN RELATIVE DENSITY OF UNDERSTORY SPECIES

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<th>Species</th>
<th>Relative Density &gt;10</th>
<th>Times Ranked</th>
<th>Times Present</th>
</tr>
</thead>
<tbody>
<tr>
<td>*Acer rubrum</td>
<td>14</td>
<td>6 6 3</td>
<td>22</td>
</tr>
<tr>
<td>Ilex opaca</td>
<td>12</td>
<td>8 1 2</td>
<td>17</td>
</tr>
<tr>
<td>*Liquidambar styraciflua</td>
<td>8</td>
<td>4 3 2</td>
<td>21</td>
</tr>
<tr>
<td>Vaccinium spp.</td>
<td>5</td>
<td>0 0 4</td>
<td>20</td>
</tr>
<tr>
<td>Oxydendrum arboreum</td>
<td>4</td>
<td>0 2 2</td>
<td>14</td>
</tr>
<tr>
<td>Carpinus caroliniana</td>
<td>4</td>
<td>1 1 1</td>
<td>10</td>
</tr>
<tr>
<td>*Fagus grandifolia</td>
<td>4</td>
<td>2 0 0</td>
<td>8</td>
</tr>
<tr>
<td>*Nyssa sylvatica</td>
<td>3</td>
<td>0 1 3</td>
<td>17</td>
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<tr>
<td>Clethra alnifolia</td>
<td>3</td>
<td>1 1 1</td>
<td>5</td>
</tr>
<tr>
<td>Asimina triloba</td>
<td>3</td>
<td>2 1 0</td>
<td>4</td>
</tr>
<tr>
<td>Cornus florida</td>
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<td>0 2 1</td>
<td>11</td>
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<tr>
<td>Persea borbonia</td>
<td>2</td>
<td>0 1 1</td>
<td>6</td>
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<tr>
<td>*Liriodendron tulipifera</td>
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<td>0 1 0</td>
<td>9</td>
</tr>
<tr>
<td>Symplocus tinctoria</td>
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<td>0 1 0</td>
<td>4</td>
</tr>
<tr>
<td>*Nyssa biflora</td>
<td>1</td>
<td>0 1 0</td>
<td>3</td>
</tr>
<tr>
<td>*Quercus pagoda</td>
<td>1</td>
<td>0 1 0</td>
<td>2</td>
</tr>
<tr>
<td>*Fraxinus pennsylvanica</td>
<td>1</td>
<td>0 0 2</td>
<td>2</td>
</tr>
<tr>
<td>*Carya glabra</td>
<td>0</td>
<td>0 0 1</td>
<td>5</td>
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</table>

*potential canopy species
TABLE III. IMPORTANCE VALUES IN EACH STAND OF ALL MAJOR CANOPY SPECIES. (I.V. ≥ 10 in at least 2 stands or be present in at least 1/3 (8) stands. For rarer species see Appendix I.)

