ABSTRACT

MORRIS, TRACY CATHARINE. Tree Composition Along Edaphic and Hydrologic Gradients in Nonriverine Wet Hardwood Forests. (Under the direction of Theodore Henry Shear.)

We sampled seven intact nonriverine wet hardwood forests to establish target ranges for vegetation, soils and hydrology and to examine trends in plant species composition along a wetness gradient. Although quantitative vegetation analysis for this community has been published, broad drainage classes were used to represent a moisture gradient. We investigated trends along a finer-scaled wetness gradient utilizing a novel wetness index that incorporated indicators of saturated soils. Understanding small-scale patterns in plant community composition is useful in planning wetland restoration projects. Although no strong relationship was found between wetness index classes and plant community composition, these data represent the vegetative community supported by soils specific to each wetness class. Absence of this relationship is most likely a result of the dominance of *A. rubrum* and *L. styraciflua* in all wetness classes as well as a history of disturbance in each forest and other unknown stochastic variables. For the restorationist hoping to restore a historic nonriverine wet hardwood forest, once known as oak flats, we can suggest guidelines for restoring hydrology to the wetness classes in which we found oaks with high importance.

TREE COMPOSITION ALONG EDAPHIC AND HYDROLOGIC GRADIENTS IN NONRIVERINE WET HARDWOOD FORESTS

by
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INTRODUCTION

In the Coastal Plain of the southeastern US, plant communities are distributed along complex gradients of elevation and soil characteristics such as moisture, texture, fertility and percent carbon (Wall and Darwin 1999; De Steven and Toner 2004; Lees 2004). Wetland restoration, however, is often focused on understanding fine-scaled patterns of plant distribution to ensure survival and establishment of planted trees. Restoration projects benefit from analyses of within-community trends in plant community composition along environmental gradients (e.g., Bledsoe and Shear 2000).

Successful restoration of wetlands requires re-establishing wetland hydrology and a hydrophytic plant community. Generally, restorationists have limited time to determine existing and desired hydrologic regimes across an area, and then appropriate tree species for planting. Soil texture and color, along with size and abundance of vegetation are quickly measured in reference and potential wetlands. In contrast to these relatively static properties, hydrologic regime is more time-consuming to determine and varies annually with precipitation. One proxy for hydrologic regime without long-term data is evidence of extent, duration, and depth of saturation in the soil profile (Vepraskas 1999). Redoximorphic features in wetland soils are evidence of chemical reduction caused by extended periods of saturation. These visible indicators of reducing conditions in southeastern US soils include loss of oxidized iron and accumulation of organic matter (USDA 2002).

Current methods for selecting tree species to plant in restoration projects are not well defined. Often, tree species are chosen by desirability and not by environmental conditions. In this manner, trees are planted haphazardly throughout a hydrologic gradient.

We used soil indicators of relative hydrologic regime to create a wetness classification index for wetland soils within one plant community. This index allowed us to investigate fine-scaled distribution of plant community composition along a moisture gradient, and to determine if species' distributions are related to specific field indicators of hydric soils. Results from such analyses can be used to guide selection of appropriate plant communities.

We applied this index in nonriverine wet hardwood forests in North Carolina. The extent of this once widespread community has been greatly reduced, and large projects to restore the community are underway. By understanding the distribution of tree species by wetness class, we can make recommendations for design and performance criteria for restoration of nonriverine wet hardwood forests.

Field Indicators of Hydric Soils

Long-term saturation of mineral soils can cause reduction of iron and create the distinctive gray and red colors that characterize many hydric soils. Reduced iron (Fe^{3+}) can move with soil water, causing redoximorphic features (iron concentrations and depletions) to form (Vepraskas 1999). Iron depletion, characterized by high value and low chroma Munsell colors, occurs in soils with wetland hydrology (Evans and Franzmeier 1986; Faulkner and Patrick 1992). By examining the extent and distribution of these features in a soil, we can determine the approximate seasonal high water table. For example, the drainage classification system developed by the US Natural Resources Conservation Service utilizes depth to redoximorphic features to predict relative drainage of a soil. The higher in the profile that these features are detected, the more poorly drained the soil is (Tiner 1999).

Another indicator of long-term saturation in the southeastern US is soil organic matter content. In mineral soils saturated long enough to adequately slow decomposition, organic matter will accumulate in a dark surface horizon (Mausbach and Richardson 1994). Even longer periods of saturation lead to organic soil layers.

Nonriverine Wet Hardwood Forests

In *Classification of the Natural Communities of North Carolina: Third Approximation*, Schafale and Weakley (1990) define nonriverine wet hardwoods as those North Carolina forests not associated with rivers or estuaries, that contain various species typical of bottomland forests. Deciduous, hydrophitic hardwoods dominate the canopies, including several *Quercus* species (oaks), *Liquidambar styraciflua* (sweetgum), *Liriodendron tulipifera* (tulip poplar), and *Acer rubrum* (red maple) (Table 1). Rheinhardt and Rheinhardt (2000) and Schafale (1999) provide excellent descriptions of plant species composition in nonriverine wet hardwood forests in North Carolina and Virginia.

Nonriverine wet hardwood forests are found on mineral soils of inter-stream divides, common in the lower Coastal Plain of North Carolina and Virginia (Pinchot 1897; Schafale and Weakley 1990). The soils are poorly or very poorly drained Alfisols, Ultisols, and Inceptisols and have characteristics of hydric soils (Rheinhardt and Rheinhardt 2000).

Without input from rivers or estuaries, precipitation is the main source of water in nonriverine wet hardwood forests. These areas have low relief, and only when the water table is at the surface does overland flow occur, which can form the headwaters for Coastal Plain streams (Chescheir *et al.* 2003). Water drains downward in these soil profiles slowly due to fine subsurface soil textures and relatively flat topography, and most nonriverine wet hardwood forests are ponded through significant portions of winter and spring. In summer and fall, the water table drops below the ground surface.

The hydrologic gradient on an inter-stream divide progresses from a well drained streamside levee to the poorly drained interior of the divide. Distance from the stream determines the soil moisture regime (Daniels 1999). The interior of an inter-stream divide is often occupied by a pocosin or cypress-gum swamp on wetter, organic soils; this area is surrounded by drier nonriverine wet hardwood forests on mineral soils (Schafale and Weakley 1990).

Rheinhardt and Rheinhardt (2000) found that neither soil texture nor drainage class corresponded to changes in plant community composition within nonriverine wet hardwood forests. Only two soil drainage classes occurred in these forests, however, prompting our exploration of trends along a more finely divided hydrologic gradient.

The flat, moist soils of nonriverine wet hardwood forests make them appealing for crop production, and they have been extensively ditched and cleared for agriculture or silviculture. These forests were once estimated to cover approximately 260,000 ha in North Carolina (Pinchot 1897). Of this, approximately 2% remains (Rheinhardt and Rheinhardt 2000). Today, wetland mitigation projects to restore this forest type are being planned and implemented.

