DOI: 10.1007/s002670010170

Early Secondary Succession in Bottomland Hardwood Forests of Southeastern Virginia

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ABSTRACT / Addressing the need for reference sites that permit wetland managers to evaluate the relative success of wetland restoration efforts, this project examines the early successional properties of a chronosequence of 17 forested wetlands that have been clear-cut and allowed to naturally revegetate. Ordinations performed on the data using CANOCO software indicated three general types of communities— one dominated by bald cypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*), one dominated by black willow (*Salix nigra*), and one with a species composition similar to that of a mature stand of bottomland hardwoods. These divisions were correlated with the percentage of stems originating as coppice on stumps leftover from the clear-cut. In particular, the bottomland hardwood stands were regenerating predominantly as coppice, while the cypress/tupelo and black willow stands were regenerating primarily as seedlings. As indicated by the earlier development of overstory basal area, coppice sites were also regenerating much faster. The hydrology of a site also exhibited a strong impact on the rate of regeneration, with the semipermanently to permanently flooded portions of sites often exhibiting little or no regeneration. The results indicate that, because of the overwhelming reliance on coppice sprouts as the main source of stems and the concomitant enhanced rates of regeneration, certain vegetative parameters of clear-cut bottomland hardwood stands would not be effective benchmarks by which to judge the relative success of creation and restoration efforts.

Efforts to create or restore wetland systems, often undertaken in response to regulatory requirements, are intended to minimize the net loss of wetland functions within an impacted ecosystem. Currently, however, the science upon which wetland creation and restoration projects are based is still in its relative infancy and there remain serious questions concerning the functionality of these efforts in bottomland hardwood systems. In an effort to ensure the effectiveness of creation and restoration efforts, regulators often require monitoring of mitigation sites as a condition of project authorization. In the case of freshwater and saltwater marshes, colonization and succession of plant communities is fairly rapid and the degree of success attained can generally be ascertained within a few years (Landin and Webb 1986). On the other hand, the time frame over which created or restored bottomland hardwoods begin to resemble natural systems is more on the order of decades rather than years (Kusler 1986, Mitsch and Gosselink 1993), much longer than the average permit applicant could reasonably be expected to monitor a mitigation site and, for that matter, much longer than the institutional memory of the regulatory agencies charged with seeing that mitigation requirements are met (Clewell and Lea 1990).

Thus, to provide a manageable protocol for monitoring of bottomland hardwood mitigation sites, emphasis is being directed towards the establishment of reference wetlands that are representative of regional and local conditions (Brooks and Hughes 1986, Clewell and Lea 1990, Mitsch and Gosselink 1993). The concept of reference wetlands has become increasingly familiar to wetland professionals during recent years with the ongoing development of the hydrogeomorphic functional assessment method (HGM) (Brinson and Rheinhardt 1996, Rheinhardt and others 1997). In the HGM methodology, reference wetlands are selected to represent a range of ecological conditions, from pristine (assumed to represent the highest level of functioning) to disturbance-mediated, within a defined wetland class and geomorphic setting. Field parameters from these sites are used to determine reference standards that, in turn, allow development of a model of the

KEY WORDS: Bottomland hardwood forest; Wetland; Clear-cut; Reference; Restoration; Monitoring; Succession; Mitigation; Vegetation

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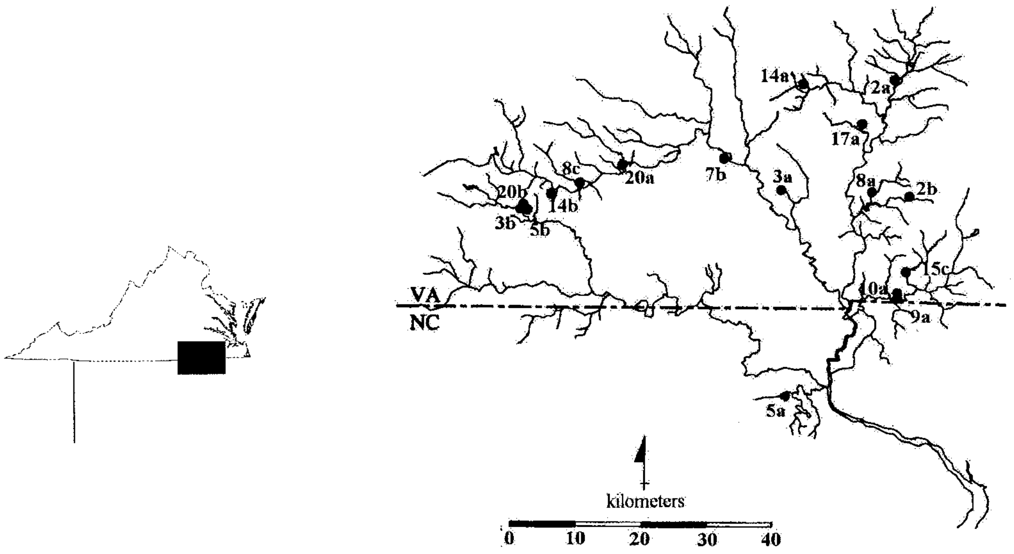

Figure 1. Locations of project sites.

wetland functions performed by that particular class of wetlands. The model quantifies the loss of functions associated with wetland impacts, as well as the recovery of functions when wetlands are created or restored, providing a defensible method of determining a ratio between acres impacted and acres compensated that is consistent with the goal of no net loss of wetland functions (Brinson and Rheinhardt 1996).

