Hydrologic Controls on Ecosystem Structure and Function in the Great Dismal Swamp

Morgan L. Schulte

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Daniel L. McLaughlin, Chair
Wallace M. Aust
J. Morgan Varner
Ryan D. Stewart

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ABSTRACT

Forested peatlands of the Great Dismal Swamp (GDS) have been greatly altered since colonial times, motivating recent restoration efforts. Community structure and function were hydrologically altered by 19th and 20th century ditches installed to lower water levels and enable early timber harvesting. Contemporary forest communities are comprised of maturing remnants from selective timber harvesting that ended in the early 1970's. Red maple (*Acer rubrum*) has become the dominant species across GDS, encroaching on or replacing the historical mosaic of cypress (*Taxodium* spp.)/tupelo (*Nyssa* spp.), Atlantic white-cedar (*Chamaecyparis thyoides*), and pocosin (*Pinus* spp.). Moreover, peat soil has been exposed to more unsaturated conditions resulting in carbon loss through decomposition and increased peat fire frequency and severity. Installation of ditch control structures aim to control drainage and re-establish historical hydrology, vegetation communities, peat accretion rates, and fire regime. To help inform restoration and management, we conducted two complimentary studies to test hypotheses regarding hydrologic influences on vegetation, peat depths, and peat fire vulnerability. First, we found thicker peat, lower maple importance, and higher species richness at wetter sites (e.g., higher mean water levels). In our second study, we evaluated the integrated effects of peat properties and water level dynamics on peat fire vulnerability. We found decreased burn vulnerability with increased wetness, suggesting that the driest sites were always at risk to burn, whereas the wettest sites never approached fire risk conditions. Together our findings demonstrate strong hydrologic controls on GDS ecosystem structure and function, thereby informing water level management for restoration goals.

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GENERAL AUDIENCE ABSTRACT

Forested wetlands, like the Great Dismal Swamp (GDS) in eastern Virginia, provide valuable ecosystem services, including wildlife habitat, biodiversity, water quality and storage, carbon storage, and many others. Many of these ecosystems have been lost to land conversion, or hydrologically altered. Ditches installed to lower water levels and enable timber harvesting altered GDS ecosystem services. Lowered water levels changed the forest from a historical mosaic of diverse tree species to a more homogeneous forest dominated by one tree species, red maple. Moreover, GDS's organic soil (peat) has been exposed to drier conditions resulting in carbon loss through decomposition and increased peat fire frequency and severity. To restore GDS ecosystem services, installation of water control structures in the ditches aim to control drainage and re-establish historical water levels (hydrology), forest cover, peat soil development rates, and fire regime. To help guide this hydrology management, we conducted two complimentary studies to test hypotheses regarding hydrology's influences on vegetation, peat soil, and peat fire vulnerability. First, we found thicker peat soil, lower red maple prevalence, and more vegetation species at wetter sites. In our second study, we evaluated the integrated effects of peat soil properties and water level dynamics on peat fire vulnerability. We found decreased fire vulnerability with increased wetness, suggesting that the driest site was always at risk to burn, whereas the wettest site never approached conditions for fire risk. Together our findings demonstrate hydrology's strong controls on GDS ecosystem services, thereby informing water level management for restoration goals.

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1.0 INTRODUCTION

1.1 Justification

Forested wetlands provide valuable ecosystem services, including wildlife habitat, biodiversity, water quality and storage, carbon sequestration, and many others (Millennium Ecosystem Assessment, 2005; Parish et al., 2008). Fifty-three percent, or 20.9 million hectares, of inland wetlands in the contiguous U.S. are forested (Dahl et al., 1991). However, 1.4 million hectares of forested wetlands were lost to urban and agricultural land conversion between the mid-1970s and mid-1980s alone (Dahl et al 1991), both small systems and large areas of extensive systems, including the Great Dismal Swamp (GDS) in southeastern Virginia and northeastern North Carolina, USA.

Once extending possibly over 500,000 hectares, GDS has been reduced to just 20 percent of its original extent. Even though 45,000 hectares of GDS were protected as a National Wildlife Refuge in the 1970s, preceding human actions, such as ditching and multiple timber harvests, have caused large-scale changes to the system (Whitehead, 1972). Hydrology, hydrophytic vegetation, and hydric soil are the key attributes of a wetland; a change in one can cause a response in the others (Carter, 1996; Mitsch and Gosselink, 2000). Through installation of 240 km of ditches to drain GDS and allow harvesting, hydrologic regimes at GDS have been substantially altered. Once an expansive mosaic of cypress (*Taxodium* spp.), Atlantic white-cedar (*Chamaecyparis thyoides*), and pocosin (*Pinus* spp.), drier soils have allowed facultative species to replace the previous obligate wetland stands (Reed, 1988; Legrand Jr, 2000). Red maple (*Acer rubrum*) has been documented as the dominant overstory species in contemporary GDS ecosystems (Whitehead, 1972; Dabel and Day Jr, 1977; Levy, 1991). Lower water levels have also exposed the peat soils to more frequent unsaturated conditions, enabling rapid peat decomposition and resulting soil elevation decreases and carbon losses (DeBerry and Atkinson, 2014). Lowered water levels have also affected peat soil characteristics and moisture regimes, both of which control peat fire vulnerability (Frandsen, 1997). In response, funds have become available to repair and install water control structures in the ditches to better manage the water levels in GDS. However, a better understanding of the hydrologic controls on community

composition, carbon storage, and fire vulnerability is critical to inform future management of GDS hydrologic regimes.

1.2 Background

1.2.1 Great Dismal Swamp Today

Great Dismal Swamp (GDS) is a temperate, forested palustrine wetland located on the border of southeastern Virginia and northeastern North Carolina, USA (Figure 1). GDS is one of the largest remaining forested wetlands in the eastern U.S. (DeBerry and Atkinson, 2014). The U.S. Fish and Wildlife Service manages the 45,000 ha GDS National Wildlife Refuge. The North Carolina State Park Service manages an additional 5,800 ha in the southern region of the swamp in North Carolina. GDS is well known for its natural history, deep peat soils, and diverse vegetative communities.

Peat Soils

Peatlands cover about 3% of the Earth's land surface (Turetsky et al., 2015). About 80% of the world's peatlands are in boreal regions, with 15 to 20% in tropical/subtropical regions and less than 5% in temperate regions (Rein et al., 2008). Peatlands are generally characterized by a minimum of 40 cm deep organic soil with greater than 50% organic matter content (Brady and Weil, 2008). Peat formation requires long durations of saturation to maintain anaerobic conditions, which reduce decomposition of organic matter inputs (Mitsch and Gosselink, 2000). As such, peatlands provide large global carbon storage (Page et al., 2002). Temperate peatlands occur in a diversity of landscapes and as mountain top bogs, fens, pocosins, and mixed-forested swamps.

GDS is a mosaic of forested wetlands characterized by peat soils, which formed due to GDS's hydrogeologic setting. Geologic studies show peat formation began around 9,000 years ago in topographic lows (Whitehead, 1972), accumulating at a rate of approximately 0.33 mm per year in pre-colonial times (Whitehead and Oaks, 1979). Requisite hydrologic conditions for peat formation (i.e., sustained saturation) are only partly supported by the region's climate, whereas geology determines lateral and/or vertical drainage. GDS is bounded on the western edge by the Suffolk Scarp, an ancient shoreline, and on the eastern edge by a subtle linear

topographic high composed of marine sediments (Oaks and Coch, 1963). This topographic setting provides water storage and limits lateral drainage. An underlying clay confining layer limits vertical drainage, providing the hydrologic conditions over time to enable peat accretion (Lichtler and Walker, 1974). Today, the majority of GDS soil is classified as Typic Haplosaprist; however, the northern edge is classified as a mineral soil, Typic Umbraquult (Web Soil Survey). Although sapric soil is classified as muck rather than peat soil, we considered the soils at GDS broadly as peat to correspond with previous literature. Peat thickness throughout GDS is variable, with peat depths ranging from 0.3 to 4 meters (Carter, 1990). Currently, the U.S. Geologic Survey is working on a large-scale project to quantify controls on such spatial variation in peat depths and thus carbon stores in GDS (Sleeter et al., 2017).

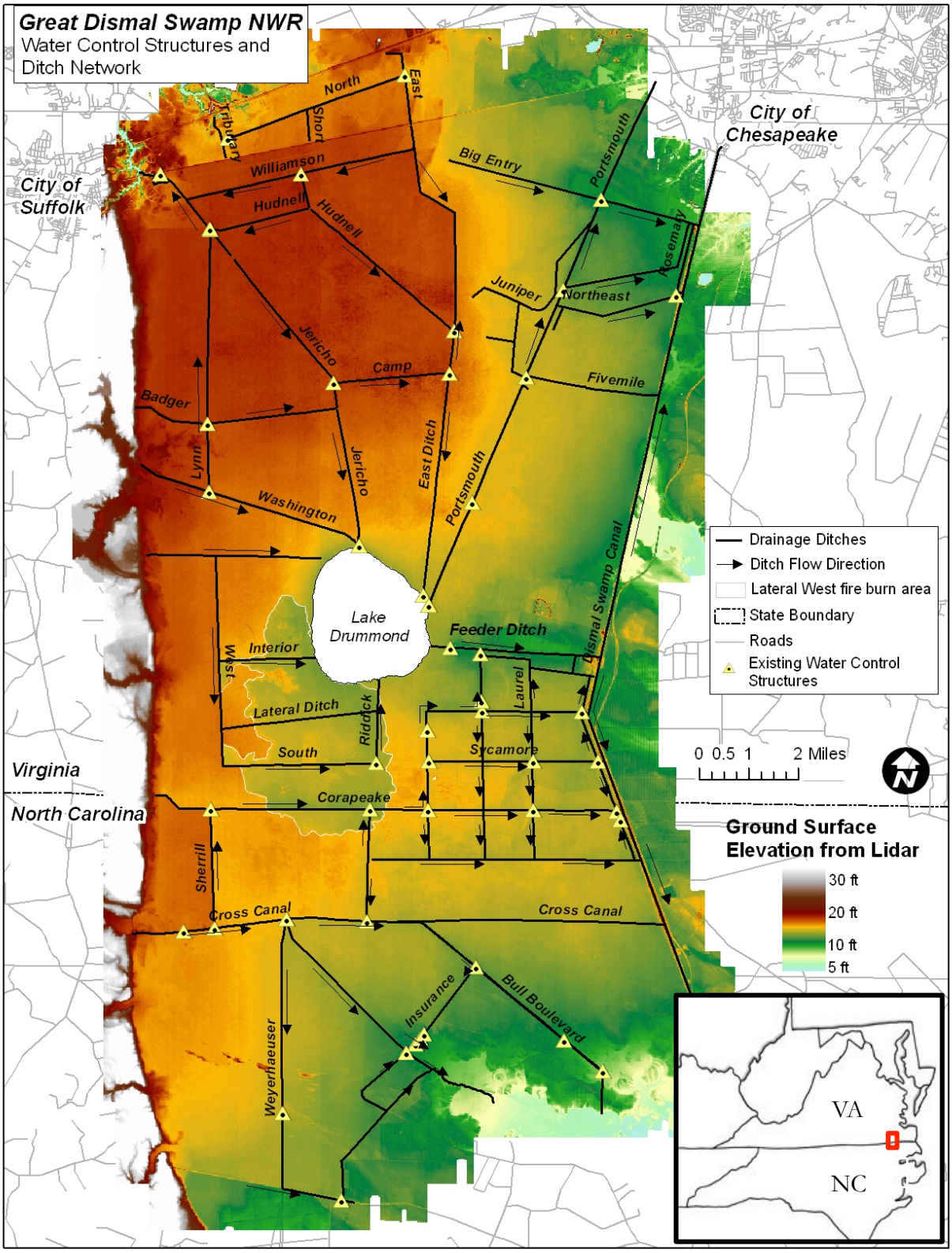


Figure 1. Great Dismal Swamp ditch network (black lines), direction of water flow in the ditches (black arrows), and land surface elevation (courtesy of the U.S. Fish and Wildlife Service).

Vegetation Composition

Forest communities in GDS include maple-gum, mixed hardwood, pocosin (e.g., pond pine), cypress-gum, and cedar stands (Dabel and Day Jr, 1977). The current dominant forest cover type is maple-gum, which dominated by red maple (*Acer rubrum*) and comprised of other species including swamp tupelo (*Nyssa biflora*), black gum (*Nyssa sylvatica*), sweetbay (*Magnolia virginiana*), sweetgum (*Liquidambar styraciflua*), and tuliptree (*Liriodendron tulipifera*) (Dabel and Day Jr, 1977; Levy, 1991; Legrand Jr, 2000). Common shrubs in the maple-gum cover type include red bay (*Persea borbonia*), sweet pepper bush (*Clethera alnifolia*), highbush blueberry (*Vacciunum corymbosum*), American holly (*Ilex opaca*), and pawpaw (*Asimina triloba*). Greenbriar (*Smilax* spp.) is an extremely common vine throughout GDS (Legrand Jr, 2000). Other vegetative communities make up less than half of GDS forest cover. Cypress-gum communities are comprised of cypress (*Taxodium distichum*), swamp tupelo, and red maple (Dabel and Day Jr, 1977). The GDS mixed hardwood community overstory is comprised of laurel oak (*Quercus laurifolia*), white oak (*Quercus alba*), sweetgum, and black gum, with a midstory of American holly and ironwood (*Carpinus caroliniana*), and a dense understory of giant cane (*Arundinaria 5igantean*; Dabel and Day Jr, 1977). Cedar stands are made up of a dense overstory of Atlantic white-cedar (*Chamaecyparis thyoides*; hereafter "cedar") with some co-dominant red maple (Dabel and Day Jr, 1977). These less extensive community types have reduced in spatial extent because of disturbances and increasing dominance of maple-gum communities (DeBerry and Atkinson, 2014).

1.2.2 A History of Disturbance

When European explorers surveyed GDS in the late 1700s, the deep peat soils were dominated by monotypic stands of cypress and cedar, and mixed stands of tupelo (*Nyssa* spp.) (Whitehead, 1972; Levy, 1991). GDS was reported to once have the single largest stand of cedar (ca. 26,000-45,000 ha; Frost, 1987). GDS formerly stretched approximately 500,000 ha; however, land conversion and ditching reduced its spatial extent by 80% and altered ecosystem structure and function, including shifts in community composition and peat characteristics (Legrand Jr, 2000).

Human disturbance has substantially altered hydrologic regimes and species composition in GDS. From the late 1700s to the early 1900s, 240 km of ditches were dug to drain the land for timber harvest (Whitehead 1972). Roads were installed parallel to these ditches for access. The

ditches lowered water levels, while roads had a damming effect, altering the overall hydrology. Lowered water levels dried the upper peat soil and selected for more facultative tree species (Whitehead and Oaks, 1979; Atkinson et al., 2003). Moreover, timber harvesting also affected the vegetation composition. Cedar was cut for shingles, and cypress was cut for ship building (Whitehead, 1972). The last primary forest was harvested in the 1950s; what trees remained matured into the overstory of GDS today. Stands of cypress and cedar, now rare at GDS, yielded to red maple. Red maple was historically present in most GDS forest community types but typically in the midstory species, whereas now it is the most abundant tree species in GDS (Whitehead, 1972; Dabel and Day Jr, 1977; Carter et al., 1994; Legrand Jr, 2000).

Disturbances to hydrology have also decreased carbon storage by increasing peat decomposition and fire vulnerability. The lowered water levels in GDS exposed peat soils more frequently to unsaturated (i.e., aerobic) conditions, causing increased decomposition rates and peat subsidence (Duttry et al., 2003). Peat subsidence has resulted in an estimated 1 m average elevation loss and associated loss of carbon storage (Whitehead and Oaks, 1979), and is visible to some extent from exposed tree roots throughout GDS (personal observation). Unsaturated peat also has a higher risk for smoldering fires (Wosten et al., 2008). Peat soils, unlike mineral soils, can be consumed in a fire because of its high organic matter content. Throughout GDS natural history, smoldering fire has consumed hectares of peat and changed surface topography (Legrand Jr, 2000). Such a peat-consuming fire is suggested as the process that formed Lake Drummond, a 1,250 ha lake in the center of GDS, about 4,000 years ago (Whitehead, 1972). However, current drier hydrologic conditions likely increase fire risk, intensity, and frequency. GDS has had two large catastrophic fires just in the past decade. In 2008 and 2011, catastrophic fires burned deep into the peat, consuming peat soil and emitting substantial carbon (DeBerry and Atkinson, 2014). By quantifying elevation loss and uncertainty using multi-temporal LiDAR, Reddy et al. (2015) estimated that the 2011 fire burned 2,500 ha, released 1.10 Tg of carbon and consumed an average of 46 cm of peat soil. Moreover, the fire killed the overstory trees, resulting in a complete conversion from closed-canopy forest to an open herbaceous marsh.

1.3 Research Objectives

The importance of hydrology to GDS structure and function has motivated recent restoration efforts. Starting in 2016, installation and repair of water control structures in drainage ditches commenced due to Hurricane Sandy relief funds. The functioning structures were installed to raise water levels in targeted areas to an optimal height with the goal of restoring GDS to more historical conditions. We developed a conceptual model (Figure 2) using three specific objectives:

1. Evaluate hydrologic controls on peat depth, microtopography, and vegetation composition.
2. Evaluate hydrologic controls on peat fire vulnerability and associated peat properties.
3. Inform hydrologic restoration of ecosystem structure and function in GDS.

1.3.1 Hydrologic Restoration

Our research aims to inform the water level management to increase carbon storage, adjust forest composition, and decrease peat fire vulnerability. Hydrology as the main driver motivated our conceptual model (Figure 2), which posits four testable hypotheses:

H1) Increased wetness (e.g., shallower water table) increases peat depth and microtopographic variation.

H2) Increased wetness decreases maple importance, increasing stand diversity.

H3) Long-term hydrologic regime influences peat properties (bulk density, organic matter content, and moisture holding capacity) that together create spatial variation in fire vulnerability.

H4) Increased wetness will decrease fire vulnerability through integrated effects of site-specific soil moisture burn thresholds, moisture holding capacity, and water level dynamics.

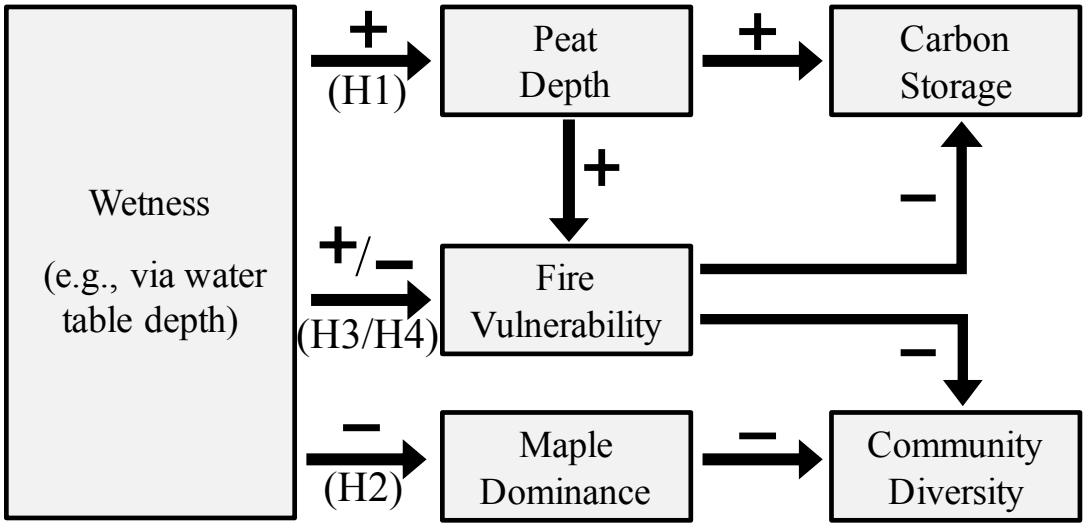


Figure 2. Conceptual model of hydrology as a major driver of ecosystem structure and function in the Great Dismal Swamp.

Literature Cited

Atkinson, R. B., J. W. DeBerry, D. T. Loomis, E. R. Crawford, R. T. Belcher, R. B. Atkinson, R. T. Belcher, D. A. Brown, and J. E. Perry. 2003. Water Tables in Atlantic White Cedar Swamps: Implications for Restoration. In *Atlantic White Cedar Restoration Ecology and Management, Proceedings of a Symposium. Christopher Newport University, Newport News*, 137–150.

Brady, N. C., and R. R. Weil. 2008. *The Nature and Properties of Soils*. 14th ed. Prentice-Hall Inc. Upper Saddle River, New Jersey.

Bruland, G. L., and C. J. Richardson. 2005. Hydrologic, Edaphic, and Vegetative Responses to Microtopographic Reestablishment in a Restored Wetland. *Restoration Ecology* 13, 3: 515–523.

Carter, V. 1990. The Great Dismal Swamp: An Illustrated Case Study. *Ecosystems of the World*.

Carter, V., P. T. Gammon, and M. K. Garrett. 1994. Ecotone Dynamics and Boundary Determination in the Great Dismal Swamp. *Ecological Applications*, 189–203.

Carter, V. 1996. Wetland Hydrology, Water Quality, and Associated Functions. *National Water Summary on Wetland Resources*, 35–48.

Dabel, C. V., and F. P. Day Jr. 1977. Structural Comparisons of Four Plant Communities in the Great Dismal Swamp, Virginia. *Bulletin of the Torrey Botanical Club*, 352–360.

Dahl, T. E., C. E. Johnson, and W. E. Frayer. 1991. Wetlands, Status and Trends in the Conterminous United States Mid-1970's to Mid-1980's. US Fish and Wildlife Service.

DeBerry, J. W., and R. B. Atkinson. 2014. Aboveground Forest Biomass and Litter Production Patterns in Atlantic White Cedar Swamps of Differing Hydroperiods. *Southeastern Naturalist* 13, 4: 673–690.

Duttry, P., R. Atkinson, G. Whiting, R. T. Belcher, M. G. Kalnins, and G. S. Thompson. 2003. Soil Respiration Response to Water Levels of Soils from Atlantic White Cedar Peatlands in Virginia and North Carolina. In *Proceedings Atlantic White Cedar Restoration Ecology and Management Symposium. Newport News: Christopher Newport University*, 165–74.