While quantitative (Rheinhardt and Rheinhardt 1999) and qualitative (Schafale 1999) surveys of nonriverine wet hardwood plant composition exist, no analysis of plant composition changes along edaphic gradients has been undertaken. Here we test a novel wetness index that integrates indicators of saturated soils to identify relative hydrologic regime of individual plots, and overall moisture gradients within the plant community. We analyze tree composition changes along wetness gradients in seven forests in the Coastal Plain of North Carolina. Wetness classes, assigned by identifying characteristics of long-term reducing conditions in soils, were used to assess hydrologic regime. By revealing ranges and trends in vegetation, soils, and hydrology, we can suggest design and performance criteria for nonriverine wet hardwood restoration.

METHODS

Study Sites

All forests described are in the lower Coastal Plain of North Carolina, between the Albemarle Peninsula and the White Oak River (Figure 1). All but two are east of the Suffolk Scarp, the most recent historical reach of the ocean (Table 2).

Each forest has:

1) hydrologic input from precipitation only;
2) vegetation that is dominantly hardwood;
3) soils that are not Histosols; and
4) subsurface soils (at depths of 30 to 90 cm) that are not sand.

Old roads and ditches are present in the forests, but not maintained. The majority of the trees are at least 50 years old.

Data Collection

Initially we explored each site and consulted county soil surveys to establish the direction of a wetness gradient by looking at changes in soil drainage classes. To capture variation in soil wetness and vegetation, a belt transect was established traversing this gradient in each forest. Along this transect, approximately thirty 10 m X 10 m plots were surveyed. Change in elevation along belt transects was measured at Gum Swamp and Gull Rock.

Transects began at least 30 m from stand edge, to avoid edge effects. When an anthropogenic disturbance (e.g. ditch, trash pile, roadbed) was encountered, sampling ended 10 m before the disturbed area and resumed 10 m on the opposite side.

The number of stems reaching breast height of each woody species was recorded in each plot, in size classes of diameter at breast height (dbh). The actual diameter of each stem over 90 cm was noted. Species' names follow those of the USDA PLANTS database (USDA, NRCS 2004).

A soil profile description was made in every even-numbered plot to a depth of 60 cm below the ground surface. Profile descriptions consisted of soil texture and color, and abundance and color of redoximorphic features (formerly called mottles). Soil texture was evaluated by hand (Thein 1979.) The matrix and redoximorphic feature colors were determined using Munsell color charts (Munsell Color 1994). The amount of redoximorphic features was classified as few (<2%), common (2-20%), or many (>20%).

Four replicates of soil samples at depths of 15, 30, 45, 60, and 90 cm were taken from each site (excluding East Dismal) for a total of 120 samples. At each of these depths, the soil from 2 cm above and 2 cm below the sample depth was composited with the soil at that depth. The samples were oven-dried at 110° C for 24 hours, and then ground and sieved to remove particles greater than 2 mm in diameter. Later, these samples were composited to give two representative samples from each depth in each site (total of 60 samples).

Soil particle size distribution was determined by the hydrometer method of Gee and Bauder (1986). Total C and N were determined for the 15 and 30 cm depth samples as percent upon ignition using combustion and frontal chromatography in a CHN ignition analyzer. Concentrations of P, Ca, K, Mg, and Na (Appendix 1) were determined by Mehlich-3 extraction (Mehlich 1984). Soil acidity (Appendix 1) was estimated using the Mehlich-buffer acidity method (Mehlich et al. 1976).

Development of Wetness Index

To evaluate hydrologic regime, we developed a soil wetness index utilizing visible indicators of reduction in wetland soils (Table 3). The class characteristics are based on Field Indicators of Hydric Soils (USDA, NRCS 2002). The wetness class of a soil was determined by examining the soil profile description for presence of one of the soil characteristics, beginning with class one, and working towards class ten. The first characteristic met in the profile corresponded to its wetness value.

Muck and mucky mineral texture are determined by percent carbon and percent clay in the soil (Figure 2). For wetness classes one through five, the depth of mucky mineral soil layers is the defining characteristic. A dark surface, in classes six and seven, is present in mineral soils with Munsell matrix colors with value of three or less *and* chroma of two or less. The dark A horizon indicates buildup of organic matter. Soils in classes eight and nine contain a depleted matrix, which is described in USDA Hydric Soil Indicator F3 (USDA, NRCS 2002) (Table 4).

The order of wetness classes, and their corresponding soil characteristics, represents a soil moisture gradient ranging from wetter (class 1) to drier (class 10). As the depth to hydric soil field indicators increases, duration of soil saturation, and high water table decrease. This ranking of moisture regimes integrates depth of water table with duration of seasonal high water table.

Data Analyses

Species surveyed were classified as canopy or non-canopy by the authors. We summarized tree species data by calculating relative basal area and relative frequency for each species in each plot. These measures were averaged to give an importance value (IV). The midpoint diameter was used to calculate basal area for each size class, and actual diameter was used for stems with dbh greater than 90 cm. To examine overall oak species' importance, we summed IV for all oaks. The importance values for each tree were averaged by wetness class, regardless of site, to evaluate trends in plant species composition. The distribution of soil wetness classes by site and the average wetness by site were determined.

We analyzed plant composition (as IV by species in each plot) by indirect ordination using the nonmetric multidimensional scaling (NMS) function of PC-ORD multivariate analysis software (McCune and Medford 1995). The input coordinates were Bray-Curtis distance scores, and an ordination was run with up to six dimensions, stepping down to one dimension, and following guidelines for instability criterion (0.0005) and number of runs by McCune and Grace (2002). We chose a three-dimensional solution for each ordination, and used the starting configuration from the best three-dimensional run in the initial ordination to produce the final ordination. This same procedure was used for the three ordinations presented here.

First, we ordinated only those plots assigned wetness values, and compared their ordination scores to the assigned wetness classes. We also ran indicator species analysis on plots with wetness values, utilizing the method of Dufrêne and Legendre (1997) in PC-ORD. After exploring trends along the moisture gradient, we ordinated all plots to further examine factors driving plant community composition. We also examined a second NMS ordination of all plots with only canopy species. Canopy and non-canopy groups are shown in Table 5.

RESULTS

Vegetation

Thirty-seven species were found in all forests (17 canopy and 20 non-canopy species) (Table 5). The only two canopy species found in every forest were *L. styraciflua* and *A. rubrum*. Mean importance of total oaks in all forests ranged from 0 to 33%. Across forests, *Q. michauxii* was the most abundant oak. The only other oaks with any appreciable presence across forests were *Q. nigra* and *Q. pagoda*. Gull Rock was the only one with no oak component.

Non-canopy dominance varied greatly among forests, and often the dominant species in one forest was absent in other forests. For example, *Clethra alnifolia,* with the highest average importance, was only found in three forests. *Asimina triloba* has the second highest importance in Scranton, and is not found in any other forest. Other non-canopy species were common, but rarely dominant. *Ilex opaca* was present in six of seven forests and *Carpinus caroliniana* and *Persea palustris* were present in five of seven. No single non-canopy species was present in all forests.

Soils

All soil textures were sandy loam or finer (Table 7). In each forest, with the exception of Alligator River, sand content decreased from the surface to the subsurface soil (from 15 to 90 cm). Only Gull Rock soils contained enough carbon to have a mucky-modified texture; all others were mineral soil materials.