<table>
<thead>
<tr>
<th>Stand #</th>
<th>17</th>
<th>11</th>
<th>12</th>
<th>20</th>
<th>14</th>
<th>22</th>
<th>21</th>
<th>7</th>
<th>5</th>
<th>16</th>
<th>6</th>
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</thead>
<tbody>
<tr>
<td>Species:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F. grandifolia</td>
<td>54.1</td>
<td>32.1</td>
<td>13.7</td>
<td>18.1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Q. falcata</td>
<td>-</td>
<td>10.9</td>
<td>6.6</td>
<td>-</td>
<td>2.3</td>
<td>-</td>
<td>1.6</td>
<td>6.9</td>
<td>1.9</td>
<td>6.4</td>
<td>2.9</td>
</tr>
<tr>
<td>Q. alba</td>
<td>3.6</td>
<td>21.6</td>
<td>45.7</td>
<td>24.6</td>
<td>34.8</td>
<td>12.0</td>
<td>17.7</td>
<td>18.6</td>
<td>16.1</td>
<td>25.4</td>
<td>4.9</td>
</tr>
<tr>
<td>Pinus taeda</td>
<td>2.2</td>
<td>1.5</td>
<td>1.8</td>
<td>10.0</td>
<td>4.5</td>
<td>17.4</td>
<td>19.3</td>
<td>11.0</td>
<td>11.5</td>
<td>12.4</td>
<td>21.2</td>
</tr>
<tr>
<td>Q. nigra</td>
<td>0.7</td>
<td>3.3</td>
<td>-</td>
<td>3.7</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>16.2</td>
<td>28.2</td>
<td>-</td>
<td>2.1</td>
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<tr>
<td>Liriodendron</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>2.9</td>
<td>1.6</td>
<td>0.6</td>
<td>-</td>
<td>7.5</td>
<td>20.1</td>
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<tr>
<td>Q. michauxii</td>
<td>1.5</td>
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<td>-</td>
<td>-</td>
<td>4.4</td>
<td>3.7</td>
<td>4.0</td>
<td>1.5</td>
<td>0.9</td>
<td>6.0</td>
<td>-</td>
</tr>
<tr>
<td>Q. pagoda</td>
<td>10.3</td>
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<td>-</td>
<td>1.1</td>
<td>7.3</td>
<td>4.1</td>
<td>0.6</td>
<td>5.4</td>
<td>-</td>
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<td>-</td>
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<td>-</td>
<td>4.7</td>
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<td>9.5</td>
<td>8.1</td>
<td>-</td>
<td>-</td>
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<td>Q. laurifolia</td>
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<td>-</td>
<td>-</td>
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<td>-</td>
<td>-</td>
<td>-</td>
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<td>1.7</td>
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<td>4.8</td>
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<td>-</td>
<td>-</td>
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</tr>
<tr>
<td>Acer rubrum</td>
<td>18.2</td>
<td>8.9</td>
<td>11.3</td>
<td>18.2</td>
<td>31.7</td>
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The rank in importance of major dominants for overstory species is listed in Table I and for understory species in Table II, and the Importance Values (I.V.) of major overstory species are given in Table III. When canopy species were arranged in Table III according to high importance values, the stands fell into two main groups. Group I stands had high values of beech, white oak, or pine, while Group II stands did not have high I.V.'s for those species, but usually had high values of either tuliptree, basket oak, cherrybark oak, willow oak or swamp laurel oak.

The soils in the study area were low in pH and low in nutrient content as they had been described by Hodges et al. (1985). The soil pH, mineral content, and soil texture for each site are recorded in Table IV. The soils of the lower Peninsula are acidic to strongly acidic with pH values ranging from 3.1 to 3.9 with one higher pH value of 5.2 on stand #4 (IX). The soils also tend to be nutrient poor. Using standards set by the Virginia Polytechnic Soil Testing Labs, only stand #23 (PQ) had soil that was high in calcium (1200 ppm) and magnesium (95 ppm). Stands #4 (IX), #7 (RW), and #14 (OH1) had medium levels of calcium and/or magnesium; the rest were all low in those two minerals. All stands had low readings for phosphorus and potassium. The amounts of zinc, which had the highest correlation with vegetation, ranged from 1.5 to 6.1 ppm.

