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Debra Willard
US Geological Survey


Christopher Bernhardt
US Geological Survey

Roger Brown
Columbus State University

Bryan Landacre
US Geological Survey

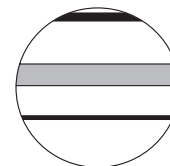
Philip A. Townsend
University of Wisconsin-Madison, ptownsend@wisc.edu

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Debra Willard,¹ Christopher Bernhardt,^{1,2} Roger Brown,³
Bryan Landacre¹ and Philip Townsend⁴

Abstract

We used pollen assemblages to reconstruct late-Holocene paleohydrologic patterns in floodplain deposits from the lower Roanoke River basin (North Carolina, southeastern USA). Using 120 surface samples from 38 transects, we documented statistical relationships between pollen assemblages, vegetation, and landforms. Backswamp pollen assemblages (long hydroperiods) are dominated by *Nyssa* (tupelo) and *Taxodium* (cypress) and have high pollen concentrations. Sediments from elevated levees and seasonally flooded forests (shorter hydroperiods) are characterized by dominant *Pinus* (pine) pollen, variable abundance of hardwood taxa, and low pollen concentrations. We apply the calibration data set to interpret past vegetation and paleohydrology. Pollen from a radiocarbon-dated sediment core collected in a tupelo-cypress backswamp indicates centennial-scale fluctuations in forest composition during the last 2400 years. Backswamp vegetation has occupied the site since land clearance began ~300 years ago. Recent dam emplacement affected sedimentation rates, but vegetation changes are small compared with those caused by pre-Colonial climate variability. The occurrence of wetter conditions from ~2200 to 1800 cal. yr BP, ~1100 to 750 cal. yr BP, and ~400 to 250 cal. yr BP may indicate changes in cyclonic circulation patterns related to shifts in the position of the Bermuda High and jet stream.

Keywords

Atlantic Coastal Plain, floodplains, hydroperiod, paleohydrology, pollen, vegetation

Introduction

Riparian forests of the Atlantic Coastal Plain of North America contain diverse wetland assemblages that include tidal marshes, freshwater marshes, southern deepwater swamps, and bottomland hardwood forests. These wetlands provide critical habitats for plant and animal communities and play an important role in maintaining water quality by trapping sediment, contaminants, and nutrients (Hupp, 2000). Extensive tracts of these wetlands have been lost since Colonial land clearance in the eighteenth and nineteenth centuries (Mitsch and Gosselink, 2000) and twentieth-century construction of dams that altered seasonal discharge rates and patterns, sedimentation, and forest composition (Graf, 2006; Pearsall *et al.*, 2005). The lower Roanoke River (LRR), located on the Atlantic Coastal Plain of North Carolina (Figure 1), is a large, minimally disturbed bottomland forest (Townsend, 2001) that provides a natural laboratory to examine wetland response to hydrologic and environmental changes associated with dam operations, land-use changes, and climate variability over a range of temporal and spatial scales.

Hydrology is the primary control on the composition and distribution of floodplain vegetation in the Atlantic Coastal Plain (Townsend, 2001). Because dam operations change the timing and magnitude of peak flows, they often are considered to have

much greater impacts on discharge and, by extension, wetland hydrology than climate change and variability (Graf, 1999; Townsend and Foster, 2002). To evaluate such hypotheses, we must consider long hydrologic records that capture the variability associated with climate processes operating on multidecadal timescales. The longest instrumental records of river discharge and precipitation extend only to the early twentieth century and cannot address questions either on hydrologic variability over long temporal scales or hydrologic patterns of the floodplain before it was substantially altered by Colonial land clearance. Hydrologic proxies preserved in sediments provide a means to compare the

¹US Geological Survey, USA

²University of Pennsylvania, USA

³Columbus State University, USA

⁴University of Wisconsin, USA

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Corresponding author:

Debra Willard, U.S. Geological Survey, Reston VA, USA.

Email: dwillard@usgs.gov

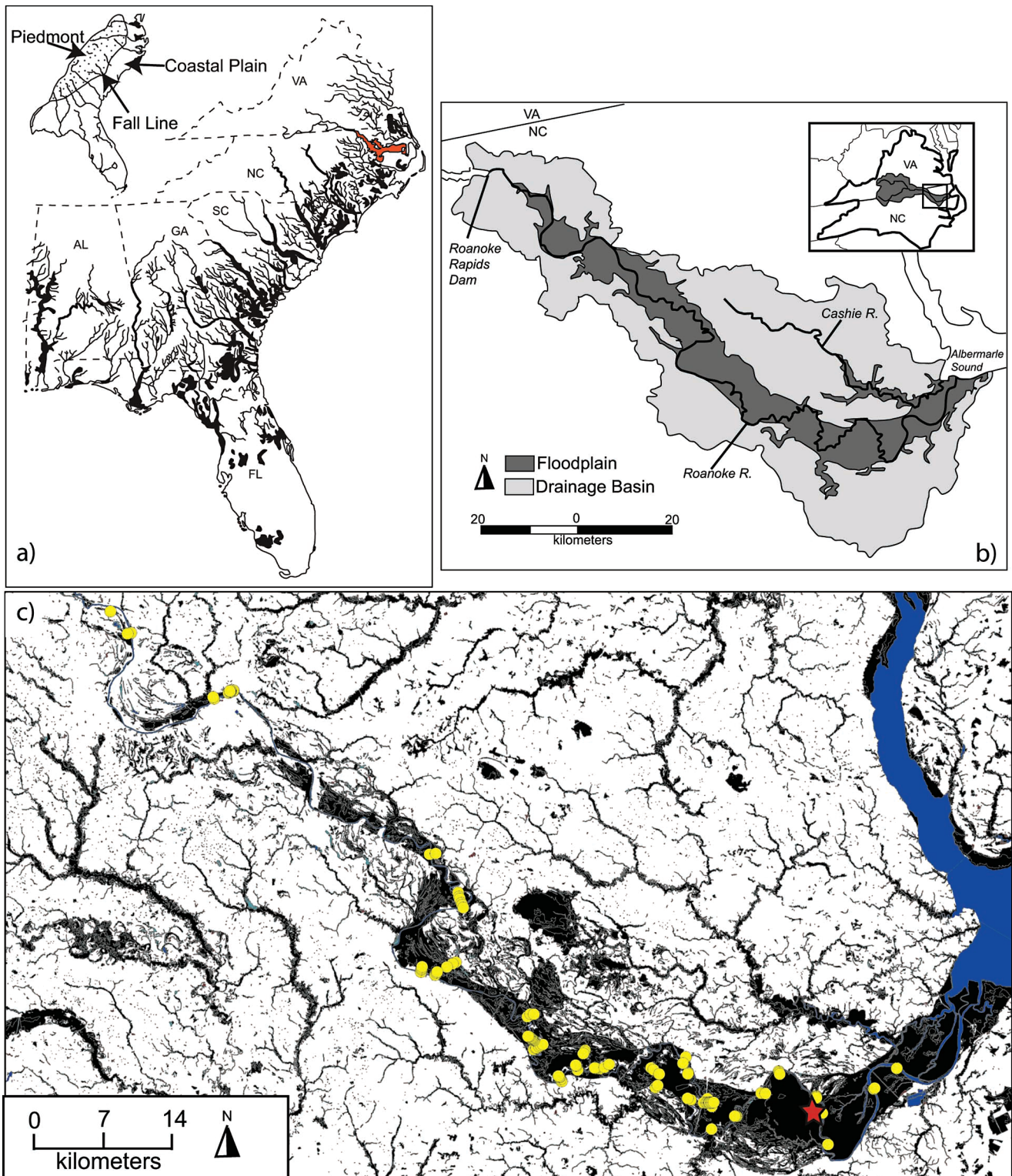


Figure 1. (a) Distribution of rivers in Coastal Plains of southeastern USA. Roanoke River is highlighted in red. Potential extent of bottomland hardwood forests is shown along major streams (modified from Putnam *et al.*, 1960). (b) Distribution of lower Roanoke River (LRR) floodplain (dark gray shading) within LRR drainage basin (light gray shading), North Carolina. Inset map shows extent of entire Roanoke River watershed in Virginia and North Carolina. (c) Satellite image of LRR showing location of study transects. Yellow circles indicate location of surface samples, and the red star indicates the location of sediment Core 01-10-11-4

natural wetland hydrology with that of the modern system and to evaluate such questions.