Variation in mean wetness class of each forest was high (Table 6). There was little pattern in wetness values along the belt transect for most forests. This was not true in Gull Rock where all plots were assigned wetness class 1. The distribution of sampling plots across wetness classes was uneven.

Wetter sites had higher amounts of carbon accumulation, confirming our use of carbon accumulation as an indicator of moisture regime in the wetness index. This relationship held true even for forests that were not assigned to wetness classes that used carbon accumulation as a characteristic.

Vegetation-Soil Relationships

L. styraciflua and *A. rubrum* maintained relatively high importance across a wide range of wetness classes (Figure 3). Other species, like *Q. michauxii,* were restricted to soils of certain wetness classes. There was much variation in importance for each species by wetness class, and standard deviations were high. This may be due to a low number of samples for a few wetness classes (Figure 3).

Gull Rock, the wettest site, contained the fewest total species and a low stem density (Table 6). However, the lowest stem density is seen in Scranton, the third driest site. Total species is generally higher for drier sites, but not without exception. More likely differences in stem density, basal area and total number of species are related to stand history.

NMS ordination of only plots assigned wetness values showed little relationship between plant community composition and wetness class (Table 9). None of the three NMS axes had a value of r^2 above 0.30. Indicator species analysis also showed little correlation of individual species with wetness class. Perfect indication (indicator value =100%) means that presence of a species points to a certain wetness class without error (McCune and Grace 2002). Here, indicator values never exceeded 40% for any species.

Stand scores for an ordination of all plots were evenly distributed along axes 1 and 2 with no obvious pattern or clumping. On axis 3, more plots were found at moderate values than at higher or lower values, but still without pattern. We did not group plots into subclasses within nonriverine wet hardwood forests. Correlations of species' importance (with r>.30) with the three axes in this ordination are shown in Table 9.

As in the previous ordination, no grouping of plots was seen on the three best-fit axes of an ordination of only canopy tree species in all plots (Figure 5). Importance of *L. styraciflua, A. rubrum*, *L. tulipifera*, *Q. michauxii*, and total oaks were the only traits with noteworthy relationships to stand scores. In Figure 5, these traits are shown as vectors, indicating direction of increase for each. Summing all oaks added little information beyond that from *Q. michauxii* alone, and both traits increased in a direction nearly opposite that of *A. rubrum*. However, none of these species has a significant relationship to plant community composition.

DISCUSSION

Plant Community Composition

More detailed analysis of plant community composition has been made by Rheinhardt and Rheinhardt (2000). As in our study, Rheinhardt and Rheinhardt noted the high importance of *A. rubrum* and *L. styraciflua* and low relative importance of oak in most stands of intact nonriverine wet hardwood forests (5 forests in this study were included). We found much lower importance of *N. biflora* than Rheinhardt and Rheinhardt, most likely because of excluding sample plots containing *Taxodium distichum*, which were considered nonriverine swamp forests. After finding no relationship between soil texture or drainage class and community composition, they concluded that more detailed soils data and hydrologic modeling were needed to determine how hydrologic regime is related to composition.

In this study, there is a low correlation between plant species composition and fine-scaled wetness index values in North Carolina nonriverine wet hardwood forests. Existing literature supports that our wetness index represents a gradient in hydrologic regime in these forests. For example, cypress-gum swamps, with a longer hydroperiod than wet flats, have more organic matter accumulation at the soil surface (Watt and Golladay 1999). Also, the depth of redoximorphic features indicates the reach of a fairly consistent water table in the growing season. As the depth to redoximorphic features increases, hydroperiod decreases. Therefore, we must conclude that other factors have a stronger influence on composition.

Further investigations into plant community dynamics suggest other explanations for variation in plant community composition. The high importance of *A. rubrum* and *L. styraciflua* in all wetness classes limits correlation of overall plant composition to changes in wetness class. In addition, microtopography, high intersite variation in non-canopy species, and stochasticity also have strong effects on plant community composition.

All of these forests show evidence of, or have a known history of disturbance by logging, ditching, and/or farming. Anthropogenic disturbances such as fire suppression and nutrient input from agriculture have increased the proliferation of *A. rubrum* well beyond its historical reaches of habitat and abundance in the eastern United States (Abrams 1998). Although *A. rubrum* was historically limited to moist sites, it is now found in a broader range of moisture regimes (Abrams 1998). In forested wetlands previously used for agriculture, *L. styraciflua* dominates early natural regeneration (Devine et al. 2000).

The low correlation of importance of canopy dominants *A. rubrum* and *L. styraciflua* to wetness helps explain the low correlation of overall species composition to wetness. Their dominance across wetness classes is especially significant on canopy composition at the community level, where gradients are identified by changes in relative abundances of species, not types of species.

Moderate disturbance in plant communities can re-initiate or arrest succession (Brown and Lugo 1994). Opportunistic species like *L. styraciflua*, *L. tulipifera*, and *A. rubrum* can quickly colonize areas impacted by logging and farming. If succession proceeds, the composition of these forests may change to one less dominated by species adapted to a wide variety of moisture regimes (lower importance of *A. rubrum* and *L. styraciflua*). This transition would require seed sources for later-successional species and limited recurrence of disturbance.

If *A. rubrum* and *L. styraciflua* have increased in abundance, they must have replaced other species, or caused a decline in the numbers of other species present in historical nonriverine wet hardwood forests. Selective logging may have excluded species with higher commercial value (e.g., *Quercus* species). Also, the wide separation of the few remaining nonriverine wet hardwood forests in a landscape dominated by agricultural fields limits propagule dipersal, especially of heavy-seeded genera like *Quercus*.

Other studies have shown that non-canopy species are better indicators of subtle changes in environmental gradients than canopy species (e.g., herbs in Drewa *et al.* 2002). However, high variance in non-canopy composition among sampled nonriverine wet hardwood forests is most likely due to a suite of random factors. Because restoration of forested wetlands focuses on canopy species, we did not describe vegetation below 1.3 m.

Each forest contained plots representing one to six wetness classes. Therefore, within any one wetness class, several possible expressions of plant community composition can be found. In each site, the small, gradual change in hydrologic regime of sampled plots over a 300 m transect made it difficult to capture more than a few wetness classes.

Microtopography is a significant factor in distribution of several tree species in nonriverine wet hardwood forests (Scherrer 2000). For example, *Q. michauxii* and four other canopy trees occur predominantly on hummocks. *A. rubrum* and *L. styraciflua* are found in both hummocks and depressions.

Microtopography varied over short distances, such that our 10 m X 10 m plots often contained at least one hummock (high, dry area) and one depression (low, wet area). We described a soil profile typical of the overall plot, averaging microtopographic variation, and discounting the significant effect micro-topography has on tree species distribution. Net change in elevation from transects at Gum Swamp and Gull Rock (30 cm and 9 cm over 260m and 170m, respectively) was no greater than typical within-plot microtopographic variation.