The amount of moisture in the soil listed as three separate environmental factors was not correlated with vegetation. Table V lists the 23 stands and their relative standings based on average moisture readings. The wettest site was
Figure 3. Detrended Correspondence Analysis (DCA) ordination of canopy species on 23 lower Peninsula hardwood stands using large tree data. The straight line in the left half of the ordination separates the sites into Groups I and II. In Group I on the right the solid curved line encloses all sites where *Fagus grandifolia* (Fg) I.V. >10; the dot-dash line encloses all sites where *Q. alba* (Qa) I.V.>10, and the solid oval encloses all sites where *Quercus nigra* (Qn) I.V.>10. In Group II the sites where *Liriodendron tulipifera* (Lt) I.V.>10 are enclosed by the notched solid line in the lower left corner. The dashed line on the left encloses all sites where *Q. michauxii* (Qm) I.V.>10, and the solid ovals enclose the sites with *Q. laurifolia* (Ql) and *Q. phellos* (Ph) I.V.>10. Arrows indicate significant correlation (p<.01) of environmental variables with the first axis.
Figure 4. DCA ordination as in Figure 3. Groups I and II and significant correlation of variables with the first axis are as in Fig. 3. For convenience in comparing with Fig. 3, the Q. alba (Qa) I.V.>10 (right dot-dash line) and the line separating Group I from Group II are repeated here. The right dashed line encloses to its right all sites where Pinus taeda (Pt) I.V.>10. The left solid line encircles sites where Q. pagoda (Qp) I.V.>10. The stand symbol on the far right with a bar indicates an outlier of Q. pagoda.
Figure 5. DCA ordination as in Fig. 3, with soil types each of site indicated. Groups I and II and significant correlation of variables with the first axis are as in Fig. 3. Tomotley Series is represented by stars, Nimmo by N's, Izagora by open circles, Bethera by a solid circle, Dragston by open squares, Chickahominy by a solid square, and Tetotum by an open rectangle. The stand numbers are given in Appendix II.
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Figure 6. DCA ordination of stands omitting *Acer rubrum* and *Liquidambar styraciflua* from large tree data. Groups I and II are separated by the slanted, straight line. On the right the solid lines encircle the sites where *Q. laurifolia* (Ql) and *Q. michauxii* (Qm) I.V.>10. The stands where *Q. phellos* (Ph) I.V.>10 are enclosed by a dashed line within the *Q. michauxii* contour. Star with a single bar to the right indicates stands where *Quercus pagoda* I.V.>10. The dashed line encircles the sites where *Liriodendron tulipifera* (Lt) I.V.>10. On the left the dot-dash line encloses to its left all sites where *Q. alba* (Qa) I.V.>10. The solid circle encloses sites where *Q. nigra* (Qn) I.V.>10, and the far left solid line encloses to its left sites where *F. grandifolia* (Fg) I.V.>10. The star with a double bar to its right indicates stands where *Pinus taeda* (Pt) I.V.>10. Arrows indicate significant correlation (p<.01) of environmental variables with the axes.
Figure 7. Soil types on the DCA ordination omitting *Acer rubrum* and *Liquidambar styraciflua*. Groups I and II and significant correlation of variables with the axes are as indicated in Fig. 6. The soil series are represented by the same symbols used in Fig. 5. The stand numbers are given in Appendix III.
Figure 8. High and low zinc on the DCA ordination omitting *Acer rubrum* and *Liquidambar styraciflua* as in Figure 6. The sites where *Quercus laurifolia* (Ql) I.V. > 10 are encircled on the far right. In the lower center a solid line encloses sites where *Liriodendron tulipifera* (Lt) I.V. > 10. On the far left a solid line encloses sites where *Fagus grandifolia* (Fg) I.V. > 10. Sites with high zinc (>4 ppm) are enclosed by a dot-dash line, and sites with low zinc (<2 ppm) are enclosed by a dashed line.
ranked first and the driest was ranked 23rd. The soil moisture ranking of stands varied according to the method used in determining the rankings.

In the initial DCA ordination the 23 stands fell into a fairly clear vegetational gradient (Figures 3 and 4). Group I stands with high I.V. of white oak, water oak, and beech fell on the right of Figure 3 while the laurel oak, willow oak, and basket oak of Group II separated on the left side. All stands with tuliptree I.V. > 10 except one fell into Group II. Similarly, in Figure 4 loblolly pine in association with white oak was found in Group I and cherrybark oak, except for one outlier, separated on the left in Group II. Zinc \( r = 0.6649, p < 0.01 \) and elevation \( r = 0.5789, p < 0.01 \) were positively correlated with the first axis. None of three moisture variables correlated with the first axis, although the sequence of species from laurel oak to beech strongly suggests a moisture gradient. The distribution of soil types across the ordination are shown in Fig. 5.

As seen in Tables III and VI, red maple and sweetgum were present in all stands and abundant in many. The influence of such widespread abundant species on ordination axes can mask distribution patterns in less widespread species. To determine whether this was true in this data, the precedents of Gemborys and Hodgkins (1971) and Ware (1988) were followed in the omission of these species from the data for further analysis. A DCA ordination of large trees was run with red maple and sweetgum omitted.

In the DCA ordination of canopy trees ignoring red maple and sweetgum (Figures 6, 7, and 8), the 23 stands again separated into two distinct groups. Group I stands with high I.V. values of white oak, beech, and/or pine fell on the left side of Figure 6 and showed the linear succession of the species as found by Monette and Ware (1983). The Group II stands with laurel oak, willow oak, and basket oak separated on the right side. Again all stands of tuliptree with I.V. > 10 except one fell into Group II. In this DCA ordination there was significant
Figure 9. Canonical correspondence analysis (CCA) ordination of 23 hardwood stands on the lower Peninsula. The solid line on the far right encloses to its right all sites where *F. grandifolia* (Fg) I.V.>10, and the solid line in the lower center encircles sites where *Q. nigra* (Qn) I.V.>10. On the left the lines enclose sites where *Liriodendron tulipifera* (Lt), *Q. laurifolia* (Ql), and *Q. phellos* (Ph) I.V.>10. Stands in Group I are represented by solid circles and in Group II by solid squares. Arrows indicate significant correlation (p<.01) of environmental variables with the axes.
Figure 10. CCA ordination of sites using large tree data. Groups I and II and significant correlation of variables with the axes are indicated as in Fig. 9. The dashed line encloses sites with *Q. alba* (Qa), the dot-dash line encloses sites with *Fagus grandifolia* (Fg), the solid line in the center encloses sites with *P. taeda* (Pt). The dot-dash line on the left encloses sites with *Q. michauxii* (Qm), where I.V. > 10; the solid line within the *Q. michauxii* area encircles stands with *Q. pagoda* (Qp), where I. V. > 11.
Sand Silt Zinc Elevation
correlation with zinc and elevation on both axes. Zinc ($r = -.5395, p<.01$) and elevation ($r = -.4795, p<.05$) were negatively correlated with the first axis, and zinc ($r = .4274, p<.05$) and elevation ($r = .4187, p<.05$) were positively correlated with the second axis. The three moisture variables still did not correlate with either axis. Figure 7 shows that there are only two soil series in Group II, Tomotley and Dragston. Again in this DCA ordination, the separation of the two groups somewhat follows the areas of high and low zinc (Figure 8). Beech (Group I) is more important in stands with high zinc, and laurel oak (Group II) is more important in stands of low zinc. With one exception the greater abundance of tuliptree is associated with low zinc. Overall, the omission of red maple and sweetgum did not result in major changes in the DCA ordination of canopy trees.