Frandsen, W. H. 1997. Ignition Probability of Organic Soils. 27, 1471–1477.

Frost, C. C. 1987. Historical Overview of Atlantic White Cedar in the Carolinas.

Legrand Jr, H. E. 2000. The Natural Features of Dismal Swamp State Natural Area, North Carolina. *The Natural History of the Great Dismal Swamp, Omni, Madison, Wisconsin*, 41–50.

Levy, G. F. 1991. The Vegetation of the Great Dismal Swamp: A Review and an Overview. *Virginia Journal of Science,* 42, 4: 411–418.

Lichtler, W., and P. Walker. 1974. Hydrology of the Dismal Swamp, Virginia-North Carolina. *Geological Survey – Water Resources Division*, 74–39.

Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-Being: Wetlands and Water. *World Resources Institute, Washington, DC*.

Mitsch, W. J., and J. G. Gosselink. 2000. Wetlands John Wiley & Sons. *Inc., New York, New York*.

Oaks, R. Q., and N. K. Coch. 1963. Pleistocene Sea Levels, Southeastern Virginia. *Science,* 140, 3570: 979–983.

Page, S. E., F. Siegert, J. O. Rieley, H. V. Boehm, A. Jaya, and S. Limin. 2002. The Amount of Carbon Released from Peat and Forest Fires in Indonesia during 1997. *Nature* 420, 6911: 61–65.

Reddy, A. D., T. J. Hawbaker, F. Wurster, Z. Zhu, S. Ward, D. Newcomb, and R. Murray. 2015. Quantifying Soil Carbon Loss and Uncertainty from a Peatland Wildfire Using Multi-Temporal LiDAR. *Remote Sensing of Environment,* 170: 306–316.

Reed, P. B. Jr. 1988. National List of Plant Species That Occur in Wetlands: National Summary. *U. S. Fish and Wildlife Service Biological Report*, 88.

Rein, G., N. Cleaver, C. Ashton, P. Pironi, and J. L. Torero. 2008. The Severity of Smouldering Peat Fires and Damage to the Forest Soil. *Catena* 74, 3: 304–309.

Sleeter, R., B. M. Sleeter, B. Williams, D. Hogan, T. Hawbaker, and Z. Zhu. 2017. A Carbon Balance Model for the Great Dismal Swamp Ecosystem. *Carbon Balance and Management* 12, 1: 2.

Turetsky, M. R., B. Benscoter, S. Page, G. Rein, G. R. van der Werf, and A. Watts. 2015. Global Vulnerability of Peatlands to Fire and Carbon Loss. *Nature Geoscience* 8, 1: 11–14.

Web Soil Survey. 2017. Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture.

Whitehead, D. R. 1972. Developmental and Environmental History of the Dismal Swamp. *Ecological Monographs*, 301–315.

Whitehead, D. R., and R. Q. Oaks. 1979. Developmental History of the Dismal Swamp. *The Great Dismal Swamp (PW Kirk, Jr., Ed.). University of Virginia Press, Charlottesville*, 25–43.

Wösten, J. H. M., E. Clymans, S. E. Page, J. O. Rieley, and S. H. Limin. 2008. Peat–water Interrelationships in a Tropical Peatland Ecosystem in Southeast Asia." *Catena* 73, 2: 212–224.

2.0 HYDROLOGIC CONTROLS ON PEAT DEPTH AND VEGETATION COMPOSITION IN THE GREAT DISMAL SWAMP

2.1 Abstract

Forested peatlands of the Great Dismal Swamp have been substantially altered since colonial times, motivating recent restoration efforts. Current forest communities are comprised largely of the maturing remnants from timber harvesting that ended in the early 1970's. Community structure and function have also been affected by hydrologic alteration resulting from 19th and 20th century ditches installed to lower water levels and enable timber harvesting. Due to these disturbances, peat decomposition rates have accelerated, resulting in peat soil elevation decreases and carbon loss. Moreover, red maple (*Acer rubrum*) has become a dominant species across the swamp, encroaching on or replacing the historical mosaic of cypress (*Taxodium* spp.), Atlantic white-cedar (*Chamaecyparis thyoides*), and pocosin (*Pinus* spp.). Recent installation and operation of ditch control structures aim to control drainage and re-establish historical hydrology, vegetation communities, and peat accretion rates. To help inform restoration and management, we established 5 transects of 15 plots (n=75) along a hydrologic gradient where we measured water levels and ecosystem attributes. Ecosystem attributes included peat depths, microtopography, vegetation composition (overstory, midstory, and understory), density and basal area, species diversity and richness. Data were analyzed at both the transect and plot level. By transect, we found significant differences among transects, with wetter sites having thicker peat, lower maple importance, and greater tree diversity and density. Similarly, at the plot-level, we found mean water level to have positive and significant correlations with peat depth, microtopography, tree density, and stand richness, and negatively and significantly correlated with maple importance. Nonmetric multidimensional scaling analysis of the suite of vegetation parameters highlighted similarities within transects and differences across transects, and comports with plot-level analysis of hydrologic controls on vegetation. Our findings underscore the degree to which hydrology affects peat carbon storage, vegetation structure, and maple importance, ultimately guiding large-scale hydrologic restoration for improved peatland community composition and ecosystem function.

2.2 Introduction

Great Dismal Swamp, Then and Now

The Great Dismal Swamp (GDS) is a forested palustrine wetland that has been substantially altered since colonial times. The GDS once extended approximately 500,000 ha with up to 5 m of peat soil (Osborn, 1919). The landscape was characterized by a mosaic of cypress (*Taxodium* spp.)/tupelo (*Nyssa* spp.), Atlantic White-cedar (*Chamaecyparis thyoides,* hereafter "cedar"), and pond pine (*Pinus serotina*) dominated stands (Legrand Jr, 2000). From the late 1700s to the early 1900s, the GDS landscape was ditched and drained to make it accessible for timber harvesting (Levy, 1991; Legrand Jr, 2000). In the 1970s, GDS became a 45,000 ha National Wildlife Refuge, preserved and managed for habitat function. However, previous disturbances resulted in an overstory now dominated by red maple (*Acer rubrum,* hereafter "maple"), which has encroached on the shrinking range of cedar (DeBerry and Atkinson, 2014) and homogenized the mosaic of other historical vegetation communities (Phipps et al., 1979). The lowered water levels left the peat soils exposed to aerobic conditions, which rapidly increased decomposition leading to reduced peat accretion and in some places peat subsidence (Whitehead and Oaks, 1979). With the installation of ditch control structures designed to restore the hydrology, a better understanding of hydrologic controls is needed to utilize hydrology as a management tool for restoring peat soil depths and historical communities in GDS.

Hydrologic Effects on Peat Soils

Hydrologic regime (mean and variation in water level) exerts strong controls on peat forming mechanisms. Peat formation occurs under constant anaerobic conditions when organic matter inputs exceed organic matter decomposition. Inundation or saturated conditions reduce oxygen diffusion, creating anaerobic conditions that greatly reduce microbial decomposition (Reddy and Patrick, 1975). If soil saturation (or flooding) is constant, peat can continue to accumulate, storing large amounts of carbon and further increasing soil water-holding capacities, providing a positive feedback on peat formation (Atkinson et al., 2003). Conversely, lowered water levels and aerobic conditions amplify decomposition rates, resulting in loss of previously accumulated peat deposits and carbon stores (Reddy and Patrick, 1975).

Peatlands occur globally in boreal, tropical/subtropical, and temperate regions, covering 3% of the Earth's land surface, but storing 30% of global land carbon (Parish et al., 2008). Peatlands cover up to 50% of boreal Canada (Kuhry et al., 1993), where peat depths can be 1.5 m to 2.3 m (Hugron et al., 2013). Indonesia contains the largest tropical peatland areas, where peat soil thickness is on average 0.5 m to 10 m (Anderson, 1983; Page et al., 1999). Tropical peat deposits of 20 m or more have also been recorded (Bruenig, 1990). Temperate peatlands occur throughout the northern and eastern U.S., including New Jersey Pinelands (Yu and Ehrenfeld, 2010), Great Lakes regional cedar swamps (Ott and Chimner, 2016), Croatan National Forest pocosins (Reardon et al., 2007), GDS (Legrand Jr, 2000), and many more. Temperate peat soil can reach several meters in thickness (Poulter et al., 2006; Ott and Chimner, 2016). However, peatlands across regions and their vast global carbon stores are at risk due to hydrologic disturbance and resulting peat subsidence via drainage for land uses and conversion (Usup et al., 2004; Watts and Kobziar, 2013).

In addition to controls on peat depths, hydrologic regimes influence spatial structure in local peat elevations, with associated effects on vegetation composition. High water levels in forested peatlands tend to favor formation of variable microtopography (Ehrenfeld, 1995a). Hummocks (local highs) and hollows (local lows) are natural microtopographic features in many peatlands, including in GDS (Day Jr, 1985). Hummocks and hollows can be formed by differential peat or litter accumulation, erosion, root growth, and often tree blow down or windthrow due to shallow rooting depths (Golet et al., 1993; Bruland and Richardson, 2005). This microtopography creates spatial variation in hydrologic regimes, where the spatial suite of resulting hydroperiods increases habitat complexity and stand-level diversity in vegetation (Vivian-Smith, 1997). In locations with high microtopographic variability, hollows are flooded more frequently and may support only obligate wetland plant species, while hummocks support a suite of facultative trees, shrubs, and vines (Reed, 1988; Bruland and Richardson, 2005).

At GDS, peat soils began forming about 9,000 years ago due to geologic confining layers and extremely flat topography promoting constant saturation and flooding (Whitehead, 1972). Based on peat core studies, rates of pre-colonial peat accretion in GDS were approximately 0.33 mm per year (Whitehead and Oaks, 1979). The peat historically ranged from approximately 1 m to 5 m in thickness, with a maximum of 5.5 m (Osborn, 1919; Lewis and Cocke, 1929). However, ditching has lowered contemporary water levels, dried surface peat, and increased peat

oxidation. Currently peat thickness ranges from only 0.3 m to 4 m throughout GDS (Reddy et al., 2015), with an observed local microtopographic variation of 0.21 to 0.36 m (Levy and Walker, 1979). Peat accumulation at GDS provides multiple functions, from carbon storage to microtopographic-induced complexity in hydrologic regime and associated vegetation composition (Vivian-Smith, 1997). Maintaining (and increasing) peat accumulation rates is thus a primary management goal at GDS.

Hydrologic Effects on Vegetation Composition

Wetland vegetation composition is largely driven by spatial and temporal dynamics of water level variation. Specific ranges of duration and depths of flooding or soil saturation select for specific vegetation communities (Casanova and Brock, 2000). Obligate wetland species are physiologically and morphologically adapted to prolonged anaerobic conditions, making them less stressed by consistently saturated or inundated environments (Reed, 1988). Cedar and cypress are obligate wetland species, whereas red maple is a facultative species (Reed, 1988). Concordantly, water levels in cedar swamps are typically higher than red maple swamps (Lilly, 1981; Parrott et al., 1981). In peatlands like GDS where hydrology has been altered by ditching, the resulting lowered water table favors aggressive facultative species over obligate species, especially during regeneration (Legrand Jr, 2000; Atkinson et al., 2003).

A gradient of hydrologic conditions exists both across and locally within GDS wetlands (Carter et al., 1994). Across GDS, most wetlands are forested palustrine (i.e., non-riverine swamp), made up of primarily maple-dominated systems with a midstory composition (i.e., maple/pocosin, maple/cane, maple/tupelo) that varies based on local hydrology (Legrand Jr, 2000). Cedar forests occurs on only 6% of GDS area, in locations with saturated (but not flooded) conditions during the growing season (Legrand Jr, 2000). Most of the area with cedar forest was planted during restoration efforts but later burned in 2008 and 2011 fires (DeBerry and Atkinson, 2014). Tupelo-gum is found in conditions of seasonal flooding, cypress can be found in conditions of near permanent flooding (Dabel and Day Jr, 1977), and pocosins occur in upland to seasonally saturated conditions (Levy, 1991). Together these three community types make up less than half of GDS forest cover (Levy, 1991). At local scales, microtopography causes spatial differences in hydroperiod, encouraging the coexistence of obligate hydrophytes growing in local lows and facultative species on local highs (Levy, 1991; Carter et al., 1994).

Although many studies of GDS vegetation types have been conducted over the past four decades (e.g., Dabel and Day Jr, 1977; Levy, 1991; Carter et al., 1994; Legrand Jr, 2000), linkages between hydrologic regime and species composition at both local and broad scales are implied but not well understood.

Purpose of the Study

To better understand the hydrologic controls on ecosystem structure and function in GDS, this research sought to empirically test relationships between hydrologic regime and peat depths, microtopography, and vegetation composition. From our conceptual model (Figure 2), we expected (H1) peat to be deeper and microtopography to be more variable at sites with higher mean water levels. We also expected (H2) that maple would be less competitive at higher mean water levels, thus increasing stand diversity and abundance of other tree species (e.g., cedar, cypress, tupelo). To test these hypotheses, we monitored peat depths, microtopography, vegetation composition and structure, and water levels across locations with varying hydrologic regime.

2.3 Materials and Methods

2.3.1 Site Description

We established sites in the northeastern corner of the Great Dismal Swamp National Wildlife Refuge (GDS), (36°42’28”N, 76°23’46”W), during summer 2015 (Figure 1). GDS is a forested palustrine wetland extending 45,000 ha in southeastern Virginia and northeastern North Carolina, USA. The climate is temperate with long, humid summers and mild winters (Lichtler and Walker, 1974). Average annual precipitation is 1090 mm at Norfolk, VA (Francis, 1959; Lichtler and Walker, 1974). The dominant forest cover type is maple-gum (Levy, 1991). Soils are predominantly hydric and organic soils. NRCS Web Soil Survey soil type classifications are provided in Table 1. Despite GDS largely considered as a peatland, Haplosaprists are not technically considered peat, but instead muck due to advanced decomposition. This suggests that GDS soils can deviate from their often considered peat soil characterization, or either potential inaccuracies in the Web Soil Survey classification. Also, SBE is classified as an ultisol, highlighting further variation across the swamp. However, going forward, we broadly refer to

GDS as a peatland following other peer-reviewed GDS studies (e.g., Osborn, 1919; Sleeter et al., 2017).

We selected five sites along an observed wetness gradient (F. Wurster, GDS Hydrologist, personal observation). Sites are referred to using site codes, which reflect locations relative to adjacent access ditches (Table 1). At each of the five sites, we established one 300 m transect perpendicular to the corresponding ditch/road (Figure 3). We established fifteen plots along each transect (Figure 4), spaced at 20 m intervals, to measure hydrologic regime, land surface elevation, peat depths, and vegetation attributes (n = 75). Plots captured a wetness gradient both within and across transects.

Table 1. List of site names and reference codes. Site soil classification from Web Soil Survey.

Site Name	Site Code	Soil Classification
West of Rosemary Ditch	WRM	Typic Haplosaprist
West of Portsmouth Ditch	WPM	Typic Haplosaprist
South of Big Entry Ditch	SBE	Typic Umbraquult
East of East Ditch	EED	Typic Haplosaprist
West of East Ditch	WED	Typic Haplosaprist

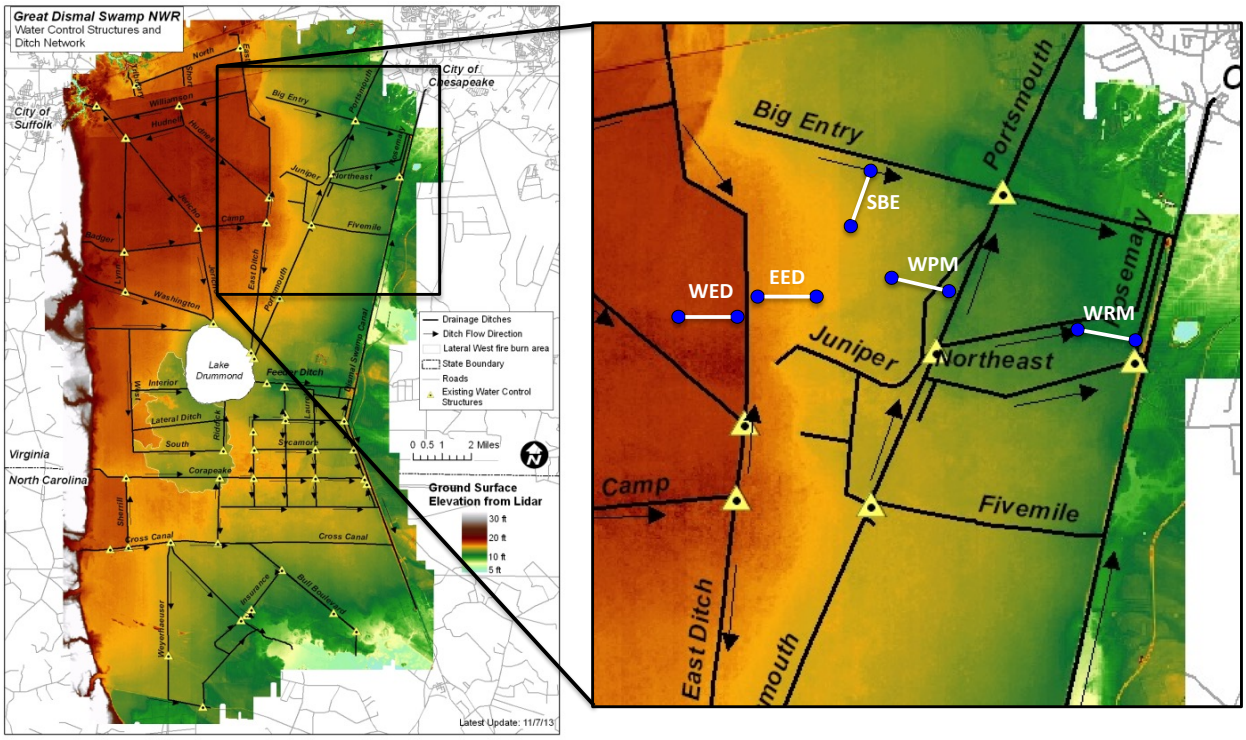
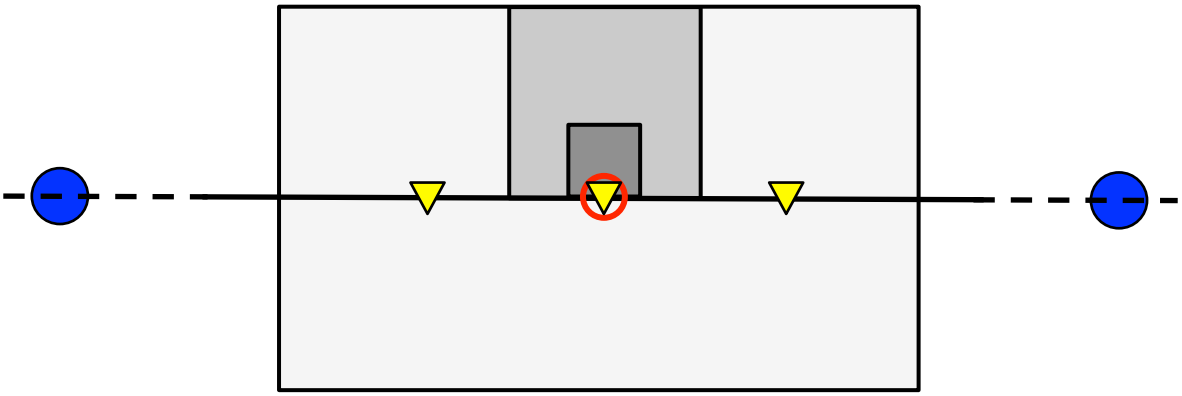


Figure 3. Transects (right pane, white lines) located in the northeastern corner of the Great Dismal Swamp with paired wells (blue circles) bookending each transect (courtesy of U.S. Fish and Wildlife Service).

2.3.2 Data Collection

Hydrologic Regime and Microtopography

To estimate hydrologic regime at each plot, we related continuous measures of water level elevation to plot land surface elevation across each transect. Monitoring wells were previously installed at each end of transects by GDS staff. Pressure transducers in each well provided continuous 15-minute water level data for 16 months. Using an optical level and leveling rod, we surveyed the relative elevation of plot center and plot center ± 3 meters to the first well at each transect (Figure 4). A microtopography index at each plot was calculated as the standard deviation of the three elevation points per plot. Using our surveyed elevations, we interpolated between wells to estimate 15-minute water level height at each of the three surveyed locations in each plot. This approach yielded spatial (3 locations per plot) and temporal water level variation at each plot to explore relationships among hydrology, peat depth, microtopography, and vegetation across all 75 plots.



	Subplot	Size	Vegetation Size Class	Measurements
	Overstory	10 m × 6 m	> 2.54 cm dbh	Dbh
	Midstory	3 m × 3 m	< 2.54 cm dbh and > 33 cm tall	Diameter at base
	Understory	1 m × 1 m	< 33 cm tall	Seedling count, % cover
	Plot Center	-	-	Peat Depth
	Survey Point	-	-	Elevation
	Well	-	-	15-min water level data

Figure 4. Diagram and description of a single plot along a transect of fifteen plots bookended by monitoring wells.

Peat Depth and Vegetation Composition

Peat depth was measured at plot center using a soil probe. The probe was hand-pushed down through the peat until stopped by resistance from the density of underlying mineral soil. To measure vegetation composition, each plot included three nested subplots established around the plot center to measure vegetation at different strata: overstory, midstory, and understory (Figure 4). In the overstory plot (10 × 6 m), diameter at breast height (dbh) and species were recorded for each tree. In the midstory plot (3 × 3 m), species and basal diameter were recorded for each stem (Dabel and Day Jr, 1977; DeBerry and Atkinson, 2014). In the understory plot (1× 1 m), percent cover was recorded by species using an ocular 0-5 (Daubenmire, 1959) ground cover scale. Seedlings were also tallied by species in the understory plots.