Although many pollen-based reconstructions come from lake sediments (Delcourt and Delcourt, 1984; Watts, 1979, 1980; Watts *et al.*, 1996; Whitehead, 1972; Whitmore *et al.*, 2005), wetland sediments increasingly are being used for paleohydrologic studies

(Chmura *et al.*, 2006; Cohen *et al.*, 1999; Goman and Leigh, 2004; LaMoreaux *et al.*, 2009; Pederson *et al.*, 2005; Whitehead, 1972; Willard *et al.*, 2006). Pollen assemblages preserved in wetland sediments typically contain a more localized pollen signature than those from lake sediments (Bunting *et al.*, 1998), and thus reflect both regional climate and a strong overprint of local

hydrologic fluctuations. In the Atlantic Coastal Plain, substantial differences in elevation and substrate exist along the length of the stream from the Fall Line to the river mouth as well as laterally from levee to backswamp. Such variability affects local hydroperiods (annual duration of inundation) and influences the amount of spatial heterogeneity within floodplain vegetation.

Here we evaluate the sensitivity of sedimentary pollen records to hydrologic variability in floodplain environments. We quantified pollen from surface samples and associated source plants and environments (hydroperiod, substrate, and elevation) from the LRR basin. Using this calibration data set, we examined late-Holocene vegetation and reconstructed hydroperiod from a sediment core collected in a tupelo-cypress backswamp in the lower reaches of the Roanoke River.

Regional setting

The Roanoke River is an alluvial river with its headwaters situated in the Blue Ridge Mountains of south-central Virginia, following a high topographic gradient from the Piedmont across the Fall Line, and flowing across the Atlantic Coastal Plain to its mouth at Albemarle Sound, North Carolina (Figure 1). The LRR basin is >200 km long with an area of ~9000 km² (US Department of Health, Education, and Welfare, 1962). Its floodplain is 5–10 km wide and contains the largest remaining contiguous bottomland hardwood forest of the Atlantic Coastal Plain (Hupp, 2000). The present river flow and floodplain hydroperiod are regulated by a series of seven dams in the upper reaches of the river. Coastal Plain rivers are characterized by two distinct hydrological seasons, a low-flow summer season when stream flow is restricted to the river channel and a high-flow winter to spring season when large areas of the floodplain are inundated (Hupp, 2000; Townsend, 2001). The annual period of inundation in wetlands is referred to as the hydroperiod, which ranges from a few days on high-elevation sites such as levees to many months in low-elevation sites of deep swamps. The dynamic nature of this hydrologic regime results in significant erosion, transport, and deposition of sediment on the floodplain and a near constant state of sediment flux within the system. Coastal Plain floodplains have acted as sediment sinks during the late Holocene, and lateral accretion of sediment during flood events has influenced the structure of the floodplain environment, with coarse-grained sediments deposited on levees and finer-grained sediments deposited in backswamps distal to the stream. Hydrologic variation is enhanced by the presence of abandoned channels and other features that retain moisture differently than surrounding sediments. The hydrologic, topographic, and geomorphic diversity (substrate elevation, distance from river mouth, soil texture and organic matter content) inherent to Coastal Plain floodplains determines the structure of floodplain vegetation (Rice and Peet, 1997; Townsend, 2001).

Hydroperiod influences oxygen availability in soils, and species adaptability to anoxic stresses plays a large role in determining community composition across bottomland hydrologic gradients (Huffman and Forsythe, 1981; Wharton et al., 1982). On floodplains, a few centimeters difference in substrate elevation can significantly influence hydroperiod, resulting in altered community composition over a distance of meters. Coastal Plain floodplains may be described as a mosaic of backswamps, flats, and levees that generally reflect the underlying geomorphology of the area.

Forested peatlands, dominated by *Nyssa biflora*, *Magnolia virginiana*, and *Persea palustris*, are centered on organic soils on

the lowest-elevation floodplains near the Roanoke River mouth (Townsend, 2001). Swamp forests, including backswamps of many Coastal Plain rivers, are dominated by *Nyssa aquatica* and *Taxodium distichum* and typically occur on organic-rich, mineral substrates with long hydroperiods (annual flooding >200 days during wet years) in areas of very low topographic relief (Table 1) (Conner and Buford, 1998). Tupelo-cypress forests are inundated from the winter through summer seasons. Other canopy species in tupelo-cypress forests include *Salix nigra*, *Acer rubrum*, and *Populus heterophylla*. Along the margins of deepwater swamps, *Quercus lyrata*, *Carya aquatica*, and *Ulmus americana* may be common (Conner and Buford, 1998).

Wet bottomland hardwood (BHW) forests occur on transitional features between swamp forests and levees, and mesic BHW forests predominate on higher levees and ridges. Wet BHW forests are flooded for one to two months during the growing season and are characterized by a greater diversity of hardwood trees than occur in tupelo-cypress swamps. Common canopy species include *Acer rubrum*, *Fraxinus pennsylvanica*, *Ulmus americana*, *Liquidambar styraciflua*, and *Celtis laevigata* (Townsend, 2001). Mesic BHW forests flood infrequently (1 week to 1 month during the growing season) and include species of *Quercus* and *Carya* as well as *Pinus taeda* in peripheral sites. Mesic *Fagus* and *Quercus* forests occur on dry sites with <50 days flooding during the wet years.

The humid temperate regional climate has mean annual temperatures of 15–16°C and precipitation of 1100–1300 mm from AD 1895 to 2007 (Southeast Regional Climate Center Historical Climate Summaries: <http://www.sercc.com/climateinfo/historical/historical.html>; viewed 19 August 2009). Although winter temperatures in the region occasionally reach freezing, average winter temperatures (5–7°C) are consistent with a warm, equable climate. Precipitation typically is highest in the summer (JJA) and lowest in the autumn (SON), and the seasonality of rainfall is influenced both by El Niño/Southern Oscillation (ENSO) cycles (Boyles et al., 2004) and the Bermuda High Index (BHI) and changes in strength of subtropical atmospheric circulation (Diem, 2006; Henderson and Vega, 1996).

Methods

Study design and site characterization

Thirty-eight transects were established from the levee into the backswamp along the length of the LRR (Figure 1). Transects were referenced by placing metal spikes into a mature tree, serving as monuments for present and future studies. Locations were recorded on maps and documented using a Global Positioning System (GPS) with horizontal accuracy of ~3.5 m. Elevations were recorded and corrected to NGVD 1929 datum (Hupp et al., 2009a). Transect lengths ranged from 100 m to 2 km with stops every 50–100 m. Tree tags were affixed to witness trees at each stop, and the locations were noted using GPS. Each stop was assigned to a particular landform (levee, flat, backswamp, ridge, etc.), and precise locations and elevations were determined. Percent cover of canopy, subcanopy, shrub, and herbaceous layers were quantified at most stops on each transect using the North Carolina Vegetation Survey (NCVS) methodology described in Peet et al. (1998). This method locates standard 10 m × 10 m quadrats at each stop to minimize within-plot environmental heterogeneity. Percent cover, defined as the percentage of ground