A CCA ordination of canopy species is presented in Figures 9 and 10. Elevation ($r = .6927, p<.01$), zinc ($r = .7432, p<.01$), and silt ($r = .5579, p<.01$) were positively correlated with the first axis while sand ($r = -.4985, p<.05$) was negatively correlated with it. Silt ($r = .4442, p<.05$) was also positively correlated with the second axis. In this ordination the first axis is reversed as compared with the DCA axis. In Figure 9 beech is separated on the high end of axis 1 with high silt, high zinc, and high elevation. Tuliptree is again separated from beech on the low end of axis 1, generally in stands with low zinc. In the CCA ordination Group I and II stands do not separate as clearly as they did in the DCA ordinations.

Understory Vegetation

The major dominants in the understory are listed in Tables II and VI. *Ilex opaca* (American holly) and red maple are most commonly the leading dominants, followed by sweetgum. Holly is not a potential canopy tree in the area, but important species in the understory which can reach the canopy include
Figure 11. DCA ordination using understory data. Solid square symbols represent Group I canopy sites while Group II canopy sites are represented by open squares. On the right the dashed line encloses sites with *Asimina triloba* (At) I.V.>10 and the solid line encloses sites with *Clethra alnifolia* (Ca) I.V.>10. Still in Group II on the lower left a solid line encloses sites where *Cornus florida* (Cf) I.V.>10. In Group I the oval encircles sites where *Persea borbonia* (Pb) I.V.>10; on the far left the solid line encloses sites where *Fagus grandifolia* (Fg) I.V.>10, and the dashed line encloses sites where *Acer rubrum* (Ar) I.V.>10. Arrows indicate significant correlation (p<.01) of environmental variables with the second axis.
Figure 12. DCA ordination with understory data as in Fig. 11. Groups I and II and significant correlation of variables with the second axis are indicated as in Fig. 11. Enclosed below the dot-dash line are the sites where *Ilex opaca* (Ix) I.V.>10. The stand symbol with a bar to the right indicates an outlier of *Ilex*. Encircled by the solid line are the sites where *Liquidambar styraciflua* (Ls) I.V.>10. The stand symbol with a star to its right marks the site with *Nyssa biflora* I.V.>10, and the dashed line encloses the sites with *N. sylvatica* (Ns), where the I.V.>10. Stands where *Oxydendrum arboreum* I.V.>10 are indicated by a single bar on top of the stand symbol.
Figure 13. CCA ordination of understory data. Stands in Group I are represented by squares within circles, and stands in Group II by open squares. The dot-dash line on the far right encloses sites where Asimina triloba (At) I.V.>10, and the solid line on the right encircles sites where Clethra alnifolia (Ca) I.V.>10. The stand symbols with a single bar to the right mark sites with N. sylvatica I.V.>10, and the stand symbol with a double bar to the right marks the site with N. biflora, where the I.V.>10. The dashed encloses the sites above it where Ilex opaca (Ix) I.V.>10. On the left the lines enclose sites with Cornus florida (Cf), Persea borbonia (Pb), and Fagus grandifolia (Fg), where the I.V.>10. Arrows indicate significant correlation (p<.01) of environmental variables with the axes.
Calcium