2.3.3 Data Analysis

We characterized hydrologic regime at both transect and plot level. Using three surveyed locations at each plot, we calculated plot water level mean (i.e., mean over time and space), 10th and 90th percentiles, and temporal standard deviation. Using plot-level water levels, we calculated transect-scale water level mean (over time and space), 10th and 90th percentiles, and temporal standard deviations. Microtopography at each plot was characterized by the index of standard deviation of the three surveyed elevation points in each plot.

To characterize vegetation attributes in each plot, we calculated several metrics separately for overstory, midstory, and seedling strata including species density, relative density (sum of species density/sum of total density), frequency, richness, and diversity (Shannon-Wiener Index). We also calculated overstory and midstory basal area for all species and relative basal area (sum of species basal area/sum of total basal area) for maple. To better understand the presence of maple, we calculated Importance Value (0-100%), which we calculated as the sum of overstory relative maple basal area and relative maple density. We also calculated overstory quadratic mean diameter (QMD) per transect, where *ba* is basal area (m^2/ha) and *tpha* is trees per hectare:

$$QMD = \sqrt{\frac{\frac{ba}{tpha}}{0.00007854}}$$

Understory cover scale numbers (0-5) by species were considered categorical variables. Mean values for all metrics across plots characterized vegetation within each transect. Presence/absence of understory obligate wetland species at each plot was also tallied by transect.

To evaluate relationships among hydrology, vegetation composition, and peat depth, we performed three different analyses. First, we performed a transect-level categorical analysis in JMP (SAS Institute Inc., 2012) using Analysis of Variance ($\alpha = 0.05$) to compare vegetation community attributes, peat depth, and microtopography across categorical wetness (via mean water level height). When a significant difference was detected, we used Tukey's honest significant difference (HSD) post-hoc test to evaluate pair-wise differences between transects. Second, we explored plot-level correlations (via Spearman's correlation analysis) among hydrologic regime metrics, vegetation attributes, microtopography, and peat depth across all 75 plots, with particular focus on correlations with maple importance. Lastly, we analyzed the suite

of vegetation and hydrologic parameters using nonmetric multidimensional scaling (NMDS) in R (R Core Team, 2016), using 'mds' function in the 'vegan' package (Oksanen et al., 2017). Vegetation parameters were input as processed data (e.g., whole strata density, basal area, diversity, richness). Data were scaled to normalize values using the 'scale' function. To ensure avoidance of local minima and maxima, the analysis was conducted using Euclidean distance and seven random starts for 10,000 iterations. A stress test was used to determine goodness-of-fit. A Shepard diagram was used to show the residual variability about the regression line and determine the adequacy of the dimensional representation. Both vegetation vectors (i.e., data input to create the NMDS ordination space) and hydrology vectors were fit to the axes using the 'envfit' function to show each parameter's relationship with the spread of data in ordination space.

2.4 Results

We evaluated relationships among hydrologic regime, peat depth, microtopography, and vegetation composition to better understand the hydrologic effects on GDS ecosystem structure and function. We examined these relationships at different spatial scales using both transect- (categorical) and plot- (continuous) level analyses.

2.4.1 Transect- and Plot-level Hydrology

We captured a gradient of hydrologic regime across transects. Transect mean water level (i.e., average of plot-level temporal means) ranged from -0.58 m (at WRM) to 0.16 m above land surface (at WED), varying significantly ($P < 0.0001$) between all transects, except SBE and EED (Figure 5a). Temporal water level standard deviation at the transect-level (i.e., mean of plot-level standard deviations) highlighted significant differences in water level variation across all transects except EED and WED (Figure 5b). Similar trends across transects (driest to wettest transect; WRM to WED) were also found for 10th (-0.97 to 0.01 m) and 90th percentiles (-0.33 to 0.24 m), revealing significant transect differences for both low and high water level conditions, respectively (data not shown).

Our sampling design also captured a gradient of hydrologic regime at the plot level. Plot mean water level ranged from -0.81 m to 0.40 m (see box-plot distributions in Figure 5a), and standard deviation ranged from 0.35 m to 0.09 m (see Figure 5b). Water level 10th and 90th

percentiles ranged from -1.33 m to 0.32 m and -0.55 m to 0.55 m, respectively (data not shown). All hydrologic parameters significantly covaried with each other (Table 2), with the wettest plots (via mean water level) also having the lowest water level variation (i.e., standard deviation) and highest 10th and 90th percentiles.

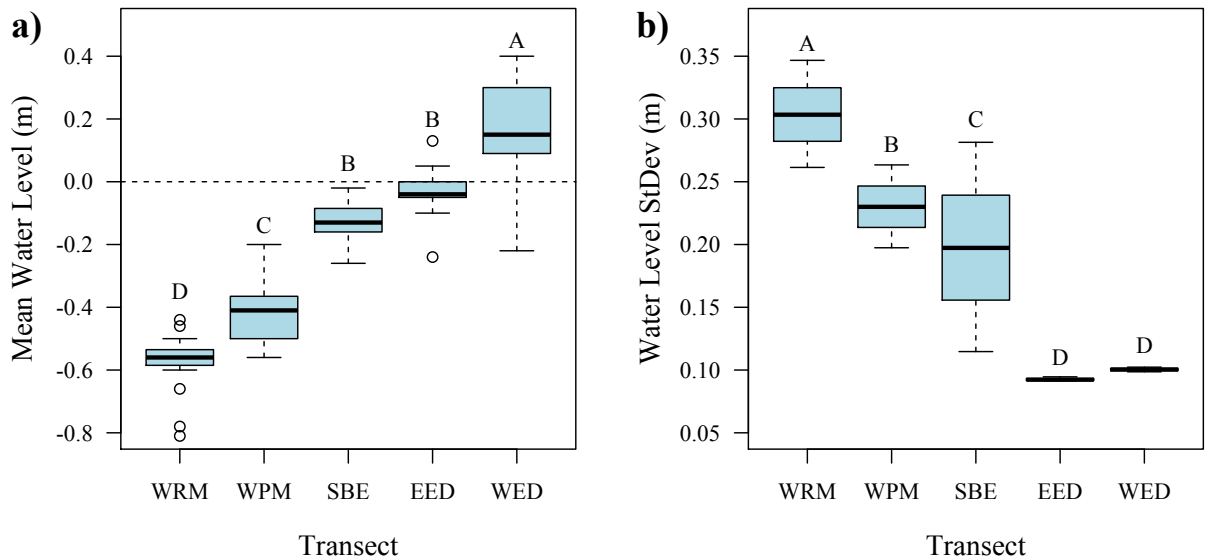


Figure 5. Hydrologic regime by transect characterized by a) mean water level (dashed line denotes ground surface) and b) water level temporal standard deviation. Box plot distributions document transect spatial variation of plot-level a) means and b) standard deviations. ANOVAs for both mean water level and standard deviation were significant ($P < 0.0001$). Letters denote significant pair-wise differences ($P < 0.0001$) between transects using Tukey HSD.

Table 2. Spearman's correlation matrix of water level (WL) metrics.

	Mean WL	StDev WL	10% WL	90% WL
Mean WL	1			
StD WL	**-0.78**	1		
10% WL	**0.96**	**-0.83**	1	
90% WL	**0.88**	**-0.59**	**0.91**	1

Bold values are significant at $P < 0.05$.

2.4.2 Transect-level Analysis

Peat Depth and Microtopography

We evaluated transect-level trends of peat depth and microtopography with wetness. Mean peat depths ranged from 59 cm to 134 cm and increased significantly with transect wetness (from WRM to WED; Figure 6a); however, the wettest two transects (EED and WED) did not significantly differ. Microtopographic index (i.e., the elevation standard deviation per plot) was

generally lower at the drier transects and highest at the wettest two transects (EED and WED), but not significantly (Figure 6b).

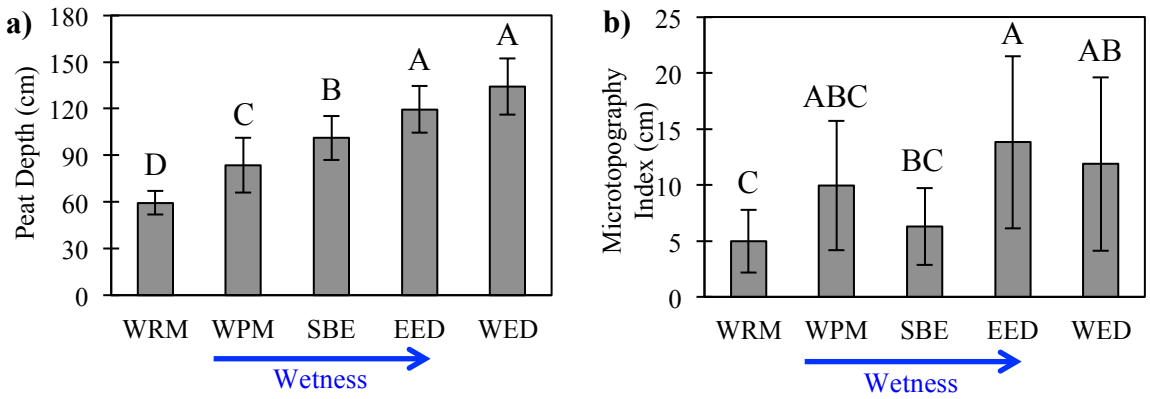


Figure 6. Transect means (± standard deviation) of plot-level a) peat depth and b) microtopography index along a gradient of increasing wetness (via transect mean water level). Microtopography index at each plot is defined as the standard deviation of three plot elevations. ANOVA for both peat depth and microtopography were significant ($P < 0.05$). Letters denote significant pair-wise differences ($P < 0.05$) between transects using Tukey HSD.

Vegetation Composition and Maple

For each stratum, we compared vegetation composition and structure across transects and thus a wetness gradient. In the overstory stratum, tree size class distributions varied across transects with higher frequencies of small diameter trees at wetter transects (Figure 7). Similarly, QMD also decreased with wetness from 25 cm (at WRM) to 13 cm (at WED; Figure 7). Tree density ranged from 750 to 2800 stems ha^{-1}, and was significantly higher at the wettest two transects (EED and WED; Figure 8a). However, maple relative tree density was highest at the three driest transects (Figure 8b). Tree basal area showed no significant trend with wetness (Figure 8c), whereas maple relative tree basal area was highest at the three driest transects (Figure 8d). As a result, maple importance value (i.e., sum of maple relative tree basal area and density) was significantly lower at the wettest transects (EED and WED; Figure 8e). Despite this trend of maple importance, tree diversity (Shannon Index) showed no clear pattern with wetness (Figure 8f). In the midstory stratum, shrub composition and structure also revealed no clear trend with wetness. SBE had significantly higher shrub density and basal area than all other transects (Figure 9a,b), but generally lower diversity (Figure 9c). Maple was not prevalent at the midstory level. In the understory stratum, richness was generally higher at the wettest three transects, but

this trend was not significant (Figure 10a). WED (the wettest site) had the highest occurrence (67% of plots) of obligate understory wetland species (Figure 10b). The three wettest transects had greater seedling density (Figure 19c) and the only occurrence of maple seedlings (Figure 10d). Lastly, across all strata, mean stand species richness ranged from 4.5 to 7.3, and was significantly greater at the 3 wettest transects (Figure 11). See Table 3 for all observed species by strata.

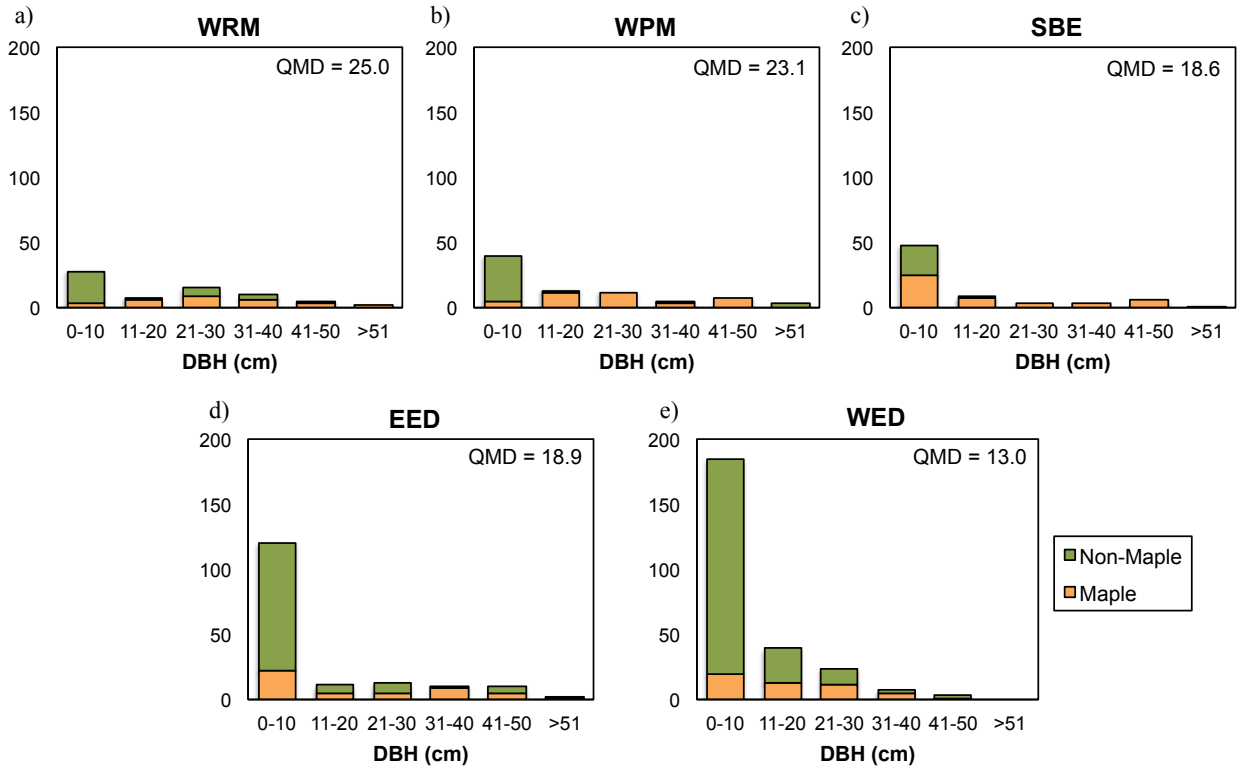


Figure 7. Overstory (dbh > 2.5 cm) size class distributions for each transect across an increasing wetness gradient: a) WRM, b) WPM, c) SBE, d) EED, and e) WED. Quadratic mean diameter (QMD; cm) is also shown for each transect.

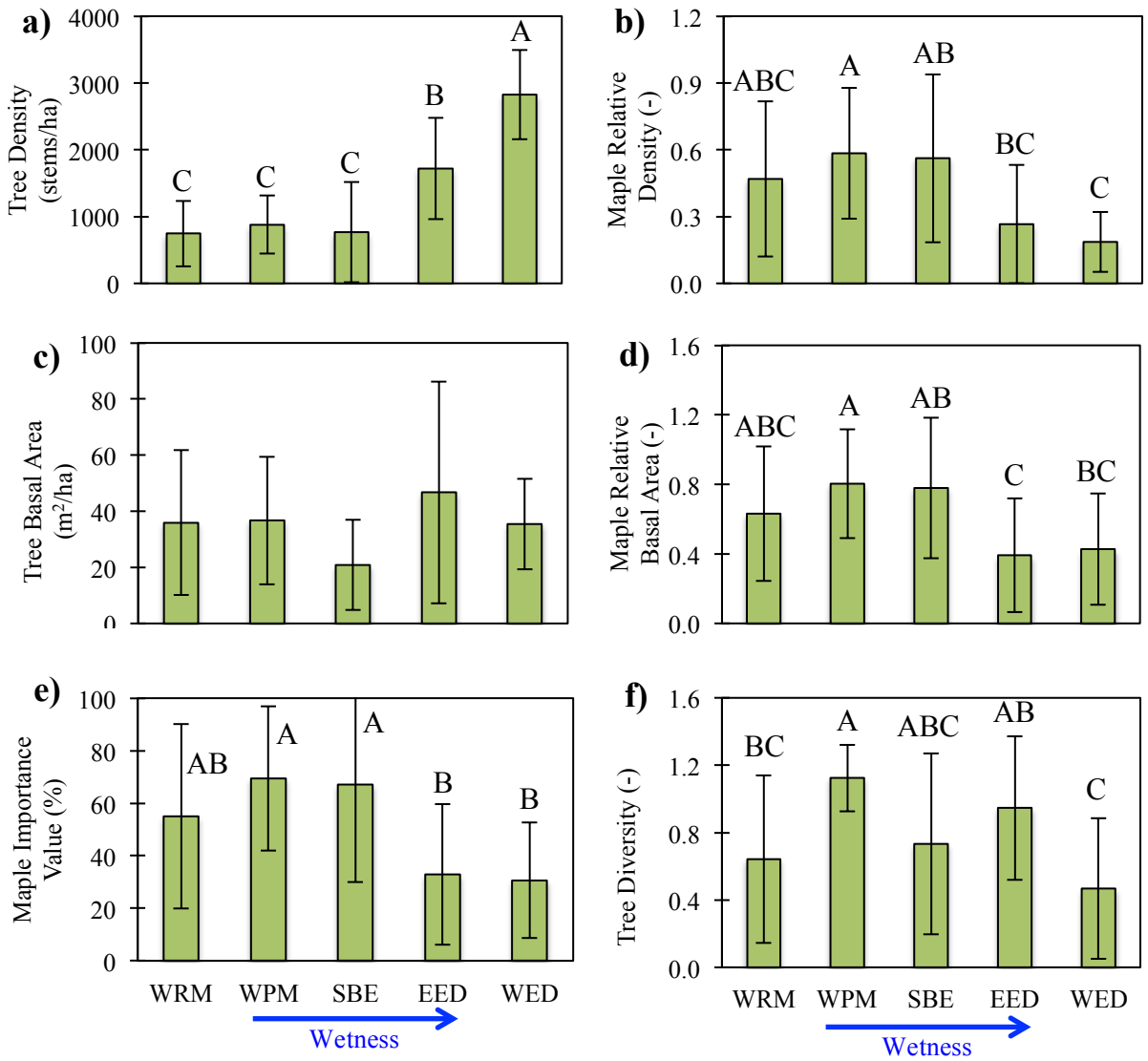


Figure 8. Overstory analysis by transect mean (± standard deviation) of plot-level a) tree density, b) maple relative tree density, c) tree basal area, d) maple relative tree basal area, e) maple importance value, and f) tree diversity along a gradient of increasing wetness (via transect mean water level). Tukey HSD ordered letters are shown on plots if ANOVA was significant ($P < 0.05$).

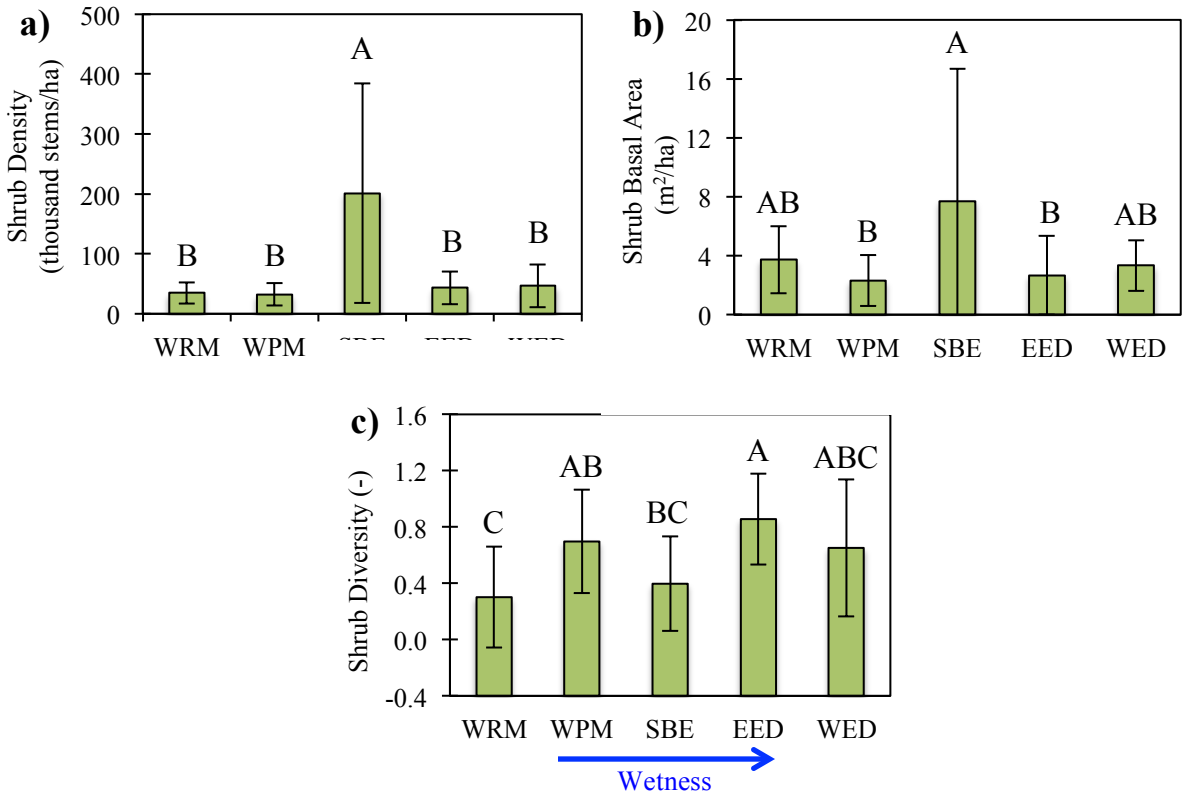


Figure 9. Shrub analysis by transect mean (± standard deviation) of plot-level a) shrub density, b) shrub basal area, and c) shrub diversity along a gradient of increasing wetness (via transect mean water level). Tukey HSD ordered letters are shown on plots if ANOVA was significant ($P < 0.05$).