While the process of developing reference wetlands pursuant to HGM methodology accounts for many of the spatial, temporal, and environmental gradients that influence the functions performed by bottomland hardwood systems, it must be realized that this procedure does not provide a means of estimating the developmental trajectory of forested wetland systems during the earliest stages of succession. These first few years, however, represent the time period during which most creation and restoration projects are monitored for success. Thus, there is a need for data on these early successional processes (Allen 1997) that can be used as a benchmark to indicate whether these compensatory wetlands are indeed proceeding towards a mature system that will adequately replace the functions previously performed by the impacted wetland.

The purpose of this project was to examine a suite of naturally revegetated forested wetlands and to quantify early secondary succession in the bottomland hardwood forests of southeastern Virginia. Vegetation analyses were conducted on a chronosequence of 17 sites that were clear-cut over the last 2–20 years and allowed to naturally revegetate. Sites were selected based on the presence of an unimpacted hydrologic regime and the lack of artificial treatments, such as seeding, burning, or use of chemicals. It was hypothesized that the data would indicate successive dominance of structural components, from herbaceous to woody understory to forest vegetation as time progresses. Dominance of particular species and structural components at a given age was expected to be correlated with hydrologic regime and the availability of stumps for coppice sprouting and, to a lesser extent, with soil characteristics and other environmental variables. In particular, the presence of extensive coppice regeneration was expected to accelerate the early development of an understory, while regeneration was expected to be stunted in those sites characterized by a stagnant hydrology with continuous or nearly continuous inundation.

Methods

Study Sites

The fieldwork for this research took place in the watersheds of the Blackwater, Nottoway, and Meherrin rivers, which together form a considerable portion of the Chowan River Basin in southeastern Virginia and northeastern North Carolina. Sites were located in the upper coastal plain, an area that has an average frost-free period of approximately 200 days (Plunkett and Hall 1995) and receives approximately 122 in. of rain per year, mostly between April and September. Seventeen sites (Figure 1), were selected for inclusion in this study, all of which are owned either by Union Camp Corporation or by private citizens who manage their land in coordination with the Virginia Department of Forestry. The presence of wetland indicators was used to determine eligibility rather than species composition, which was one of the factors expected to influence successional trajectory and, thus, would have biased the results. Each site has been clear-cut at some point within the last 20 years and their respective ages are determined by the number of years since the area was logged. Maps and descriptions of each site are available in Spencer (1997).

Field Data Collection

Prior to the initiation of sampling, vegetation was divided into three sampling components: herbaceous (or ground plane), understory, and overstory. The herbaceous component included all herbaceous species, all vines, and woody plants (trees and shrubs) <50 cm tall. Understory vegetation consisted of saplings and shrubs ≥ 50 cm tall but <2.5 cm dbh (diameter at 1.5 m above ground). Overstory included all woody vegetation ≥ 2.5 cm dbh (Mader 1990, Rheinhardt 1991).

Because of the relative lack of overstory in early successional forested wetlands and the necessity of avoiding upland/wetland ecotones in some of the more narrow project sites, 2.81-m-radius (25 m^2) circular plots were selected as an efficient, yet reasonably thorough, means of sampling both understory and overstory vegetation. The number of circular plots varied from five to as many as 13, depending on such factors as density of understory and dimensions of the cutover area. Within each circular plot, stems were tabulated by species, sampling component, and origin (i.e., seedling or sprout). The dbh of overstory stems was measured to the nearest half centimeter, while understory vegetation was measured at 40 cm above the base for trees and at 3 cm above the base for shrubs, also to the nearest half centimeter (Mader 1990). Each stem was classified as either a seedling or sprout, being considered sprouts if they originated below 40 cm on residual stumps and were counted separately if they forked within 3 cm of the base (Mader 1990).

The herbaceous component was sampled using quadrats of dimensions 1×0.5 m (0.5 m^2) that were positioned in a stratified random manner based on the centerpoints of the radial plots. Density for each species was measured by counting only those plants actually rooted within the quadrat. Total herbaceous cover and coverage of each species present within the quadrat, regardless of root location, was determined by a modified Daubenmire (1968) technique, involving ocular estimation of cover and assignment into one of seven coverage classifications: trace, 1–5%, 5–25%, 25–50%, 50–75%, 75–95%, or 95–100% (Rheinhardt 1991).

At each site, a soil sample was taken from 10 cm below the surface at an elevation representative of the vegetation sampling points. A standard chemical analysis, including measurements of pH, organic carbon, and cation exchange capacity, was performed on each sample by the Department of Crop and Soil Environmental Sciences at Virginia Polytechnic Institute and State University.

Hydrologic characteristics of study sites were evaluated through installation and monitoring of PVC groundwater wells. Wells were constructed of screened 4-in. PVC pipe positioned from approximately 1–2 m below ground to within 15 cm of the surface and attached to solid 4-in. PVC pipe that extended about 1 m above the ground surface. Because of the unavailability of remote dataloggers and the resulting time considerations involved in checking the wells manually, only one well was installed at most sites. At three project sites, two monitoring wells were established to indicate any possible differences in microsite hydroperiod. Water levels were recorded biweekly for one year, although occasional datapoints are missing where high water levels rendered sites inaccessible.

Data Analysis

Information obtained during field sampling was used to calculate estimates for population densities and dominance. Dominance was defined by basal area in overstory and understory strata and by cover for herbaceous layer. The relative values according to species and sampling component was then determined for each of these measures by dividing the value for each species by the total value for all species in a given strata. Species importance values were then formulated for each sampling component by taking half of the sum of relative density and relative dominance for each species present.

Community dynamics were than analyzed using a variety of ordination techniques available as part of the CANOCO software package. Results of the canonical correspondence analysis are presented here using species–site biplots that detail the first two ordination axes. The role of measured environmental variables, such as hydrology and soil chemistry, was evaluated by examining their correlation with each other and with the first two ordination axes. The changes in community characteristics associated with age were minimized by using age as a covariable.

