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Vegetation of Headwater Wetlands in the Inner Coastal Plain of Virginia and Maryland

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ABSTRACT

Canopy, woody understory, and herbaceous strata of headwater wetlands were quantitatively sampled in the inner coastal plain of Virginia and Maryland. Canopy species distribution patterns were then compared with field indicators of hydrologic regime using Detrended Correspondence Analysis (DCA). Sixteen canopy species, 21 subcanopy species, 9 vine species, and 40 herbaceous species were encountered in the 18 sampled stands. One third of sampled sites were overwhelmingly dominated (IV > 50) by *Acer rubrum* L., while *Liquidambar styraciflua* L. was important (IV > 15) in half of the stands. The DCA ordination separated stands dominated by *Nyssa biflora* Walter and *Fraxinus* spp. from stands dominated by *Liriodendron tulipifera* L. along a moisture gradient measured by a field indicator of microtopographic depressional storage.

Sapling strata of most sites were overwhelmingly dominated by *Liquidambar styraciflua* L., although *Acer rubrum* L. and *Fraxinus* spp. were also important in many sites. In the subcanopy stratum, *Carpinus caroliniana* Walter, *Lindera benzoin* (L.) Blume, and *Ilex opaca* Aiton occurred in 60–70% of the sites sampled. In the herb layer, *Boehmeria cylindrica* (L.) Swartz, *Glyceria striata* (Lam.) Hitchcock, and *Thelyptris palustris* Schott occurred in 40–60% of sampled sites. The subcanopy and herb layers differed substantially in composition from headwater wetlands in North Carolina, perhaps a reflection of differences in climatic conditions and site histories relative to past logging and/or fire frequencies.

INTRODUCTION

Much information has been published on the vegetation and hydrodynamics of floodplain swamps of high-order streams and rivers in the southeastern United States (for overviews see Wharton et al. 1982, Sharitz and Mitsch 1993). However, comparatively little information is available about wetlands of low-order streams (hereafter referred to as headwater wetlands) in spite of their abundance in the landscape.

Headwater wetlands differ substantially from wetlands associated with larger rivers in a number of hydrologic attributes: (1) low order stream systems have much lower hydrologic energy and so are not capable of carrying large amounts of sediment or debris, (2) water table fluctuations are more flashy, flooding durations shorter, and flooding depth much less, and (3) flooding is primarily in response to groundwater discharge and overland flow from surrounding uplands rather than from overbank flow. These differences in hydrodynamics and water source may lead to differences in the floristic composition of headwater wetlands compared to wetlands associated with higher stream orders.

Many headwater wetlands located in the inner coastal plain of Maryland and Virginia have been altered directly or indirectly by human activities. Historically, many activities (i.e., stream channelization and straightening, interception and diversion of overland flow from headwater wetlands directly to stream channels) were directed toward converting headwater wetlands to drier conditions that could be used for agriculture. Other headwater wetlands were

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converted to ponds for water supply, flood prevention, or mill ponds. The hydrology of many headwater wetlands has also been altered by road construction. Headwater wetlands upstream of roads typically flood more frequently and have higher sediment deposition rates (Whigham et al. 1988). Culverts at road crossings are also used by beaver (*Caster canadensis* Kuhl) for siting dams (pers. obs.), thus accentuating the depth and duration of upstream flooding. Agricultural activities, and more recently, urban and suburban development, have often resulted in further hydrologic alterations and increased sediment deposition in headwater wetlands. Many headwater wetlands have been repeatedly logged, further modifying both vegetation and creating physical disturbance. Microtopographic conditions are also often altered by human activities resulting in vegetation changes (Thomas 1998).

The numerous alterations associated with headwater wetlands have likely been responsible not only for changes in hydrologic conditions, but also for changes in vegetation and functions related to nutrient cycling. To our knowledge, there have not been systematic efforts to characterize current ecological conditions of headwater wetlands in the inner coastal plain of Maryland and Virginia. In this paper, we describe the vegetation in reference standard (relatively unaltered) wetlands that were sampled as part of an effort to develop and test hydrogeomorphic (HGM) functional assessment models for headwater wetlands on 1st to 3rd order streams (Whigham et al. 1999). We also compare these data with those from low order bottoms in North Carolina (Rheinhardt et al. 1998) and southeastern Virginia (Glascock and Ware 1979, Parsons and Ware 1982). In addition, we provide quantitative data on the composition of woody subcanopy and herbaceous strata in headwater wetlands, about which little has been published.

Study Area

The inner coastal plain of Virginia and Maryland north of the James River is dissected by several wide tidal rivers (subestuaries) of Chesapeake Bay, creating a series of northwest-to-southeast trending peninsulas (Figure 1). Numerous freshwater streams originate in these peninsulas but few of them ever converge to form streams that are greater than 3rd order, because the peninsulas are relatively narrow, watersheds are small, and streams never get very large before they reach tidal influence at sea level. This landscape differs geomorphically from land south of the James River where relatively narrow non-tidal rivers dissect the inner coastal plain, and large, flat, poorly-dissected interfluvial areas are prevalent. It is unclear whether these geomorphic differences in the landscape have led to any vegetational differences in headwater wetlands.

Climate of the inner coastal plain of Virginia and Maryland is humid temperate (Holdridge 1967), with hot summers and relatively mild winters. The area's proximity to the Atlantic Ocean and Chesapeake Bay somewhat ameliorates climatic fluctuations. Although precipitation is evenly distributed throughout the year, stream discharge is highest during winter months when evapotranspiration (ET) is low and generally lowest during summer months when ET rates are high. However, nor'easters in winter and hurricanes in late summer and fall can temporarily and radically increase stream flow.