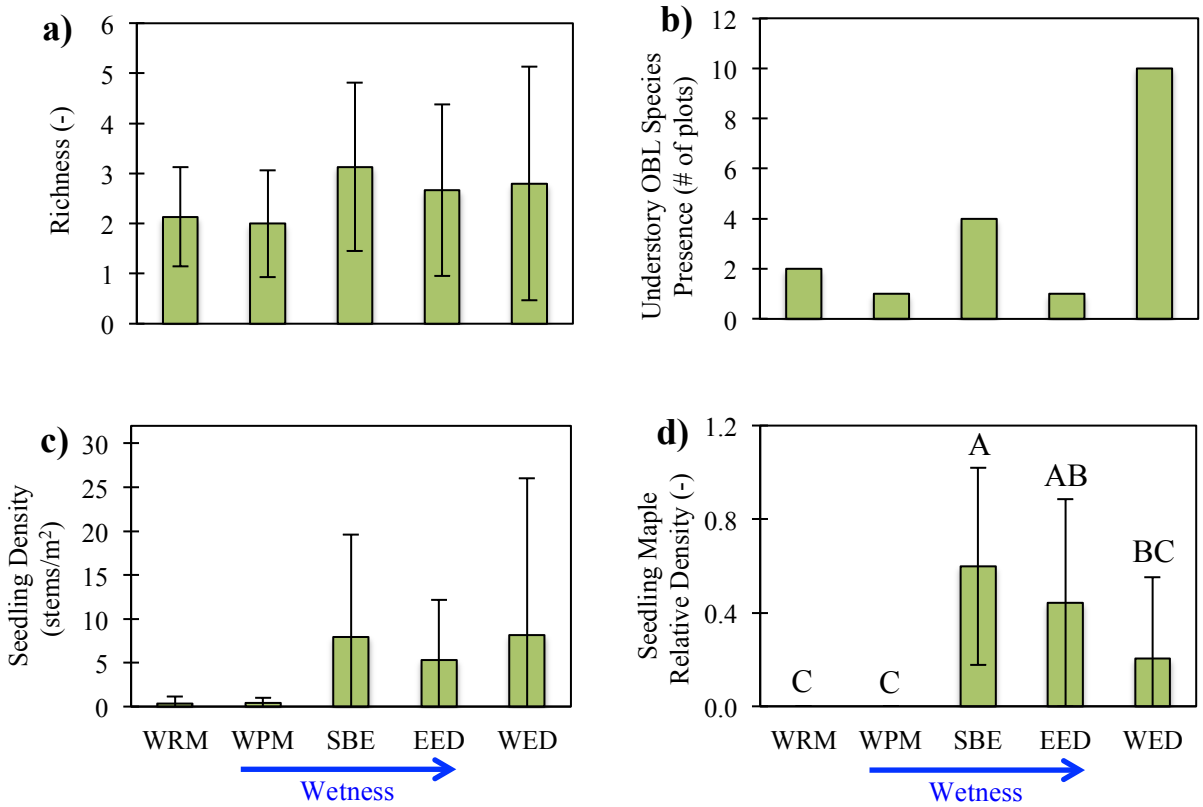


Figure 10. Understory analysis by transect mean (± standard deviation) of plot-level a) richness, b) count of plots with presence of obligate wetland (OBL) species, c) seedling density, and d) seedling maple relative density along a gradient of increasing wetness (via transect mean water level). Tukey HSD ordered letters are shown on plots if ANOVA was significant ($P < 0.05$).

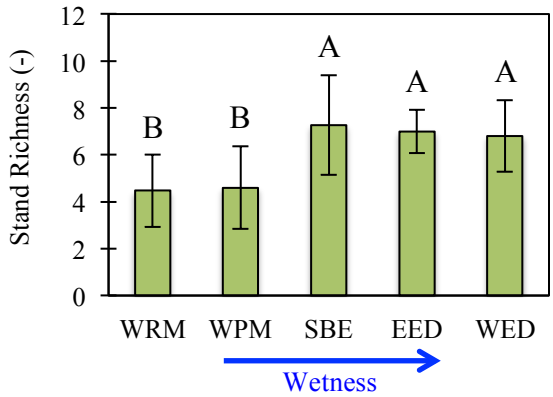


Figure 11. Transect mean (± standard deviation) of plot-level species richness across all strata along a gradient of increasing wetness (via transect mean water level). Letters denote significant differences ($P < 0.0001$) between transects using Tukey HSD.

Table 3. List of observed species. Species are included in the stratum where it appeared most, with 4-letter code used in this study and the Atlantic and Gulf Coastal Plain (AGCP) Regional Wetland Plant List Classification: upland (UPL), facultative upland (FACU), facultative (FAC), facultative wetland (FACW), and obligate wetland (OBL).

Common Name	Scientific Name	Code	AGCP
Tree			
Loblolly pine	*Pinus taeda* L.	PITA	FAC
Pond pine	*Pinus serotina* Michx.	PISE	FACW
Bald cypress	*Taxodium distichum* L.	TADI	OBL
Pond cypress	*Taxodium ascendens* Brongn.	TAAS	OBL
Tulip-poplar	*Liriodendron tulipifera* L.	LITU	FACU
Sweetbay	*Magnolia virginiana* L.	MAVI	FACW
Redbay	*Persea borbonia* L.	PEBO	FACW
Pawpaw	*Asimina triloba* L.	ASTR	FAC
Sweetgum	*Liquidambar styraciflua* L.	LIST	FAC
American holly	*Ilex opaca* Ait.	ILOP	FAC
Red maple	*Acer rubrum* L.	ACRU	FAC
Blackgum	*Nyssa sylvatica* Marsh.	NYSY	FAC
Swamp Tupelo	*Nyssa biflora* Walt.	NYBI	OBL
Black Oak	*Quercus velutina* Lam.	QUVE	UPL
Shrub			
Sweet pepperbush	*Clethra alnifolia* L.	CLAL	FACW
Giant cane	*Arundinaria gigantea* Walt.	ARGI	FACW
Highbush blueberry	*Vaccinium corymbosum* L.	VACO	FACW
Herb			
Virginia creeper	*Parthenocissus quinquefolia* L.	PAQU	FACU
Netted chain fern	*Woodwardia areolata* L.	WOAR	OBL
Muscadine grape	*Vitis rotundifolia* Michx.	VIRO	FAC
Bladderwort	*Utricularia* spp	UTRI	OBL
Poison Ivy	*Toxicodendron radicans L.*	TORA	FAC
Greenbriar	*Smilax* spp	SMSP	FAC
Sphagnum moss	*Sphagnum* spp	SPHA	OBL
Wild strawberry	*Fragaria vesca* L.	FRVE	UPL
Virginia chain fern	*Woodwardia virginica* L.	WOVI	OBL

2.4.3 Plot-level Analysis

Peat Depth and Microtopography

We evaluated relationships of peat depth and microtopography with hydrologic metrics at the plot level. Peat depth had a strong positive relationship with mean water level (Figure 12a) and a strong negative relationship with water level standard deviation (Figure 12b). Microtopographic index had a weak but positive relationship with mean water level (Figure 12c) and a negative (but stronger) relationship with water level standard deviation (Figure 12d). Peat depth and microtopographic index covaried significantly (Spearman's ρ = 0.36; data not shown).

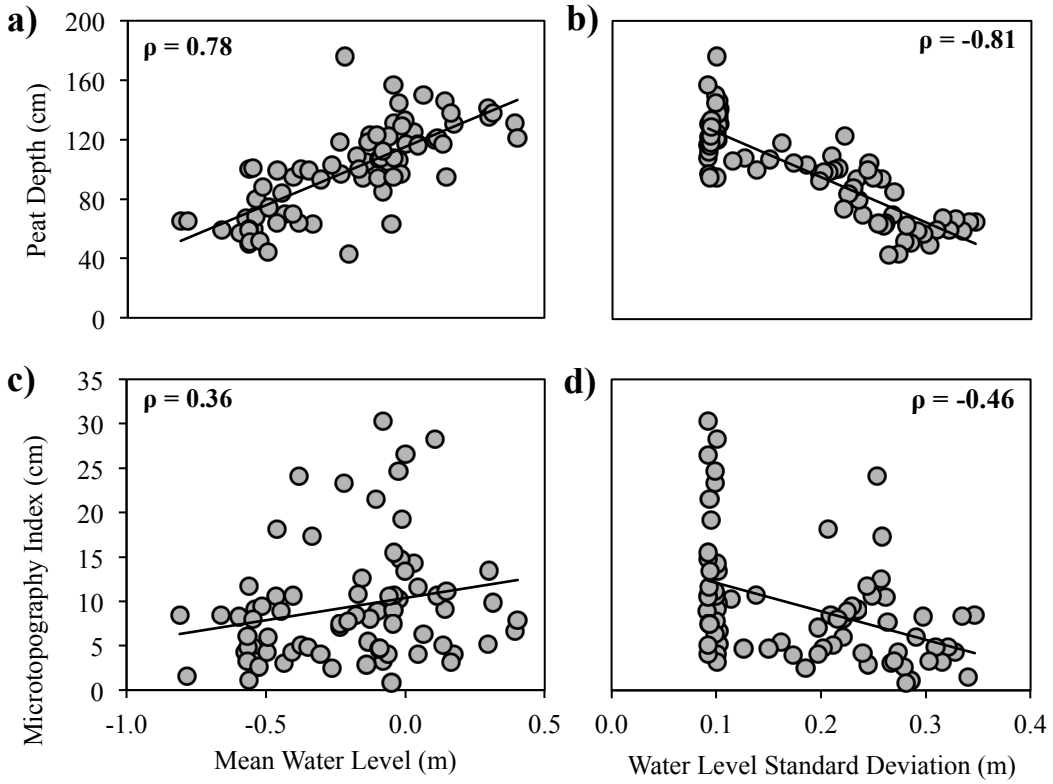


Figure 12. Plot-level analysis of a-b) peat depth and c-d) microtopography vs. hydrologic metrics (mean water level and standard deviation). All relationships were significant via Spearman's correlation ($P < 0.05$).

Vegetation Composition and Maple

At the plot level, we evaluated correlations among hydrologic and vegetation metrics across strata, with a focus on maple importance. At the overstory stratum, plot tree density significantly increased with mean water level (Figure 13a), and had a strong significant correlation with all other hydrology metrics (Table 4). In contrast, tree basal area and tree

diversity showed no significant relationships with hydrologic metrics (Table 4). Maple relative tree density, relative basal area, and importance value (Figure 13b) were all negatively correlated with mean water level and positively correlated with water level standard deviation (Table 5). However, absolute maple tree density and basal area had no significant correlation with hydrologic metrics (Table 5). At the midstory stratum, plot shrub density and shrub basal area showed no significant relationships with hydrologic metrics (Table 4). However, shrub diversity was positively correlated with mean water level and negatively correlated with water level standard deviation (Table 4). While understory richness showed no significant relationships with hydrology (Table 4), seedling diversity and density were significantly correlated with some hydrologic metrics, including negative correlations with water level standard deviation (Table 4). Maple seedling density and relative density were positively correlated with mean water level and negatively correlated with water level standard deviation (Table 5).

Overall stand richness (across all strata) increased significantly with mean water level ($P = 0.0001$; Figure 13c, Table 4). Stand richness was also positively correlated with 10th percentile and 90th percentile water level, negatively correlated with water level standard deviation, and had no significant correlation with microtopography (Table 4, Figure 13d). Lastly, stand richness had a significant ($\rho = -0.36$) negative relationship with maple importance; however, maple importance did not significantly covary with any other non-maple vegetation parameters (Table 6).

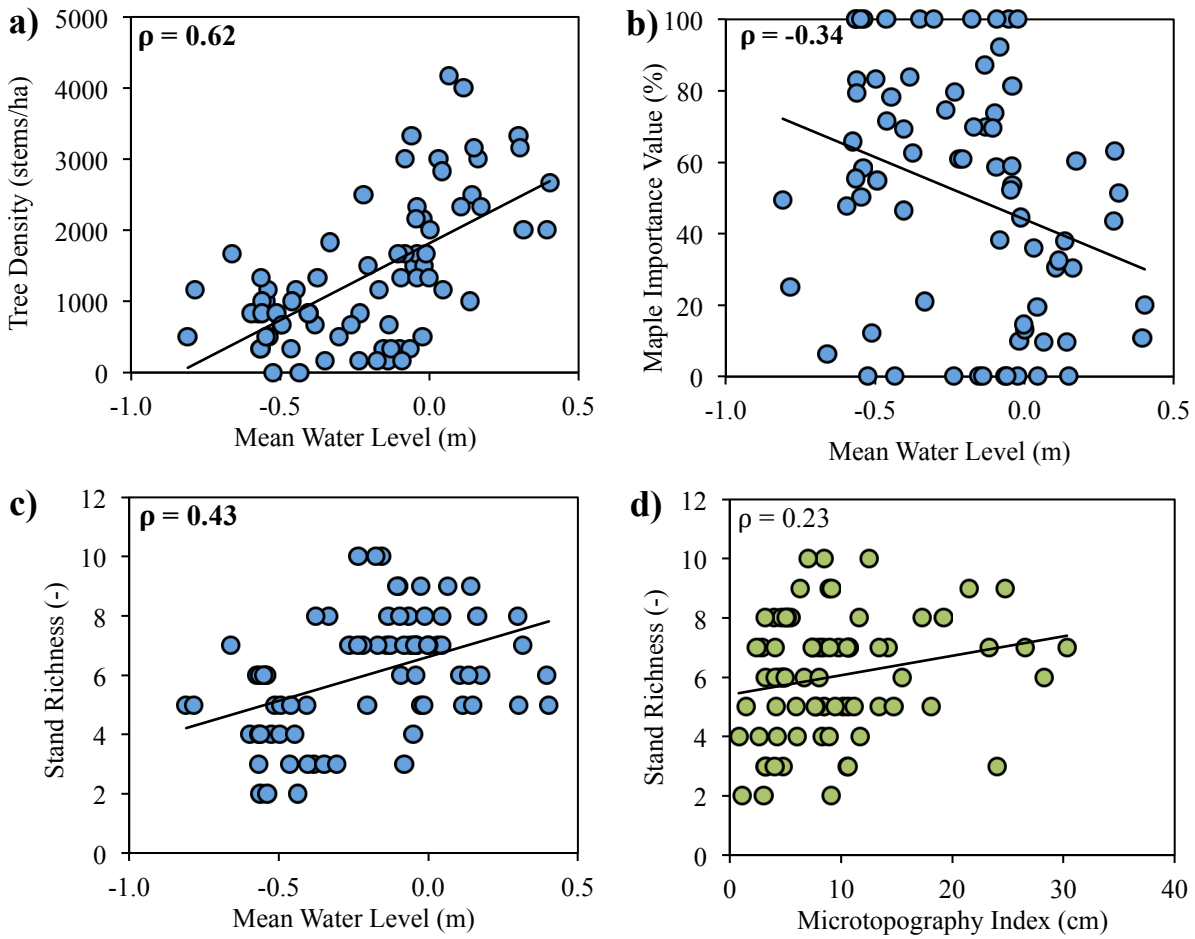


Figure 13. Plot-level analysis of vegetation parameters: a) tree density vs. mean water level, b) maple importance value vs. mean water level, c) stand richness vs. mean water level, d) stand richness vs. microtopography index. Bold values denote Spearman's correlation significance ($P < 0.05$).

Table 4. Spearman's correlation matrix of vegetation vs. hydrologic metrics.

	Mean WL	StDev WL	10% WL	90% WL	Microtopo
Stand Richness	**0.43**	**-0.46**	**0.42**	**0.30**	0.23
Tree Diversity	-0.19	0.03	-0.16	-0.05	0.07
Tree Density	**0.62**	**-0.51**	**0.58**	**0.50**	**0.31**
Tree Basal Area	0.00	-0.12	0.05	0.00	0.11
Shrub Diversity	**0.28**	**-0.40**	**0.27**	0.21	0.15
Shrub Density	0.12	-0.09	0.07	0.00	0.04
Shrub Basal Area	-0.02	0.07	-0.06	-0.10	-0.10
Understory Richness	0.02	-0.14	-0.05	-0.20	0.10
Seedling Diversity	0.21	**-0.31**	0.20	0.11	**0.24**
Seedling Density	**0.33**	**-0.41**	**0.28**	0.10	0.16

Bold values are significant at $P < 0.05$.

Table 5. Spearman's correlation matrix of maple vs. hydrologic metrics.

	Mean WL	StDev WL	10% WL	90% WL	Microtopo
Maple Importance Value	**-0.34**	**0.30**	**-0.31**	-0.23	-0.14
Tree Maple Density	0.09	-0.06	0.11	0.14	0.04
Tree Maple Relative Density	**-0.38**	**0.32**	**-0.34**	-0.26	-0.13
Tree Maple BA	-0.19	0.06	-0.12	-0.15	-0.06
Tree Maple Relative BA	**-0.32**	**0.30**	**-0.30**	-0.23	-0.16
Seedling Maple Density	**0.35**	**-0.41**	**0.31**	0.17	0.09
Seedling Maple Relative Density	**0.33**	**-0.39**	0.31	**0.19**	0.08

Bold values are significant at $P < 0.05$.

Table 6. Spearman's correlation matrix of vegetation vs. maple importance value (IV).

	Maple IV
Stand Richness	**-0.36**
Tree Diversity	0.10
Tree Density	-0.34
Tree Basal Area	0.07
Shrub Diversity	-0.02
Shrub Density	0.01
Shrub Basal Area	-0.03
Understory Richness	-0.06
Seedling Diversity	-0.03
Seedling Density	-0.13

Bold values are significant at $P < 0.05$.

Nonmetric Multidimensional Scaling

To analyze all covariates, we evaluated correlations among all vegetation parameters (listed in Table 7) in a nonmetric multidimensional scaling analysis (NMDS). We used two-dimensions with a stress of 0.17; no additional interpretable information was derived from additional axes. The NMDS shows the same data with two separate vectors displayed: vegetation metrics in the axes (Figure 14a, Table 7) and hydrologic metrics and microtopography for plots within the ordination space (Figure 14b, Table 8). Note that hydrologic metrics were not included in the axes. The arrows show the direction of increasing parameter gradient. The arrow length is proportional to the correlation between the parameter and the ordination. The driest transect plots (WRM and WPM) grouped together, as did the wettest transect plots (EED and WED). SBE plots, intermediate wetness, grouped out separately. Increasing tree metrics (i.e., tree maple basal area, tree maple density, tree basal area, tree density) opposed shrub density and basal area (Figure 14a). Notably, hydrologic metrics (i.e., mean, 10%, 90% WL) significantly explained variation in the ordination space (Figure 14b; Table 8), where increasing wetness negatively covaried with maple importance.

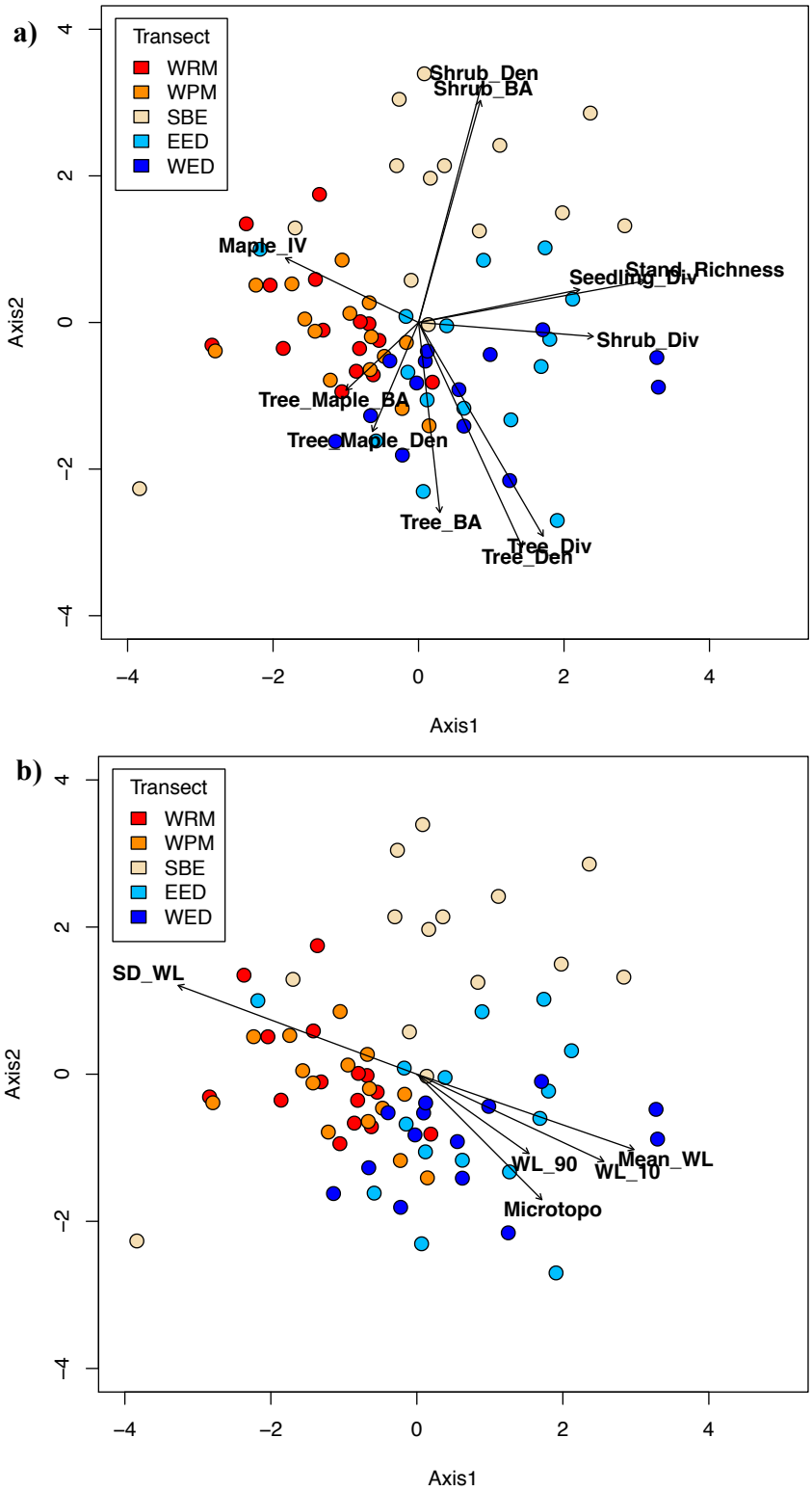


Figure 14. Nonmetric multidimensional scaling (NMDS) analysis with two-dimensions to visualize vegetation parameters with a) vegetation vectors present in axes and b) hydrology vectors not in axes.