Results

Structural Characteristics

The results for each site, without respect to the particular species present, are presented in Table 1.

Table 1 Structural vegetation data from project sites[a]

	Overstory			Understory			
Site	Density (stems/ha)	Basal area (m^2/ha)	Stem origin (% sprouts)	Density (stems/ha)	Basal area (m^2/ha)	Stem origin (% sprouts)	Herbaceous (mean % cover)
2a	320	0.18	38	14,720	1.997	38	80.5
2b	320	0.21	75	9,600	1.006	87	85.5
3a	0	0	0	10,293	0.65	2	75.3
3b	1,280	1.03	44	16,320	4.21	11	56.5
5a	686	1.19	33	6,686	1.066	54	94.2
5b	2,080	2.401	46	10,880	2.399	28	47.5
7a	933	1.09	64	8,267	2.27	43	53.8
8a	743	0.57	23	28,114	5.245	11	25
8b	2,600	9.53	73	30,500	3.72	17	58.8
9a	2,800	10.46	83	17,520	2.06	82	38
10a	3,040	20.4	87	10,160	0.957	79	43
14a	5,920	21.64	75	11,440	1.771	47	9.5
15a	4,533	36.39	85	4,200	0.866	79	22.5
15b	8,300	31.42	46	7,400	1.7	11	3.7
17a	3,133	20.36	60	15,000	2.719	52	42.1
20a	3,943	18.81	36	1,543	0.491	48	3.3
20b	4,400	35.28	66	1,600	0.139	75	1.9
Mean	2648.88	12.40	54.9	12014.29	1.96	44.9	43.6
Median	2,600	9.53	60	10,293	1.77	0.47	43

[a] Site number indicates years since harvest when sampled. Percent sprouts indicates the percentage of stems originating as coppice.

Densities and basal areas have been standardized to hectares to facilitate comparison with other studies. Overstory densities range from 0 stems/ha at site 3a to 5920 stems/ha at 14a. Site 3a, which was whole-tree chipped at harvest, leaving few visible stumps, also had the lowest proportion of stems originating as coppice in both the overstory and understory. Site 14a, on the other hand, exhibited a prevalence of coppice sprouts that was characteristic of a number of project sites and that generally corresponded with enhanced stem densities. Likewise, site 15a, which had the second highest percentage of overstory stems originating as coppice, was the most productive site in terms of total basal area, more so than even the 17- and 20-year-old sites. In comparing the overstories of sites of the same age, a notable discrepancy exists between the two 20-year-old sites. Despite having roughly similar densities, site 20b exhibited almost twice the basal area as site 20a. Not accounted for in the data, though, was a considerable mortality among the canopy trees at site 20a, limited almost entirely to *Salix nigra* and, to a lesser extent, *Populus heterophylla*. Understory densities displayed considerable variability throughout the 17 project sites, ranging from just over 1500 stems/ha to greater than 30,000 stems/ha. Some notable aberrations would appear to be sites 8a, 8b, and 17a. At the latter two, beaver activity resulted in numerous stumps that produced a prodigious number of new sprouts, while at site 8a, suckering at the base of *S. nigra* saplings substantially augmented understory stem densities. This explains the notably higher understory basal area at site 8a, since it was not subjected to the postestablishment reduction in basal area associated with beaver activity.

Species Composition

Tables 2 and 3 list the importance values of the dominant and codominant species within the overstory and understory components, respectively, for all of the project sites combined. Although a total of 27 species were sampled in the overstories of project sites, only nine were dominant or codominant on at least one project site. Dominance and codominance were determined by the species or group of species, respectively, as ranked by importance values, necessary to accumulate a combined importance value (IV) greater than 50 within a particular site. It should be noted that, because of difficulty in identifying the particular species of such young specimens from the genus *Fraxinus*, all occurrences were classified as *Fraxinus* spp. Several species and subspecies are, in fact, known to occur within this geographical region, including *F. caroliniana*, *F. profunda*, and, primarily, *F. pennsylvanica* (Rheinhardt 1991, Glascock and Ware 1979). As indicated by the total importance value for all sites combined, *A. rubrum* and *S. nigra* were the dominant species throughout the study. However, the fact that *S. nigra* was the only species occurring in the overstory of site 2b enhances its relative importance with respect to this measure. Three

Table 2 Importance values of overstory species[a]

	Site																	
	2a	2b	3a	3b	5a	5b	7a	8a	8b	9a	10a	14a	15a	14b	17a	20a	20b	Total I.
Acer rubrum					23	55		44.4	61.6	50		27.6	6.2	25.6	15.7	17.9	49.5	22.1
Salix nigra	100			58.4	13.1	2.7	66.3	48.1		13.4				22.7	5.6	22.3	7.2	21.2
Fraxinus spp.				36.6		28.8		7.4	21.7			11.9	53.7	22.7	9.4	8.2	28	13.4
Liquidambarstyraciflua											50.3	46.6		4.3		11.9	11.3	7.3
Nyssa aquatica									7.1	16.2	14		32.6		40.7			6.5
Platanus occidentalis		76.1													14.5			5.3
Taxodium distichum					8.9		23.3		2.3	20.3	21.6				6.3			4.9
Ulmus americanus					37.1											8.2		2.7
T2b10 (unidentified)		23.9																1.4
Other species	0	0	0	5	17.9	13.5	10.4	0.1	7.3	0.1	14.1	13.9	7.5	24.7	7.8	31.5	4	15.2

[a]Species include those classified as dominant or codominant, as defined in the text, on at least one project site. Site number indicates years since time of harvest at time of sampling. Total importance value = (sum of importance value for all sites)/1700 * 100.