Magnesium
Figure 14. CCA ordination with understory data as in Figure 13. Group I and II and significant correlation with variables with the axes are as in Fig. 13. The solid line in the center encloses below it all stands where *Liquidambar styraciflua* (Ls) I.V.>10. The dashed line encircles sites where *Oxydendrum* (Ox) I.V.>10, and the dot-dash line encloses to its left all sites where *Acer rubrum* (Ar) I.V.>10.
red maple, sweetgum, beech, and blackgum. *Vaccinium* spp. (blueberry) are strictly understory species and despite occurring in 20 stands were too low in relative density (maximum = 14) to ever rank first or second in a stand. *Asimina triloba*, a clonal understory species, was usually very important if present at all. The only oak to reach a relative density > 10 was cherrybark oak, which occurred in the understory of two stands. White oak, basket oak, and water oak were present in the understory in 10, 8, and 7 stands, respectively, but the highest relative density reached by any was 6.3 by white oak in one stand.

On the DCA ordination of understory species pictured in Figures 11 and 12, potassium (r = .4642, p<.05), zinc (r = .4111, p<.05), and elevation (r = .5345, p<.01) were positively correlated with the second axis. Beech and red maple separated from pawpaw and *Clethra alnifolia* along axis 1 of the ordination, and these separations largely coincided with Groups I and II of the canopy ordination, except for two stands in Group II with red maple (Fig. 11). Sweetgum and holly were abundant in stands of both Groups I and II, but largely separated from one another along the second axis (Fig. 10). *Cornus florida* (dogwood) and *Persea borbonia* (redbay) and blackgum also separated along the gradient of axis 2 (Fig. 12). Dogwood (Fig. 11) was most abundant in stands with low zinc and potassium. The two stands with high values of redbay, located adjacent to the line separating Groups I and II, are stands #5 and #7, which also had the highest values of water oak and high values of white oak in the canopy. Sourwood was abundant only in Group I stands at the high end of the second axis.

Different correlations not found in the DCA ordination appeared in the CCA ordination for understory trees (Fig. 13 and 14). Calcium (r = .4948, p<.05) and magnesium (r = .4378, p<.05) correlated positively with the first axis (the only case in which these two variables correlated with any axis), and silt (r = .4399, p<.05) correlated positively with the second axis. Red maple was concentrated
Figure 15. DCA ordination of hardwood stands on the Coastal Plain of Virginia. DeWitt and Ware’s (1979) stands are represented by stars. The star on the left indicates an overcup oak stand which was not included in their study. Parsons and Ware’s (1982) wetter sites (Group I) are solid squares, and the drier ones (Group II) are open squares. The stands in Group I in this study are solid circles, and those in Group II are open ones. The arrow points to the top side of the figure.
Figure 16. DCA ordination of hardwood stands in the Coastal Plain. The symbols are as indicated in Fig. 16. On the left the curved line separates Parsons' wet sites from the drier ones. The dashed line in the center represents the separation between Group I and Group II in this study. The straight line on the right separates DeWitt's dissected upland woods from the undissected upland woods to the left.
TABLE VII. Comparison of leading dominants in three vegetation studies in the Coastal Plain of Virginia. The number indicates the number of stands in which that species was the leading dominant. The percent of stands in each study in which the species reached I.V.>10 is given in parentheses.

(n=18)

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<td>Q. pagoda</td>
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<td>2 (8%)</td>
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<tr>
<td>Pinus taeda</td>
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<tr>
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<td>5 (28%)</td>
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<tr>
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<td>3 (17%)</td>
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<tr>
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TABLE VIII. Number of stands in which characteristic species reached an I.V.>10 in each group of Coastal Plain forest stands. The percent of stands with the species divided by the total number of stands in that group is written in parenthesis for comparison among the three groups.

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<td>Fraxinus pennsylvanica</td>
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on the low level end of axis 1 while pawpaw and pepperbush segregated on the high end of the axis where calcium and magnesium levels were higher. Dogwood, redbay, beech, and sourwood were all on the low end of axis 1 in Figures 12 and 13.

The grand DCA ordination of 72 Coastal Plain stands is found in Figures 15 and 16. Parsons’ wettest bottomland sites are found on the far left, while her drier stands mixed with the wetter sites (Group II) from this study in the left center. Group I stands of the lower Peninsula are in the right center, while DeWitt’s dissected upland stands are generally on the far right. Tables VII and VIII further compare the dominant species of the three vegetation studies in Virginia’s Coastal Plain.
DISCUSSION