METHODS

Bottomlands of 18 headwater wetlands were sampled between June 15 and July 28, 1995 in Virginia and Maryland. In this paper, the term headwater wetland includes both active floodplains (where present) and seepage wetlands located at the toe of adjacent upland slopes. None of the sampled sites showed evidence of recent human alteration (logging, stream channelization, hydrologic alteration from road crossings), and none were flooded by beaver impoundments at the time of sampling. At each site, an area of relatively homogeneous, mature forest was located, and two non-overlapping sampling locations (described below) were randomly placed within each stand.

At each sampling location, canopy trees were tallied by species using the Bitterlich plotless technique (Grosenbaugh 1952, Lindsey et al. 1958) to obtain basal area in m^2/ha. Canopy trees were defined as stems >10 cm dbh (diameter at breast height: 1.5 m above ground). Absolute basal area of canopy trees was converted to relative basal area for each species by

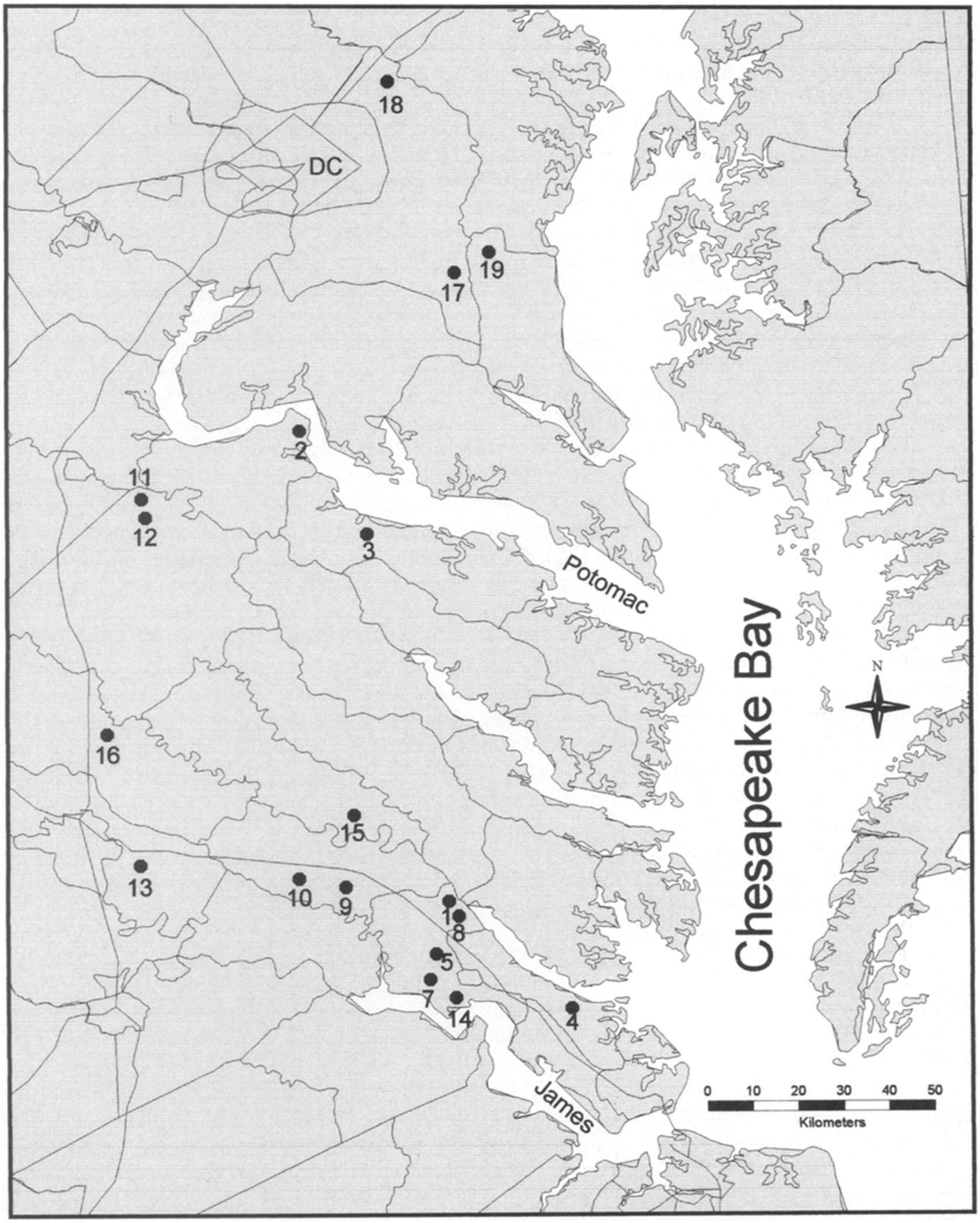

Figure 1. Study area and site locations (dots). Numbers for sites correspond to stands in Tables, except that N (for North Carolina) and M (for Maryland) designations not provided. There is no site 6.

dividing each species' absolute basal area by total canopy basal area. In a 10 m radius plot centered on each Bitterlich point, trees were also tallied by species to obtain tree density in stems/ha. Absolute density of canopy trees was converted to relative density by dividing the absolute density of each species by total tree density. An importance value (maximum IV =

100) for each tree species was derived by averaging relative basal area and relative density. These IVs were used to compare the sites using the Detrended Correspondence Analysis (DCA) algorithm (Hill 1979, Hill and Gauch 1980) using PC-ORD software (McCune and Mefford 1995).