Table 3 Importance values of understory species[a]

	Site																	
	2a	2b	3a	3b	5a	5b	7a	8a	8b	9a	10a	14a	14b	15a	17a	20a	20b	Total I.
Acer rubrum	7.7	0.7	0.9		11.4	35.5	3.4	0.6	57.6	25.5	2.4	17.6	48	7.8	9.4	47.1	62.9	1
Fraxinus spp.	9.9	29.5		17		19.5	0.5	3.4	29.4		18.9	16.4	17.8	78	2.7	18.9	31	1
Salix nigra	59.8	14.4	5.9	14.9	38.7	1.2	12.3	85.9		29.2	2.5				1.4			1
Taxodium distichum		10	59.6		16.8		57.2	0.8	0.2	14.8	8			5.2	47.9			
Liquidambar styraciflua	1.8	13.7	13.7	1.6	18.9				0.5	10.1	13.8	3.1		3.8	2.5			
Celtis occidentalis				61.5	0.9	3.4	2.4		1.4		1.9	1.1						
Nyssa aquatica							19		3.4	16.9	31.9				0.6			
Quercus lyrata									1.2				21.6			23.4		
Platanus occidentalis	3	24.3	0.1	4.1	1.1							0.7	0.8		2.9			
Magnolia virginica	0.4	6.8										18.2		4.3				
Leucothoe racemosa					5.1	18.4						0.9			2.6			
Ilex opaca											1.1	15	0.7					
Other species	17.4	0.	19.8	0.9	7.1	22	5.2	9.3	6.3	3.5	19.5	27	11.1	0.9	30	10.6	6.1	1

[a]Species listed include those classified as dominant or codominant, as defined in the text, on at least one project site. Site number indicates years since harvest at time of sampling. Total importance value = (sum of importance values for all sites)/1700 * 100.

species—*Platanus occidentalis*, *Ulmus americanus*, and one unidentified species referred to as T2b10—occurred in the overstories of no more than two project sites. In the case of *P. occidentalis* and T2b10, they were generally found to occur on the edges of or on hummocks within the sampled wetlands, while limited *U. americanus* populations possibly reflect the lingering impact of Dutch elm disease, which tends to reduce seed production in mature trees (G. Silverhorn, personal communication, S. Ware, personal communication).

When understory importance values are summed for all stands, *Acer rubrum* and *S. nigra* are joined by *Fraxinus* spp. and *T. distichum* as the dominant species among all 17 sites, as indicated by total IVs > 200. The presence of *S. nigra*, dominant in the understories of several project sites, greatly diminishes between the seventh and tenth growing seasons, correlating with the early stages of canopy development. Between years 10 and 20, the increasing presence of an understory of shade-tolerant subcanopy and canopy species is indicated by the presence of *Ilex opaca* and *Quercus lyrata*, respectively.

Hydrology

Data obtained from monitoring groundwater wells is shown in Table 4. Fluctuation, indicated by the range of measured water levels at a given site, was greatest at the two 20-year-old sites, where measured highs and lows were over a meter apart. Flooding regimes at these two sites were somewhat different, though, with site 20a exhibiting flooding at the surface for approximately 68% of the year compared to 28% of the year for site 20b. At the other end of the hydrologic spectrum, sites

Table 4 Depth and frequency of inundation at project sites[a]

Depth (cm)	2a	2b	3a	3b	5a	5b	7a	8a	8b	9a	10a	14a	14b	15a	17a	20a	20b
100																	
90																	
80							0.00										
70							0.08		0.00								
60				0.00			0.15		0.07	0.00						0.00	
50				0.20			0.31	0.00	0.07	0.06			0.00			0.05	
40			0.00	0.40		0.00	0.46	0.68	0.07	0.33			0.05	0.00		0.05	0.00
30			0.05	0.53		0.14	0.54	1.00	0.07	0.78		0.00	0.05	0.05		0.05	0.06
20			0.10	0.60	0.00	0.86	0.77		0.07	0.89	0.00	0.06	0.05	0.11	0.00	0.05	0.06
10		0.00	0.30	0.67	0.05	1.00	1.00		0.29	0.94	0.06	0.06	0.26	0.21	0.27	0.47	0.06
0	0.00	0.06	0.60	0.73	0.26				0.64	0.94	0.38	0.41	0.89	0.26	0.67	0.68	0.28
−10	0.82	0.22	0.70	0.80	0.68				0.86	1.00	0.81	0.71	0.89	0.63	1.00	0.74	0.39
−20	0.94	0.67	0.90	0.80	1.00				0.93		1.00	0.88	1.00	0.79		0.84	0.61
−30	1.00	0.83	0.90	0.87					0.93			0.94		0.95		0.95	0.67
−40		1.00	0.95	1.00					1.00			1.00		0.95		0.95	0.78
−50			0.95											0.95		0.95	0.83
−60			0.95											0.95		1.00	0.89
−70			1.00											0.95			0.94
−80														1.00			1.00
−90																	
−100																	

[a] Depth is in relation to soil surface. Data indicates the portion of the year a site was inundated at a particular depth, i.e. at site 2a, water was present at 10 cm below the surface for 82% of the year.

8a and 2a had water levels fluctuating within a 20 cm range throughout the year. Again, this was not necessarily indicative of an overwhelming similarity between the hydrologic regimes of the two sites. Water levels never dropped below 30 cm at site 8a, while at site 2a surface flooding was never observed (although there were secondary indicators of its presence). At two sites, 7a and 8a, measurements do not accurately reflect the high end of water level ranges with respect to the other sites because on several occasions the logging roads by which they were accessed were impassable due to high water levels.