Table 1. Vegetation classes represented in Lower Roanoke River floodplain study. Hydroperiod tolerances are provided for vegetation classes rather than individual species. Median annual hydroperiods indicate the median number of days of inundation, but hydroperiods during extremely wet years determine floodplain forest composition by eliminating species that cannot tolerate longer than average flood regimes (Townsend, 2001). Median annual hydroperiods for forest classes were compiled from Townsend (2001). Post-dam hydroperiods for wet years represent hydroperiod ranges for sites included in study. Percent cover values for species in LRR sites are derived from measurements made using the North Carolina Vegetation Survey (NCVS) methodology (Peet *et al.*, 1998). Elevations are corrected to NGVD 1929 datum

| Class name | Primary canopy species | Vegetation class median annual hydroperiod ^a | Hydroperiod, post-dam, wet years ^b | Percent cover | Elevation above Roanoke River surface (cm) |
|----------------------------------|--|---|---|---------------|--|
| <i>Swamp forests</i> | | | | | |
| Tupelo-Cypress backswamps | | 227–230 | 200–350 | | 0–50 |
| | <i>Nyssa aquatica</i> | | | 63–85 | |
| | <i>Taxodium distichum</i> | | | 4–18 | |
| | <i>Populus heterophylla</i> | | | 0.5–38 | |
| Low ridges and flats | | 96–213 | 130–300 | | 30–100 |
| | <i>Nyssa aquatica</i> | | | ≤38 | |
| | <i>Taxodium distichum</i> | | | ≤38 | |
| | <i>Populus heterophylla</i> | | | ≤63 | |
| | <i>Acer</i> spp., <i>Carya aquatica</i> , <i>Fraxinus pennsylvanica</i> , <i>Platanus occidentalis</i> , <i>Liquidambar styraciflua</i> , <i>Quercus</i> spp. | | | ≤18 each | |
| <i>Wet bottomland forests</i> | | | | | |
| Maple-Oak-Tupelo | | 77 | 10–180 | | 33–190 |
| | <i>Acer rubrum</i> | | | ≤38 | |
| | <i>Fraxinus pennsylvanica</i> | | | ≤63 | |
| | <i>Nyssa aquatica</i> | | | ≤38 | |
| | <i>Ulmus americana</i> | | | ≤38 | |
| | <i>Populus heterophylla</i> | | | ≤18 | |
| Ash-Maple-Boxelder | | 46 | 40–120 | | 100–190 |
| | <i>Fraxinus pennsylvanica</i> | | | 18–85 | |
| | <i>Acer rubrum</i> , <i>Acer negundo</i> | | | ≤18 | |
| <i>Mixed mesic hardwoods</i> | | | | | |
| High levee bottomlands | | <10 | <50 | | >200 |
| | <i>Acer</i> spp., <i>Celtis</i> , <i>Fraxinus</i> , <i>Platanus</i> , <i>Fagus</i> | | | 18–63 each | |
| Mixed mesic hardwoods | | <10 | <50 | | 133–397 |
| | Diverse assemblages including <i>Acer</i> , <i>Celtis</i> , <i>Carya</i> , <i>Fagus</i> , <i>Fraxinus</i> , <i>Liquidambar</i> , <i>Populus</i> , <i>Quercus</i> | | | 4–18 each | |

^aMedian annual hydroperiods for vegetation classes were compiled from Townsend (2001).

^bPost-dam, wet-year hydroperiods for sites in this study were derived from a model of potential flood inundation for the lower Roanoke River floodplain as described in Townsend and Walsh (1998).

surface obscured by the vertical projection of all aboveground parts of a given species onto the ground, was noted for each quadrat. The NCVS system uses a ten-point scale in which successively higher increments indicate approximate doubling of cover (Peet *et al.*, 1998), and the sum of cover estimates across all species may exceed 100%. These data ultimately were used to assign specific vegetation classes to observed forests at each stop (Table 1). Hydroperiod for each site was derived by integrating GIS coverages, Landsat Thematic Mapper time series, and synthetic aperture radar images into a model of potential flood inundation for the lower Roanoke River floodplain (Townsend and Walsh, 1998). Because annual flooding during wet years is the strongest predictor of spatial distribution of floodplain vegetation in the LRR (Townsend, 2001), we used that value for each site to reconstruct hydroperiod from surface pollen assemblages.

Palynological sampling and analysis

The upper 1 cm of sediment was collected using mini-cores in 50 ml centrifuge tubes after removal of plant litter. Sediment texture and color were described for each sample. Pollen was isolated from 120 sediment samples representing distinct vegetation types from 38 transects using standard palynological techniques

outlined in Willard *et al.* (2003, 2005). Approximately 3–10 g of dry sediment was used for palynological analysis, depending on lithology. After drying and weighing samples, one *Lycopodium* marker tablet was added to each dried sample for eventual calculation of absolute pollen concentrations (Stockmarr, 1971). Samples were demineralized using HCl and HF before being acetolyzed (nine parts acetic anhydride:one part sulfuric acid) in a hot-water bath (100°C) for 10 min. After neutralization, they were treated with 10% KOH in a hot-water bath for 15 min. Neutralized samples were sieved with 10 µm and 200 µm sieves, and the 10–200 µm fraction was stained with Bismarck Brown, mixed with warm glycerin jelly, and mounted on microscope slides. Raw data and metadata for pollen samples are deposited in the North American Pollen Database (NAPD) at the World Data Center for Paleoclimatology in Boulder, Colorado, USA (<http://www.ncdc.noaa.gov/paleo/napd.html>) and in Supplementary Tables 1–5, available online). Pollen and spore identification (minimally 300 grains per sample) was based on reference collections of the US Geological Survey (Reston, Virginia).

Absolute pollen concentrations were calculated using the marker-grain method described by Benninghoff (1962). The number of *Lycopodium* spores in the marker tablets was determined by the manufacturer with a Coulter Counter following the

procedures of Stockmarr (1973) as $10\,679 \pm 191$: absolute pollen concentration was calculated using the formula (Maher, 1981):

$$\text{Pollen per gram dry sediment} = \frac{(\text{Pollen grains counted} / \text{markers counted}) * 10,679}{\text{Weight of the sediment}} \quad (1)$$

Roanoke sediment core

We collected a sediment core in a tupelo-cypress backswamp in the lower reach of the river (35.85°N, 76.90°W; Figure 1c) to evaluate past patterns of vegetation and hydrologic variability. Using a vibracorer with a 7.8 cm diameter aluminum core barrel, we penetrated 267 cm of sediment; the resulting core was 170 cm long after compaction. After describing the core lithology, we removed 1–2 cm increments of sediment for pollen analysis and processed them as outlined above. The modern hydroperiod at the site is 218 days, and elevation is 0 cm above the mean river level. The pre-dam (pre-AD 1950) hydroperiod for the site is estimated at 167 days, which would support bottomland hardwood forests characteristically found on low ridges and flats in the current system.

Chronology for the core was based on 14 radiocarbon dates obtained on plant macrofossils, pollen biostratigraphy, and lithostratigraphy. Conventional radiocarbon dates were converted to calibrated years before present (cal. yr BP, where present is defined as AD 1950) using the Pretoria Calibration Procedure (Stuiver *et al.*, 1998; Talma and Vogel, 1993). Increased abundance of *Ambrosia* pollen to >2% at 48 cm and a change from dark brown, highly organic muds of unit C to gray-brown to olive-greenish-gray muds of unit B (Figure 2) mark the initiation of Colonial land clearance in the Piedmont early in the eighteenth century. The change to oxidized organic-rich muds/clays of unit A at 16 cm is correlated with completion of the John H. Kerr dam in AD 1953 (Manooch and Rulifson, 1989); a radiocarbon date of 120.7 ± 0.4 pMC (percent modern carbon) at 10.5 cm is consistent with this assignment. We used Bchron (Haslett and Parnell, 2008; Parnell *et al.*, 2008) to generate age models for the sediment core (Figure 2); this program combines stochastic linear interpolation between points with uncertainty associated with age assignments to generate a series of chronologies.