Conclusions

Generalizations about trends in plant community composition along gradients in the lower Coastal Plain of North Carolina have been affected by large-scale alteration of natural environments. Our results illustrate the difficulty in characterizing fine-scaled trends in plant community composition in isolated remnants of nonriverine wet hardwood forests now dominated by generalist canopy species. Variables not measured in this study are controlling distribution of plant species in these forests.

Implications for Restoration

Historical documentation points to oak dominance in nonriverine wet hardwood forests (Pinchot 1897). Today, *A. rubrum*, *L. styraciflua*, and *L. tulipifera* join *Q. michauxii* in dominating these forests. However, because many restoration sites have disturbance regimes and isolated natures similar to those of the sampled forests, the dominance of non-oak species is what we can realistically expect to persist in the long-term in restoration projects of nonriverine wet hardwood forests.

While we found little pattern in plant community composition along the moisture gradient to guide restoration, these data represent subsets of useful reference information. These data indicate which species are known to grow in individual wetness classes. When divided by wetness class, they provide guidelines for planning and evaluation of nonriverine wet hardwood restoration. For example, *A. rubrum* and *L. styraciflua* can be planted across wetness classes. Areas with soils corresponding to wetness classes one through three can also support *L. tulipifera* and *N. biflora*. In soils corresponding to wetness classes four through eight, *Q. michauxii* and *Q. nigra* may be planted in addition to *A. rubrum* and *L. styraciflua.*

However, many restoration projects aim for more than just viable vegetation; their goal is to restore a historical plant community. Today all identified remnants of nonriverine wet hardwood forests are previously-cut stands that have grown back to a variation of the past community composition (Schafale and Weakley 1990; Rheinhardt and Rheinhardt 2000). Although once classified as oak flats (Pinchot 1897), most of these remaining stands have only a small portion of oaks in their canopies. And according to Abrams (1998) we can expect *A. rubrum* to increase in dominance in the next century, eventually replacing some of the historically dominant trees of the eastern United States.

These sites likely once contained higher quantities of oak species, mainly cherrybark oak (*Q. pagoda*), swamp chestnut oak (*Q.michauxii*), water oak (*Q.nigra*) and laurel oak (*Q. laurifolia*), but logging and disturbance have allowed opportunistic species like *L. styracifula*, *A. rubrum,* and *L. tulipifera* to dominate. *Quercus* saplings can be found in many sites, indicating that in the absence of disturbance, *Quercus* species could dominate the canopy (Schafale 1999.) It is possible that historical *Quercus* dominance was over-estimated (Rheinhardt and Rheinhardt 1999). However, from current reports of *A. rubrum* dominating, or at least increasing abundance (Abrams 1998) in eastern North American plant communities, it is rational to conclude a lesser historical importance for *A. rubrum* in these forests.

For the restorationist intending to replace a historical nonriverine wet hardwood forest, the range of species' importance values reported in this study may not suffice. Unfortunately, quantitative data on historical *Quercus* importance are not available. Reference sites for restoration of this historical community are difficult to find because of the widespread low importance of oak in remaining stands. Even in Aurora, which has the highest overall oak importance, *Q. michauxii* has high importance (27%), but other *Quercus* species are very low (< 3%).

This study illustrates that total importance values for *Quercus* species are highest in wetness classes four through eight. While more research into detailed hydrologic regimes and other variables controlling plant community composition is needed in the future, we currently suggest restoring hydrology to support soils in these wetness classes to support growth of hydrophytic oaks on inter-stream divides. Wetter classes will not likely support a community with high oak importance.

For other plant communities, this method has great potential as a means of determining appropriate species for restoration projects. As in this study, the climate, soils, and geomorphic position of the sampled sites should be similar. The wetness index and indicators will depend on field conditions of the particular community.

Table 1. Common plant species in nonriverine wet hardwood forests (Schafale 1999)

Plant Layer	*Common Species*
Trees	sweetgum *(Liquidambar styraciflua),* swamp chestnut oak *(Quercus michauxii),* laurel oak*(Quercus laurifolia),* cherrybark oak *(Quercus pagoda),* water oak *(Quercus nigra),* loblolly pine *(Pinus taeda),* red maple *(Acer rubrum),* tuliptree *(Liriodendron tulipifera)*
Understory Trees	red bay *(Persea palustris),* red maple *(Acer rubrum),* American hornbeam *(Carpinus caroliniana),* American holly *(Ilex opaca)*
Shrubs	coastal sweet pepperbush *(Clethra alnifolia),* coastal doghobble *(Leucothoe axillaris),* giant cane *(Arundinaria gigantea)*
Herbs	netted chainfern *(Woodwardia areolata),* Virginia chainfern *(Woodwardia virginica),* royal fern *(Osmunda regalis)*

Table 2. Names of forests sampled, North Carolina county of location, and mapped soil series sampled

Forest	**County**	**Mapped Soil Series**
Alligator River National Wildlife Refuge	Dare	Hyde loam
Aurora	Beaufort	Tomotley fine sandy loam
Bethel Grindel Hardwoods	Pitt	Pantego loam
East Dismal Swamp	Washington	Portsmouth fine sandy loam
Gull Rock National Wildlife Refuge	Hyde	Bellhaven muck Weeksville loam
Gum Swamp (Croatan National Forest)	Craven	Pantego fine sandy loam Rains fine sandy loam
Scranton Harwoods	Hyde	Brookman loam Stockade mucky sandy loam

Table 3. Soil wetness index. Beginning with wetness class one, examine soil profile for characteristics until one is encountered, corresponding to its wetness class. For classes one through five, depth of muck in the surface is combined with depth of mucky mineral layers.

Wetness Class	Soil Characteristics
1	Mucky Mineral layer greater than 41 cm thick
2	Mucky Mineral layer 32 cm - 40 cm thick
3	Mucky Mineral layer 22 cm - 31 cm thick
4	Mucky Mineral layer 7 cm - 21 cm thick
5	Mucky Mineral layer 0.5 - 6 cm thick
6	Thick Dark Surface: 18 cm - 31 cm of value 3 or less, chroma 2 or less
7	Thin Dark Surface: 0.5 cm - 17 cm of value 3 or less, chroma 2 or less
8	Depleted Matrix within 25 cm of surface (see USDA Hydric Indicator F3)
9	Depleted Matrix within 25 cm - 61 cm of surface (see USDA Hydric Indicator F3)
10	None of the above indicators

Table 4. Soil profile characteristics requirements to meet USDA hydric soil indicator F3 for depleted matrix (USDA, 2002)

Matrix Color		Horizon	*Redox Concentrations*	
Value	Chroma	Type	Types	Contrast
6	≤ 2	A or E Bg	2% or more None	Distinct, Prominent
5	≤ 1	A or E Bg	2% or more None	Distinct, Prominent
4 or 5	≤ 2	All	2% or more	Distinct, Prominent
4	≤ 1	All	2% or more	Distinct, Prominent

Table 5. Mean importance value for each species by forest and overall. From left to right, forests are driest to wettest.