Soils Chemistry

Table 5 represents soil data for the entire suite of measured variables. In general, there were few apparent trends associated with site age. Soil pH levels ranged from 4.2 to 5.7 and organic carbon content ranged from 0.34% to 8.36% at a depth of 10 cm. Although there did appear to be a general decrease in soil pH over time at a depth of 10 cm, the lack of multiple samples from project sites and the considerable within-site variability, particularly at sites with a high degree of microtopographic variability, precluded analysis of the significance of apparent trends in soil data. Site 2a was notable in that it exhibited among the highest values for each of the variables indicated in Table 5.

Multivariate Analysis

The initial ordination of the 17 sampled stands (Figure 2) revealed a fairly even distribution of stands along the vertical axis. However, site 2b was so vegetatively different from the other 16 sites that, along the horizontal axis, it proved to be obviously disjunct from the other sites, which themselves exhibited little variation along that particular axis. The most obvious reason for this difference is the dominance of *P. occidentalis* in the overstory and its codominance in the understory, with IVs = 76 and 24, respectively. With regard to morphology of the site, 2b is more adequately characterized as a braided stream complex, separated by the hummocks on which *P. occidentalis* is regenerating predominantly as coppice. The site also was the only one at which no surface flooding was recorded during well checks, being observed only once during the entire monitoring period in the course of other research on the site. Instead, water was generally confined to the well-defined channels, a trait not shared by any of the other project sites. Of note also in this ordination was the inverse relationship between the presence of organic

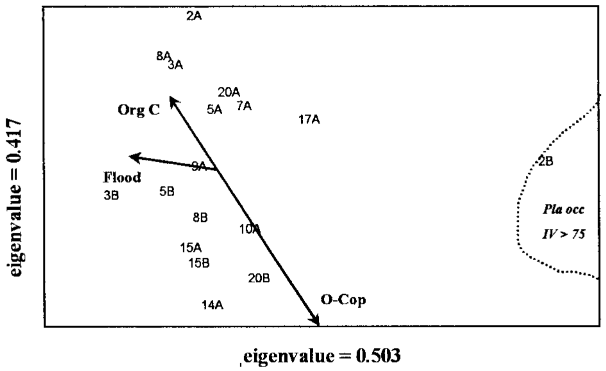

Figure 2. Canonical correspondence analysis of all project sites with no covariables. Vegetation data include understory and overstory importance values for each species recorded in those strata (i.e., two values may exist for each species). Environmental variables included information related to hydrologic regime, soil chemistry, and stem origin. Only those environmental variables exhibiting the highest correlation with ordination results are depicted by arrows in the figure. Org C = organic carbon; Flood = duration of flooding as a percentage of the calendar year; O-Cop = percentage of overstory stems originating as coppice. The dashed line encloses the only site in which *Platanus occidentalis* exhibited an overstory importance value greater than 75.

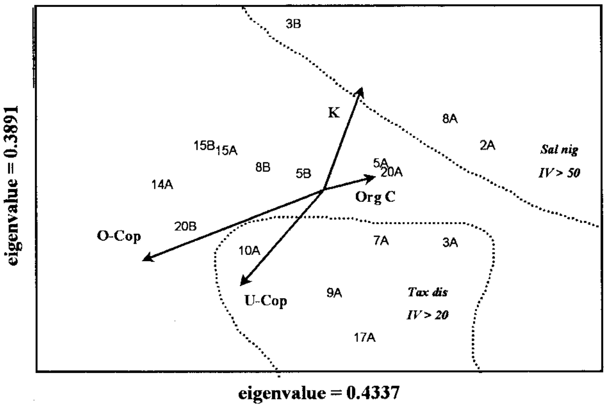

Figure 3. Canonical correspondence analysis with site 2b removed and no covariables; other covariables identical to Figure 2. U-Cop = percentage of understory stems originating as coppice. The upper dashed line encloses those sites in which *Salix nigra* exhibited an overstory importance value greater than 50. The lower dashed line encloses those sites in which *Taxodium distichum* exhibits an understory importance value greater than 30.

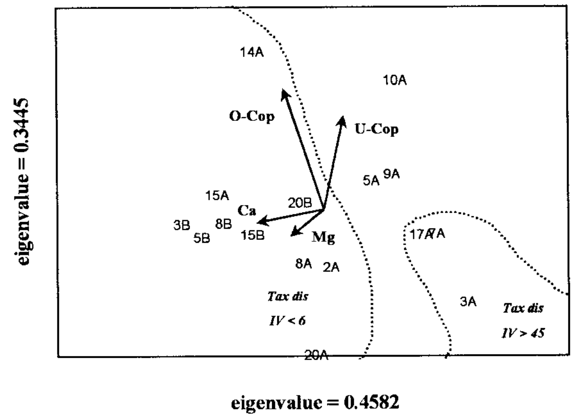

Figure 4. Canonical correspondence analysis with site 2b removed from the ordination and age inserted as a covariable. The dashed line to the right encloses those sites in which *Taxodium distichum* exhibits an understory importance value greater than 45. The dashed line to the left encloses those sites in which *Taxodium distichum* exhibits an understory importance value less than 6.

carbon in the soil and the percentage of overstory stems originating as coppice.

Because of these differences, site 2b was removed from subsequent ordinations. With the disjunct stand removed, a considerably more distinct grouping of the sites was revealed (Figure 3). By delineating the understory importance values of *T. distichum* and *S. nigra* as indicated in the biplot, the presence of three types of sites is indicated—cypress, willow, and mixed hardwood. The environmental parameter most highly correlated with the first ordination axis is the percentage of overstory stems originating as coppice, which clearly separates the mixed hardwood sites from the cypress and willow sites. Potassium is most highly correlated with the second axis, although the significance of this is not readily apparent.