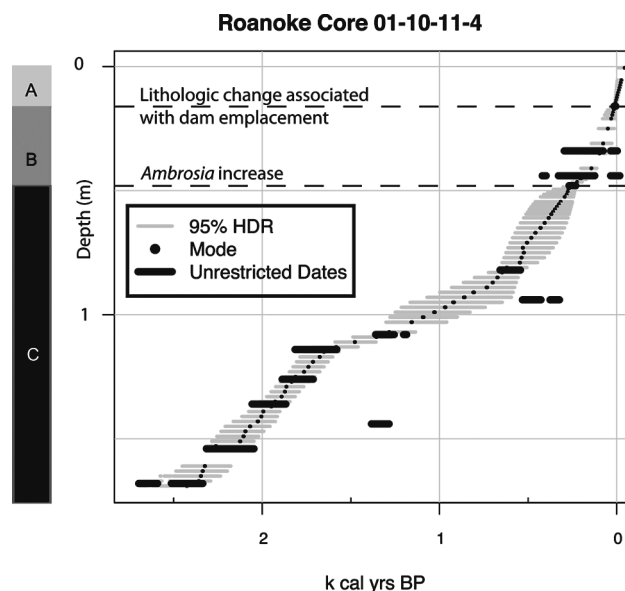


Figure 2. Lithologic zones and calendar year chronologies and for Core 01-10-11-4. Lithologic zone A is an oxidized organic-rich mud/clay (Munsell 10YR 5/6); zone B includes basal gray-brown mud (5Y 5/1) grading into olive greenish-gray organic-rich mud/clay (5Y 5/2); zone C is a dark brown, organic-rich mud (10YR 2/1) with interspersed wood fragments. The calendar year chronology was constructed with Bchron v 2.1 (Haslett and Parnell, 2008). The 95% highest posterior density regions (HDR) indicate the uncertainty of the ages assigned to the samples between the dated depths. Thick black lines represent the calibrated radiocarbon ages. Horizontal dashed lines indicate events discussed in the text.

Statistical analysis of palynological data

Statistical analysis of pollen assemblages included all arboreal taxa that comprise >1% of pollen assemblages in at least four surface samples. *Ambrosia* (ragweed) pollen was excluded from percentage calculations for statistical analyses of surface samples because it responds primarily to land use rather than climate variability. Its removal from percentage calculations facilitates comparison of modern and fossil assemblages to infer past hydroperiods. *Ambrosia* is an early successional plant that occupies cleared sites.

Table 2. Radiocarbon dates from Core 01-10-11-4, collected in backswamp forest of lower Roanoke River floodplain, located on transect 38 near tree tag 35 (35.85°N, 76.90°W, indicated by red star in Figure 1)

| Lab no. | Depth (cm) | Material dated | Method | Conventional age (yr BP) | $\delta^{13}\text{C}$ | Cal age 2σ plus ^a | Cal 2σ minus ^a |
|------------------------|------------|----------------|----------|----------------------------------|-----------------------|-------------------------------------|----------------------------------|
| <i>Core 01-10-11-4</i> | | | | | | | |
| Beta 202684 | 10-11 | wood | AMS | 120.7 ± 0.4 pMC ^b | -26.6 | | |
| Beta 202685 | 34-36 | twig | AMS | 170 ± 40 | -27.9 | 300 | 0 |
| Beta 202686 | 44-45 | wood | AMS | 220 ± 40 | -28.0 | 310 | 0 |
| Beta 202687 | 72-74 | wood | AMS | 210 ± 40 | -26.7 | 310 | 0 |
| Beta 202688 | 82-84 | wood | AMS | 610 ± 40 | -24.3 | 660 | 540 |
| Beta 202689 | 94-96 | wood | AMS | 420 ± 40 | -24.3 | 530 | 0 |
| Beta 202690 | 100-102 | twig | AMS | 240 ± 40 | -28.4 | 430 | 0 |
| Beta 202691 | 108-110 | wood | AMS | 1380 ± 40 | -25.6 | 1330 | 1260 |
| Beta 202692 | 114-116 | wood | AMS | 1770 ± 40 | -25.0 | 1810 | 1570 |
| Beta 202693 | 126-128 | wood | AMS | 1870 ± 40 | -26.2 | 1890 | 1710 |
| Beta 202694 | 136-138 | wood | AMS | 2000 ± 40 | -27.3 | 2030 | 1870 |
| Beta 202695 | 144-146 | wood | AMS | 1420 ± 40 | -23.1 | 1380 | 1280 |
| Beta 162199 | 154-160 | wood | Standard | 2160 ± 60 | -26.5 | 2330 | 1990 |
| Beta 202697 | 168 | wood | AMS | 2400 ± 40 | -24.7 | 2710 | 2340 |

^a Calibrations are based on Stuiver and van der Plicht (1998), Stuiver *et al.* (1998), and Talma and Vogel (1993).

^b pMC (percent modern carbon) indicates an age of post 0 BP and is reported as a percentage of the modern reference standard. Such values indicate that the material was living within the last 50 years.

within a year of land clearance (Bazzaz, 1974; Keever, 1983). The abundance of *Ambrosia* pollen in eastern US sediments increased sharply from $\leq 1\%$ before European colonization to much higher percentages after the onset of Colonial land clearance (Brush, 1984; Willard *et al.*, 2003). Using cluster analysis on the resulting data set, we examined relationships among different samples based on species abundance in those samples. We used average-linkage clustering (UPGMA) with the Pearson product moment correlation coefficient and the computer program MVSP 3.1 (Kovach, 1999).

The modern analog technique (MAT) is used commonly to derive quantitative estimates of past environments from paleontological proxies (Jackson and Williams, 2004; Overpeck *et al.*, 1985). Typically, dissimilarity coefficients are calculated between modern and fossil assemblages, and samples with dissimilarity coefficients less than a specified critical value are identified as analogs. The analogous fossil and modern assemblages are assumed to represent similar vegetational composition and, by extension, similar environmental conditions, forming the basis for quantitative paleoenvironmental reconstructions. Although spatial autocorrelation of closely spaced samples may invalidate the statistical validity of transfer functions based on such data sets (Telford and Birks, 2005, 2009), our sample design minimizes its impacts. Adjacent samples on a transect were at least 50 m apart and collected in different forest classes with differing hydrology; although this spatial scale is very small compared with regional- and continental-scale studies, ecotones associated with hydrologic variability occur over short distances (meters) in floodplain habitats.

We calculated dissimilarity coefficients (squared chord distance, SCD) among all modern samples and used the leave-one-out cross validation technique (Malmgren and Nordlund, 1997; Williams and Shuman, 2008) to determine the critical SCD value for the wetland data set. When hydrologically transitional sites and those in disturbed sites (i.e. drained backswamps, forest regrowth) were excluded from consideration, modern samples fall into two clear groupings: tupelo-cypress backswamps (long hydroperiods with flooding persisting into the summer) and all other BHW forests (shorter, seasonal hydroperiods). Intragroup SCD values among backswamp samples average 0.13 (SD 0.06, range 0.03–0.35, $n=15$), whereas intergroup comparisons between backswamps and other BHW forests yield mean SCD values of 0.43 (SD 0.19, range 0.03–1.32, $n=74$). Bottomland hardwood forest classes span a hydrologic continuum from moderate hydroperiod forests on flats adjacent to backswamps to short-hydroperiod forests on high levees, and the resulting vegetational diversity makes it difficult to distinguish subtypes of BHW forests based solely on palynological evidence. Although the mean SCD value among all BHW forests is 0.28 (SD 0.15, range 0.02–1.25, $n=74$), nearly every sample has at least five analogs with $SCD \leq 0.15$. We developed and tested a method to estimate hydroperiod based on the MAT. We selected a subset of 79 modern samples, eliminating those in hydrologically transitional sites. For each modern sample, we identified all analogs ($SCD \leq 0.15$), eliminated samples with fewer than five analogs, and calculated the predicted hydroperiod as the average hydroperiod of all analogs. When actual and predicted hydroperiods were compared (Figure 3), most predictions were within 1 standard deviation of the actual hydroperiod. Estimated hydroperiods for tupelo-cypress assemblages differ strongly from all BHW assemblages, and we used this method to reconstruct past hydroperiods from downcore samples.