Table 7. Factor averages (or vectors) of vegetation variables in the NMDS axes. Columns Axis 1 and Axis 2 show correlation coefficients of vegetation variables with each axis. R^2 values quantify the degree to which the ordination space affects the variable distribution. P-values show significance.

	Axis1	Axis2	R^2	P
Stand Richness	0.98	0.18	0.46	<0.0001
Tree Diversity	0.51	-0.86	0.53	<0.0001
Tree Richness	0.53	-0.85	0.66	<0.0001
Tree Maple BA	-0.73	-0.68	0.09	0.0386
Tree Maple Density	-0.39	-0.92	0.12	0.0232
Tree BA	0.11	-0.99	0.31	<0.0001
Tree Density	0.42	-0.91	0.53	<0.0001
Maple Importance Value	-0.90	0.43	0.19	0.0002
Shrub Diversity	1.00	-0.08	0.27	0.0002
Shrub Richness	0.78	0.62	0.50	<0.0001
Shrub BA	0.27	0.96	0.46	<0.0001
Shrub Density	0.26	0.97	0.52	<0.0001
Seedling Diversity	0.98	0.20	0.24	0.0003
Seedling Richness	0.98	0.20	0.47	<0.0001
Seedling Density	0.99	0.16	0.61	<0.0001
Seedling Maple Density	0.98	0.20	0.54	<0.0001

Table 8. Factor averages (or vectors) for correlation between hydrology and microtopography variables and the vegetation NMDS ordination space. Columns Axis 1 and Axis 2 show correlation coefficients of variables with each axis. R^2 values quantify the degree to which the ordination space affects the variable distribution. P-values show significance.

	Axis1	Axis2	R^2	P
Mean WL	0.95	-0.33	0.21	0.0002
SD WL	-0.94	0.35	0.25	<0.0001
10% WL	0.91	-0.42	0.17	0.0014
90% WL	0.82	-0.57	0.07	0.0598
Microtopography	0.71	-0.71	0.12	0.0139

2.5 Discussion

In this work, we sought to explore hydrologic controls on peat depth, microtopography, and vegetation composition, testing two specific hypotheses:

H1) Increased wetness (e.g., shallower water table) increases peat depth and microtopographic variation.

H2) Increased wetness decreases maple importance and increases overall diversity.

To do so, we coupled in situ hydrologic monitoring with surveys of peat depths, surface elevation, and vegetation along a gradient of wetness. Our findings highlight hydrologic variation at plot and transect scales and how such variation influences peat depth, microtopography, and vegetation composition. As such, research findings will inform hydrologic restoration at GDS and, more broadly, advance our understanding of interactions between hydrology and ecosystem structure and function in temperate peatlands.

Hydrology

Our hydrologic monitoring approach allowed estimates of continuous water level across 75 plots, capturing variation in hydrologic regime among and within transects. Differences in water level dynamics across transects demonstrate marked spatial variation in our focus area of GDS (i.e., NE corner; Figure 3), and likely effects of ditches and roads to induce such variation across landscape sections. Transects ranged from wet with stable water levels (e.g., mean water level ± standard deviation at WED = 0.16 ± 0.1 m) to relatively dry with more variable water levels (e.g., WRM = -0.58 ± 0.3 m; Figure 5). Differences in plot water levels highlight variation within transects, pointing to local controls (e.g., elevation, distance to ditch) and likely increasing local habitat complexity. Plot mean water level and standard deviation data captured end members of deep (-0.81 ± 0.35 m) and shallow water table conditions (0.40 ± 0.09 m), where wetter plots also had more stable water levels (Figure 5b; Table 2). Of the 75 plots monitored, 39 were never flooded, 25 were intermittently flooded, and 11 were perennially flooded; as such, plots captured a gradient of hydroperiod conditions.

The range of hydrologic regimes we measured spanned typical values of dominant swamp community types (e.g., cedar to cypress) found at GDS. At the driest end, pocosins (in New Jersey) typically have mean water levels between -0.35 and -0.55 m, with variable water level fluctuation (standard deviation of 0.28 m; Zampella et al., 2001; Yu and Ehrenfeld, 2010).

Similarly, more shallow and variable water tables (ca. -0.20 to -0.25 m ± 0.22 m) also typify New Jersey maple swamps (Zampella et al., 2001; Yu and Ehrenfeld, 2010). Cedar swamp water levels are generally more stable and shallower (-0.10 to 0.03 m above land surface; Little, 1950; Yu and Ehrenfeld, 2010), and typically do not fall below -0.15 m (Parrott et al., 1981; Atkinson et al., 2003). At the wettest end, cypress-tupelo swamp mean water level occurs between 0.1 to -0.5 m, ranging from 0.9 to -1.0 m (Aust and Lea, 1992; Crownover et al., 1995; Keeland et al., 1997).

Despite capturing a hydrologic gradient between transects, our sampling design did somewhat limit our ability to infer hydrologic variation and controls on ecosystem properties across GDS. For example, our transects were solely in the northeastern corner of GDS, potentially missing other forest communities, as well as wetter, drier, and more hydrologically variable locations. Moreover, we only had two wells per transect and relied on land surface elevations and interpolation to estimate water levels at each plot. However, high saturated conductivity in the upper peat, and thus especially at high water levels (Lichtler and Walker, 1974), likely minimized local deviation from a broader hydraulic gradient over the 300 m transects. Lastly, hydrologic data were only collected for 16 months. However, *relative* differences in hydrologic regime among plots over this monitoring period likely hold across longer periods and varying climate, provided there are no changes to ditch control. Despite these limitations, our monitored sites exhibit clear and significant differences in hydrologic regime to evaluate relative controls on peat depth, microtopography, and vegetation.

Peat and Microtopography

We found clear hydrologic controls on peat depth confirming our hypothesis of increased peat depth with increased wetness. Constant soil saturation is an important regulator of organic matter decomposition and thus peat accretion and carbon storage (Reddy and Patrick, 1975). As expected, peat depth increased significantly with mean water level at both the transect-level (Figure 6a) and plot-level (Figure 12a). Peat depth also increased with decreasing water level standard deviation (Figure 12b). However, there was a strong (negative) covariance between mean water level and standard deviation; that is, we did not capture sites with both high mean water level and high standard deviation water level, limiting our ability to separate controls of mean and variation in water levels. Plot peat depth ranged from 40 cm to 160 cm (Figure 12a),

with a mean of 1 m across all plots. These depths are similar but somewhat smaller compared to peat depths in temperate cedar swamps with similar hydrologic regimes (i.e., water levels ranging from -20 to 30 cm above land surface; Golet and Lowry, 1987). For example, Ott and Chimner (2016) measured peat depths from 40 cm to 325 cm, with an average of 112 cm in cedar peatlands in northern Minnesota and Michigan. Yu and Ehrenfeld (2010) found peat depths up to 200 cm in New Jersey cedar swamps. Note that our peat depth observations were constrained to one region of GDS, and previous work has documented depths exceeding 3 m in other GDS locations (Oaks and Coch, 1973). To our knowledge, however, our work is the first in GDS to link peat depths with hydrologic regime, thereby highlighting hydrologic controls on the carbon storage function valued in GDS.

We also found differences in microtopography across both transects and plots, with a moderate but significant relationship with hydrologic regime. We defined our microtopographic index as the local standard deviation in elevations at three surveyed points per plot. The highest microtopographic variation was found at the wettest two sites, where plot elevation standard deviations ranged from 3 cm to 30 cm, possibly due to windthrow. Concordantly, microtopographic index had a significant positive correlation with mean water level (Figure 12c) and negative correlation with water level standard deviation (Figure 12d), highlighting the influence of sustained, wet conditions to support hummock and hollow formation. Formation mechanisms for peatland microtopography vary but all require saturated soils. Ehrenfeld (1995b) identified windthrow as the main mechanism for hummock formation (up to 70-100 cm in height) in cedar swamps, where shallow rooted trees (due to high water level) in peat soils are vulnerable to wind disturbance. Spatially varying organic matter accumulation through concentrated litter fall or root turnover on more productive (less anaerobic) hummocks can further feedback to hummock development (Ehrenfeld, 1995a; Bruland and Richardson, 2005). Sediment deposition is another mechanism for microtopography (Bruland and Richardson, 2005), but minimal sediment-rich surface flow within GDS (Lichtler and Walker, 1974) makes those inputs an unlikely formative process. Regardless of formation processes, our findings point to hydrologic controls on microtopography and its feedback to spatial heterogeneity in hydrologic regime and associated habitat.

Microtopographic variation, and thus spatial variation in hydrology, is known to influence species richness in wetlands. Studies have observed increased herbaceous richness with

increased microtopographic heterogeneity, with different species showing a preference for either high or low elevation locations (Vivian-Smith, 1997; Bruland and Richardson, 2005). Although, Ehrenfeld (1995a) found that wetland woody plant species, especially tree seedlings, prefer only high elevation sites. In our work, microtopographic index had a positive significant correlation with tree density and seedling diversity (Table 4), highlighting possible roles of local elevation variation on vegetation composition. Overall, stand richness was also positively correlated with microtopographic index, though not significantly. Due to covariance in mean water level, microtopography, and vegetation composition, more plots in locations with diverse hydrologic regimes may be necessary to completely isolate and test the relationships between microtopography and vegetation composition.

Vegetation Composition and Maple Importance

Hydrologic regime can exert strong controls on wetland vegetation by influencing productivity (e.g., stand basal areas), tree regeneration, and species composition. More specifically, wetter sites can exclude more facultative species (e.g., mixed hardwoods; Burke et al., 2003) but also reduce productivity of remaining obligate species through anaerobic stress (Vann and Megonigal, 2002); both the degree of species selection and influence of anaerobic stress vary across species and hydrologic conditions (Angelov et al., 1996). At both transect and plot levels, we observed hydrologic influences on vegetation composition and structure, although the significance and direction of this influence varied across strata and vegetation metric. While we did not directly measure stand productivity, our measurements of shrub and tree densities and basal areas provide some inferences. There was no correlation between hydrologic regime and basal areas; however, both transect and plot-level analyses demonstrated strong positive associations between wetness and tree density (Figure 7, 8a, 13a; Table 4). No increase in tree basal area along with increase in tree density suggests smaller trees at wetter sites, as demonstrated with transect size class distributions (Figure 7). This is possibly a result of reduced productivity of individual trees due to water stress (e.g., Vann and Megonigal, 2002) and/or stand history and age. There were no evident associations between shrub structure and hydrologic regime, but clearly a site-level effect (e.g., SBE; Figure 9, Table 4). In contrast, seedling density (and for maple, a facultative species) increased significantly with mean water level (Figures 10c-d; Table 4, 5), which is in agreement with measured tree density but not with

often observed lower regeneration under wetter conditions (Malecki et al., 1983; Ehrenfeld, 1995a). We could not explicitly test hydrologic influences on stand level diversity (H2) due to varying nested plot sizes, but diversity at each stratum failed to confirm our general prediction. However, stand-level richness did increase with wetness, at both transect (Figure 11) and plot levels (although weakly; Figure 13d, Table 4), which both points to hydrologic and additional (e.g., seed source, selective logging) controls on species selection and composition.

Our hypothesis of increased species diversity with wetness (H2) was founded on predictions that wetness decreases maple importance, thereby increasing community diversity. At both transect and plot levels, we found decreases in maple relative basal area, relative tree density, and importance value with increased wetness, comporting with our prediction. However, correlation between maple importance and stand richness was only weakly negative (but significant; Table 6), and no significant associations were found between other stand-level vegetation characteristics and maple, suggesting other influences on composition, such as selective logging. Also, we found no significant relationship between absolute maple tree density or basal area with wetness (Table 5). But, we did find significantly decreased relative maple tree density and basal area at wetter sites, meaning there were more non-maple trees at wetter sites. More non-maple trees at wetter sites is consistent with increased tree densities and the inference of more but smaller trees at wetter sites.

To synthesize our suite of measured variables (e.g., composition and structure across strata, hydrologic regimes), we conducted NMDS ordination analysis. To do so, we only used vegetation parameters as axes inputs to explore how plots were grouped by vegetation characteristics, and then to quantify the degree to which hydrologic parameters explained vegetation variation among plots. When delineated by transect (colored plots in Figure 14), grouping of plots within their own transect was clear, highlighting within and in some cases between (WRM and WPM, EED and WED) transect similarities. Hydrologic parameters significantly correlated with the ordination space (Figure 14b, Table 8), further demonstrating the hydrologic control on vegetation composition in GDS. For example, the maple importance vector falls opposite the mean water level vector, indicating a negative relationship between the two.

Our work points to possible stress to maple trees (but not seedlings) under wetter conditions, with associated increases in stand richness. Higher water levels could reduce maple

canopies (i.e., leaf area but not tree density), allowing more non-maple trees to compete for light and increasing tree density and stand richness across strata (Malecki et al., 1983; Vann and Megonigal, 2002). In contrast to our overstory maple measurements, we found increased relative density of maple seedlings with wetness (Figure 10d, Table 5), suggesting a potential for continued maple presence (via regeneration from similar absolute maple tree densities) across hydrologic regimes (Malecki et al., 1983).

Previous work at GDS has called for hydrologic restoration (via more controlled and reduced drainage) to restore vegetation composition back to a more historical state and sequester carbon in the form of peat accretions. For example, Atkinson (2003) concluded that without hydrologic restoration, it is likely that previous cedar-dominated sites will continue to yield to species other species, including maple. Our findings add to this work by providing quantified relationships to target locations and specific hydrologic regimes to meet restoration goals. Future work should conduct measurements of leaf area index (LAI) to explore possible reduction in canopy cover (especially maple), and associated effects to tree and seedling densities, with increased wetness. Moreover, work is needed to understand ongoing stand succession under contemporary hydrologic regimes, paying attention to shade tolerance (especially maple regeneration) and possible canopy stress. This could include exploring if maple can sustain as a climax community, and if so, exploring the possibility that hydrologic regimes can be altered to make maple less competitive.

Conclusions

In this work, we sought to elucidate hydrologic controls on vegetation composition and peat depths, and ultimately to inform ongoing restoration efforts at GDS. Findings support our predictions in that at sites of increased wetness, we found thicker peat, more microtopographic variation, lower maple importance, and higher stand richness. However, more research is needed, especially to examine how maple importance affects community composition in other locations across GDS. Moreover, while the hydrologic control on peat depths is clear, more work is needed to understand the complex interactions between hydrologic regime and vegetation organic matter inputs that together determine peat accretion rates. Going forward, new restoration efforts at GDS should be coupled with continued research and monitoring to adaptively achieve restoration goals. From our findings, we conclude that the hydrologic

influences to maple importance and peat thickness (and resulting carbon storage) at GDS support the use of hydrology as a major management tool.

Literature Cited

Anderson, J. A. R. 1983. The Tropical Peat Swamps of Western Malesia. *Mires: Swamp, Bog, Fen and Moor: Regional Studies*.

Angelov, M. N., S. S. Sung, W. R. Harms, P. P. Kormanik, and C. C. Black. 1996. Long-and Short-Term Flooding Effects on Survival and Sink-Source Relationship of Swamps-Adapted Tree Species. *Tree Physiology* 16, 5: 477–484.

Atkinson, R. B., J. W. DeBerry, D. T. Loomis, E. R. Crawford, R. T. Belcher, R. B. Atkinson, R. T. Belcher, D. A. Brown, and J. E. Perry. 2003. Water Tables in Atlantic White Cedar Swamps: Implications for Restoration. In *Atlantic White Cedar Restoration Ecology and Management, Proceedings of a Symposium. Christopher Newport University, Newport News*, 137–150.

Aust, W. M., and R. Lea. 1992. Comparative Effects of Aerial and Ground Logging on Soil Properties in a Tupelo-Cypress Wetland. *Forest Ecology and Management* 50, 1–2: 57–73.

Bruenig, E. F. 1990. Oligotrophic Forested Wetlands in Borneo. *Ecosystems of the World* 15: 299–334.

Bruland, G. L., and C. J. Richardson. 2005. Hydrologic, Edaphic, and Vegetative Responses to Microtopographic Reestablishment in a Restored Wetland. *Restoration Ecology* 13, 3: 515–523

Burke, M. K., S. L. King, D. Gartner, and M. H. Eisenbies. 2003. Vegetation, Soil, and Flooding Relationships in a Blackwater Floodplain Forest. *Wetlands* 23, 4: 988–1002.

Carter, V., P. T. Gammon, and M. K. Garrett. 1994. Ecotone Dynamics and Boundary Determination in the Great Dismal Swamp. *Ecological Applications*, 189–203.

Casanova, M. T., and M. A. Brock. 2000. How Do Depth, Duration and Frequency of Flooding Influence the Establishment of Wetland Plant Communities? *Plant Ecology* 147, 2: 237–250.

Crownover, S. H., N. B. Comerford, D. G. Neary, and J. Montgomery. 1995. Horizontal Groundwater Flow Patterns through a Cypress Swamp-Pine Flatwoods Landscape. *Soil Science Society of America Journal* 59, 4: 1199–1205.

Dabel, C. V., and F. P. Day Jr. 1977. Structural Comparisons of Four Plant Communities in the Great Dismal Swamp, Virginia. *Bulletin of the Torrey Botanical Club*, 352–360.

Day Jr, F. P. 1985. Tree Growth Rates in the Periodically Flooded Great Dismal Swamp. *Castanea*, 1985, 89–95.

Daubenmire, R. 1959. A Canopy-Coverage Method of Vegetational Analysis. *Northwest Science* 33, 1: 43–64.

DeBerry, J. W., and R. B. Atkinson. 2014. Aboveground Forest Biomass and Litter Production Patterns in Atlantic White Cedar Swamps of Differing Hydroperiods. *Southeastern Naturalist* 13, 4: 673–690.

Ehrenfeld, J. G. 1995. Microsite Differences in Surface Substrate Characteristics in Chamaecyparis Swamps of the New Jersey Pinelands. *Wetlands* 15, 2: 183–189.

Ehrenfeld, J. G. 1995. Microtopography and Vegetation in Atlantic White Cedar Swamps: The Effects of Natural Disturbances. *Canadian Journal of Botany* 73, 3: 474–484.

Francis, H. E. 1959. Soil Survey for Norfolk County, Virginia, 53.

Golet, F.C., A.J.K. Calhoun, W.R. DeRagon, D.J. Lowry, and A.J. Gold. 1993. *Ecology of Red Maple Swamps in the Glaciated Northeast: A Community Profile*. Washington, D.C.

Hugron, S., J. Bussières, and L. Rochefort. 2013. Tree Plantations within the Context of Ecological Restoration of Peatlands: Practical Guide. *Peatland Ecology Research Group, Université Laval, Québec, Québec, Canada*.

Keeland, B. D., W. H. Conner, and R. R. Sharitz. 1997. A Comparison of Wetland Tree Growth Response to Hydrologic Regime in Louisiana and South Carolina. *Forest Ecology and Management* 90, 2: 237–250.

Kuhry, P., B. J. Nicholson, L. D. Gignac, D. H. Vitt, and S. E. Bayley. 1993. Development of Sphagnum-Dominated Peatlands in Boreal Continental Canada. *Canadian Journal of Botany* 71, 1: 10–22.

Legrand Jr, H. E. 2000. The Natural Features of Dismal Swamp State Natural Area, North Carolina. *The Natural History of the Great Dismal Swamp, Omni, Madison, Wisconsin*, 41–50.

Levy, G. F. 1991. The Vegetation of the Great Dismal Swamp: A Review and an Overview. *Virginia Journal of Science* 42, 4: 411–418.

Levy, G. F., and S. W. Walker. 1979. Forest Dynamics in the Dismal Swamp of Virginia. *The Great Dismal Swamp. Old Dominion University Research Foundation, Inc*.

Lewis, I. F., and E. C. Cocke. 1929. *Pollen Analysis of Dismal Swamp Peat*. Elisha Mitchell Scientific Society.

Lichtler, W., F., and P. Walker. 1974. Hydrology of the Dismal Swamp, Virginia-North Carolina. *Geological Survey - Water Resources Division*, no. 74–39.

Lilly, J. P. 1981. A History of Swamp Land Development in North Carolina.

Malecki, R. A., J. R. Lassoie, E. Rieger, and T. Seamans. 1983. Effects of Long-Term Artificial Flooding on a Northern Bottomland Hardwood Forest Community. *Forest Science* 29, 3: 535–544.

Oaks, R. Q., and N. K. Coch. 1973. *Post-Miocene Stratigraphy and Morphology, Southeastern Virginia*. Commonwealth of Virginia, Division of Mineral Resources.

Oksanen, J, F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. Minchin, et al. 2017. *Vegan: Community Ecology Package* (version 2.4-2).

Osborn, C. C. 1919. Peat in the Dismal Swamp, Virginia and North Carolina. *Contribution to Economic Geology* Bull 711, 4.

Ott, C. A., and R. A. Chimner. 2016. Long-Term Peat Accumulation in Temperate Forested Peatlands (Thuja Occidentalis Swamps) in the Great Lakes Region of North America. *MIRES AND PEAT* 18.

Page, S. E., J. O. Rieley, ØW Shotyk, and D. Weiss. 1999. Interdependence of Peat and Vegetation in a Tropical Peat Swamp Forest. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 354, 1391: 1885–1897.

Parish, Faizal, A. Sirin, D. Charman, H. Joosten, T. Minayeva, M. Silvius, and L. Stringer. 2008. Assessment on Peatlands. *Biodiversity and Climate Change: Main Report*.

Parrott, W. R., P. E. Reynolds, D. C. Hain, and J. R. Maurer. 1981. Computer Mapping of Seasonal Groundwater Fluctuations for Two Differing Southern New Jersey Swamp Forests I. In *LARS Symposia*, 485.

Phipps, R. L., D. L. Ierley, and C. P. Baker. 1979. Tree Rings as Indicators of Hydrologic Change in the Great Dismal Swamp, Virginia and North Carolina. US Geological Survey, Water Resources Division.

Poulter, B., N. L. Christensen, and P. N. Halpin. 2006. Carbon Emissions from a Temperate Peat Fire and Its Relevance to Interannual Variability of Trace Atmospheric Greenhouse Gases. *Journal of Geophysical Research: Atmospheres* 111, D6.