In the final ordination (Figure 4), age was inserted as a covariable, effectively minimizing its influence on the outcome. Three of the willow sites now fell into the larger cluster with the mixed hardwood stands, indicating that, as these sites age, they are most likely succeeding into communities more representative of those regenerating as coppice after the clear-cut. The three sites most dominated by *T. distichum* still fell out distinctly as cypress stands; however, three other sites—5a, 9a, and 10a—fell out between the mixed hardwood stands and the cypress stands on the first axis. On the second axis, these sites were distinguished from the cypress stands by the generally higher prevalence of coppice. As observed in the field, these sites tended to have a substantial degree of microtopographic variability. Thus, they exhibited a wider range of environmental conditions, resulting in species compositions similar to mixed hardwood stands in some areas and cypress stands in others. Calcium was the variable exhibiting the greatest correlation with the horizontal axis, a result also noted by a decrease in average values for the clusters moving from left to right on the biplot.

Discussion

Vegetative Communities

Analysis of the data indicated the presence of three general community types—cypress, willow, and mixed hardwood. Site 2a was excluded from analysis because the prevalent areal extent of drier hummocks resulted in the presence of more upland species.

The cypress community is characterized by an understory of *T. distichum* and is represented primarily by three sites and by portions of three others. The hydrology of these sites varied considerably in terms of both the range of water levels and the persistence of flooding. The characteristic common to all three of the primary cypress stands is a low percentage of stems originating as coppice, occurring only in the stumps of young trees impacted by beavers.

The mixed hardwood sites were generally dominated by *Fraxinus* spp. and *A. rubrum* in both the understory and overstory. A significant portion of early regeneration in these sites can be attributed to coppice sprouts, which were noted by Messina and others (1997) as accounting for 83% of stems one year after the clear-cutting of a Texas floodplain forest. The mixed hardwood sites also tend to exhibit greater fluctuations in water levels, which is believed to reflect the ability of established root networks to enhance evapotranspiration rates relative to sites regenerating predominantly from seed.

The two willow sites are characterized by a dominant overstory of *S. nigra* and water-level fluctuations of <20 cm. Although multiple stems are exhibited by *S. nigra* specimens at both sites, actual coppicing is rare, a condition not unexpected given the fact that the species was not a likely constituent of the canopy prior to clear-cutting. The third willow site, 20a, is important in that it offers an insight into the time frame over which this community is succeeding into a more typical mixed hardwood stand. *Salix nigra*, overwhelmingly dominant during the first 10–15 years of regeneration, as indicated by remaining live specimens and substantial amounts of both standing and fallen deadwood, has, within 20 years, begun to reach the end of its life span and is not reproducing either vegetatively or by seed under the limiting conditions of a closed canopy. Also of importance is the presence of ecologically desirable mast-producing species in the understory of the 20-year-old willow site. It is thought that the success of this component, so often sought after in creation and restoration efforts and generally uncommon in the secondary growth characterizing many of the bottomland hardwood forests remaining in southeastern Virginia, is directly related to the stabilization of site hydrology and the sporadic canopy openings associated with the mortality of *S. nigra.* Under these conditions, species best adapted to specific microsites are more likely to succeed because they are insulated from the dramatic changes in site conditions during the years immediately following timber harvest.

Glascock and Ware (1979) noted that, aside from a few geographically limited species, there was a remarkable similarity in the composition and structure of stream bottoms from New Jersey all the way down to Florida. This study generally corresponds with their findings regarding the dominant species associations. The most notable difference would be the reduced significance of *Carpinus caroliniana* among sites in the current study, whereas Glascock and Ware (1979) and Plunkett and Hall (1995) consistently found it to be a prevalent constituent of the overstories of bottomland hardwood forests in southeastern Virginia. Characterized as a small understory tree, its presence in the overstories of mature sites is, again, probably the result of past selective harvests throughout the region, which allowed economically undesirable understory species like *C. caroliniana* to take advantage of the increased resource availability and become important components of the overstory. Given the lack of old growth bottomland hardwood forests in the region, one can only speculate as to the role of the species under natural circumstances; however, it is apparent that the species is quickly outcompeted during the earlier stages of post-clearcut regeneration.

Quantitative Aspects of Project Data

Generally speaking, the limited amount of past research on the early successional development of bottomland hardwood forests and the inconsistent data collection protocols make comparison with the quantitative data of other studies problematic. However, the results of these other studies can provide a context by which to gauge the successional rates of projects examined as part of this study. Within the same region, Doumlele and others (1985) recorded a total basal area of 91.35 m^2/ha and overstory densities of nearly 2750 stems/ha in a mature tidal freshwater swamp. This was substantially more standing biomass than the four Savannah River floodplain forests examined by Jones and others (1994), where overstory basal areas ranged between 29 and 38 m^2/ha, and the 17 sites examined by Megonigal and others (1997), where basal areas ranged from 13.6 to 54.5 m^2/ha and densities of live stems ranged from 330 to 930 stems/ha. Given natural variation of this magnitude and the lack of pre-clear-cut quantitative data on project sites, the difficulty of estimating the rate at which they are proceeding towards a mature canopy becomes evident. In a similar study, Bowling and Kellison (1983) noted bottomland hardwood overstories developing at rates remarkably similar to those noted for mixed hardwood stands in this study. In fact, the slight differences that did occur can likely be accounted for by the fact that overstory stems in the former study were limited to those over 10 cm. Like the present study, much of the regeneration was attributed to coppice sprouts; however, data from the cypress and willow stands, where coppice sprouts were few and regeneration much slower, suggest that physical and/or biological characteristics may be influencing the successional trajectory of project sites.

Two possible characteristics that have not been previously addressed are the presence of wetland soils and the proximity of mature stands to provide a seed source. Given the consistent presence of established wetland soils at project sites, it is difficult to estimate their relationship to early successional trajectory following clearcut. Moreover, the condition of adjacent lands ranged from agricultural uplands to mature forested wetlands. Two previous studies indicate the potential complications introduced by these and, possibly, other factors: a chronosequence of early successional old-field sites in the coastal plain of New Jersey indicates no tree layer whatsoever until 25 years after abandonment (Hanks 1971), and Noon (1996) noted the presence of no trees in the first 11 years following wetland creation on the mineral soils of reclaimed mine lands.