The bottom of each canopy tree in the 10 m radius plots was examined for the presence of vines climbing more than 1 m up the tree. Each vine was tallied by species to obtain vine density in stems/ha. Absolute density of vines was converted to relative density by dividing the absolute density of each species by total vine density.

In a 5 m radius plot centered on each Bitterlich point, woody stems <10 cm dbh and >1 m tall were tallied by species to obtain densities in stems/ha. Woody species in this size class were partitioned into two life-forms: saplings (juveniles of potential canopy trees) and subcanopy (shrubs and trees restricted to the understory at maturity). Absolute densities of species belonging to each life-form were converted to relative densities by dividing absolute density of each species by total density of its respective life-form. Saplings and subcanopy stems were analyzed separately because they provide different information about understory dynamics and may be useful in clarifying forest dynamics (Rheinhardt 1992).

Five randomly placed 1 m^2 plots were placed at each of the two sampling locations (10 plots per site). In each plot, we estimated cover (using the categories below) for two parameters that we believed might indicate the magnitude of flooding duration or depth: (1) the proportion of the plot potentially capable of ponding water (a potential indicator of water storage capacity in microtopographic depressions) and (2) the proportion of unvegetated ground in the plot (a potential indicator of ponding duration). Cover in each 1 m^2 plot was estimated and assigned the midpoint (in parentheses) of one of the following nine cover categories: 0% (0), 1–5% (2.5), 5–25% (15), 25–50% (37.5), 50% (50), 50–75% (67.5), 75–95% (85), 95–100% (97.5), 100% (100). At each plot, we also measured the height of water marks on the tree nearest to each plot (a potential indicator of flooding height). Each of these three parameters was used in the ordination to construct environmental jointplot arrows, which depict the direction and relative strengths of changes along environmental gradients radiating from the centroid of ordination scores (McCune and Mefford 1995). We used PC-ORD's default cutoff value of $r^2 > 0.20$. We also determined whether any of the variables correlated significantly with stand positions along the two ordination axes.

Herbaceous species were identified in each site and their presence recorded. Although herbs were not quantitatively sampled, presence/absence information among the sites was used to provide a generalized characterization of the groundcover stratum.

RESULTS AND DISCUSSION

Canopy

At least 16 canopy species were encountered in the eighteen headwater streams sampled. The most abundant canopy species were *Acer rubrum* L. (red maple), *Liquidambar styraciflua* L. (sweetgum), *Fraxinus* spp. (ash), *Nyssa biflora* Walter (swamp blackgum), *Liriodendron tulipifera* L. (yellow poplar), and *Ulmus* spp. (elm), including *U. rubra* Muhl. (slippery elm) and *U. americana* L. (American elm) (Table 1). Six oak species (*Quercus phellos* L., *Q. palustris* Muenchh), *Q. michauxii* Nutt., *Q. lyrata* Walter, *Q. shumardii* Buckley, and *Q. alba* L.) were also associated with the bottoms. In addition, *Pinus taeda* L. (loblolly pine), *Fagus grandifolia* Errhart (beech), and *Juniperus virginiana L.* (eastern red cedar) occasionally occurred in headwater reaches.

The DCA ordination was useful in showing relationships among stands with respect to where the most common canopy species show their highest importance values. For example, *Acer rubrum* occurred at all stands, but was very important (IV > 50) in the 7 stands (38%) located in the top center of the first DCA ordination axis (Figure 2). *Liquidambar styraciflua* also occurred in almost all stands and was important (IV > 15) in 9 of the stands (50%). *Liquidambar styraciflua* was important in 3 of the 4 stands in which *Liriodendron tulipifera* was important (IV > 15) and 4 of the 7 stands that *A. rubrum* was most important. However,

Table 1. **Importance values of canopy species (Maximum = 100). Absolute basal areas and densities of trees can be obtained from the senior author by request. Taxonomic nomenclature follows Radford et al. (1968), except that** *Nyssa sylvatica* **var.** *biflora* **is herein called** *Nyssa biflora.* **There is no site 6**