Species	Forest Name							Mean IV	SD
	Aurora	Gum Swamp	Scranton	East Dismal	Bethel Grindel	Alligator River	Gull Rock		
				Canopy					
Liquidambar styraciflua L.	0.12	0.17	0.26	0.18	0.20	0.12	0.35	0.19	0.18
Acer rubrum L.	0.06	0.18	0.10	0.15	0.11	0.15	0.39	0.15	0.15
Quercus michauxii Nutt.	0.27	0.06	0.11	0.05	0.03	0.04		0.08	0.15
Liriodendron tulipifera L.	0.03	0.04	0.10	0.05	0.12			0.05	0.11
Pinus taeda L.		0.05	0.01	0.02		0.11	0.01	0.03	0.08
Quercus nigra L.	0.03	0.06		0.01		0.09		0.03	0.07
Nyssa biflora Walt.	0.02	0.04		0.01	0.01	0.05	0.05	0.02	0.06
Quercus pagoda Raf.		0.05	0.02	0.02		0.02		0.02	0.05
Fagus grandifolia Ehrh.	0.07	0.03		0.01				0.02	0.05
Fraxinus pennsylvanica Marsh.	0.07	<0.01	0.02			0.01		0.01	0.06
Ulmus americana L.	0.01	<0.01	0.03	<0.01				0.01	0.03
Quercus laurifolia Michx.	0.02	<0.01	0.01	<0.01	<0.01			0.01	0.03
Nyssa sylvatica Marsh.				0.03				0.01	0.03
Carya ovata			0.02			0.01		<0.01	0.03
Quercus lyrata Walt.	0.01	0.01				<0.01		<0.01	0.01
Ulmus rubra Muhl.							0.02	<0.01	0.01
Quercus phellos L.		<0.01		<0.01				<0.01	0.01
Total Oaks	0.33	0.18	0.14	0.09	0.03	0.15		0.14	0.18
A. rubrum + L. styraciflua	0.17	0.35	0.36	0.32	0.31	0.27	0.73	0.34	0.23

Table 5 (continued). Mean importance value for each species by forest and overall. From left to right, forests are driest to wettest.

Species	Forest Name							Mean IV	SD
	Aurora	Gum Swamp	Scranton	East Dismal	Bethel Grindel	Alligator River	Gull Rock		
	Non-canopy								
Persea palustris (Raf.) Sarg.	0.03	0.22			<0.01	0.11	0.09	0.07	0.12
Carpinus caroliniana Walt.	0.22	0.01	0.07	0.02		0.15		0.07	0.12
Ilex opaca Ait.	0.01	0.04	0.09	0.18	0.06	0.05		0.06	0.13
Asimina triloba L. Dunal			0.14					0.02	0.09
Symplocos tinctoria (L.) L'Her	0.01	0.01		<0.01	<0.01	0.06		0.01	0.05
Morella cerifera (L.) Small		0.01				<0.01	0.06	0.01	0.04
Vaccinium sp.					<0.01	0.03		<0.01	0.02
Ostrya virginiana (P. Mill.) K. Koch	0.02			<0.01				<0.01	0.02
Magnolia virginiana L.	<0.01						0.02	<0.01	0.02
Gordonia lasianthus (L.) Ellis				0.01				<0.01	0.01
Unknown							0.01	<0.01	0.01
Vaccinium corymbosum L.	<0.01	<0.01		<0.01				<0.01	0.01
Morus rubra L.	<0.01							<0.01	0.01
Crataegus sp.			<0.01					<0.01	0.01
Ligustrum sinense Lour.					<0.01			<0.01	<0.01
Cornus amomum P.Mill		<0.01						<0.01	<0.01
Euonymus americana L.	<0.01							<0.01	<0.01
Callicarpa americana L.	<0.01							<0.01	<0.01
Hamamelis virginiana L.	<0.01							<0.01	<0.01

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Table 6. Mean wetness and standard deviation, stem density, basal area and total number of species found in each forest.

Site	Mean Wetness	SD	Stems per ha	Basal Area m^2/ha	Total Species
Gull Rock	2.0	3	1247	7.3	9
Alligator River	3.9	0.5	2097	7.5	16
Bethel Grindel	4.0	1.6	3781	7.8	12
East Dismal	4.2	1.4	2641	7.6	20
Scranton	4.6	0.9	993	7.4	15
Gum Swamp	6.4	2.0	3258	6.7	22
Aurora	6.5	1.7	2200	6.8	22

Table 7. Selected soil properties by depth in nonriverine wet hardwood forests (n=4; -- indicates samples missing). (m) indicates mucky-mineral soil texture due to amount of carbon.

Site	Depth	% Sand		% Silt		% Clay		Texture	% Carbon		% Nitrogen	
	(cm)	Mean	SD	Mean	SD	Mean	SD		Mean	SD	Mean	SD
Bethel Grindel	15	62	4	24	<1	15	5	sandy loam	2.8	0.4	0.8	0.7
	30	61	<1	23	<1	16	1	sandy loam	1.7	1.4	0.2	0.0
	45	55	1	29	<1	16	1	sandy loam				
	60	59	1	24	<1	17	<1	sandy loam				
	90	51	7	33	7	16	0	loam				
Aurora	15	68	4	19	2	14	2	sandy loam	1.7	0.4	0.1	0.0
	30	67	2	16	1	17	3	sandy loam	0.7	0.0	0.0	0.0
	45	66	11	12	3	22	8	sandy clay loam				
	60	56	3	15	1	29	2	sandy clay loam				
	90	62	8	13	4	25	5	sandy clay loam				
Alligator River	15	38	9	31	4	31	5	clay loam	7.6	0.9	0.5	0.0
	30	44	3	27	4	29	1	clay loam	5.1	2.9	0.3	0.2
	45	40	4	30	4	30	<1	clay loam				
	60	40	3	28	2	32	1	clay loam				
	90	62	3	21	1	17	1	sandy clay loam				
Gull Rock	15	42	2	33	<1	25	1	loam (m)	11.8	0.0	0.5	0.0
	30	34	5	39	6	26	<1	loam (m)	10.2	1.7	0.4	0.1
	45	31	3	44	2	24	5	loam				
	60	36	--	43	<1	21	<1	loam				
	90	23	13	56	12	22	1	silt loam				
Gum Swamp	15	60	4	22	1	18	3	sandy loam	1.9	1.1	0.1	0.1
	30	57	4	24	<1	19	4	sandy clay loam	0.7	0.3	0.0	0.0
	45	55	2	23	<1	22	2	sandy clay loam				
	60	52	5	22	2	26	3	sandy clay loam				
	90	54	7	22	1	24	6	sandy clay loam				
Scranton	15	28	2	50	2	22	<1	silt loam	3.6	0.0	0.2	0.0
	30	29	3	47	2	23	1	loam	2.4	0.7	0.1	0.0
	45	23	--	54	12	35	5	clay loam				
	60	--	--	62	6	37	1	--				
	90	23	--	53	19	36	1	clay loam				

Table 8. R-squared values for ordination axes in NMS ordinations.
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Dataset	No. of plots	No. of species	r^2				Monte Carlo p value	Final stress	Final instability
			Axis 1	Axis 2	Axis 3	Cumulative			
All plots all species	209	38	0.24	0.19	0.28	0.71	0.02	19.35	<0.01
All plots canopy only	209	18	0.23	0.27	0.23	0.73	0.02	28.78	0.03
Plots with wetness values	100	35	0.23	0.23	0.26	0.72	0.02	18.70	<0.01