An unexpected finding in this study was few environmental variables showed significant correlations with the composition of the vegetation in the lower Peninsula. Throughout this paper, the stands in the current study will be called the "lower Peninsula", and those studied by DeWitt and Ware will be referred to as "dissected uplands". While DeWitt and Ware (1979) did not find good correlations between vegetation and soil pH and mineral content in their Coastal Plain uplands, Monette and Ware (1983) were able to show that this was because much of the difference among Coastal Plain upland stands was related to successional status rather than the usual environmental variables. Further, in their study of Peninsula bottomlands, Parsons and Ware (1982) found strong correlation between vegetation and soil pH and mineral content (Ca, Mg, and NO$_2^-$), and more particularly, between vegetation and soil moisture. On the basis of degree of mesophytism/hydrophytism of the dominant trees, the lower Peninsula stands fall into a more mesophytic group (Group I) and a more hydrophytic group (Group II), and stands of these two groups fairly consistently separated from one another along the axes of the various ordinations. One would then expect certain environmental variables, particularly soil moisture, to be related to vegetational composition of the stands.

The highest correlation coefficient related levels of zinc to vegetation in all ordinations of canopy species. Red maple, tuliptree, laurel oak, water oak, and willow oak were all most important in areas of low zinc, while beech was associated with high zinc (Fig. 3 and 8). Zinc is a mineral not generally reported to be correlated with vegetational composition; nevertheless, it is zinc soil content
which most consistently has the highest correlation with ordination axes including the one along which Group I and Group II stands separate.

More importantly, vegetation on the low, flat lands was correlated with elevation and related to soil types and physiographic subdivisions. Elevation, which in an area of low relief might be expected to be related to depth of the water table, is strongly correlated with the axes along which Group I and Group II separate. Group II stands occurred only in poorly drained Tomotley soils and somewhat poorly drained Dragston soils (Hodges et al. 1985), and Group II sites are mostly located on the lower Hampton Flat (Fig. 2). On the other hand, Group I stands were found on a variety of soil series including the moderately well-drained Izagora and Tetotum. Beech, a Group I species, was found in Nimmo and Izagora soils and on higher elevations (4.5-16.8 meters).

Percent silt and percent sand correlated with the axes along which Group I and Group II separate in the CCA ordination, but they did not in the DCA ordination. These correlations are the reverse of what one might expect if the relative amounts of silt and sand are taken as indications of soil moisture. The more mesophytic sites are in finer textured soils, which normally would be regarded as more moist, and the more hydrophytic sites are on coarser textured soils, which normally would be regarded as drier. However, soil texture may not be an important determinant of moisture when the water table is usually near the surface (Levy and Walker 1976, Parsons and Ware 1982).

Despite the relationships between vegetation and elevation, physiographic area, and soil types, there was no correlation between vegetational pattern and any of the three moisture variables (growing season mean, mean of the four driest readings, and mean of the three driest readings). Probably the reason the moisture data did not correlate with vegetation is best explained by the unusually great amount of subsurface drainage that occurs in this area (Mike Newhouse,
personal communication). Drainage ditches, constructed along the perimeters of the study sites, make the stands drier than they were when the woods were established. Soils that are of a hydric type that should be wet during wet seasons are not now as wet because of this artificial drainage. Most of the trees in the canopy were established before these drainage ditches were dug, so that the present-day canopy composition reflects moisture correlations of the past, rather than the moisture condition that exists at present.

Calcium and magnesium, while usually showing correlation with distribution of vegetation (Parsons and Ware 1982; Farrell and Ware 1991; Kasmer, Kasmer, and Ware 1984), were correlated in this study only with the CCA first axis for understory species. *Clethra* and pawpaw were found at the high end of the calcium and magnesium gradient, while beech, redbay, dogwood, red maple, and sourwood were at the low end (Fig. 13 and 14). The levels of calcium and magnesium are actually very low compared with those found by Farrell and Ware (1991); Kasmer, Kasmer, and Ware (1984); and Parsons and Ware (1982). Perhaps, the levels are so low everywhere that there is too little variation in these minerals to have a major effect on vegetation.

The soils of the lower Peninsula are more acidic than the upland soils in neighboring areas (Rice and Ware 1983, DeWitt and Ware 1979). While no direct correlation was found between the soil pH and vegetation, the distribution of hardwood species is doubtless influenced by the extreme acidity of the soil. Parsons and Ware (1982) found sweetgum, *Carpinus*, willow oak, and water oak important in stands with low pH as well as low magnesium, calcium, and nitrogen. In the Piedmont of southeastern Pennsylvania beech, white oak, and red maple were found in association with lower values of pH, calcium, and magnesium (Kasmer, Kasmer, and Ware 1984). Beech, white oak, and red maple were described as species of less fertile sites by Johnson and Ware
Such studies suggest that the abundance of these species in the lower Peninsula may be enhanced by low soil pH and low levels of nutrients.