Canopy	V12	V15	V3	M17	M19	V7	V9	V4	V10	V2	V8	V1	V14	V13	V5	V16	M18	V11
Total basal area (m²/ha)	27	31	27	28	39	32	26	38	28	33	28	36	29	32	38	27	30	33
Total density (stems/ha)	508	445	605	588	413	683	620	366	445	588	541	636	318	477	477	524	572	413
Acer rubrum L.	81.4	60.8	72.0	70.8	56.3	51.0	49.3	33.6	40.2	20.5	19.5	8.5	18.6	28.9	32.8	29.1	34.2	5.4
Liquidambar-styraciflua L.	16.8	17.1	—	15.6	28.8	7.1	9.6	14.7	—	17.5	3.3	4.2	16.9	9.6	4.6	39.3	8.4	20.7
Fraxinus spp.	—	—	2.5	4.1	7.0	34.3	11.5	34.7	28.1	49.0	38.3	33.7	15.1	—	31.7	—	3.0	—
Nyssa biflora Walter	—	—	—	—	—	2.4	4.4	—	10.5	—	22.6	39.6	—	24.3	17.6	—	—	—
Liriodendron tulipifera L.	—	15.3	—	4.9	—	2.7	—	—	5.2	—	4.8	9.8	5.9	3.2	—	4.9	39.4	67.1
Betula nigra L.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3.0	—
Fagus grandifolia Ehrhart	—	1.9	—	—	—	—	—	—	—	—	—	—	—	—	—	11.3	—	—
Juniperus virginiana L.	—	—	—	—	—	—	—	—	3.5	—	—	—	—	—	—	1.5	—	—
Pinus taeda L.	1.9	—	—	—	—	—	3.2	—	—	—	—	—	—	—	1.3	13.8	—	—
Platanus occidentalis L.	—	1.6	—	—	—	—	6.4	7.5	—	3.0	—	—	—	—	—	—	3.0	5.0
Quercus alba L.	—	—	25.5	—	—	—	—	—	1.8	—	—	—	—	—	—	—	—	—
Quercus lyrata Walter	—	—	—	—	—	—	—	—	—	—	—	—	—	14.6	6.0	—	—	—
Quercus michauxii Nutt.	—	—	—	—	—	—	4.5	—	—	—	3.3	—	23.8	9.7	—	—	—	—
Quercus palustris Muenchh.	—	—	—	—	1.3	—	—	—	—	—	—	—	—	—	—	—	—	—
Quercus phellos L.	—	—	—	—	6.6	—	—	—	—	—	—	—	—	9.7	—	—	—	—
Quercus shumardii Buckley	—	—	—	—	—	—	—	—	—	—	—	—	9.4	—	—	—	—	2.0
Ulmus spp.	—	3.5	—	4.5	—	2.7	10.9	9.5	10.6	10.0	8.1	4.2	10.3	—	6.0	—	8.8	—

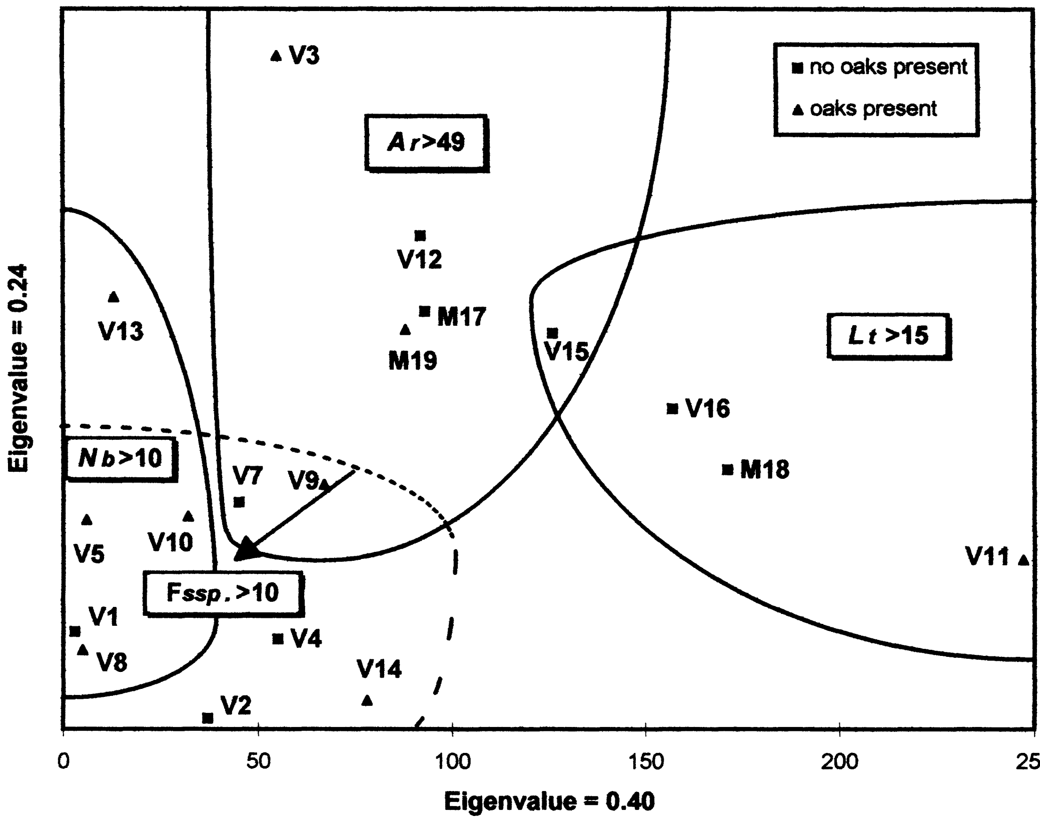

Figure 2. Ordination of sampled sites based on importance values (IV) of canopy trees. Lines delimit stands in which the IV for a species exceeds that defined within the boxes. Abbreviations: *Nb* = *Nyssa biflora* (within solid line, lower left); *F*spp. = *Fraxinus* spp. (within dotted line, lower left); *Lt* = *Liriodendron tulipifera* (within solid line, center right); *Ar* = *Acer rubrum* (within solid line, upper center). The jointplot arrow depicts the direction of the microtopographic depression variable ($r^2 > 0.20$). This variable also correlated negatively with Axis 2 ($P < 0.01$, $r^2 = 0.502$).