Table 9. R values for selected attributes in NMS ordinations ($r^2 > 0.30$ on at least one axis)

	All plots all species r-values			All plots canopy only r-values			Plots with wetness values r-values		
Attribute	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
A. rubrum	0.46	0.36	-0.32	-0.49	-0.53	-0.31	-0.17	-0.15	0.69
L. styraciflua	0.24	-0.53	-0.53	-0.30	-0.35	0.74	-0.52	0.51	-0.03
L. tulipifera	0.10	-0.09	0.57	-0.13	0.68	-0.02	-0.07	-0.59	-0.15
Q. michauxii	-0.69	0.04	0.09	0.71	-0.17	-0.10	0.62	-0.25	0.05
Total oaks	-0.63	0.26	-0.02	0.58	-0.10	-0.25	0.62	0.10	0.17
Wetness values							0.29	0.06	-0.04

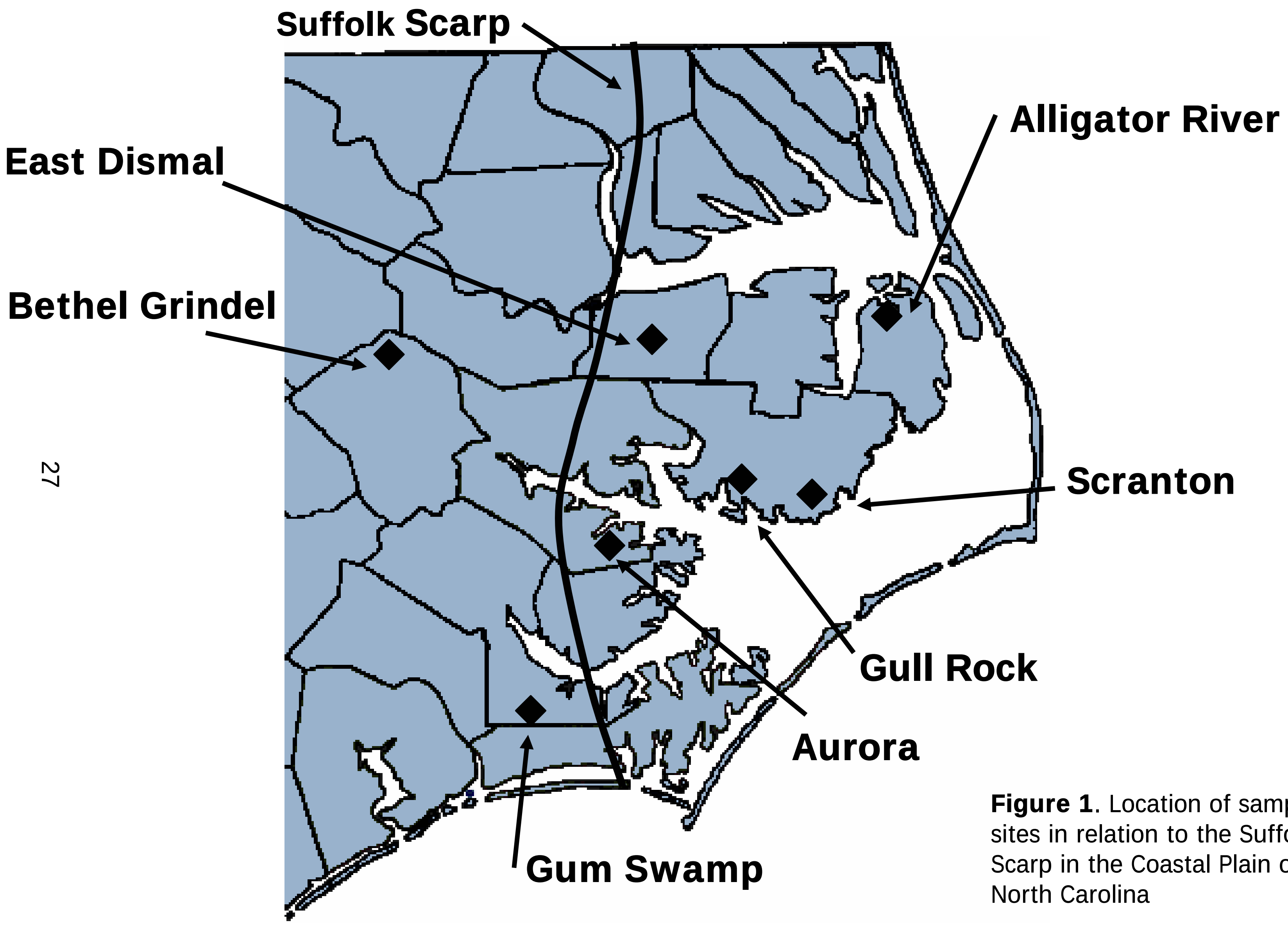


Figure 1. Location of sampling sites in relation to the Suffolk Scarp in the Coastal Plain of North Carolina

Figure 2. Relationship between % organic carbon and % clay for distinguishing organic and mucky-modified soil material from mineral soil texture.

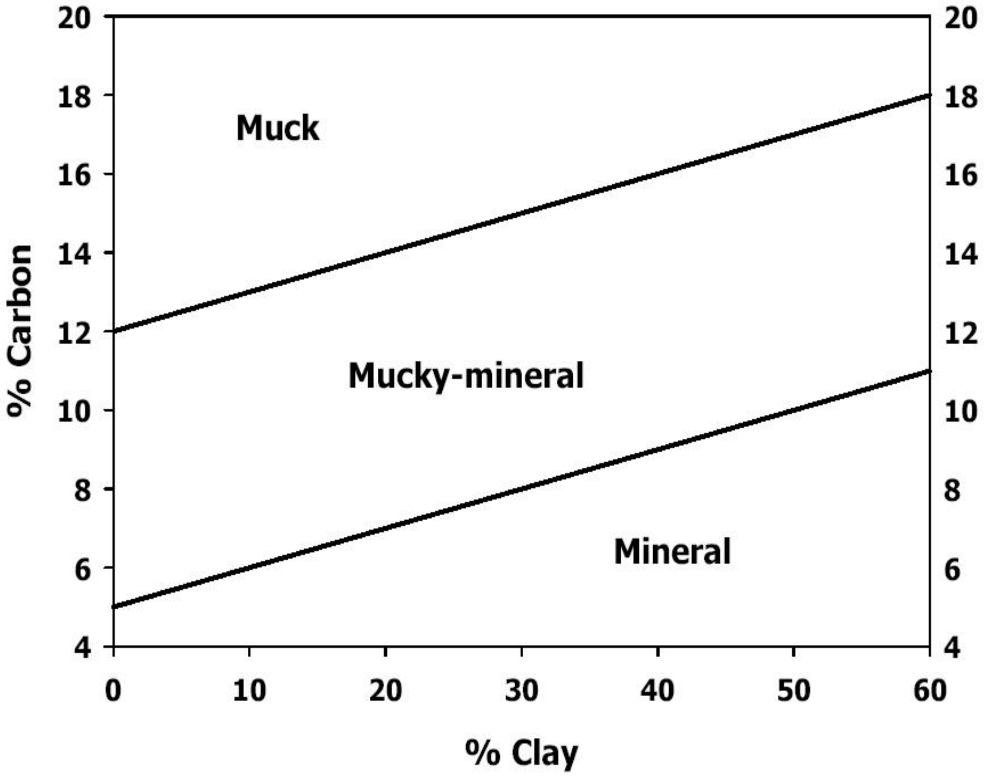


Figure 3. Trends in importance for selected canopy trees along wetness gradient (wet to dry) in nonriverine wet hardwood forests.