R Core Team. 2016. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Reardon, J., R. Hungerford, and K. Ryan. 2007. Factors Affecting Sustained Smouldering in Organic Soils from Pocosin and Pond Pine Woodland Wetlands. *International Journal of Wildland Fire* 16, 1: 107–118.

Reddy, A. D., T. J. Hawbaker, F. Wurster, Z. Zhu, S. Ward, D. Newcomb, and R. Murray.2015. Quantifying Soil Carbon Loss and Uncertainty from a Peatland Wildfire Using Multi-Temporal LiDAR. *Remote Sensing of Environment* 170: 306–316.

Reddy, K. R., and W. H. Patrick. 1975. Effect of Alternate Aerobic and Anaerobic Conditions on Redox Potential, Organic Matter Decomposition and Nitrogen Loss in a Flooded Soil. *Soil Biology and Biochemistry* 7, 2: 87–94.

Reed, P. B. Jr. 1988. National List of Plant Species That Occur in Wetlands: National Summary. *U. S. Fish and Wildlife Service Biological Report*, no. 88.

SAS Institute Inc. 2012. Using JMP 10 (version 10). Cary, NC: SAS Institute Inc.

Usup, A. Y. Hashimoto, H. Takahashi, and H. Hayasaka. 2004. Combustion and Thermal Characteristics of Peat Fire in Tropical Peatland in Central Kalimantan, Indonesia. *Tropics* 14, 1: 1–19.

Vann, C. D., and J. P. Megonigal. 2002. Productivity Responses of Acer Rubrum and Taxodium Distichum Seedlings to Elevated CO 2 and Flooding. *Environmental Pollution* 116: S31–S36.

Vivian-Smith, G. 1997. Microtopographic Heterogeneity and Floristic Diversity in Experimental Wetland Communities. *Journal of Ecology*, 71–82.

Watts, A. C., and L. N. Kobziar. 2013. Smoldering Combustion and Ground Fires: Ecological Effects and Multi-Scale Significance. *Fire Ecol* 9, 1: 124–32.

Whitehead, D. R. 1972. Developmental and Environmental History of the Dismal Swamp. *Ecological Monographs*, 301–315.

Whitehead, D. R., and R. Q. Oaks. 1979. Developmental History of the Dismal Swamp. *The Great Dismal Swamp (PW Kirk, Jr., Ed.). University of Virginia Press, Charlottesville*, 25–43.

Yu, S., and J. G. Ehrenfeld. 2010. Relationships among Plants, Soils and Microbial Communities along a Hydrological Gradient in the New Jersey Pinelands, USA. *Annals of Botany* 105, 1: 185–196.

Zampella, R. A., C. L. Dow, and J. F. Bunnell. 2001. Using Reference Sites and Simple Linear Regression to Estimate Long-term Water Levels in Coastal Plain Forests. *JAWRA Journal of the American Water Resources Association* 37, 5: 1189–1201.

3.0 HYDROLOGIC EFFECTS ON SMOLDERING PEAT FIRE VULNERABILITY IN THE GREAT DISMAL SWAMP

3.1 Abstract

Catastrophic wildfires in 2008 and 2011 occurred in the forested peatlands of the Great Dismal Swamp (GDS), motivating hydrologic restoration efforts. The most recent fire in August 2011 burned 2,500 ha, released 1.10 Tg of carbon, and consumed an average of 0.46 m of peat soil depth. Historical fire regimes at GDS have been altered by peat desiccation due to 19th and 20th century ditches installed to lower water levels. As a result, water level control structures are being installed and repaired in ditches, in an effort to re-establish historical hydrology and fire regime. To help inform water level management and fire prediction at GDS, we established four sites along a hydrologic gradient where we evaluated short- and long-term hydrologic controls on peat fire vulnerability. We measured *in situ* water levels, peat properties (i.e., bulk density, organic matter content), moisture holding capacity (via moisture release curves), and soil moisture thresholds for smoldering combustion. Using equations parameterized for each site, we estimated the soil moisture content at which each site had a 50% probability to burn (i.e., soil moisture burn threshold) and the water tension necessary to create this soil moisture (i.e., burn tension). Additionally, we estimated site-specific water level heights that maintain saturated conditions at the surface (i.e., capillary fringe height). Differences in long-term hydrologic regime (and related bulk density and organic matter content) between sites were reflected in these three parameters (soil moisture thresholds, burn tensions, and capillary fringe heights). To integrate both short- and long-term hydrologic effects on fire vulnerability, we evaluated site-specific water level time series, identifying how often water levels crossed two different thresholds of fire vulnerability that corresponded to burn tension and capillary fringe height. Both thresholds showed that burn temporal probablities decreased with wetness. Our findings suggest that the driest GDS site was always at risk to burn, while the wettest site maintained saturated conditions at the surface (via capillary fringe) and thus never reached conditions of burn vulnerability. This work is among the first to integrate soil moisture thresholds, moisture holding capacities, and water level dynamics to explore temporal and spatial variation in burn vulnerability. In doing so, our study emphasizes that such interactions need to be addressed in future research and fire management programs in peat-dominated systems.

3.2 Introduction

Smoldering Peat Fire

Smoldering fires are natural disturbances in peatland systems that influence ecosystem structure and function, with potential positive (e.g., controls on vegetation composition) and negative (e.g., carbon and smoke emissions) consequences. In contrast to flaming fires that exclusively burn above-ground fuels, smoldering combustion occurs in and can consume organic-rich soils (Watts et al., 2015) and lasts for long durations (days to months; Page et al., 2002). The consumption of peat soils can change wetland bathymetry and thus hydrologic regime (Watts et al., 2015). Additionally, in some ecosystems such as cypress swamps, low to moderate severity fires can provide stand maintenance, leaving cypress trees alive while killing potential competitors (Watts and Kobziar, 2013). Severe fires, however, can cause total tree mortality and induce species shifts from forested swamp to herbaceous marsh species (Casey and Ewel, 2006). Moreover, the smoldering nature makes the fire front difficult and costly to locate and extinguish (Rein et al., 2008), generating thick smoke into the atmosphere that can cause local health problems and traffic hazards (Poulter et al., 2006). Critically, along with above and below ground plant biomass, extensive consumption of peat soil can release enormous amounts of carbon to the atmosphere (Usup et al., 2004). Peat drainage and drought can amplify fire severity (Page et al., 2002). Across the globe, hydrologically altered peatlands have been devastated by smoldering fires (Turetsky et al., 2015), calling for hydrologic restoration and new research to inform such restoration.

Peatlands and Carbon

Peatlands only cover about 3% of the Earth's land surface, but store almost one third of the Earth's land carbon (Turetsky et al., 2015). About 80% of the world's peatlands are in boreal regions, 15-20% are in tropical or subtropical regions, and less than 5% are in temperate regions (Rein et al., 2008). The amount of carbon stored in these peatlands is a function of both peat depths and carbon content, varying by location due to differing organic matter inputs and formative processes. Tropical peatland soils in Central Kalimantan, Indonesia have a carbon content of about 57-61 kg m^{-3} C and peat depths of 0.5 to 10 m (Sorensen, 1993; Page et al., 1999; Shimada et al., 2001). Boreal peatland soils in northern latitudes have similar carbon contents (mean = 58 kg m^{-3} C; Gorham, 1991), with peat deposits of 2-3 meters (Hugron et al.,

2013). Temperate peatland soils in Pocosin Lakes, North Carolina have high carbon contents of 88 kg m^{-3} C, but depths to only 0.5 to 3 m (Poulter et al., 2006). Peatland drainage across these different regions is a huge threat to peatland carbon stores, where lowered water table can put peat soil at risk to rapid loss by both decomposition and fire (Atkinson et al., 2003). For example, smoldering fires in 1997 burned 0.73 Mha of forested peatland in Central Kalimantan, Indonesia, releasing an estimated 190-230 Tg of carbon (Page et al., 2002). Even though temperate peatlands fires tend to be relatively small in area, they typically release substantially more carbon per unit area than boreal or tropical peat fires due to the high organic content of temperature peat soils (Reddy et al., 2015). Such substantial carbon stores make understanding and managing controls on fire vulnerability across regions and environmental settings important at both local and global scales.

Mechanisms of Peat Fire

The characteristics of smoldering fires that make them difficult to extinguish also make them difficult to study *in situ*. Ignition starts on the surface, burns down into the soil, and spreads laterally, making the active fire front difficult to locate (Watts and Kobziar, 2013). Smoldering fires burn at lower oxygen contents and lower temperatures than flaming fires and spread at a much slower rate (Rein et al., 2008). Remote sensing technology has provided new information to measure scale and magnitude of soil and carbon loss from fire (e.g., Reddy et al., 2015), but not about fire driving mechanisms in the field. However, laboratory experiments have found that smoldering peat fire vulnerability is driven by three primary variables: soil moisture content, mineral content, and bulk density (Frandsen, 1987, 1997; Reardon et al., 2007; Rein et al., 2008). More specifically, the soil moisture threshold at which smoldering is possible decreases (i.e., drier requirements) with increases in bulk density and mineral content (Frandsen, 1997). Conversely, soils with higher organic contents and lower bulk densities will burn at higher soil moistures. As such, fire vulnerability varies over space (across and within peatland systems) and time due to variation in peat properties and hydrologic regime. In peatland systems, particularly those hydrologically altered, understanding hydrologic controls on fire vulnerability is paramount both to inform fire danger protocols (e.g., soil moisture monitoring) and hydrologic restoration to decrease fire risk.

Hydrologic Effect on Smoldering Peat Fire

Hydrologic controls on peat fire vulnerability are twofold. First, soil moisture is the primary driver of peat ignition (Frandsen, 1997; Reardon et al., 2007; Rein et al., 2008). As such, antecedent rainfall, evapotranspiration, and water level largely control fire ignition vulnerability over time in a given location. However, the soil moisture threshold below which smoldering is possible depends on peat properties such as bulk density, organic matter, and mineral content (Reardon et al., 2007). The secondary effect of hydrology is then through its long-term influence on these properties. Peat with increased long-term wetness typically has lower mineral content and bulk density due to higher organic matter accumulation (Verry et al., 2011), which likely increases the burn threshold moisture content and thus fire vulnerability. For example, both Frandsen (1997) and Reardon et al. (2007) found significant positive relationships between organic matter and burn thresholds, though the exact thresholds widely ranged between peatland systems. However, these studies explored such relationships across southeastern US regional peatland systems; similar work to examine such controls of peat properties within systems at more local scales has been limited.

Additionally, moisture holding capacity, which is quantified via relationships between water tension and resulting soil moisture (i.e., moisture release curves; Verry et al., 2011), is also influenced by peat properties, particularly bulk density. Specifically, increased bulk density decreases moisture holding capacity (Boelter, 1968; Verry et al., 2011). Again, such properties are strongly controlled by long-term hydrologic regime (Chambers et al., 2011). These differences in moisture holding capacities will then cause surface soil moisture to diverge between soils, even for similar antecedent short-term hydrology. That is, equivalent water table depths and evapotranspiration rates (and thus water tensions) can result in different surface soil moistures. Thus, hydrology will also influence fire vulnerability through long-term influences on peat properties that control <u>soil moisture burn thresholds</u> and <u>moisture holding capacities</u>. However, it is not yet understood how spatial variation in hydrologic regime within a peatland system creates local variation in smoldering soil moisture thresholds, moisture holding capacities, and resulting fire vulnerability.

Great Dismal Swamp Fire History

Understanding hydrologic controls on fire vulnerability is particularly important in southeastern USA peatlands, like the Great Dismal Swamp (GDS), where pervasive hydrologic alteration and recent large-scale fires have occurred. The GDS is a palustrine forested peatland that has been substantially altered since colonial times. GDS once extended across approximately 500,000 ha with up to 5 m deep peat soils (Osborn, 1919). GDS forests were characterized by a mosaic of cypress (*Taxodium* spp.), tupelo (*Nyssa* spp.), pond pine (*Pinus serotina*), and Atlantic White-cedar (*Chamaecyparis thyoides,* hereafter cedar) stands (Legrand Jr, 2000). From the late 1700s to the early 1900s, GDS was ditched and drained to make it accessible for timber harvesting (Levy, 1991; Legrand Jr, 2000). In the 1970s, GDS became the 45,000 ha Great Dismal Swamp National Wildlife Refuge, preserved and managed as habitat; however, the historical hydrological alterations have had a lasting effect on GDS ecosystem functions. GDS drainage resulted in lowered water levels leaving peat exposed, which rapidly increased decomposition and fire vulnerability, resulting in carbon loss.

Fire at GDS has historically been an important natural disturbance. In pond pine (*Pinus serotina*)- dominated pocosin systems, fire killed competing vegetation and caused the release of seeds from serotinous pine cones, allowing pocosin vegetation to reestablish and dominate (Legrand Jr, 2000). In cedar stands, fire historically consumed vegetation and some upper peat, but saturated peat protected cedar seed banks and allowed them to regenerate into pure cedar stands (Legrand Jr, 2000; Atkinson et al., 2003). These fire regimes coupled with high water levels generated substantial landscape diversity. However, it is thought that lowered water levels combined with logging resulted in a red maple-dominated overstory (Phipps et al., 1979), and exposed peat soils more susceptible to severe fire (Atkinson et al., 2003).

Two recent catastrophic peat wildfires have occurred at GDS during drought conditions. In June 2008, the South One Fire started when equipment caught fire and ignited soils, ultimately burning 1,980 ha over 4 months. The South One Fire resulted in complete overstory tree mortality, converting closed canopy forest to herbaceous marsh. In August 2011, the Lateral West Fire was ignited by lightning and spread within the 2008 fire scar, once again igniting the underlying peat soil. After 4 months, the Lateral West Fire burned 2,500 ha, released 1.10 Tg of carbon, and consumed an average of 0.46 m of peat soil depth with 1 m deep burns in some places (Reddy et al., 2015). As a result, hydrologic ditch control structures are currently being

installed and repaired to better manage water levels at GDS, with the goal of reducing such catastrophic fire vulnerability and restoring resilient vegetative communities. A better understanding of hydrologic controls on peat properties and associated fire vulnerability is needed to fully utilize hydrology as a management tool to reduce fire vulnerability.

Purpose of the Study

To evaluate short- and long-term hydrologic controls on peat fire vulnerability and associated peat properties at GDS, we coupled continuous hydrologic data, peat property characterization, and laboratory smoldering tests. From our conceptual model of feedback between soil wetness and fire vulnerability (Figures 2, 15), we expected (H3) peat at higher long-term water levels to have lower bulk density and mineral content and thus higher soil moisture burn thresholds (i.e., burn under wetter conditions). However, we also expected that peat moisture holding capacities would be higher with increased long-term wetness, thereby potentially reducing the likelihood that burn thresholds will be passed (H3). Lastly, we predicted that wetter sites would have lower fire vulnerabilities through the integrated effects of site-specific soil moisture thresholds, moisture holding capacities, and short-term water level dynamics (H4). In our overall approach to this objective, we used a three-step method. First, we used a complimentary dataset to evaluate relationships between hydrologic regime and peat soil characteristics (i.e., bulk density, carbon and mineral content). Second, we sampled soil across a hydrologic gradient and performed laboratory analyses to document site-specific threshold soil moisture values for smoldering and moisture holding capacities. Lastly, we combined those identified thresholds with continuous water level data to explore temporal trends in burn probabilities across our sampled sites.

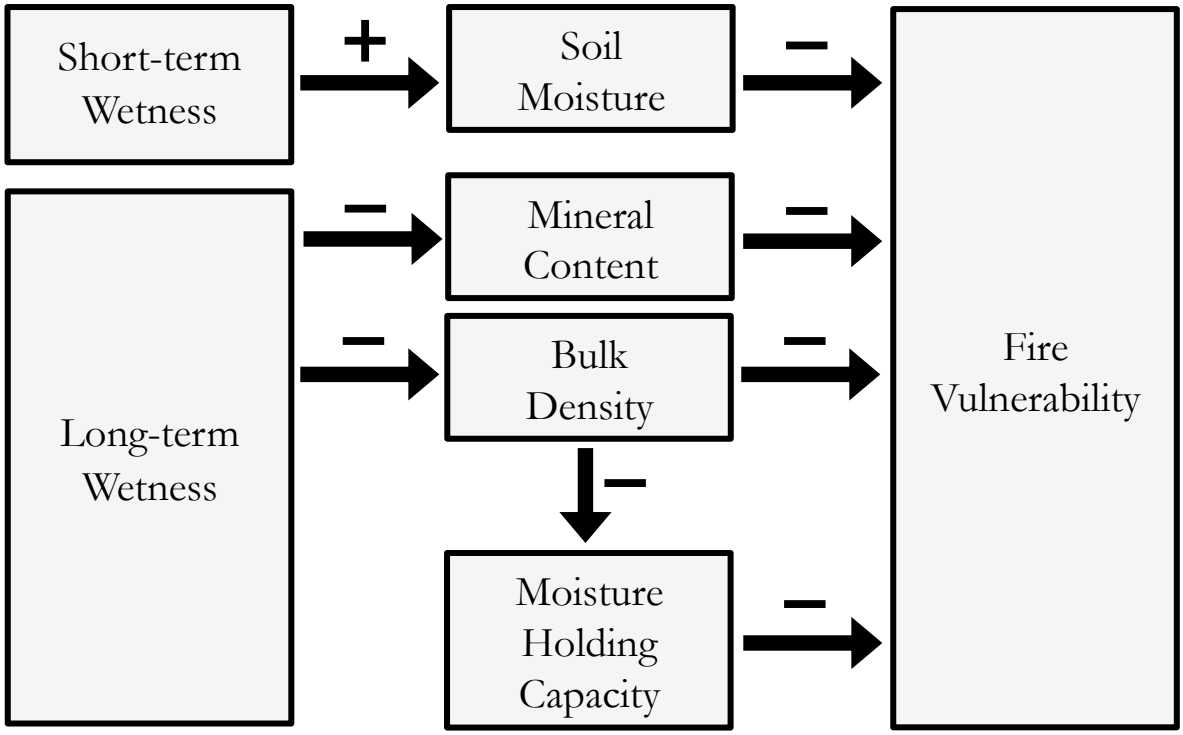


Figure 15. Conceptual model depicting hydrology's short- and long-term influences on peat properties and subsequent fire vulnerability.

3.3 Materials and Methods

3.3.1 Site Description

In summer 2016, we established sites in the northeastern corner of the Great Dismal Swamp National Wildlife Refuge (GDS). GDS is a freshwater, forested peatland covering 45,000 ha in the coastal plain of southeastern Virginia and northeastern North Carolina, USA (36°42’28”N, 76°23’46”W). The climate is temperate with long, humid summers and mild winters (Lichtler and Walker, 1974). Average annual precipitation is 109 cm at Norfolk, VA (Francis, 1959; Lichtler and Walker, 1974). Maple-gum (*Acer-Nyssa*) is the dominant forest cover type (Levy, 1991). Soils are predominantly hydric and organic soils. NRCS Web Soil Survey soil type classifications are provided in Table 9. Despite GDS largely considered as a peatland, Haplosaprists are not technically considered peat, but instead muck due to advanced decomposition. This suggests that GDS soils can deviate from their often considered peat soil characterization, or either potential inaccuracies in the Web Soil Survey classification. Also, SBE is classified as an ultisol, highlighting further variation across the swamp. However, going

forward, we broadly refer to GDS as a peatland following other peer-reviewed GDS studies (e.g., Osborn, 1919; Sleeter et al., 2017).

We selected four sites along an observed wetness gradient (F. Wurster, GDS Hydrologist, personal observation). Sites are referred to using site codes, which reflect locations relative to adjacent access roads/ditches (Table 9). Wells were established at each site at least one year prior to sampling to provide continuous 15-minute water level data.

Table 9. List of sites, site codes used to refer to sites, and site soil classification from Web Soil Survey.

Site Name	Site Code	Soil Classification
West of Rosemary Ditch	WRM	Typic Haplosaprist
West of Portsmouth Ditch	WPM	Typic Haplosaprist
South of Big Entry Ditch	SBE	Typic Umbraquult
East of East Ditch	EED	Typic Haplosaprist

3.3.2 Sample Collection

Soil samples were collected near the wells at each site. To maintain field bulk density, we first cut the root mat with hand tools and removed to expose underlying peat. The root mat was easily distinguishable from peat due to the root mat's lighter color and higher abundance of living roots, but varied in depth from ca. 5 to 20 cm. A flat edge, large diameter corer (diameter D=15 cm) was used to cut a 5 cm deep circle vertically down into the peat, yielding a sample volume of 930 cm^3. A PVC pipe of identical dimensions as the corer was fit into the vertical cut to house the sample and protect the soil structure. A hand tool was used to cut the bottom of the sample horizontally and free it from underlying soil. Samples were carefully removed, reinforced with cardboard, and sealed in plastic bags. All samples were stored in a cooler at 4°C until analyzed to minimize decomposition.

3.3.3 Lab Methods

Peat Soil Properties

Samples (3 per site) were analyzed for bulk density, organic matter content, and carbon content. Analysis took place in the Latham Forest Soils and Hydrology Lab at Virginia Tech. Samples were oven-dried at 105°C until they reach a constant dry weight. Bulk density was calculated by dividing dry weight by sample volume (via corer dimensions). Oven dry samples were ground with mortar and pestle, and then subsampled for combustion in an electric muffle

furnace at 500°C for 24 hours. Loss on ignition (i.e., mineral fraction; %) was calculated by dividing weight after combustion by oven dry weight of precombusted sample. Carbon content (g/g) was measured using a CN Elemental Analyzer (Shimada et al., 2001).

In complimentary work, additional samples were collected at 5 additional locations (not at wells) per site (yielding 20 sampling locations with replicates of 3) and also analyzed for bulk density and organic matter content. We explored linear regressions between these peat properties and mean water levels (interpolated via well and elevation data, see Chapter 2).