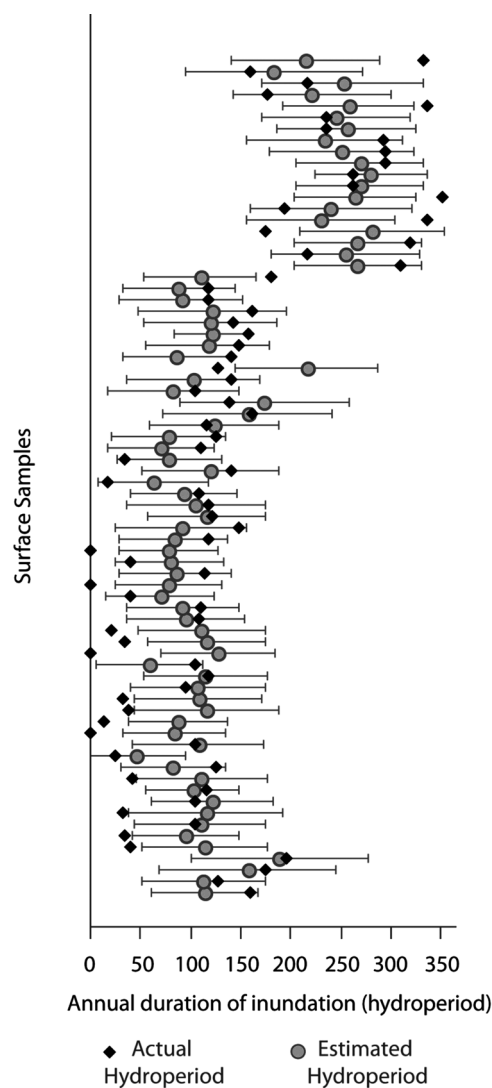


Figure 3. Comparison of predicted and actual hydroperiods in surface samples from lower Roanoke River basin, North Carolina. Circles indicate predicted hydroperiod from comparison with analogs ($SCD \leq 0.15$). Error bars represent one standard deviation from the mean. Diamonds indicate actual hydroperiod for each site

Results and discussion

Pollen assemblages from surface samples

Four pollen species groupings are indicated by R-mode cluster analysis (Figure 4). *Pinus* and *Juglans* cluster separately from the other taxa and represent the only genera that were not observed in the study area. Although they are native to the floodplain, they were not present on any transect. *Pinus*, *Juglans*, and *Carya* are grouped into cluster A, which represents taxa characteristic of short median annual hydroperiods (0–7 days: Townsend, 2001) most common in upland forests or mesic BHW forests. Cluster B consists of *Quercus*, *Fagus*, *Liquidambar*, and *Ulmus*, which tolerate slightly longer annual hydroperiods (< 50 days) and minimal spring flooding (< 12 days) (Townsend, 2001); these taxa are most common in mesic BHW forests. Cluster C includes *Fraxinus*, *Acer*, and *Celtis*, which tolerate longer median annual hydroperiods (34–80 days) and are most common in wet BHW forests. Cluster D consists of *Taxodium* and *Nyssa*, which have median annual hydroperiods > 200 days and are most common in tupelo-cypress swamp forests.

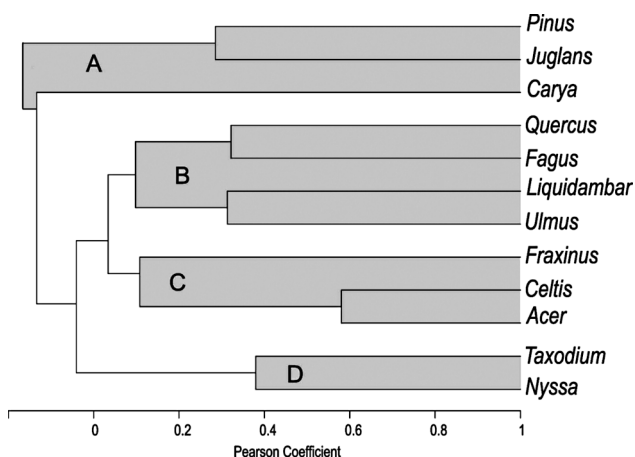


Figure 4. Dendrogram from R-mode cluster analysis (using UPGMA and Pearson correlation coefficient) of pollen assemblages from surface samples in the lower Roanoke River basin. Cluster A represents taxa characteristic of short annual hydroperiods, most commonly occurring in upland forests or mesic bottomland forests. Taxa in cluster B tolerate short annual hydroperiods and minimal spring flooding, most commonly growing in mesic bottomland forests. Taxa in cluster C tolerate longer annual hydroperiods and are most common in wet bottomland forests. Cluster D includes taxa characteristic of long hydroperiods that are abundant in tupelo-cypress swamps

Comparison of pollen assemblages on a site-by-site basis using Q-mode cluster analysis clearly separates tupelo-cypress swamps from bottomland hardwood forests present on levees, flats, and transitional areas (Figure 5). Tupelo-cypress swamps (cluster 1) are characterized by a combined average of 33% *Nyssa* and *Taxodium* pollen and the highest pollen concentrations of the floodplain deposits in this study (Figure 5). Backswamp sediments typically were brown organic clays, in contrast with gray-brown to dark brown silty clays, sandy clays, and sands of other landforms. Their median annual hydroperiod ranges from 150 to 300 days. Cluster 2 consists primarily of wet and mesic BHW forests that are characterized by >20% *Pinus* pollen. Samples in cluster 2a include a range of landforms and forest types. Some of these sites are located in mixed swamp forests (flats) and ash-maple-boxelder bottomlands in the lower half of the river (40–90 km upstream of the river mouth), which have a median annual hydroperiod of 40–70 days. Also included in cluster 2a are sites from the middle reaches of the river that include transitions from flats to backswamps or backswamp sites near the transition with median annual hydroperiods of 60–175 days; in these, *Nyssa* and *Taxodium* each may comprise 7–12% of assemblages. Samples included in cluster 2b contain >40% *Pinus* pollen, typically are located >90 km from the river mouth in the middle and upper reaches of the LRR floodplain, and have median annual hydroperiods of <50 days. Dominant forest types in cluster 2b include ash-maple-boxelder bottomlands and high-levee bottomlands. Assemblages dominated by *Quercus* occur in cluster 3 and were produced by mesic BHW forests on levees and upland terraces with median annual hydroperiods of <50 days per year. *Carya* is abundant (>24%) in cluster 4, which consists of wet BHW forests in transitional areas near backswamps; hydroperiods for cluster 4 range from 90 to 180 days per year.

Percent abundance of *Nyssa*, *Taxodium*, and *Pinus* pollen and total pollen concentration provide the primary means to discriminate

between long-hydroperiod backswamps and bottomland hardwood forests (Figure 6). The highest abundance of *Nyssa* pollen occurs in backswamp sediments (average 19% (14–44%) and 87345 grains/g), followed by low levees (8%). *Nyssa* pollen averages less than 5% (and < 7343 grains/g) of assemblages in medium and high levees, flats, and intermediate sites with elevations >1 m above river level. *Taxodium* pollen is most abundant in backswamps (averaging 7% (1–20%) and 19889 grains/g); when reported as percent abundance, it also is common in low and medium levee deposits (4.7–5%), but its pollen concentration is significantly lower in transitional and levee surfaces (averaging <5500 grains/g). *Pinus* pollen percent abundance is greatest in sediments from high levees, flats, and intermediate sites, in which it averages >40% of assemblages. Lowest percentages of *Pinus* pollen occur in backswamps, where it averages 26%. However, *Pinus* pollen concentrations are greatest in backswamps (81762 grains/g), compared with 28441 grains/g in intermediate sites and 19788 grains/g on levees. The greater concentration of these taxa in backswamps is mirrored by total pollen concentration, which is at least three times greater in backswamps than in other landforms. This pattern may reflect some combination of lower sedimentation rates in backswamps (effectively concentrating pollen), greater connectivity of backswamps with the river and fluvial transport of pollen to the site, and poorer palynomorph preservation in levees and other exposed/oxidized sediments. The uniformly high concentration of *Pinus* pollen across the landscape is due to its great abundance in southern mixed forests of the southeastern USA and the large quantities of wind-dispersed pollen that it produces (Delcourt et al., 1984).