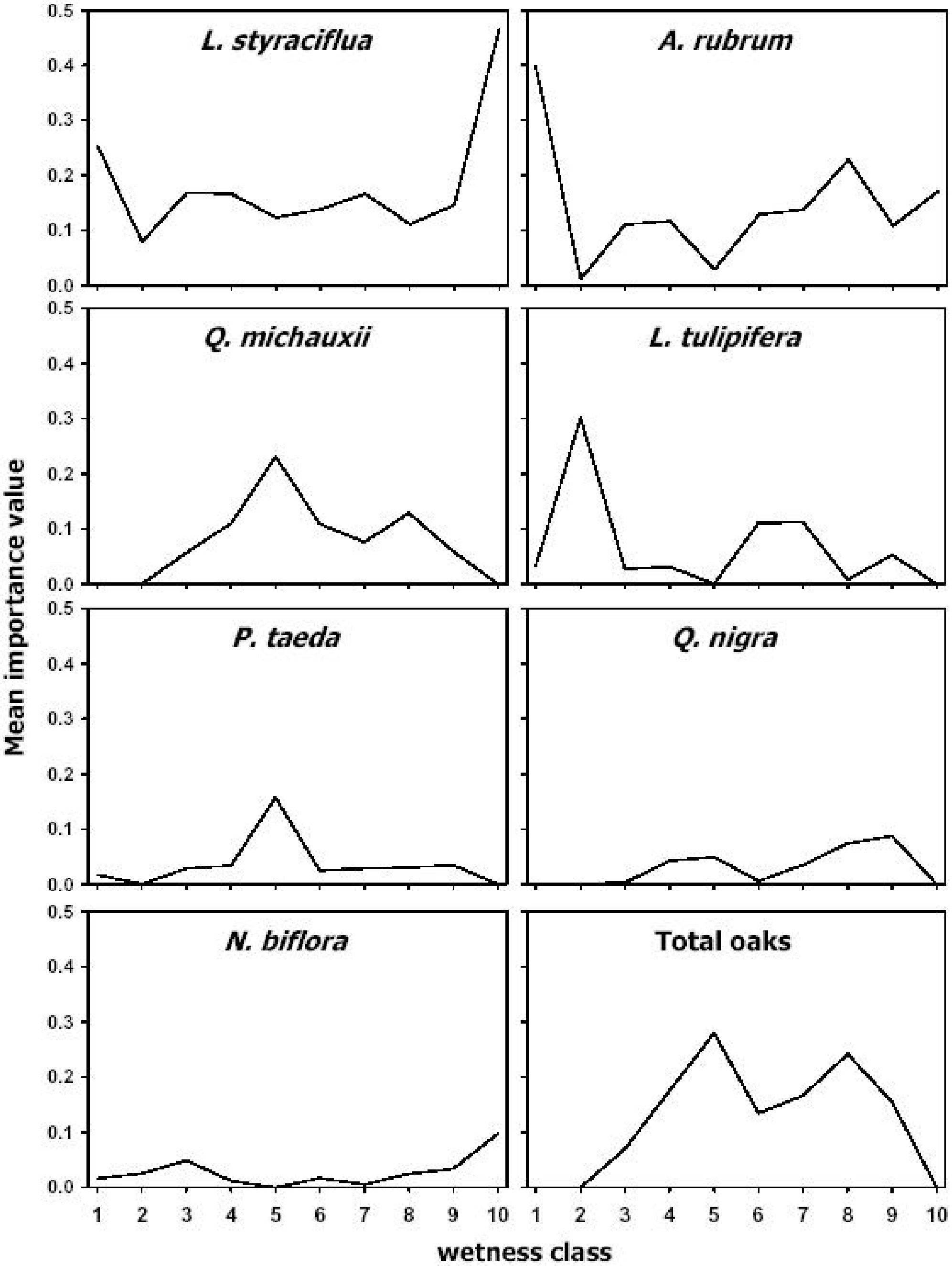


Figure 4. Percent organic carbon at 15 cm in relation to mean wetness by site.

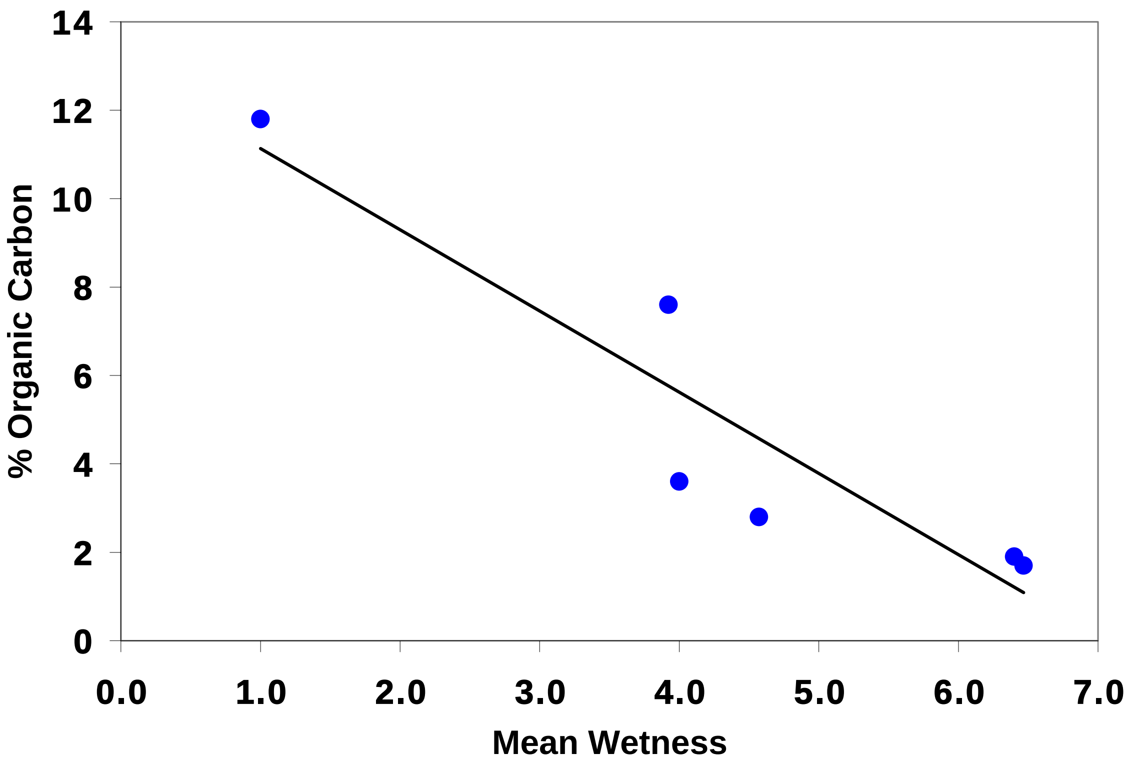
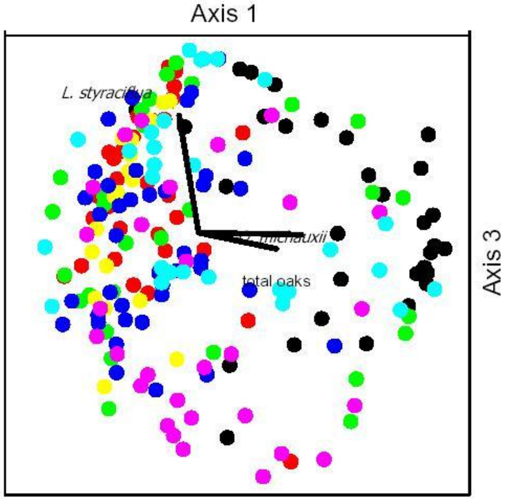