Smoldering Threshold Analysis

To identify site-specific threshold soil moisture values at which peat will ignite and burn, smoldering tests were conducted in the Forest Harvesting Lab at Virginia Tech, using eighteen samples collected at well locations from each of the four sampled sites. Sample moisture content was manipulated by air-drying samples (covered with cheese cloth) on an open rack over time. Smoldering testing, following methods reported by Frandsen (1997), took place in 10 × 10 × 10 cm (inner dimensions) open-topped combustion frames lined with cement board. The circular sample was cut into a 10 × 10 × 5 cm square and placed in the combustion frame. The remaining sample was weighed, oven-dried at 65 °C for two days, and weighed again to find gravimetric moisture content (g H_2O/g dry soil).

To estimate ignition thresholds, we used a hot iron (electric coal starter) held to the peat sample in the combustion frame. After 5 minutes, the iron was removed. After an additional 5 minutes, if any portion of the sample was still independently smoldering, the sample was categorized as "burned". A binary response was recorded: burn (1) or no burn (0). Moisture content was manipulated to identify and focus around observed burn threshold moisture content.

For each site, data were fit with a logistic regression ("glm") function in R (R Core Team, 2016) to quantify smoldering probability, P(burn), at each moisture content. Using developed site-specific equations (eq. 1), we solved for gravimetric moisture content (*GMC*) for 50% burn probability (hereafter GMC_{burn}) using (eq. 2), where B_o and B_1 are unitless fitted parameters:

[1] $$P(burn) = \frac{1}{1+e^{-[B_0+B_1(GMC)]}}$$

[2] $$GMC = \frac{-\ln\left(\frac{1}{P(burn)}-1\right)-B_0}{B_1}$$

Peat Soil Moisture Holding Capacity

To quantify moisture holding capacity across sites, we constructed site-specific moisture release curves that describe the relationship between water tension and moisture content of a soil. Moisture release curves for each sampling location were developed using four replicate samples from each site. Curves were developed using a pressure plate extraction method (Dane and Hopmans, 2002) in the Smyth Soil Physics Lab at Virginia Tech. A subsample was taken from each field sample using a soil ring (D=5 cm, H=5 cm). Saturated samples were weighed and placed on a porous ceramic plate. Inside a pressure chamber, positive pressure was added in three steps (0.33 bar, 1 bar, and 3 bar). At each pressure step, the samples were weighed after reaching soil moisture equilibration (i.e., no more water leaving the chamber). After the last pressure step, samples were oven dried and weighed to determine dry soil mass, which was then used to calculate gravimetric moisture content (g H_2O/g dry soil) at each pressure step. The points were fit with the Brooks and Corey (1964) model (eq. 3) to calculate moisture release curves and quantify moisture holding capacity, where θ_{sat} is defined as moisture content at saturation, λ is a unitless variable related to pore size distribution, and h_b is the air entry matric potential (cm):

[3] $$GMC = \theta_{sat}\left(\frac{h_b}{h}\right)^{\lambda}$$

[4] $$h = \frac{h_b}{\left(\frac{GMC}{\theta_{sat}}\right)^{(1/\lambda)}}$$

We solved for water tension (h) as a function of gravimetric moisture content (GMC; eq. 4), allowing us to estimate site-specific tension burn thresholds (h_{burn}) using 50% burn probability (GMC_{burn}). Assuming hydrostatic equilibrium, h_{burn} represents the water table depth at which surface peat will be at GMC_{burn}. As such, we used continuous water level records at each sampling site to calculate the proportion of time over a 16-month period that the distance from water table to surface exceeded h_{burn}.

If hydrostatic equilibrium is not maintained over daily timescales (e.g., due to evapotranspiration losses), soil moisture values could approach GMC_{burn} even with a relatively shallow water table (i.e., distance from water table to surface less than h_{burn}). Capillary fringe height represents the deepest water table depth at which the surface soil will remain saturated. Once the water level relative to the soil surface is lower than capillary fringe height, the surface

soil can become decoupled from the water table and unsaturated (Brady and Weil, 2008). As such, we calculated the proportion of time a site had water levels deeper than site-specific capillary fringe heights (via moisture release curve parameters) as a *conservative* estimate of temporal burn vulnerability. We estimated site-specific capillary fringe heights, Λ, using the Brooks and Corey parameters (eq. 5) to solve the equation developed by Raats and Gardner (1971):

$$\Lambda = \frac{-h_b(3\lambda + 2)}{(3\lambda + 1)} \quad [5]$$

3.3.4 Uncertainty Analysis

We compared burn threshold water contents (GMC_{burn}) and tensions (h_{burn}) across sites to evaluate the integrated effects of peat properties (and thus hydrologic regime) on burn probability. As part of this comparison, we quantified uncertainty of GMC_{burn} and h_{burn} calculations using a resampling method in R (R Core Team, 2016). We randomly sampled model parameters from eq. 2 and 4 (i.e., B_0, B_1, λ, h_b) 1000 times from 90% model confidence intervals using standard methods, yielding means and standard deviations at each site for both GMC_{burn} and h_{burn} over 1000 simulations.

3.4 Results

We explored hydrologic controls on peat fire vulnerability at GDS by evaluating hydrologic regime, peat properties, soil moisture burn thresholds, and moisture holding capacity across four soil transects that captured a gradient of hydrologic regime (Table 10).

3.4.1 Peat Soil Properties

Using our complimentary data set that captured 5 sampling locations per site, we evaluated trends between soil properties and mean water level. For soil property analysis, SBE was a clear outlier due to its mineral soil type; thus, we examined relationships with (Figure 16a,c) and without SBE (Figure 16b,d). Excluding SBE, and as expected, bulk density decreased with increasing mean water level (Figure 16b). Unexpectedly, however, organic matter content also decreased with increased wetness, albeit weakly ($R^2 = 0.16$; Figure 16d), possibly due to differences in organic matter inputs and site productivity.

We also separately evaluated peat properties at our four sampling locations used for smoldering testing and moisture release curve analysis (Table 10). Excluding SBE, we found site mean bulk densities ranging from 0.20 to 0.26 g cm^{-3}, equivalent mean organic matter contents (81%), and carbon contents ranging from 0.08 to 0.12 g cm^{-3} (Table 10). SBE had the highest bulk density (0.53 g cm^{-3}), the lowest organic matter (20%), and the lowest carbon content (0.03 g cm^{-3}), highlighting clear differences at SBE, likely due to its mineral soil type.

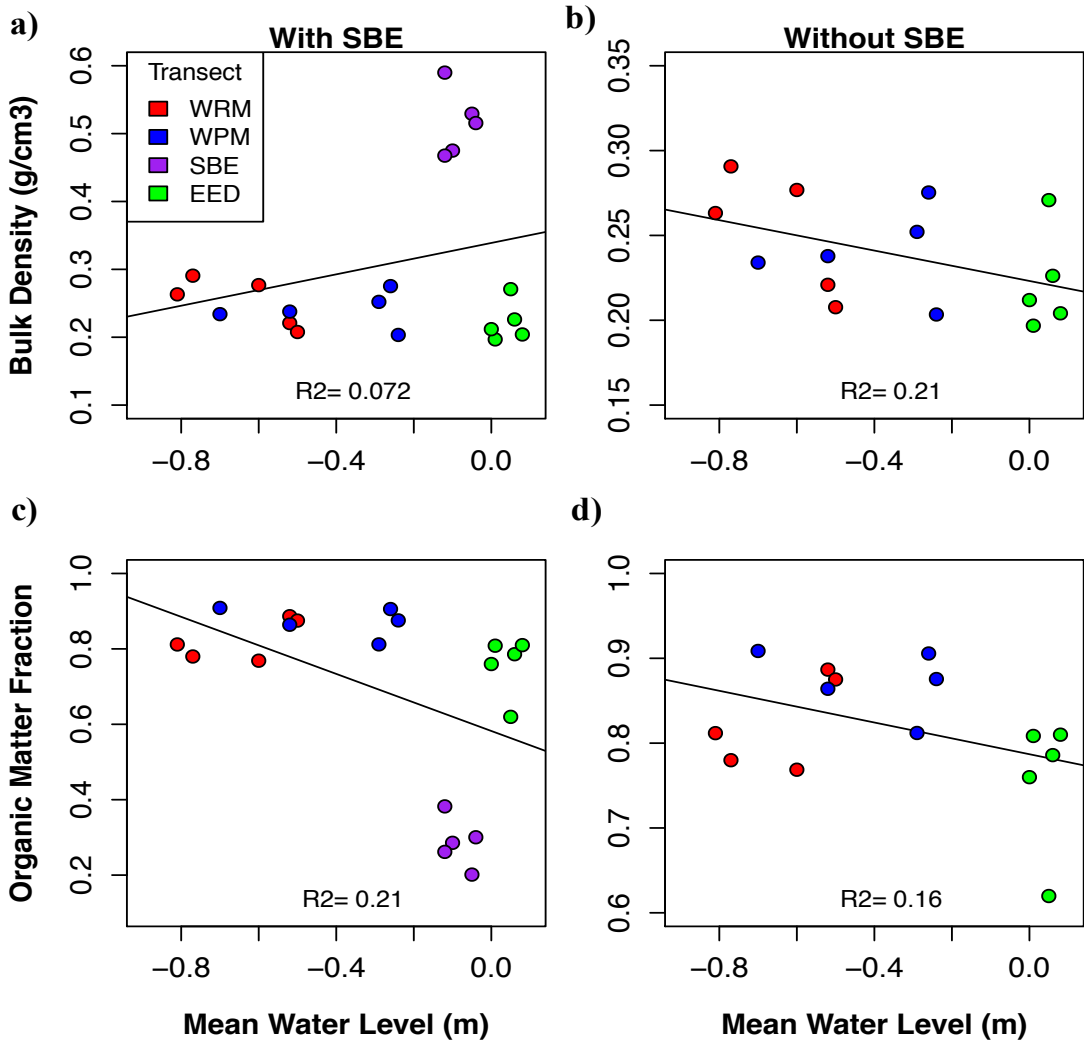


Figure 16. Complimentary data showing a-b) bulk density and c-d) organic matter content vs. mean water level using 5 plots from each site with three replicates (N=60). SBE is excluded in b) and d) due to its differing soil type.

Table 10. Mean (standard deviation) bulk density, organic fraction, carbon content, and mean water level at the four sampling locations used in smoldering testing and moisture release curve analysis.

Site	Bulk Density (g/cm^3)	Organic Fraction (g/g)	Carbon Content (g/cm^3)	Mean Water Level (m)
WRM	0.26 (0.03)	0.81 (0.03)	0.11 (0.01)	-0.81 (0.35)
WPM	0.25 (0.02)	0.81 (0.06)	0.12 (0.003)	-0.29 (0.26)
SBE	0.53 (0.01)	0.20 (0.02)	0.03 (0.02)	-0.05 (0.28)
EED	0.20 (0.02)	0.81 (0.02)	0.08 (0.003)	0.01 (0.09)

3.4.2 Smoldering Thresholds

Using 18 samplings at each site, ignition testing yielded 18 binary responses of burn (1) or no burn (0) per site. With these data, we developed site-specific logistic relationships to predict burn probability (%) at a given moisture content (Figure 17, Table 11). Using the gravimetric moisture content value at 50% burn probability (GMC_{burn}), we compared sites by wetness and soil properties. As expected, at WRM, WPM, and EED, we found increasing GMC_{burn} (Table 11) with increased mean water level and decreased bulk density; that is, the wettest site (EED) was most vulnerable to ignite and burn at the highest gravimetric moisture content (290%). SBE had the lowest GMC_{burn} (i.e., it requires drier conditions to burn), concordant with its highest bulk density and lowest organic matter content.

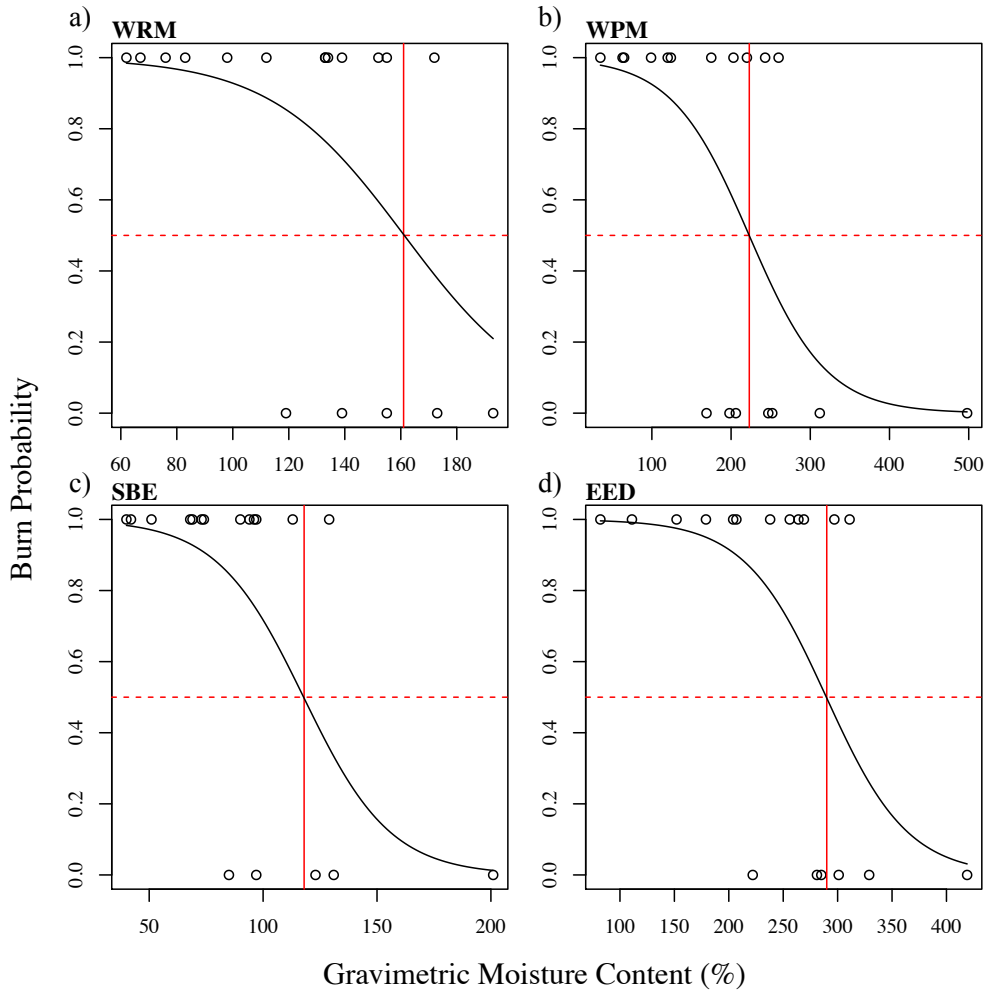


Figure 17. Logistic regression of burn probability as a function of gravimetric moisture content (%) at a) WRM, b) WPM, c) SBE, d) EED. The solid red line shows GMC_{burn} (i.e., the moisture content at which the 50% burn probability occurs).

Table 11. Modeled parameters in equation 2 for burn probability logistic regressions at each site, along with gravimetric moisture content (%) solved for 50% burn probability (GMC_{burn}).

Site	B_0	B_1	GMC_{burn} (%)
WRM	6.74	-0.042	161
WPM	4.55	-0.020	223
SBE	6.16	-0.052	118
EED	7.70	-0.027	290

3.4.3 Moisture Holding Capacities

To explore differences in moisture holding capacities across sites and to link soil moisture burn thresholds with their associated tensions (h_{burn}), we developed site-specific moisture release curves using the Brooks and Corey model (Figure 18). As expected, at WRM, WPM, and EED, we found an increase in moisture holding capacity with increasing wetness and decreasing bulk density. SBE had the lowest moisture holding capacity and the highest bulk density. Using these curves, we calculated site-specific burn tensions (h_{burn}; Table 12) required to yield site-specific values of GMC_{burn} (Table 11). EED had the highest burn tension (h_{burn} = 8.1 m), with much lower values (h_{burn} < 0.2 m) at all other sites (Table 12). We also used developed moisture release curves to estimate site-specific capillary fringe heights, which represent height of saturated conditions (thus no fire vulnerability) above water table. Similar to h_{burn}, capillary fringe height was highest at EED, consistent with its higher moisture holding capacity (Figure 18), and lowest at the drier sites (WPM, WRM; Table 12).

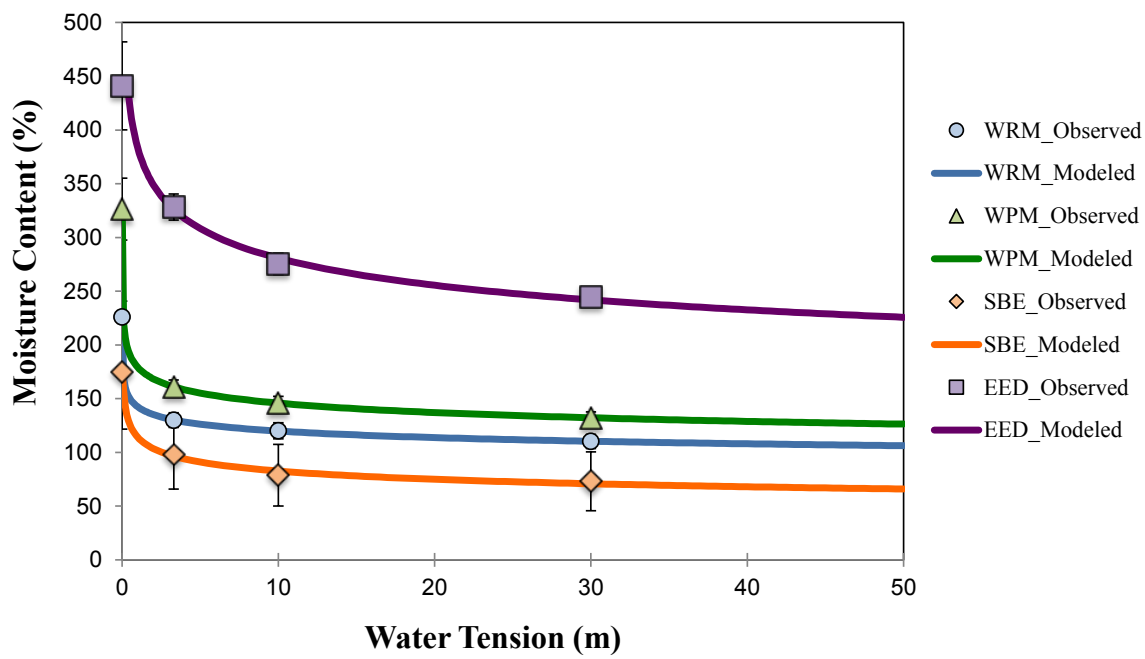


Figure 18. Moisture release curves developed for each site using the Brooks and Corey model (Brooks and Corey, 1964).

Table 12. Model parameters in equation 4 for moisture release curves at each site along with the tensions (h_{burn}) for soil moisture burn thresholds at 50% probability and estimated capillary fringe heights (CF; via eq. 5).

Site	Θ_{sat} (%)	λ	h_b (m)	h_{burn} (m)	CF (m)
WRM	226	0.0749	0.0021	0.1941	0.0038
WPM	326	0.0893	0.0012	0.0877	0.0022
SBE	175	0.1402	0.0472	0.8117	0.0805
EED	441	0.1353	0.3545	8.083	0.6066

3.4.4 Uncertainty and Site Comparisons of Burn Vulnerability

Using our developed equations from the smoldering tests (logistic regressions) and moisture release curves (Brooks and Corey model), we solved for burn threshold values for both GMC_{burn} and h_{burn} at each site. We resampled equation parameters within 90% confidence intervals to estimate uncertainty around threshold values (Figure 19). Uncertainty was largely due to the logistic regressions, which then propagated through the h_{burn} values (i.e., moisture release curve equations had less parameter uncertainty). Given these uncertainties, EED and WPM had the highest burn GMC_{burn} values suggesting highest burn vulnerability when considering soil moisture alone (Figure 19). However, when also considering moisture holding capacity, EED had the highest h_{burn} value, indicating higher required tension for burn and thus a lower burn vulnerability. The h_{burn} threshold describes the required water table depth to reach GMC_{burn}, while assuming hydrostatic equilibrium. As such, we calculated percent time each site's water levels were below such water table depth thresholds (via site mean h_{burn} values) over the 16-month observation period. Because hydrostatic equilibrium does not necessarily occur in the field, we also calculated the proportion of time that water levels at each site were below capillary fringe heights, representing an alternative (and more conservative) estimate of temporal burn probability. WRM water levels were always lower than both thresholds (h_{burn} and capillary fringe heights; Table 13), suggesting it was always at risk to burn. In contrast, EED water levels were always higher than both thresholds, suggesting the site was never at risk to burn. WPM and SBE intermittently experienced water levels crossing both thresholds. Differences in temporal variation in burn vulnerability (via water level below site-specific h_{burn}) across sites are clearly demonstrated in Figure 20.

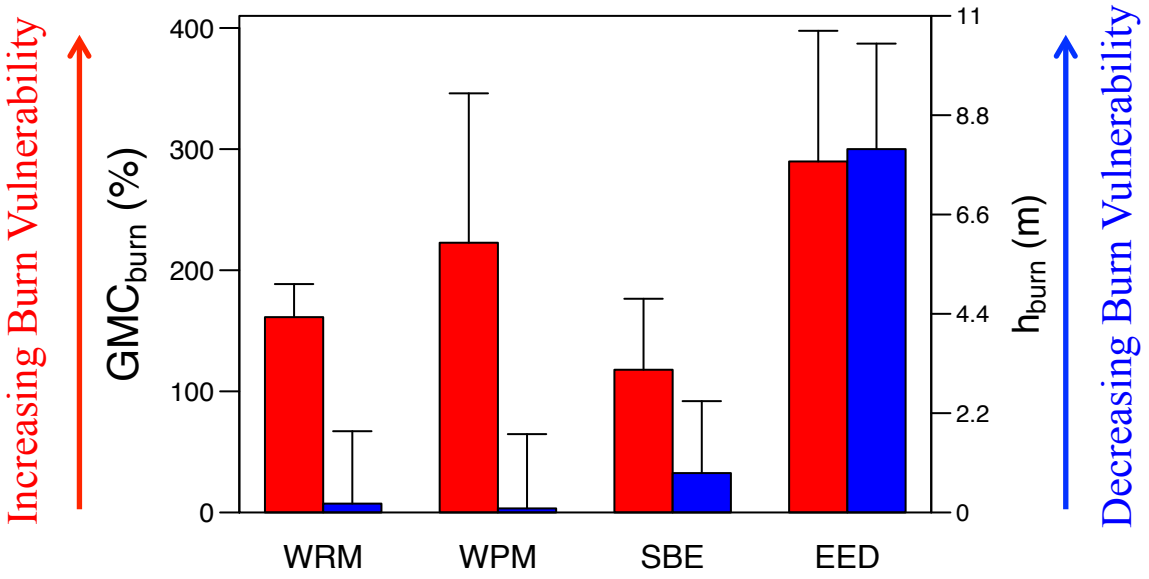


Figure 19. Comparison of mean burn threshold moisture content (GMC_{burn}) and burn tension (h_{burn}) across sites along with estimated uncertainty using 1000 simulations (shown with error bars for 1 standard deviation).