Successional Processes

Noon (1996) developed a model of wetland primary succession on reclaimed mine sites using a chronosequence similar to this study. As in van der Valk's (1981, 1982) Gleasonian model of succession, two distinct phases in early wetland succession were identified—the arrival and establishment phase, followed, after 3 years, by the autogenic dominance phase. The development of species composition during the arrival and establishment phase is the result of a combination of factors, particularly the availability of resources and species' life history traits. Then, during the autogenic dominance phase, established species compete for dominance through biomass production.

Although used to describe primary succession by Noon (1996), this concept would seem to have applications useful in describing secondary succession of forested wetlands as well. It would seem that the naturally regenerating sites represent an accelerated version of Noon's model of succession, with the rate of acceleration being determined by such factors as coppice sprouting, hydrology, and soil characteristics. This acceleration is in fact accomplishing a goal inherent in many creation and restoration projects of quickly replacing vegetative community structure, which is often used by regulators as a surrogate for measuring complex ecosystem functions. Specifically, the results of this study are consistent with the presence of an arrival and establishment phase, albeit one that is by no means linked inextricably to the time frame of roughly 3 years described by Noon (1996). The presence of wetland soils alleviates much of the competition for resources evident during primary succession and allows near total cover often by the end of the first growing season. At this point, the site has already begun entering the autogenic dominance phase, the dynamics of which are determined by the species ability to produce biomass, as well as the stress related to the physical regime of the location.

Both of the above factors seem to contribute to dominance by one or several species as the site moves farther into this second successional phase. In the mixed hardwood stands, the proliferation of coppice sprouts and subsequent development of a canopy once again creates a resource limitation, except the availability of light is the limiting factor rather than soil nutrients or water. In those sites characterized by the harsh physical regime associated with continuous flooding or high sedimentation rates, an overwhelming dominance is displayed by the few species capable of surviving in those conditions. This idea is consistent with Odum's (1969) assertion of an inverse relationship between environmental stress and diversity and was also evident in the results of Johnson and others (1985), who attributed the success of *S. nigra* on early successional islands in the Atchafalaya River Delta, Louisiana, USA, to the species ability to withstand high sedimentation rates and quickly develop large fibrous root systems. Specific examples in this study were sites 8a, 7a, and 3b. Site 8a, which is densely populated by *S. nigra* except for a few higher points where *Acer rubrum* has sprouted, is bordered by steeply sloping, early successional pine uplands, providing the high energy, high sedimentation environment that largely prevents successful seedling establishment by competing wetland species. In a similar manner, *Celtis occidentalis* and *Polygonum* spp. were able to outcompete other species over a significant portion of site 3b, located in the first bottom of the alluvial Meherrin River and, thus, subject to a physical environment largely reflective of climatic events across the much larger piedmont watershed. Finally, at site 7a,

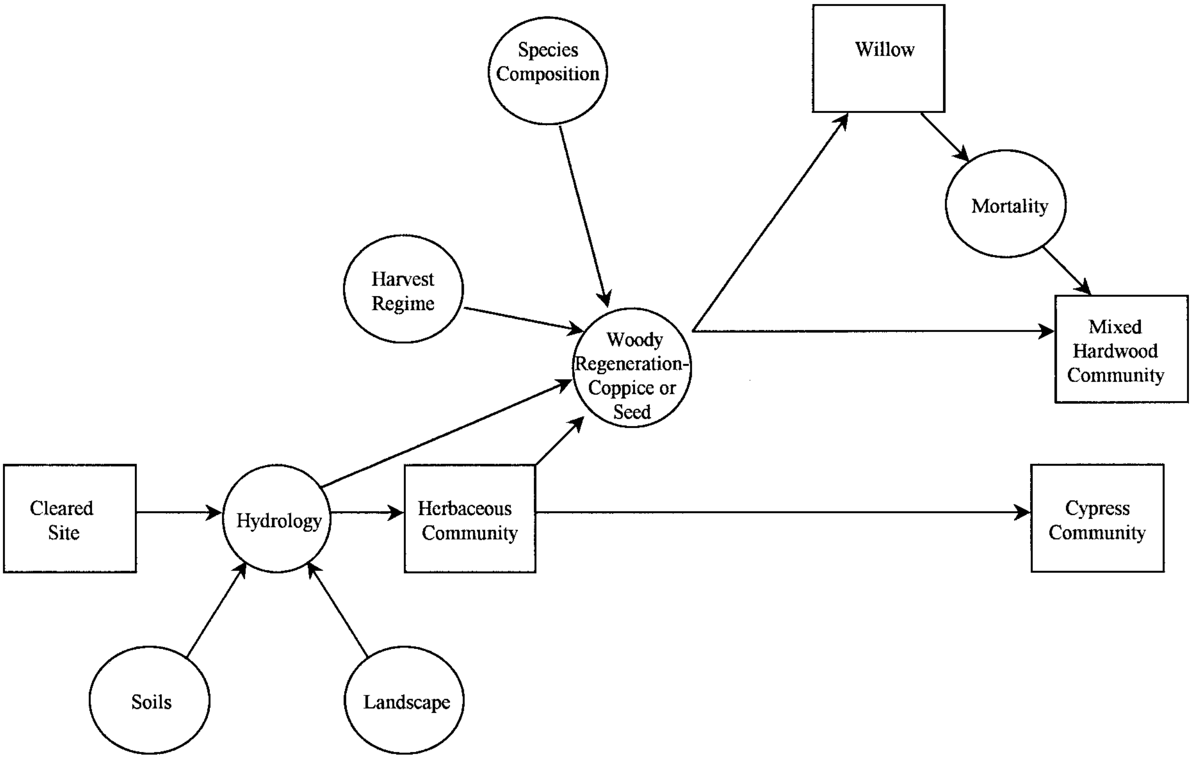

Figure 5. Conceptual model of early secondary succession following clear-cut of bottomland hardwood forests in southeastern Virginia.

where the intense flooding of the adjacent Meherrin River is possibly exacerbated by logging-road-induced impoundment, much of the site is covered by dense stands of herbaceous perennials characterized by low species richness. However, towards the edges of the site, where drawdowns are more prevalent and flooding less intense, a more diverse assemblage of both woody and herbaceous species is found.