Paleohydrologic reconstruction from floodplain sediment core

Pinus pollen dominates assemblages in the organic-rich muds deposited before Colonial land clearance, oscillating between extremely high (60–80%) and lower (40–50%) abundances throughout the sequence (Figure 7). In post-Colonial sediments, *Nyssa* co-dominates with *Pinus*, and herbaceous, weedy taxa are more common than any time prior to land clearance. Constrained cluster analysis of assemblages (CONISS: Grimm, 1992) and visual inspection of data were used to assign four pollen zones.

Pollen zone 1 (170–152 cm; 2438–2196 cal. yr BP) is dominated strongly by *Pinus* (58–75%), with common fern spores and *Nyssa* pollen. Modern analogs for zone 1 consist almost exclusively of BHW forests (Figure 7). In pollen zone 2 (152–124 cm; 2159–1790 cal. yr BP), *Pinus* pollen is less abundant (typically 38–53%), and *Taxodium* pollen is subdominant (8–33%). *Nyssa* pollen typically comprises >10% of assemblages. Modern analogs consist primarily of backswamp sites, although analogs from wet BHW forests also were identified for the upper samples of zone 2. Although *Pinus* pollen dominates pollen zone 3 (124–40 cm; 1762–151 cal. yr BP), four subzones were identified (Figure 7). Basal subzone 3a (124–100 cm; 1762–1151 cal. yr BP) is dominated strongly by *Pinus* pollen (65–90%), and modern analogs consist entirely of BHW forests. In pollen subzone 3b (100–88 cm; 1093–754 cal. yr BP), fern spores are subdominant (16–27%), and *Nyssa* and *Taxodium* pollen collectively exceed 10% of assemblages. Modern analogs include a mix of BHW forests and backswamp sites. *Pinus* pollen is strongly dominant (61–80%) in subzone 3c (88–48 cm; 714–260 cal. yr BP), and modern analogs consist entirely of BHW sites. Pollen subzone 3d

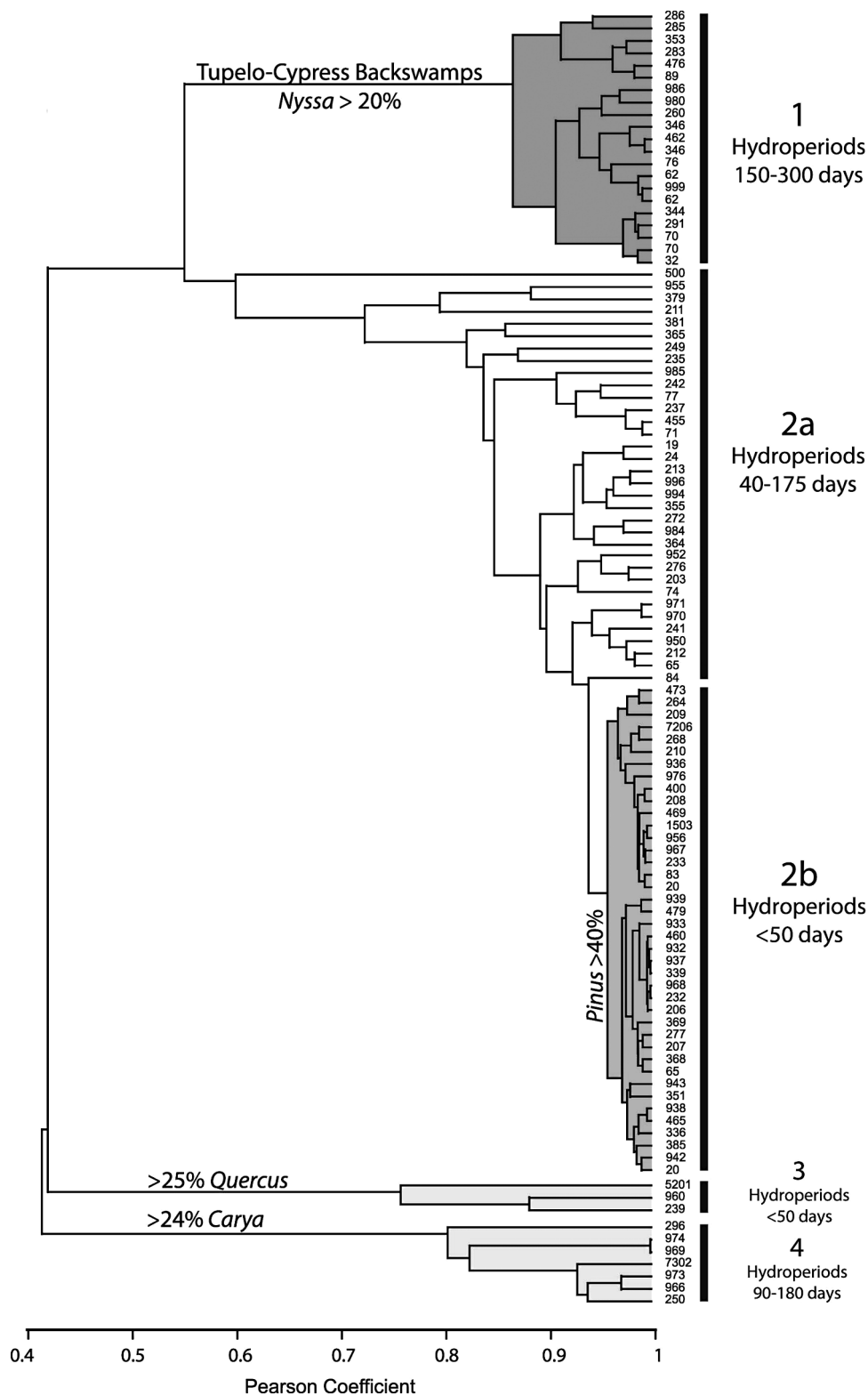


Figure 5. Dendrogram from Q-mode cluster analysis of pollen data from surface samples in the lower Roanoke River (LRR) basin. Numbers indicate the tree tag nearest each sample site. Cluster 1 includes samples from backswamp forests, characterized by $>20\%$ *Nyssa* pollen. Cluster 2 includes samples with $>25\%$ *Pinus* and $<20\%$ *Nyssa* pollen. Subcluster 2a includes samples located in transitional areas near backswamps or edges of backswamps, are characterized by 25–40% *Pinus* pollen and varying percentages of bottomland hardwood and backswamp taxa, depending on location within the floodplain. Subcluster 2b consists of levee and transitional sites located in the middle and upper reaches of the LRR; these assemblages have $>40\%$ *Pinus* pollen. Clusters 3 and 4 represent samples from mesic bottomland forests on levees, upland terraces, and transition zones adjacent to backswamps

(48–40 cm; 242–151 cal. yr BP) includes the first occurrence $>2\%$ *Ambrosia* and more *Nyssa* (10–19%). Modern analog sites include a mix of backswamp and BHW sites. Pollen zone 4 (35–0 cm; 108

cal. yr BP to present) is co-dominated by *Nyssa* and *Pinus* pollen, and *Ambrosia* is abundant; its modern analogs predominantly are backswamps.