L. styraciflua was important in only 3 of the 9 stands that *Fraxinus* spp. were important (IV > 10) and in none of the 5 stands in which *Nyssa biflora* was important (IV > 10). Both *N. biflora* and *Fraxinus* spp. were most important in stands toward the left of the ordination and overlapped in 4 stands (Figure 2).

Of the three hydrologic indicators measured, none correlated with the first ordination axis and only the indicator of microtopographic depressional area correlated negatively with Axis 2 ($P < 0.01$, $r^2 = -0.502$). Also, this microtopographic variable was the only one of the three measured that met the $r^2 > 0.20$ default for jointplots. The jointplot arrow points from the centroid of all stands (above and to the right of stand V9) toward the lower left of the ordination diagram (Figure 2). Both the correlation analysis and the jointplot results suggest that the sites in the lower left corner of the ordination have more microtopographic depressional storage than the other stands and are probably more hydric. This makes sense in that the most flood-tolerant species in headwater systems (*Nyssa biflora* and *Fraxinus* spp.) show their highest IVs in the stands located in the wettest part (in lower left) of the ordination diagram.

Liriodendron tulipifera is generally considered to be successional in stream bottoms (Ashe 1915, Braun 1950, Burns and Honkala 1990). In our sites, it occurred in 61% of sampled stands, but reached an IV > 15 in 4 sites (22%). Similarly, *L. tulipifera* occurred in 88% of headwater bottoms in North Carolina and was important (IV > 15) in 32% of stands sampled (Rheinhardt et al. 1998). In relatively mature stands, *L. tulipifera* appears to be more prevalent in headwater (lower order) reaches than in more downstream reaches (R. Rheinhardt, pers. obs.). This may account for its concentration at the sites on the far right, which are furthest removed from the wettest portion of the ordination diagram.

Acer rubrum is a common species in many forested wetlands throughout eastern North America, and Abrams (1998) has proposed that it may be increasing in dominance at the expense of other species. In southeastern Virginia, Parsons and Ware (1982) found that in about half of their stands, *A. rubrum, Fraxinus,* and *Ulmus* spp. were important. Most of the other stands supported a mixture of *Quercus* spp. Only one of Parson and Ware's 14 stands in southeastern Virginia and none of the 17 headwater stands sampled by Rheinhardt et al. (1998) in North Carolina had an IV > 50 for *A. rubrum.* In contrast, 38% of the headwater stands we sampled in Virginia and Maryland had *A. rubrum* with an IV > 50. It is unclear why *A. rubrum* is so important in more northerly stands.

Six *Quercus* spp. occurred in half of our Virginia and Maryland stands, but only 3 species attained an IV > 10, each species in a different stand (*Q. alba,* IV = 25.5 in V3; *Q. michauxii,* IV = 23.8 in V14; *Q. lyrata,* IV = 14.6 in V13). In North Carolina, *Quercus* spp. were important (IV > 10) in 18% of the stands (Rheinhardt et al. 1998) with only 3 species attaining an IV > 10 in any stand (*Q. laurifolia* Michaux., *Q. pagodaefolia* (Ell.) Ashe, and *Q. michauxii*). In contrast, *Quercus* spp. were important (IV > 10) in 36% of the bottomlands sampled by Parsons and Ware (1982) in the southeastern coastal plain of Virginia. It is unclear why Parson and Ware found that *Quercus* spp. were more important in their study sites. However, our study covered a wider geographic area than that of Parsons and Ware. In addition, when scouting for appropriate sites to sample in 1995, we found that many of the sites that Parsons and Ware had sampled in 1980 had been dammed by beaver or had been clear-cut. Perhaps beaver dams and/or preferential logging of stands with oaks have been responsible for the apparent decline in oak abundance over the 15 years between the two studies.

We found *Ulmus* spp. in the canopy of 67% of stands sampled (Table 1), while 28% of stands harbored *Ulmus* spp. with an IV > 9. Parsons and Ware (1982) found *Ulmus* spp. in 78% of stands sampled in Virginia, with an IV > 9 occurring in 43% of all stands sampled. *Ulmus* was also prevalent in swamps sampled by Monk (1966) in north Florida (83% of stands). In contrast, *Ulmus* spp. occurred in only 32% of stands sampled in the inner coastal plain of North Carolina and in no stand did *Ulmus* exceed 9 in IV (Rheinhardt et al. 1998). It is unclear why *Ulmus* is less prevalent in low order streams south of the James River than north of it. Perhaps preferential logging of stands with *Ulmus* spp. (and stands with both *Quercus* spp. and *Ulmus* spp.) is responsible for the relatively lower *Ulmus* importance in North Carolina stands.

Saplings

We encountered eleven species of saplings in the understory, ten of which occurred in the canopy stratum. The sapling stratum of most sites was dominated by *Liquidambar styraciflua* (Table 2), contributing to 50% or more of the saplings in 67% of the sites. Saplings of *Acer rubrum* were abundant (relative density >10%) in 55% of the sites and *Fraxinus* spp. in 22% of the sites. Saplings of *Quercus* spp. and *Fagus grandifolia* were present in only 3 (17%) sites while *Nyssa biflora* was not encountered in any sites. Based on sapling composition alone, it would appear that in the future most stands will be dominated by *L. styraciflua* and *A. rubrum* and that there will be few *Quercus* spp. or *Fraxinus* spp. Also, *Fagus grandifolia* may become more important in the canopy of three sites (V11, V16, and M19), all of which have incised channels (M19 may have been channelized).