Figure 5. NMS ordinations of plant species data by plots.



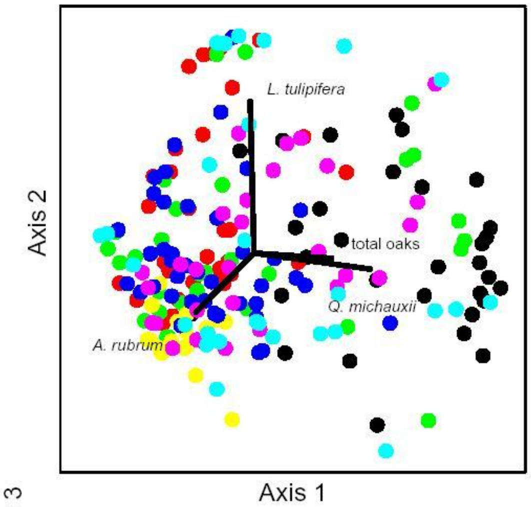


Figure 4. NMS ordination of all plots with only canopy trees included. Vectors shown are for traits with r^2 >.300.

APPENDIX 1

Selected Soil Chemical Properties for Nonriverine Wet Hardwood Forests.

Forest	Depth (cm)	meq/100 cm^3											
		P		K		Ca		Mg		Na		Buffer Acidity	
		Sample1	Sample2	Sample1	Sample2	Sample1	Sample2	Sample1	Sample2	Sample1	Sample2	Sample1	Sample2
Bethel Grindel	15	22.20	29.60	0.15	0.11	0.36	0.30	0.09	0.15	0.10	0.10	4.70	6.70
	30	7.10	24.20	0.10	0.10	0.33	0.29	0.12	0.12	0.10	0.10	6.00	6.50
	45	0.00	5.40	0.09	0.11	0.30	0.33	0.11	0.13	0.10	0.10	5.10	5.70
	60	0.00	0.80	0.10	0.11	0.35	0.39	0.13	0.14	0.10	0.10	5.20	5.80
	90	0.00	2.20	0.50	0.60	0.21	0.24	0.09	0.10	0.10	0.10	2.60	4.00
Aurora	15	16.10	28.30	0.05	0.08	0.37	0.36	0.17	0.20	0.10	0.10	2.70	4.80
	30	3.60	0.00	0.06	0.09	0.34	4.75	0.19	0.57	0.10	0.10	2.80	2.30
	45	0.00	0.00	0.07	0.11	2.60	5.34	0.44	0.69	0.10	0.20	2.10	2.00
	60	0.00	0.00	0.15	0.19	6.28	7.37	0.77	0.77	0.20	0.20	1.90	1.10
	90	0.00	0.00	0.22	0.15	8.13	6.97	0.89	0.71	0.30	0.30	0.80	0.60
Alligator River	15	77.60	22.30	0.10	0.06	0.50	0.22	0.61	0.26	0.20	0.10	6.00	3.30
	30	80.50	2.00	0.10	0.06	0.40	0.22	0.56	0.38	0.20	0.20	3.40	5.40
	45	49.60	2.30	0.13	0.06	0.56	0.26	0.81	0.41	0.20	0.20	3.00	2.20
	60	26.30	9.80	0.10	0.06	0.40	0.23	0.61	0.41	0.20	0.20	2.30	2.10
	90	10.30	12.70	0.06	0.11	0.24	0.44	0.41	0.78	0.30	0.30	2.00	4.50

Selected Soil Chemical Properties for Nonriverine Wet Hardwood Forests (cont.).

Forest	Depth (cm)	meq/100 cm^3											
		P		K		Ca		Mg		Na		Buffer Acidity	
		Sample1	Sample2	Sample1	Sample2	Sample1	Sample2	Sample1	Sample2	Sample1	Sample2	Sample1	Sample2
Gull Rock	15	66.70	48.90	0.22	0.19	0.52	0.73	1.04	1.33	2.60	2.70	6.00	6.80
	30	93.80	70.10	0.19	0.14	0.72	0.68	1.20	1.10	2.10	1.60	4.00	4.80
	45	59.00	43.60	0.15	0.10	0.71	0.56	1.07	0.85	1.50	1.20	4.80	4.80
	60	21.00	19.00	0.19	0.14	1.17	0.85	1.93	1.44	2.20	2.20	5.00	4.90
	90	0.20	9.10	0.28	0.20	1.40	1.12	3.82	2.40	2.20	2.10	2.20	3.20
Gum Swamp	15	15.20	28.40	0.08	0.10	0.29	0.24	0.20	0.22	0.10	0.10	3.60	4.50
	30	0.00	11.40	0.08	0.08	0.27	0.22	0.20	0.19	0.10	0.10	5.10	3.50
	45	0.00	0.00	0.10	0.10	0.29	0.23	0.26	0.21	0.20	0.10	5.40	5.10
	60	0.00	0.00	0.10	0.13	0.25	0.32	0.27	0.35	0.10	0.10	3.80	5.40
	90	0.00	0.00	0.11	0.15	0.27	0.46	0.29	0.46	0.10	0.10	3.90	4.00
Scranton	15	6.50	0.00	0.13	0.06	1.41	0.47	0.68	0.29	0.10	0.10	4.10	4.50
	30	8.40	6.90	0.05	0.06	0.54	0.54	0.29	0.27	0.10	0.10	3.20	3.60
	45	0.00	0.00	0.05	0.06	0.61	0.41	0.32	0.31	0.10	0.20	3.20	2.60
	60	0.00	0.00	0.08	0.10	1.01	0.69	0.56	0.72	0.20	0.20	3.00	2.80
	90	0.00	0.00	0.08	0.12	0.97	1.03	1.14	1.35	0.20	0.30	2.60	4.10

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