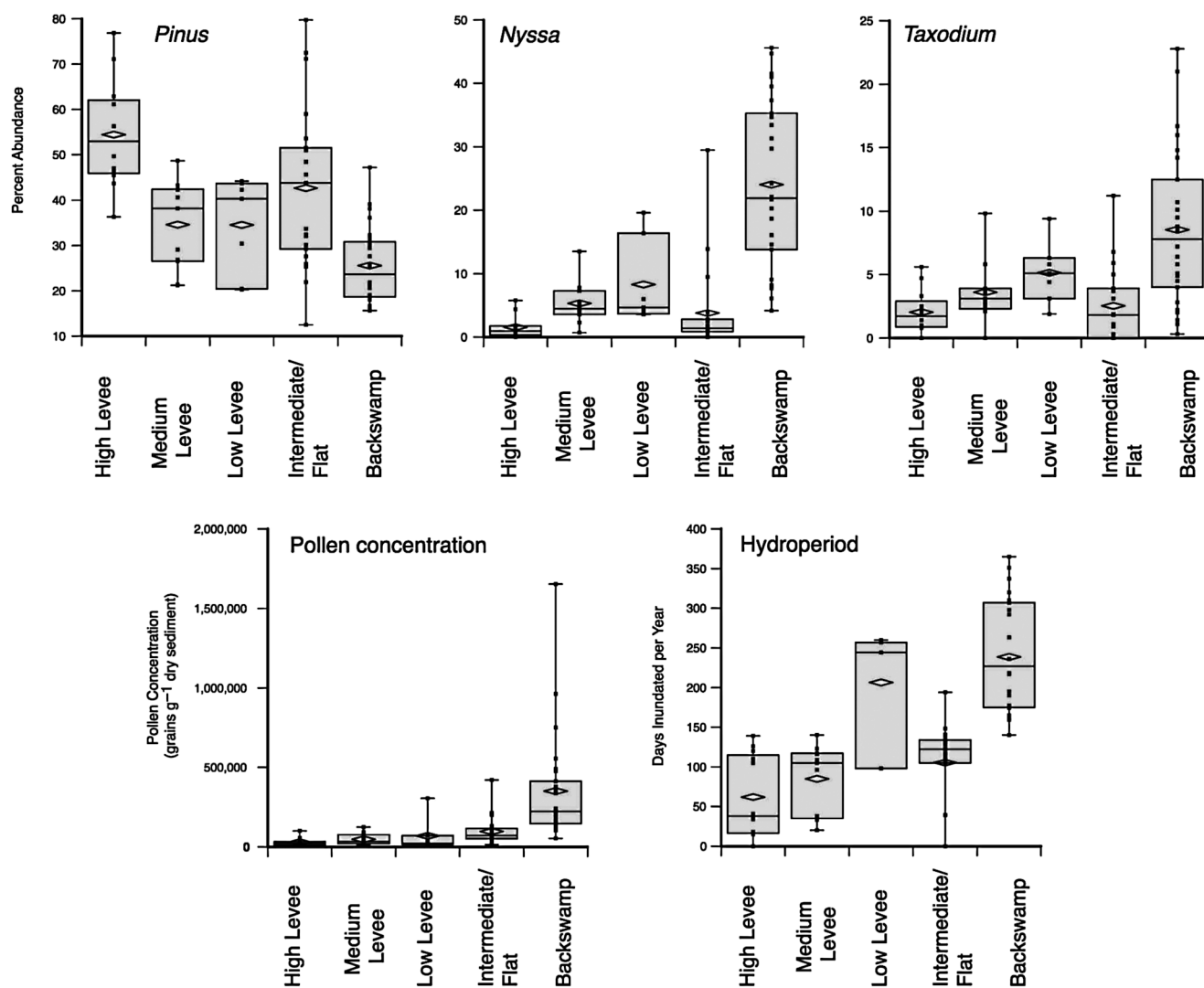


Figure 6. Tukey box and whisker plots of pollen percent abundance of diagnostic taxa, total pollen concentration, and hydroperiod in surface samples from five landforms in the lower Roanoke River basin. Points indicate individual sample abundance, and the diamond indicates the mean. The horizontal line within the box indicates median abundance for the vegetation type, and the box indicates values for the lower and upper quartile

Reconstructed hydroperiods at the site indicate centennial-scale variability between dry periods (inundation ~100 days per year) and wet periods (inundation >200 days per year) throughout the last ~2400 years (Figure 7). Between ~2400 years BP and the onset of Colonial land clearance in the early eighteenth century, dry intervals supporting short-hydroperiod bottomland hardwood forests alternated with wet intervals that supported long-hydroperiod cypress-tupelo swamps and transitional forests. Three wet intervals were identified: ~2200 to ~1800 cal. yr BP, ~1100 to ~750 cal. yr BP, and ~370 cal. yr BP until Colonial land clearance. Much longer hydroperiods occurred by ~AD 1850, followed by significant fluctuations throughout the last 150 years. The magnitude of observed late-Holocene fluctuations in *Nyssa* abundance (and by extension, hydroperiod) are comparable with the differences reported between early- and late-Holocene sediments from floodplains in Georgia and North Carolina (Goman and Leigh, 2004; LaMoreaux et al., 2009).

Paleoclimatic interpretations

Long hydroperiod, tupelo-cypress swamps of the Atlantic Coastal Plain require inundation extended past the period of maximum

river discharge (winter and spring) through the summer months. In the natural system, flooding throughout the summer is maintained by summer precipitation, including tropical storm systems (Gamble and Meentemeyer, 1997). Hydroperiods at the Roanoke floodplain core fluctuated by an order of magnitude during the last 2400 years. Because no lithologic changes indicative of altered floodplain morphology exist within the unit deposited before Colonial land clearance altered floodplain geomorphology, we suggest that the observed pre-Colonial hydroperiod fluctuations resulted from sustained changes in atmospheric circulation patterns. Summer storm frequency increases when anticyclonic atmospheric patterns off the coast draw moisture both from the Gulf of Mexico and Atlantic Ocean (Curtis, 2008; Gamble and Meentemeyer, 1997). Such changes in atmospheric flow are influenced by the configuration of the jet stream and position of the Bermuda high (Diem, 2006; Liu and Fearn, 2000).

The three wet intervals observed in the Roanoke floodplain record (~2200 and ~1800 cal. yr BP, ~1100 to ~750 cal. yr BP, and ~370 cal. yr BP) generally correspond to proxy records indicating periods of increased storminess in New York, Florida and Puerto Rico (Donnelly and Woodruff, 2007; Liu and Fearn, 2000; Scileppi and Donnelly, 2007) and reduced salinity in Chesapeake