Generally, sapling abundance is a more reliable indicator of future canopy composition than seedling abundance because mortality is usually lower among saplings than seedlings. However, the relative abundance of *Liquidambar styraciflua* saplings may not provide a reliable prediction of its future abundance because *L. styraciflua* may be more susceptible to beaver predation.

Beavers and their lodges have become much more prevalent in the last 20 years (R. Rheinhardt, pers. obs.). In many watersheds, they have created a contiguous, step-wise pattern

Table 2. Relative densities of saplings (Maximum = 100). Absolute densities of individual species can be obtained by multiplying relative densities by total density of the site. P (present) denote species observed in the site, but not sampled in plots. Taxonomic nomenclature follows Radford et al. (1968), except that *Nyssa sylvatica* var. *biflora* is herein called *Nyssa biflora*

Sapling	V12	V15	V3	M17	M19	V7	V9	V4	V10	V2	V8	V1	V14	V13	V5	V16	M18	V11
Total density (stems/ha)	3,111	64	825	444	1,587	1,080	190	64	254	317	700	0	190	1,782	255	1,465	64	700
Liquidambar styraciflua L.	100.0	100.0	85.0	57.0	76.0	82.6	33.3	—	50.0	80.0	—	—	66.7	46.4	—	65.2	100.0	72.7
Acer rubrum L.	—	—	15.0	43.0	—	5.9	33.3	100.0	—	20.0	18.2	—	33.3	14.3	25.0	—	—	—
Fraxinus spp.	—	—	—	—	4.0	11.8	—	—	50.0	—	81.8	—	—	—	75.0	—	—	—
Fagus grandifolia Ehrhart	—	—	—	—	20.0	—	—	—	—	—	—	—	—	—	—	13.0	—	18.2
Liriodendron tulipifera L.	—	—	—	—	—	—	33.3	—	—	—	—	—	—	7.1	—	—	—	—
Prunus serotina Ehrhart	—	—	—	—-	—	—	—	—	—	—	—	—	—	—	—	4.3	—	—
Nyssa sylvatica Marsh	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17.4	—	—
Quercus michauxii Nutt.	—	—	—	—	—	—	—	—	—	—	—	—	—	10.7	14.3	—	—	—
Quercus nigra L.	—	—	—	—	—	—	—	—	—	—	—	—	—	7.1	—	—	—	—
Quercus lyrata Walter	—	—	—	—	—	—	—	—	—	—	—	—	—	3.6	—	—	—	—
Quercus shumardii Buckley	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9.1
Nyssa biflora Walter	—	—	—	—	—	—	—	—	—	—	—	—	—	3.6	—	—	—	—
Betula nigra L.	—	—	—	—	—	—	—	—	—	—	—	—	—	7.1	—	—	—	—

of dams along long stretches of most low order streams in the inner coastal plain, making it difficult to locate suitable sites to sample. It is unclear how the recent increase in beaver populations will affect the composition of headwater areas over the long-term; additional research is needed.

Subcanopy

Twenty-one subcanopy species were encountered in headwater bottoms. The most frequently occurring species were *Carpinus caroliniana* Walt. (ironwood) in 67% of the sites, *Lindera benzoin* L. Blume (spicebush) in 61% of the sites, and *Ilex opaca* (Ait.) Spreng (American holly) in 61% of the sites. However, although *C. caroliniana* occurred in 67% of the sites, it was abundant (relative density >25%) in only 25% of the sites in which it occurred (Table 3). Likewise, although *I. opaca* occurred in 61% of the sites, it was not abundant in any site. In contrast, spicebush also occurred in 61% of the sites, but was abundant in 54% of the sites in which it occurred. Several other shrubs followed this general pattern of high abundance when present: *Clethra alnifolia* L. (coast pepperbush) was very abundant in 50% of the sites in which it occurred, *Viburnum dentatum* L. (southern arrowwood) in 50%, *Viburnum nudum* L. (southern wild raisin) in 40%, and *Asimina triloba* Adanson (pawpaw) in 28%. The subcanopy differed substantially from that in headwater bottoms in North Carolina where *C. caroliniana, L. benzoin,* and *A. triloba* were rarely found (Rheinhardt et al. 1998). Rather, in North Carolina bottoms *C. alnifolia* and *Magnolia virginiana* L. (sweetbay) were more prevalent.

In site V4, *Asimina triloba* obtained the highest relative abundance of any subcanopy species (97%) with virtually no regeneration of canopy species in that site. It was obvious that V4 had been extremely over-browsed by deer: browse lines were clearly evident in surrounding uplands and deer were abundant in broad daylight nearby (the site is in a National Historic Park in which hunting is prohibited). Obviously, deer avoided the astringent leaves of pawpaw and consumed all other understory forage instead. If left unchecked, over-grazing could lead to an eventual loss of the forest. Although site V4 represents an extreme case, more headwater swamps may become altered by over-grazing as hunting pressure is reduced following suburban expansion.

Vines

With the exception of one stand (in which no vines were located in plots), vine density ranged from 48 to 875 stems/ha (Table 4). Nine species were encountered. *Rhus radicans* L. (poison ivy) occurred in 89% of the stands and was dominant in 56% of them. *Smilax rotundifolia* L. (common greenbrier) was the second most prevalent vine species, occurring in 44% of stands sampled. *Decumaria barbara* L. (climbing hydrangea) was encountered in only three stands, but exceeded 70% relative density in all three stands. *Vitis rotundifolia* Michx. (muscadine grape) was the only other common vine species, occurring in 28% of stands.