DeWitt and Ware (1979) sampled well-dissected, well-drained hardwood stands in Virginia's Coastal Plain, finding white oak and American beech each ranked first in importance value in 11 stands. Southern red oak and tuliptree were the leading dominants in the remaining five stands. Sweetgum and red maple, the major dominants in the present study, were of low importance in DeWitt and Ware's (1979) work. There are other significant differences in DeWitt and Ware's (1979) stands and the present study. They found that beech and tuliptree were often both important in the same stand; they found that *Carya* spp. (hickories) were important, and that willow oak, basket oak, laurel oak, and cherrybark oak were not important. Only the first four stands in Group I of the undissected uplands of the lower Peninsula, which have high values of beech and white oak (Tables III, Appendix I), are very similar to the upland hardwoods studied by DeWitt and Ware (1979).

Bottomland hardwood forests in the Coastal Plain were studied by Glascock and Ware (1979) and Parsons and Ware (1982). They found three types of bottomland stands: 1) those with year-round high water tables, with high levels of *Fraxinus pennsylvanica* (swamp ash), *Ulmus americana* (American elm), red maple, and some *Taxodium distichum* (bald cypress); 2) drier sites, with high importance values of *Carpinus caroliniana* (ironwood) and sweetgum; and 3) those with low moisture in the dry season but flooding in the wet season, with willow oak. Bald cypress did not occur on any of the 23 non-bottomland hardwood stands on the lower Peninsula, and swamp ash, American elm, and ironwood were never leading dominants (see Table VIII) in the present study. Some of these differences may be related to the lower Peninsula's low soil pH and low calcium, since Parsons and Ware's (1979) wettest bottomland containing
ash, elm, and bald cypress, had pH values of 5.8 to 7.5 and high levels of calcium (from 797-1679 ppm).

The low, flat hardwoods on the lower Peninsula east of the Suffolk Scarp are not swamps as the stands were in Parsons and Ware's (1979) study, because the lower Peninsula forests are not in floodplains of streams. There are, however, several stands that are dominated by swamp species. Stands #15 and #19 have high importance values of Quercus laurifolia (swamp laurel oak) which is common in floodplains and swamp margins (Brown and Kirkman 1990), and Nyssa biflora (swamp blackgum), a bottomland species (Duncan and Duncan 1988). These sites also have swamp understory species, Clethra alnifolia and Lyonia ligustrina.

In Table VII one can see that the hardwood stands of the undissected lower Peninsula are a transition between DeWitt and Ware's (1979) dissected uplands and Parsons and Ware's (1982) stream bottomlands. Three leading dominants of DeWitt and Ware's uplands (white oak, beech, tuliptree) and five dominants of Parsons and Ware's swamps (red maple, sweetgum, willow oak, basket oak, and water oak) are leading dominants in the transitional lower Peninsula. Two species were important on the lower Peninsula (swamp laurel oak and Quercus palustris or pin oak) but were not dominant in either of the other two studies. The transitional nature of the lower Peninsula is further shown in Table VIII which lists all species with I.V.>10 in the three studies.

The grand ordination in Figures 15 and 16, as well as Tables VII and VIII, shows the transitional nature of the stands of the undissected, low uplands of the lower Peninsula, as they largely fall between Parsons' swamps and DeWitt's dissected uplands on the ordination. On the lower Peninsula some Group II stands, especially #23, are such poorly drained sites that they most resemble
Parsons' better drained bottomlands. Only three stands from the lower Peninsula (#11, #12, and #17) are grouped with DeWitt's upland stands.

Thirty-eight of the 45 species represented on the grand ordination occurred on the 23 lower Peninsula stands. Species richness averaged 10.8 per stand. Species richness was greater in DeWitt and Ware's 27 stands (1979) averaging 13.6 species per stand, while Parsons and Ware's (1982) bottomland stands averaged 11 species per stand.

DeWitt and Ware (1979) argued that the dissected uplands of the Coastal Plain should be considered a northern extension of Quarterman and Keever's Southern Mixed Hardwood Forests because of the similarities in vegetation composition. There are fourteen species of high importance values in the SMHF: beech, upland laurel oak, southern magnolia, white oak, sweetgum, mockernut hickory, water oak, southern red oak, pignut hickory, blackgum, American holly, loblolly pine, dogwood, and Vaccinium arboreum. Eight of the fourteen species listed above were found to have high importance values in at least two stands in the lower Peninsula. One important SMHF species that is missing, Magnolia grandiflora (southern magnolia), is north of its range on the Peninsula and would not be expected to be found here (Ware 1978). Another SMHF species, upland laurel oak (Quercus hemisphaerica) (Ware 1988, Greller 1980) is not the physically similar swamp laurel oak (Quercus laurifolia) found on the lower Peninsula.