Two events appear capable of interrupting this cycle of dominance during the autogenic dominance phase. First, as dominant species begin to reach the end of their life span, species growing beneath them are given access to previously limiting resources. This is believed to have occurred at site 20a, where a significant dieback of *S. nigra* and *P. heterophyllus* is underway and the overstory is in transition from one composed almost entirely of early colonizers to that of a more traditional mixed hardwood stand. The second means of breaking this cycle of dominance is a dramatic alteration in the physical regime of the site, such as the prolonged drawdown of water levels necessary for the germination of *T. distichum.* It is hypothesized that the lack of a drawdown has effectively stalled the regeneration of site 7a and allowed domination of the site by a few species of herbaceous perennials. Both of these situations appear consistent with the inhibition model of succession introduced by Connell and Slayter (1977), which states that initial colonists will inhibit the establishment of later colonists until such time as the former are damaged or die.

These processes are represented conceptually in Figure 5. Following clearing of the site, vegetation development is driven largely by hydrologic regime, which is modified on a site-specific basis by soil characteristics and landscape factors, such as positioning of the site in the broader geomorphologic setting and microtopographic variation within a site. The herbaceous community then proceeds towards one of two communities—mixed hardwood or cypress. Development of the cypress community is mediated largely by the hydrology regime, especially interannual changes related to climatic factors, although factors not specifically examined as part of this study, such as viability of the seed bank, are likely to play a role as well. Development of the mixed hardwood community is more directly related to the extent of coppice regeneration on the site, which is driven by such factors as hydrology, harvest regime, and species composition prior to timber harvest. A time scale is deliberately excluded from this model, as this is perhaps the most difficult factor to scale when predicting early successional changes in community structure, a point in case being the length of time that a site is "dominated" by herbaceous cover, which in this study ranged from less than two to at least seven years.

Relevance of Clear-Cut Swamps to Monitoring Created and Restored Wetlands

Given the overriding economic considerations and the often conflicting objectives of development and environmental interests, the establishment of success criteria for compensation wetlands is and will surely remain a contentious issue. In fact, it is clear from this research that the complex interaction of factors influencing successional trajectories—including the extent of vegetative reproduction, hydrologic regime, seed source, and soil characteristics, to name a few—result in a natural variability that makes efforts to develop vegetative success criteria, and still maintain the short time frames now typical of most monitoring programs, prohibitively speculative and not scientifically justifiable.

Despite the variability of this data set, it has nevertheless illustrated successional processes that are germane to any attempt to create or restore forested wetlands in the region. Principally, the role of the willow community, as a precursor to the subsequent development of a mixed hardwood stand, speaks to the need for allocation of more resources to engineering of creation and restoration projects and then monitoring that recognizes the early successional processes of bottomland hardwood forests, as opposed to intensive, short-term vegetation monitoring in the absence of scientifically justifiable criteria. Basically, except in cases of extreme drought or intensive ponding, regeneration will occur; the question becomes one of whether the community structure will resemble that of the natural system being replaced. Planners must take into consideration such factors as the quantity and source of water available to the proposed project, the relationship between hydrology and geomorphology of the site, and how this will influence the natural colonization of the site, as well as factors not evaluated in this study, such as the presence of wetland soils and the proximity of seed source. The emphasis should be on ensuring that conditions are favorable to the development of a mature cypress swamp, while reducing the need for costly, and often unsuccessful, plantings and avoiding the imposition of monitoring requirements, such as seedling survival rates, that are not consistent with the natural development of the system. In another case, where the reestablishment of mast-producing species is a priority and mature specimens of the desired species may not be in close enough proximity to serve as an adequate seed source, planting regimes should not be front-loaded or completed entirely within the first few years following restoration. Rather, they should recognize the potential of sites to stabilize through natural colonization. This would allow the natural variation in hydrologic regime related to evapotranspiration to reach an equilibrium and encourage the natural establishment of species optimally suited to microtopographic environmental gradients, increasing the efficiency of the project as well as the potential for achieving desired species composition in the long run. As the early successional colonizers begin to reach the end of their natural life span, 10–15 years for *S. nigra* in southeastern Virginia, the progress of the site can be reevaluated and supplemental plantings can be pinpointed where they will enjoy the greatest chance of survival. Basically, these observations support the assertions by Mitsch and Wilson (1996) that mitigation projects must be allowed a greater amount of time before judgment of success or failure is attempted and that projects should be allowed a greater element of self-design.

Acknowledgments

Many thanks to Amanda Meuller, Rebecca Smith, Rose Laird, and Michael Campana for their help with fieldwork and to Sharon Dewing for her assistance in development of maps. This project would not have been possible without the assistance of Union Camp Corporation, which assisted in the location of sites and allowed us access to their land, and the Virginia Department of Forestry, which assisted in the location of privately owned sites. We are also grateful to the private landowners that were kind enough to permit our intrusions.

This project was funded by a grant from the Environmental Protection Agency.

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