Rheinhardt et al. (1998) is the only other study of headwater wetlands that examined vine composition and abundance. The same four species (*Rhus radicans, Smilax rotundifolia, Decumaria barbara,* and *Vitis rotundifolia*) were also important in headwater systems in North Carolina. However, North Carolina stands supported additional species that are considered more southern in their affinity: *Berchemia scandens* (Hill) K. Koch, *Gelsemium sempervirens* Jussieu, and *Smilax laurifolia* L. All three of these species occur in Virginia, but are at the northern limit of their range and are primarily restricted to coastal counties (Harvill et al. 1986).

Herbaceous stratum

We encountered at least 40 species in the herbaceous stratum of headwater bottoms (Table 5), of which the following were most frequently encountered: *Boehmeria cylindrica* (L.) Swartz (56% of the sites), *Glyceria striata* (Lam.) Hitchcock (50%), *Thelypteris palustris* Schott (44% of the sites), *Impatiens capensis* Meerburg (39%), *Arisaema triphyllum* (L.) Schott (39%), *Saururus cernuus* L. (39%), and *Senecio aureus* L. (33%). Because the herb stratum was quantitatively surveyed (presence in plots), it is likely that many species with low cover and/or

Table 3. Relative densities of woody subcanopy stems (Maximum = 100). Absolute densities of individual species can be obtained by multiplying relative densities by total density of the site. P (present) denote species observed in the site, but not sampled in plots. Taxonomic nomenclature follows Radford et al. (1968)

Subcanopy	V12	V15	V3	M17	M19	V7	V9	V4	V10	V2	V8	V1	V14	V13	V5	V16	M18	V11
Total density (stems/ha)	1,018	7,574	1,400	2,419	254	1,782	1,909	1,909	3,819	954	1,273	1,082	3,373	7,747	1,400	5,347	2,673	3,310
Lindera benzoin (L.) Blume	—	11.8	23.0	8.0	25.0	—	10.0	—	63.3	73.0	—	—	52.8	—	68.2	—	93.0	98.1
Asimina triloba (L.) Dunal.	—	21.8	23.0	—	—	3.6	—	96.7	—	9.0	P	—	34.0	—	—	—	—	—
Carpinus carolinana Walter	—	5.0	—	—	75.0	21.4	10.0	3.3	5.0	—	20.0	70.6	7.6	—	22.7	—	P	P
Vaccinium corymbosum L.	68.7	—	—	—	—	—	—	—	—	—	—	—	—	0.8	4.5	3.6	—	—
Ilex opaca (Ait.) Spreng	18.8	3.4	—	P	—	7.1	3.3	—	6.7	18.0	—	5.9	1.9	0.8	—	4.8	—	—
Clethra alnifolia L.	12.5	—	—	—	—	—	43.3	—	5.0	—	—	—	—	40.2	—	30.9	—	—
Viburnum nudum L.	—	—	54.0	—	—	7.1	10.0	—	6.7	—	—	—	—	41.0	—	—	—	—
Viburnum dentatum L.	P	57.1	—	71.0	—	—	23.3	—	—	—	—	—	—	—	—	5.9	7.0	—
Ilex verticillata (L.) Gray	—	—	—	16.0	—	—	—	—	—	—	—	—	—	—	0.8	—	—	—
Rhododendron viscosum (L.) Torrey	—	—	—	5.0	—	—	—	—	—	—	—	—	—	1.6	—	—	—	—
Itea virginica L.	—	—	—	—	—	53.6	—	—	—	—	5.0	—	—	—	—	—	—	—
Alnus serrulata (Ait.) Willd.	—	—	—	—	—	3.6	—	—	—	—	P	—	—	—	—	—	—	—
Cornus stricta Lam.	—	0.8	—	—	—	3.6	—	—	1.7	—	45.0	—	—	—	—	—	—	—
Magnolia virginiana L.	—	—	—	—	—	—	—	—	—	—	—	—	—	4.9	—	50.0	—	—
Stewartia malacodendron L.	—	—	—	—	—	—	—	—	—	—	30.0	23.5	—	—	—	3.6	—	—
Corylus americana Walter	—	—	—	—	—	—	—	—	11.7	—	—	—	3.8	—	4.5	—	—	—
Leucothoe racemosa (L.) Gray	—	—	—	—	—	—	—	—	—	—	—	—	—	9.1	—	—	—	—
Amelanchier canadensis (L.) Medicus	—	—	—	—	—	—	—	—	—	—	—	—	—	0.8	—	—	—	—
Cornus florida L.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.9
Ilex decidua Walter	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.2	—	—
Ostrya virginiana (Miller) K. Koch	P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Table 4. Relative densities of vines (Maximum = 100). Absolute densities of individual species can be obtained by multiplying relative densities by total density of the site. Taxonomic nomenclature follows Radford et al. (1968)