Table 13. Percent time that water levels (WL) at each site were below the thresholds for capillary fringe heights (CF) and burn tension (h_{burn}).

	WRM	WPM	SBE	EED
Time WL < CF (%)	100	86	32	0
Time WL < h_{burn} (%)	100	79	4	0

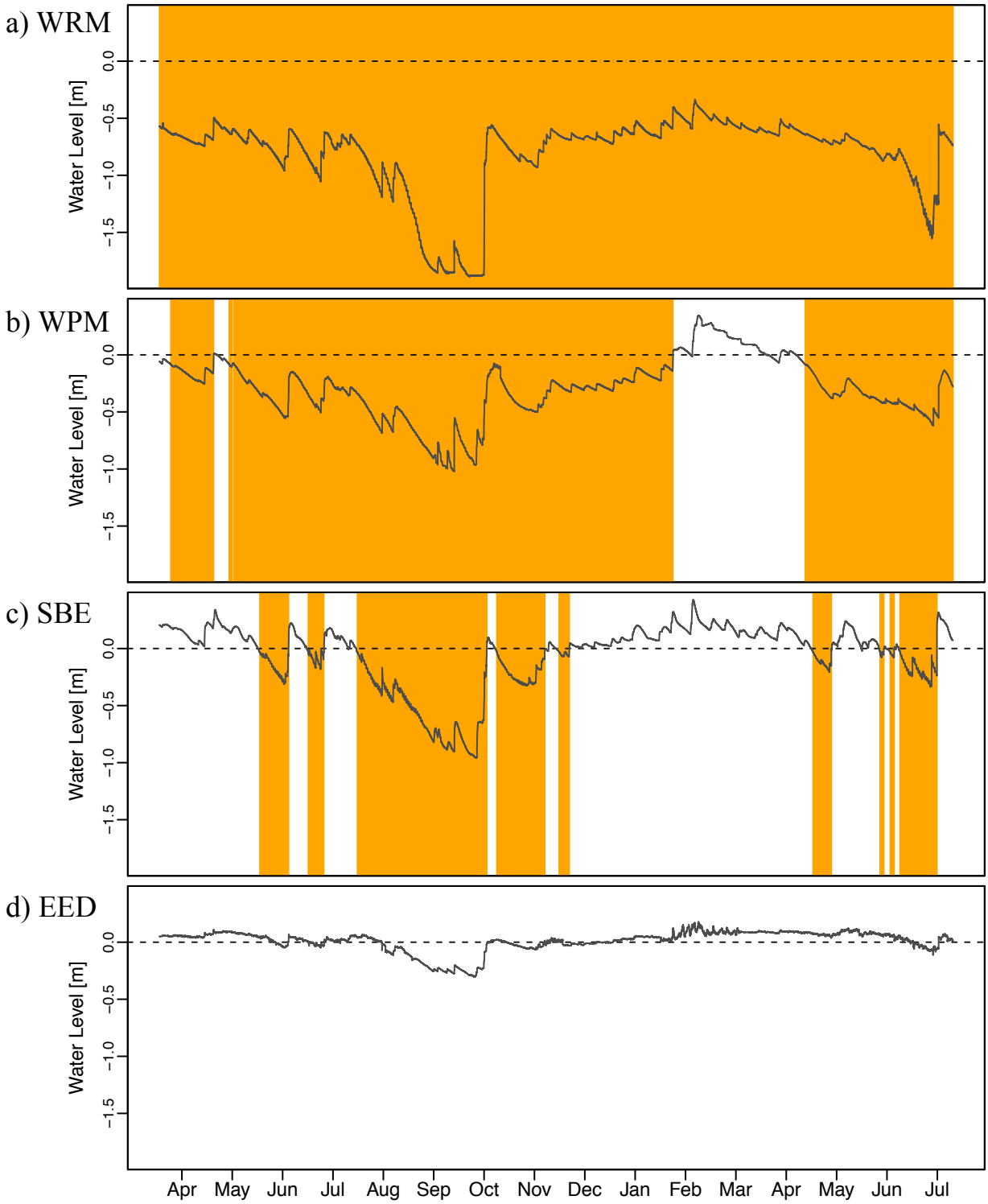


Figure 20. Time series of sub-daily water levels at a) WRM, b) WPM, c) SBE, d) EED. Orange shading indicates periods when water levels were below the site-specific burn threshold (h_{burn}) and vulnerable to burn. Dashed black line denotes ground surface.

3.5 Discussion

In this work, we sought to explore hydrologic controls on peat fire vulnerability, testing two hypotheses:

> H3) Long-term hydrologic regime influences peat properties (bulk density, organic matter, and moisture holding capacity) that together create variation in fire vulnerability across sites.
>
> H4) Increased wetness will decrease fire vulnerability through integrated effects of site-specific soil moisture burn thresholds, moisture holding capacity, and water level dynamics.

To first explore hydrologic controls on peat fire, we used evaluated relationships between mean water level and peat properties thought to influence fire vulnerability. To do so, we used a larger complimentary dataset spanning 20 locations varying in hydrologic regime. As expected (H3), with the exception of SBE, bulk density decreased with increased wetness (Figure 16b), consistent with previous work (Chambers et al., 2011). In contrast, we found decreasing organic matter content with increased wetness when removing SBE (Figure 16d). However, this negative correlation with wetness was weak and highly leveraged by one outlier at EED; removing this outlier results in a non-significant relationship (data not shown), suggesting other possible influences (e.g., quantity or lability of vegetation inputs; Chambers et al., 2011). Soil type at SBE (see Table 9) clearly differed from the other sites, with higher bulk density and lower organic matter content. At WRM, WPM, and EED, bulk densities ranged between 0.18 to 0.29 g cm^{-3}, and organic matter ranged from 75% to 85%, similar to global peatland ranges (bulk density = 0.02 to 0.3 g cm^{-3}; organic matter = 50 to 100%; Verry et al., 2011). At just our sampling locations for smoldering and moisture holding capacity analysis (only one per site), WRM, WPM, and EED samples had similar organic matter content (all with mean of 81%) and (slightly) decreasing bulk density with wetness. Although we did not capture a large gradient in soil properties across these three sites, the endmember of SBE afforded important insights regarding peat property controls on fire vulnerability. Specifically, SBE had the highest mineral content, lowest organic matter content, and highest bulk density.

Burn vulnerability is often quantified via soil moisture burn thresholds, which help to document variability across sites and how peat properties influence such variability. Across our sites, soil moisture burn thresholds for 50% burn probability (GMC_{burn}) clearly varied (Table 11). EED had the highest GMC_{burn} (290%), while SBE had the lowest (118%). A high GMC_{burn}

suggests EED would burn even when very wet, which comports with its high organic content and low bulk density. Alternatively, SBE may not ignite until a much lower moisture content is reached, due to its high mineral content and bulk density. Comparing these two sites alone, the trend of decreased fire vulnerability (via soil moisture burn thresholds) with increased mineral content and bulk density is consistent with our prediction (H3) and other studies (Hartford, 1993; Frandsen, 1997; Reardon et al., 2007; Benscoter et al., 2011). Excluding SBE, the other three sites had similar organic matter content but decreasing bulk density with wetness (Table 10); across these sites, the expected negative relationship between bulk density and fire vulnerability was also observed (Table 11).

Soil moisture burn thresholds widely vary across systems and studies. Similar to our findings, Reardon et al. (2007) found GMC_{burn} values in southeastern USA peat soils between 140 to 240%. In hardwood swamp soils with similar mineral content as our study (~20%), Frandsen (1997) found a GMC_{burn} of 76%, lower than our observed ranges and values in Reardon et al. (2007). Differences in studies are likely due to method variation. Our developed approach was conservative, in that a burn/no burn response was determined only 5 minutes after the heat source was removed, neither waiting for the sample to be consumed nor measuring consumption. Nonetheless, the consistent method applied across our sites documented clear relative differences in GMC_{burn} within one peatland system. Notably, most studies have focused on differences across regional peatland systems. Our findings emphasize that local variation should be addressed both in future work and in fire prediction protocols. For example, fire prediction at GDS currently relies on soil moisture monitoring using one system-wide soil moisture threshold that identifies fire risk (F. Wurster, GDS Hydrologist, personal communication). More work at GDS, and in other peatland systems, should seek site-specific relationships between easily measured parameters (e.g., bulk density) and soil moisture burn thresholds to better inform such fire risk monitoring. Our work was limited in sampled locations and in the resulting range of mineral contents and bulk densities, highlighting future research needs at GDS.

While soil moisture burn thresholds varied across sites, site variation in moisture holding capacity together with variation in soil moisture burn thresholds determines the required antecedent wetness for fire vulnerability. To quantify moisture holding capacity, we developed moisture release curves, allowing comparison of moisture contents between sites at the same water tension and showing clear site differences in moisture holding capacity (Figure 18). EED

had the highest moisture holding capacity, while SBE had the lowest, comporting with bulk density differences and supporting H3. Comparing GMC_{burn} alone to indicate fire vulnerability suggests that EED would burn at the highest soil moistures, followed by WPM, WRM, and SBE (Table 11; Figure 17). However, by taking site-specific GMC_{burn} values and estimating the water tension (h_{burn}) required to create those moisture contents (via moisture release curves), site differences in fire vulnerability substantially changed. EED had the highest h_{burn} value, indicating that EED requires the deepest water tables to reach its GMC_{burn} threshold (Figure 19) and critically underscoring the need to consider both soil moisture thresholds and moisture holding capacities. To improve confidence in our estimated thresholds (see error bars in Figure 19), more samples per site should be tested to reduce uncertainty in logistic regression relationships. Moreover, additional tension measurements should be taken at lower (< 3 m) tensions to better parameterize moisture release curves within ranges of h_{burn} tensions.

To integrate both short- and long-term hydrologic effects on burn vulnerability, we evaluated water level time series at each site, identifying times when water tables crossed two different thresholds of fire vulnerability: h_{burn} and capillary fringe hight (Table 13; Figure 20). The former assumes hydrostatic equlibrium, which is often not the case due to diurnally varying inputs/outputs of soil moisture (e.g., precipitation, evapotranspiration; Brady and Weil, 2008). As such, we included capillary fringe heights as an alternative and more conservative threshold. Supporting H4, we found that burn temporal probablities using both thresholds decreased with wetness (Table 13). Our findings suggest that WRM was always at risk to burn, while EED maintained saturated conditions at surface (via capillary fringe) and thus never reached conditions of burn vulnerability. Notably, these predictions integrate site-specific soil moisture burn thresholds, moisture holding capacities, and water level dyanmics.

Our work points to research needs at GDS and temperate peatlands in general. More specifically, at GDS, additional study sites are needed to better link measured peat parameters to soil moisture burn thresholds and burn tensions. Such information is important to adjust now constant soil moisture burn thresholds used across GDS locations for fire risk warning. More broadly, research is needed to better address the hydrologic controls on peat properties that influence soil moisture burn thresholds, but especially those that influence tensions required to reach such thresholds. Critically, this role of moisture holding capacity is not currently recognized. Ultimately, research should seek predictive models that couple water level

monitoring and measured soil parameters to predict surface peat fire vulnerability over both time and space.

Conclusions

Our findings highlight long-term hydrologic influences on peat properties that in turn influence peat fire vulnerability as a function of daily water level dynamics. As such, research findings will help inform both hydrologic restoration and fire monitoring at GDS and, more broadly, advance our understanding of integrated interactions among hydrologic regime, peat properties, and fire vulnerability in temperate peatlands.

Literature Cited

Atkinson, R. B., J. W. DeBerry, D. T. Loomis, E. R. Crawford, R. T. Belcher, R. B. Atkinson, R. T. Belcher, D. A. Brown, and J. E. Perry. 2003. Water Tables in Atlantic White Cedar Swamps: Implications for Restoration. In *Atlantic White Cedar Restoration Ecology and Management, Proceedings of a Symposium. Christopher Newport University, Newport News*, 137–150.

Benscoter, B. W., D. K. Thompson, J. M. Waddington, M. D. Flannigan, B. M. Wotton, W. J. De Groot, and M. R. Turetsky. 2011. Interactive Effects of Vegetation, Soil Moisture and Bulk Density on Depth of Burning of Thick Organic Soils. *International Journal of Wildland Fire* 20, 3: 418–429.

Boelter, D. H. 1968. Important Physical Properties of Peat Materials.

Brady, N. C., and R. R. Weil. 2008. *The Nature and Properties of Soils*. 14th ed. Prentice-Hall Inc. Upper Saddle River, New Jersey.

Brooks, R. H., and A. T. Corey. 1964. Hydraulic Properties of Porous Media and Their Relation to Drainage Design. *Trans. ASAE* 7, 1: 26–28.

Casey, W. P., and K. C. Ewel. 2006. Patterns of Succession in Forested Depressional Wetlands in North Florida, USA. *Wetlands* 26, 1: 147–160.

Chambers, F.M., D.W. Beilman, and Z Yu. 2011. Methods for Determining Peat Humification and for Quantifying Peat Bulk Density, Organic Matter and Carbon Content for Palaeostudies of Climate and Peatland Carbon Dynamics." *Mires and Peat* 7, 7: 1–10.

Dane, J. H., and J. W. Hopmans. 2002. 3.3.2.4 Pressure Plate Extractor. *Methods of Soil Analysis: Part 4 Physical Methods*, 671–973.

Francis, H. E. 1959. Soil Survey for Norfolk County, Virginia, 53.

Frandsen, W. H. 1987. The Influence of Moisture and Mineral Soil on the Combustion Limits of Smoldering Forest Duff. *Canadian Journal of Forest Research* 17, 12: 1540–1544.

Frandsen, W. H. 1997. Ignition Probability of Organic Soils 27, 1471–1477.

Gorham, E. 1991. Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic Warming. *Ecological Applications* 1, 2: 182–195.

Hartford, Roberta A. 1993. Smoldering Combustion Limits in Peat as Influenced by Moisture Mineral Content and Organic Bulk Density.

Hugron, S., J. Bussières, and L. Rochefort. 2013. Tree Plantations within the Context of Ecological Restoration of Peatlands: Practical Guide. *Peatland Ecology Research Group, Université Laval, Québec, Québec, Canada*.

Legrand Jr, H. E. 2000. The Natural Features of Dismal Swamp State Natural Area, North Carolina. *The Natural History of the Great Dismal Swamp, Omni, Madison, Wisconsin*, 41–50.

Levy, G. F. 1991. The Vegetation of the Great Dismal Swamp: A Review and an Overview. *Virginia Journal of Science* 42, 4: 411–418.

Lichtler, W., F., and P. Walker. 1974. Hydrology of the Dismal Swamp, Virginia-North Carolina. *Geological Survey - Water Resources Division*, no. 74–39.

Osborn, C. C. 1919. Peat in the Dismal Swamp, Virginia and North Carolina. *Contribution to Economic Geology* Bull 711, 4.

Page, S. E., J. O. Rieley, ØW Shotyk, and D. Weiss. 1999. Interdependence of Peat and Vegetation in a Tropical Peat Swamp Forest. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 354, 1391: 1885–1897.

Page, S. E., F. Siegert, J. O. Rieley, H. V. Boehm, A. Jaya, and S. Limin. 2002. The Amount of Carbon Released from Peat and Forest Fires in Indonesia during 1997. *Nature* 420, 6911: 61–65.

Phipps, R. L., D. L. Ierley, and C. P. Baker. 1979. Tree Rings as Indicators of Hydrologic Change in the Great Dismal Swamp, Virginia and North Carolina. US Geological Survey, Water Resources Division.

Poulter, B., N. L. Christensen, and P. N. Halpin. 2006. Carbon Emissions from a Temperate Peat Fire and Its Relevance to Interannual Variability of Trace Atmospheric Greenhouse Gases. *Journal of Geophysical Research: Atmospheres* 111, D6.

R Core Team. 2016. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Raats, P. A. C., and W. R. Gardner. 1971. Comparison of Empirical Relationships between Pressure Head and Hydraulic Conductivity and Some Observations on Radially Symmetric Flow. *Water Resources Research* 7, 4: 921–928.

Reardon, J., R. Hungerford, and K. Ryan. 2007. Factors Affecting Sustained Smouldering in Organic Soils from Pocosin and Pond Pine Woodland Wetlands. *International Journal of Wildland Fire* 16, 1: 107–118.

Reddy, A. D., T. J. Hawbaker, F. Wurster, Z. Zhu, S. Ward, D. Newcomb, and R. Murray. 2015. Quantifying Soil Carbon Loss and Uncertainty from a Peatland Wildfire Using Multi-Temporal LiDAR. *Remote Sensing of Environment* 170: 306–316.

Rein, G., N. Cleaver, C. Ashton, P. Pironi, and J. L. Torero. 2008. The Severity of Smouldering Peat Fires and Damage to the Forest Soil. *Catena* 74, 3: 304–309.

Shimada, S., H. Takahashi, A. Haraguchi, and M. Kaneko. 2001. The Carbon Content Characteristics of Tropical Peats in Central Kalimantan, Indonesia: Estimating Their Spatial Variability in Density. *Biogeochemistry* 53, 3: 249–267.

Sorensen, K. W. 1993. Indonesian Peat Swamp Forests and Their Role as a Carbon Sink. *Chemosphere* 27, 6: 1065–1082.

Turetsky, M. R., B. Benscoter, S. Page, G. Rein, G. R. van der Werf, and A. Watts. 2015. Global Vulnerability of Peatlands to Fire and Carbon Loss. *Nature Geoscience* 8, 1: 11–14.

Usup, A. Y. Hashimoto, H. Takahashi, and H. Hayasaka. 2004. Combustion and Thermal Characteristics of Peat Fire in Tropical Peatland in Central Kalimantan, Indonesia. *Tropics* 14, 1: 1–19.

Verry, E. S., D. H. Boelter, J. Päivänen, D. S. Nichols, T. Malterer, and A. Gafni. 2011. Physical Properties of Organic Soils. *Peatland Biogeochemistry and Watershed Hydrology at the Marcell Experimental Forest (Eds Kolka RK, Sebestyen SD, Verry ES, Brooks KN)*, 135–176.

Watts, A. C., and L. N. Kobziar. 2013. Smoldering Combustion and Ground Fires: Ecological Effects and Multi-Scale Significance. *Fire Ecol* 9, 1: 124–32.

Watts, A. C., C. A. Schmidt, D. L. McLaughlin, and D. A. Kaplan. 2015. Hydrologic Implications of Smoldering Fires in Wetland Landscapes. *Freshwater Science* 34, 4: 1394–1405.

4.0 HYDROLOGIC RESTORATION OF ECOSYSTEM STRUCTURE AND FUNCTION IN THE GREAT DISMAL SWAMP

Hydrologic restoration is coming to GDS in 2016-2017 with the management objectives to increase species diversity, increase carbon storage via peat depth, and decrease fire vulnerability. Our third objective was to inform hydrologic restoration of ecosystem structure and function in GDS. To do so, we conducted two complimentary studies to test developed hypotheses regarding hydrologic influences on vegetation, peat depths, and peat fire vulnerability.

In our first study, we explored hydrologic controls on peat depth, microtopography, and vegetation composition. At higher water levels, we expected (H1) peat to be deepest and microtopography to be most variable. We also expected (H2) that red maple would be less competitive at higher mean water levels, thus increasing tree diversity and desired species (e.g., cedar, cypress, tupelo) abundance. We tested these hypotheses by coupling *in situ* hydrologic monitoring with peat, elevation, and vegetation surveys along a gradient of wetness both at the transect and plot level. We found evidence to support H1 and H2. Specifically, at sites of increased wetness (e.g., higher water levels), we found: 1) thicker peat and more microtopographic variation; 2) lower maple importance; and 3) higher tree species richness.

In our second study, we examined hydrologic controls on peat fire vulnerability and associated peat properties. We expected (H3) long-term hydrologic regime to influence peat properties (bulk density, mineral content, and moisture holding capacity) that collectively determine site variation in fire vulnerability. We also expected (H4) increased wetness to decrease fire vulnerability through integrated effects of site-specific soil moisture burn thresholds, moisture holding capacity, and water level dynamics. We measured *in situ* water level data, peat properties, burn probability as a function of soil moisture, and moisture holding capacity at four sites. Due to differences in soils (more mineral-rich), one site (SBE) served as an endmember in our analyses and is excluded from the following conclusions. We found that wetter sites burn at higher soil moistures but also have higher moisture holding capacities, supporting H3. Burn tension (i.e., h_{burn}; tension necessary to create site-specific soil moisture burn thresholds) is a better representation of how soil moisture and thus smoldering fire

vulnerability is realized in the field. Through integrated analysis of water level time series, capillary fringe heights, and h_{burn} values, we compared the duration (%) that each site was at risk to ignition. Burn vulnerability decreased with wetness (supporting H4), suggesting that the driest site (WRM) was always at risk to burn, and the wettest (EED) never approached conditions for ignition vulnerability.

Together, findings from these two studies demonstrate strong hydrologic controls on GDS ecosystem structure and function. As such, results can be used to begin informing water level management for specific restoration goals. Critically, this research also provides baseline data for comparison with post-restoration monitoring to empirically evaluate the effects of hydrologic restoration on peat depth, microtopography, and vegetation composition. Going forward, continued research across more GDS locations should focus on hydrology-vegetation interactions and spatial variation in burn vulnerability, ultimately guiding adaptive management and restoration in the Swamp.