Despite the importance of these eight species, these lower Peninsula stands have less overall similarity to the SMHF than they do to the dissected upland stands of DeWitt and Ware (1979), and the lower Peninsula stands with their high importance values of red maple, sweetgum, tuliptree, and cherrybark oak, are actually more similar to the bottomland stands of the Coastal Plain. Though Harvill (1966) said red maple and beech are the dominant species in
TABLE IX. IMPORTANT VALUES OF OAK SPECIES. Superscript 1 indicates the top ranking oak species and superscript 2 the second ranked oak in each site.

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<th>PALUSTRIS</th>
<th>PHELLOS</th>
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<td>24.6(^1)</td>
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<td></td>
<td>5.5(^2)</td>
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</tr>
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<tr>
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<td>14.2(^1)</td>
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very mesic sites on the Coastal Plain of the Middle Peninsula between the York and Rappahannock Rivers of Virginia, Ware (1979) never found red maple a leading dominant in the upland woods of the Coastal Plain. According to several authors, red maple is often found in the canopy of hardwood swamps (Christensen 1988, Braun 1950, Monk 1968, Dabel and Day 1977). Likewise, sweetgum, a leading dominant five times on the lower Peninsula, was not important in the canopy of Monette and Ware's (1983) coastal plain sites, but it was in the bottomlands (Parsons and Ware 1982). These two species would be expected to be more important in wetter sites.

Mohler (1990) has theorized that the two most abundant oak species in any stand will be of different subgenera. The explanation for this is that two white oak species or two black oak species would be competing for the same niche, while species of the different subgenera could share dominance. In only three sites were two oak species ranked first and second. In #5 (LR), water oak and white oak were first and second; in #7 (RW), their order was reversed; and in #8 (WH), cherrybark oak and basket oak ranked first and second. In each of the three stands, one dominant oak was of one subgenus and the other of another. Because of the frequent dominance of red maple and sweetgum, only rarely did two oaks be codominate. In eleven other stands, however, one of the top two ranked species was an oak. Never in any stand were the top-ranked and second-ranked oak species from the same subgenus. Table IX lists the oak species and their importance values. Thus, Mohler's rule holds true for all 23 study sites on the lower Peninsula.

Certain hardwood species were found on sites in the lower Peninsula where they had not previously been recorded in the Atlas of the Virginia Flora (Harvill et al. 1986). Three species, *Symplocus tinctoria*, *Fraxinus pennsylvanica*, and *Quercus coccinea* were county distributional records for York County. *Carya*
ovata (shagbark hickory), a species not previously recorded in the lower Peninsula and primarily an upland Piedmont and mountain species in Virginia, occurred in six stands in York County, Poquoson, and Hampton. These sites with shagbark hickory were all on the Hampton Flat in Tomotley or Dragston soil.

This study has shown that the lack of dissection clearly affects the vegetation on the lower Peninsula. These level, low elevation upland woods are markedly different from highly dissected upland hardwood stands studied by DeWitt and Ware. In fact, the Group I stands with the highest elevation and hence the greatest dissection were most like DeWitt and Ware’s woods. These Group I stands had high importance values of beech and white oak. On the other hand, Group II stands were generally lower in elevation and shared more affinities with Parsons’ bottomlands. Thus, the hardwood forests on the flat, low land east of the Suffolk Scarp represent a transition between the dissected uplands and stream bottomlands of the eastern Coastal Plain of Virginia.
APPENDIX I. IMPORTANCE VALUES OF ALL CANOPY SPECIES IN ALL STANDS

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<th>20</th>
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<td>DN</td>
<td>HH</td>
<td>OH2</td>
<td>RM</td>
<td>KW</td>
<td>RW</td>
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<td>MW</td>
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67
APPENDIX II. STAND NUMBERS ON DCA ORDINATION OF CANOPY SPECIES

Zinc Elevation

68
APPENDIX III. STAND NUMBERS ON DCA ORDINATION OMITTING ACER RUBRUM AND LIQUIDAMBAR STYRACIFLUA

Zinc
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Elevation

69
LITERATURE CITED


VITA

Penelope Williams Cazier


In September 1989, the author entered the College of William and Mary as a graduate assistant in the Department of Biology.