Vine	V12	V15	V3	M17	M19	V7	V9	V4	V10	V2	V8	V1	V14	V13	V5	V16	M18	V11
Total density (stems/ha)	0	429	143	541	48	95	286	48	159	509	334	652	509	397	64	223	80	48
Rhus radicans L.	—	66.7	89.0	91.0	100.0	67.7	94.4	33.3	100.0	100.0	4.8	—	43.8	—	50.0	28.6	100.0	—
Vitis rotundifolia Michx.	—	—	11.0	—	—	33.3	—	—	—	—	9.5	—	6.2	—	25.0	—	—	100.0
Smilax rotundifolia L.	—	11.1	—	9.0	—	—	—	—	—	—	4.8	4.9	43.8	100.0	—	71.4	—	—
Decumaria barbara L.	—	—	—	—	—	—	—	—	—	—	71.4	85.4	—	—	25.0	—	—	—
Calycocarpum lyonia (Pursh) Gray	—	—	—	—	—	—	5.6	—	—	—	—	—	—	—	—	—	—	—
Bignonia capreolata L.	—	22.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Parthenocissus quinquefolia L.	—	—	—	—	—	—	—	—	—	—	—	—	6.2	—	—	—	—	—
Campsis radicans L.	—	—	—	—	—	—	—	—	—	—	9.5	9.8	—	—	—	—	—	—
Lonicera japonica Thunberg	—	—	—	—	—	—	—	66.7	—	—	—	—	—	—	—	—	—	—

Table 5. Presence (X) of herbaceous species in the sites. Taxonomic nomenclature follows Radford et al. (1968)

Herbs	V12	V15	V3	M17	M19	V7	V9	V4	V10	V2	V8	V1	V14	V13	V5	V16	M18	V11
Arisaema triphyllum (L.) Schott		X		X		X			X		X	X			X			
Aster spp.		X				X		X	X	X	X		X			X		
Aster vimineus Lam.												X			X			
Boehmeria cylindrica (L.) Swartz		X	X			X		X	X	X	X	X				X	X	
Carex comosa Boott							X											
Carex spp.	X	X				X		X	X		X			X				X
Carex stricta Lam.												X						
Cryptotaenia canadensis (L.) DC.								X										
Eupatorium sp.							X											
Galium sp.						X	X					X	X					
Geum canadense Jacquin													X					
Glyceria striata (Lam.) Hitchcock	X							X	X		X	X	X		X	X		X
Impatiens capensis Meerburg				X		X				X	X		X		X	X		
Juncus effusus L.		X									X							
Juncus sp.							X											
Lonicera japonica Thunberg							X											
Lycopus virginicus L.	X					X												X
Microstegium vimineum (Trinius) A.								X										
Mitchella repens L.		X					X								X			
Muhlenbergia sp.						X		X		X	X	X	X		X			
Nuphar luteum (L.) Sibthrop & Smith				X														
Onoclea sensibilis L.		X	X														X	
Panicum sp.	X																	X
Peltandra virginica (L.) Kunth.									X							X		
Podophyllum peltatum L.															X		X	

Table 5. Continued

Herbs	V12	V15	V3	M17	M19	V7	V9	V4	V10	V2	V8	V1	V14	V13	V5	V16	M18	V11
Polygonum arifolium L.			X	X						X								
Polygonum pensylvanicum L.												X		X		X		
Polygonum punctatum Ell.				X														
Polystichum acrostichoides (Michaux) Schott		X				X												
Rhus radicans L.				X			X		X								X	
Saururus cernuus L.			X			X				X	X	X			X	X		
Senecio aureus L.						X	X	X				X	X		X			
Thalictrum thalictroides (L.) Boivin									X						X			
Thelypteris hexagonoptera (Michaux) Weatherby												X						
Thelypteris palustris Schott	X	X		X	X	X	X									X		X
Tovara virginiana (L.) Raf.											X	X	X					
Uniola latifolia Michaux							X											
Viola sp.							X		X			X			X			
Woodwardia areolata (L.) Moore	X	X				X									X	X		X
Woodwardia virginica (L.) Smith		X																

density were overlooked. However, it is likely that most of the abundantly occurring species were recorded. Total herbaceous species richness (n = 41) was similar to a that found by Rheinhardt et al. (1998) in headwater bottoms in the inner coastal plain of North Carolina (n = 42). However, the most frequently occurring species differed between the two study areas. In the North Carolina sites, the most commonly occurring herb species were *Arundinaria gigantea* (Walter) Muhl., *Athyrium asplenioides* (Michx) A. Eaton, *Woodwardia areolata* (L.) Moore, and *Osmunda cinnamomea* L.

Some of the uplands and pocosins of the inner coastal plain south of the James River likely burned relatively frequently (every 1–3 yr for savannas and 15–30 yr for pocosins) before the arrival of Europeans (Christensen 1989), and it is likely that ground fires would have occasionally burned through headwater areas as well, particularly those dominated by *Arundinaria gigantea* in the understory. Due to the more dissected landscape and absence of pocosins west of the Suffolk Scarp north of the James River, fire was probably much less frequent in headwater areas and so herb flora in headwater bottoms was unlikely to have developed with the influence of fire. This is speculation, and further work is needed to determine the importance of upland fire regime to headwater flora and whether differences in past fire regime north and south of the James River have influenced herb composition in the two areas.

SUMMARY

Forested wetlands of headwater streams in the inner coastal plain of Virginia and Maryland are primarily dominated by red maple and sweetgum in the canopy with mixtures of ash, blackgum, yellow poplar, elms, and various oak species. The availability of microtopographic depressions (an indicator of relative wetness) correlates with the canopy distribution in the ordination: swamp blackgum and ash were more important in the wettest sites with yellow poplar important in the least wet sites.

Although the canopy composition of the sites north of the James River was similar to sites south of the river, the woody subcanopy and herbaceous layers appeared to differ significantly in species composition. These differences could be related to differences in logging histories or fire histories in surrounding landscapes.

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