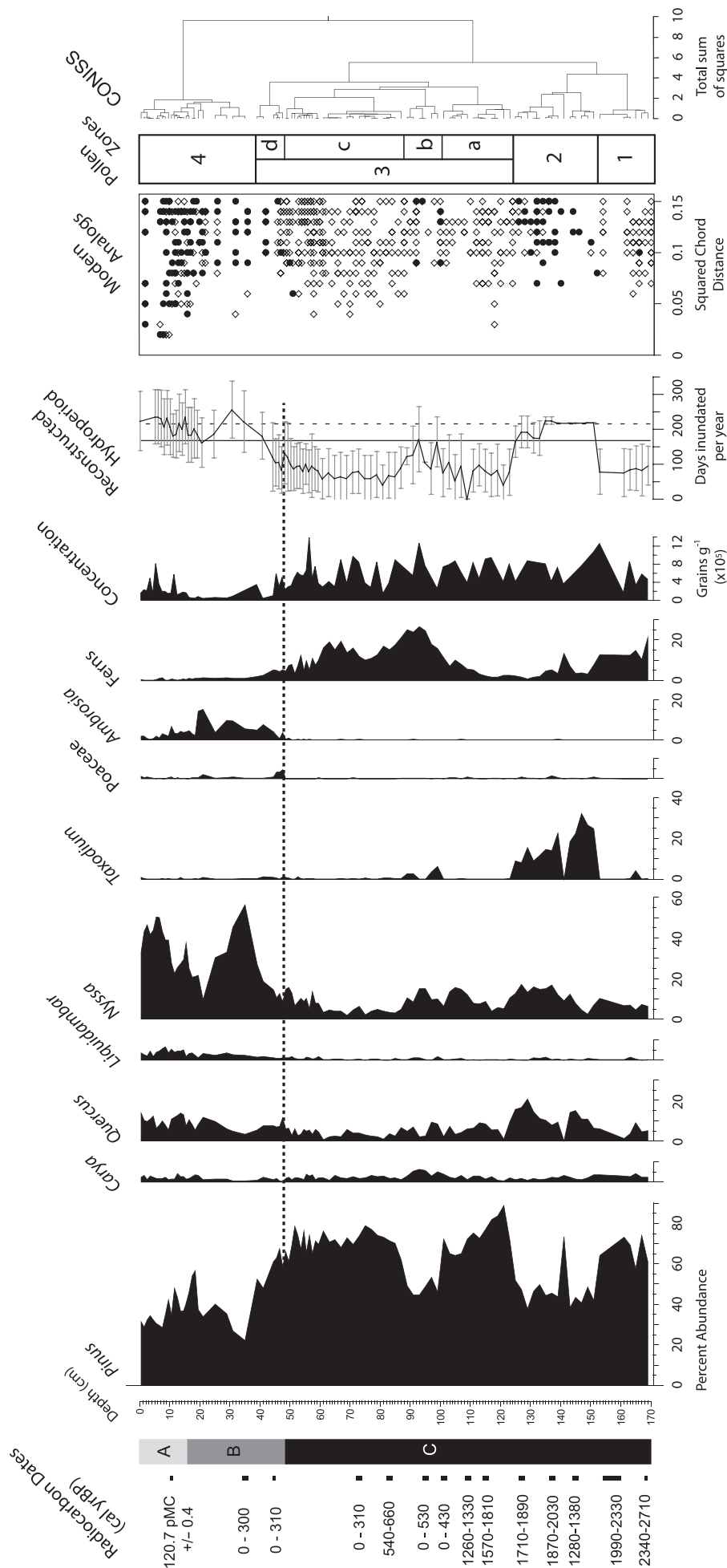


Figure 7. Percent abundance of pollen of major plant taxa and total pollen concentration, Core 01-10-11-4, collected on transect 38 near tree tag 35 in a backswamp forest, lower Roanoke River basin. Radiocarbon dates indicate 2 sigma ranges of calibrated dates. Bold horizontal dashed line at 49 cm indicates depth of initial Colonial land clearance at ~AD 1700, based on the increase in abundance of *Ambrosia* pollen and lithologic change. Hydroperiod reconstructions are averaged from hydroperiods of close modern analogs ($SCD \leq 0.15$). Error bars indicate 1 standard deviation from the mean. Vertical dashed line indicates modern hydroperiod at the site (218 days), and vertical solid line indicates estimated pre-dam hydroperiod (167 days). Modern analogs are based on SCD calculations of arboreal taxa > 1%. Filled circles indicate backswamp analogs, and open diamonds indicate bottomland hardwood forest analogs. Stratigraphically constrained cluster analysis (CONISS) is based on the total assemblage, including *Ambrosia*

Bay (Cronin *et al.*, 2005). A particularly robust record of increased storm frequency during the late sixteenth century is provided by archival reports from the American colonies of Spain between AD 1492 and 1825 (García-Herrera *et al.*, 2005). These patterns have been attributed to changing modes of climate variability, including El Niño/Southern Oscillation (ENSO) and the Atlantic Multi-decadal Oscillation (AMO) (Donnelly and Woodruff, 2007; Gray *et al.*, 2004). Although these modes clearly affect precipitation and hydrology of the southeastern USA (Henderson and Vega, 1996; Enfield *et al.*, 2001), they operate on much shorter time periods than the multicentury wet-dry trends observed in the Roanoke floodplain record, and its temporal resolution precludes further interpretation of their impacts on this site. Because such modes involve changes in atmospheric circulation patterns tied to position of the jet stream and subtropical high, the Roanoke River record supports the hypothesis that long-term fluctuations in their positions exert significant control on floodplain hydrology within the Atlantic Coastal Plain.

Human impacts on Lower Roanoke River floodplain

Two phases of anthropogenic alteration affected floodplain vegetation in the LRR basin. The first began very early in the eighteenth century, with initial European colonization of the Piedmont (http://www.usgennet.org/usa/topic/colonial/book/chap4_3.html; viewed 6 October 2009). The resulting land clearance for agriculture not only altered forest composition but greatly increased sediment load to Coastal Plain rivers, floodplains, and downstream estuaries. Increased sediment load from land clearance has deposited up to 5 m of post-Colonial sediment within the LRR floodplain (Hupp *et al.*, 2009b; Townsend *et al.*, 2004). This pattern is mirrored clearly in the Roanoke backswamp core by a three-fold decrease in pollen concentration from pre- to post-Colonial sediments. Hydroperiod at the downstream Roanoke core site also may have been influenced by post-Colonial changes in floodplain geomorphology throughout the length of the river. Increased levee height in upper reaches of the river can reduce overbank flood duration and increase channel flow velocities (Hupp, 2000), effectively increasing flow to downstream reaches of the river. The combined effects of such anthropogenic flow alterations and natural climate variability complicate attempts to determine their relative roles in forcing post-Colonial floodplain hydroperiods.

The second phase of human impacts on the LRR involved construction of a series of seven dams in the mid-twentieth century. These reduced sediment flux to the LRR, indicated by greater pollen concentrations in the Roanoke floodplain core, and altered the seasonal hydrology of the system through dam regulation schedules. The John H. Kerr dam, completed in AD 1953 has the greatest impact on the LRR because of the large storage capacity of its reservoir, Kerr Lake, and its influence on operation of the downstream dams (Manooch and Rulifson, 1989). Its operations reduced the amplitude of maximum flows by more than half, reduced the frequency of high and low flows, and increased the frequency of moderate flow (Hupp *et al.*, 2009b). Changes in the timing and magnitude of peak flows associated with dam operations have been thought to be greater than those associated with climate variability and change (Graf, 1999; Townsend and Foster, 2002). However, data from this core indicate that natural hydrologic variability of the last 2400 years greatly exceeded that related to dam management. Pollen evidence documents sustained occurrence of conditions 50% drier than any of the last century (hydroperiods

~100 days) periodically throughout the last 2400 years. Such results indicate the need for further long-term analysis of floodplain hydrology to better assess the relative impacts of dam operations and natural climate fluctuations on floodplain ecosystems.

Conclusions

Calibration of modern floodplain pollen assemblages with source vegetation indicates that:

- Long-hydroperiod tupelo-cypress backswamp pollen assemblages differ distinctly from short-hydroperiod bottomland hardwood assemblages.
- Hydrology, forest composition, and pollen signature are closely correlated, and floodplain pollen assemblages primarily record a local pollen signature.
- Cross-validation of hydroperiod estimates among modern samples indicates that they provide a robust estimate of modern hydroperiod and can be used to infer past hydroperiod from sediment core assemblages.
- Because floodplain forests of Atlantic Coastal Plain rivers share common forest composition and geomorphology, this dataset provides a means to estimate floodplain hydrology on a regional scale.

Pollen assemblages from the Roanoke River floodplain sediment core indicate:

- Sustained, multicentury periods of wet and dry conditions alternated throughout the last 2400 years. Floodplain hydroperiods varied by an order of magnitude.
- Long-hydroperiod intervals in the LRR appear to be correlated with times of increased storm frequency and reduced estuarine salinity documented in other western Atlantic Ocean records. These patterns suggest the occurrence of periodic, sustained shifts in atmospheric circulation patterns during the late Holocene.
- Although anthropogenic alteration of the landscape and river discharge have significantly affected forest composition throughout the watershed, the resulting hydrologic changes in the study site were minor compared with those resulting from natural climate variability. Study of cores from other landforms throughout the length of the river is necessary to assess the relative influences of human activity and climate on a larger scale.

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