Lower Roanoke River hydroperiods: Altered hydrology and implications for forest health and species response

by

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Abstract

Hydrology is the principal physical factor governing the ecology of floodplain forests (Gosselink et al. 1990, Poff et al. 1997). When managed hydrology is significantly different from unregulated hydrologic regimes it can fundamentally alter ecosystem processes on the floodplain, resulting in: range shifts of tree species, reduced regeneration, altered recruitment patterns, invasion of new taxa and ultimately changes in community composition (Johnson 1992, Johnson 1994, Johnson et al. 1995, Molles et al. 1998, Nilsson et al. 1991, Nilsson and Jansson 1995, Power et al. 1995, Rood and Mahoney 1990, Toner and Keddy 1997). Interest in assessing previous impacts and predicting future effects of managed hydrology on floodplain vegetation is increasing as restoration of river systems and dam re-licensing becomes an important issue to State and Federal agencies and private conservation organizations (Dahm et al. 1995, Duel et al. 1994, Johnson 1992, Johnson 1994, Johnson et al. 1995, Nilsson et al. 1991, Nilsson and Jansson 1995, Power et al. 1995, Rood and Mahoney 1990, Toner and Keddy 1997). Like many other dams across the country, the Roanoke Rapids Dam, NC is under examination for re-licensing. Historical water management on the Roanoke River (the Roanoke) drastically changed the character of the hydrologic regime on the LRR, and analysis of regeneration patterns in alluvial hardwood forest communities suggests that some communities are not compositionally stable (Rice 1997). A thorough understanding of how hydrology on the LRR has impacted floodplain forest ecosystem processes is necessary to re-structure flow management protocols to meet conservation goals.

The Nature Conservancy, NC manages a preserve on the LRR floodplain. Because of their conservation interests, they will provide input to the dam re-licensing process and suggest management plans that meet their conservation goals. The first step in the development of any management program, is a detailed investigation of extant knowledge regarding the system, its component species, and environmental forcing variables. The purpose of the two documents that comprise this report is to do just that. Specifically, *Lower Roanoke River Hydroperiods: Part I. Altered Hydrology and Implications for Forest Health*, examines what is known regarding hydroperiod (depth, return interval, duration, seasonality) effects on bottomland hardwood growth and regeneration and provides hypotheses regarding how managed flow regimes might have affected and continue to affect LRR floodplain forests; *Lower Roanoke River Hydroperiods: Part II. Approaches to Clarifying the Affects of Altered Hydrology on Forest Health and Species Specific Parameters* provides general suggestions on techniques for testing these hypotheses and examples of species that might be most affected by the ecosystem processes explained in the hypotheses, and includes a list of tree species found on the LRR floodplain, their flowering, fruiting, dispersal and germination phenology; their tolerance of shading, and various levels of flooding from soil saturation to submergence at seed, seedling and mature tree stages. Thus, these reports provide a thorough evaluation of current literature regarding hydrologic impact on floodplain forest tree species known to reside on the LRR floodplain.

Lower Roanoke River Hydroperiods, Part I.
Altered Hydrology and Implications for Forest Health

Introduction

Nearly all major river systems in the world are impounded (Johnson et al. 1976, Nilsson et al. 1997, Reily and Johnson 1982), with the consequence that downstream ecological processes are significantly altered. Among the well-known and documented changes to hydrologic regimes of dammed rivers are longer duration of flood periods, removal of both high and low-discharge periods, and significant differences from natural hydroperiod during the early-growing-season (Schneider et al. 1989). When hydrology is significantly altered, it can fundamentally change floodplain forest ecosystem processes, resulting in reduced regeneration, altered recruitment patterns, invasion of new taxa and ultimately changes in community composition and dynamics. In addition, reduced variability in hydroperiod may in turn reduce diversity of floodplain communities (Johnson 1992, Johnson 1994, Johnson et al. 1995, Molles et al. 1998, Nilsson 1996, Nilsson et al. 1991, Rood and Mahoney 1990, Toner and Keddy 1997).

Water management on the Roanoke River (the Roanoke) has drastically changed the character of the hydrologic regime on the lower Roanoke River floodplain (LRR) (Figure 1). Six dams were built on the Roanoke River system between 1950 and 1963. The dam that exerts the most influence on the LRR flows is Kerr Dam, managed by the Army Corps of Engineers (Pearsall 1998). Releases from Kerr are determined on a weekly basis, thus any excesses over required lake levels at the Roanoke Rapids Lake are available for power production. The Roanoke Rapids Dam, managed by Virginia Power and Light, is the farthest dam downriver, thus it is the regulation point where all up-river influences combine to affect downstream conditions on the LRR floodplain. Therefore management policies focus on output at the Roanoke Rapids Dam.

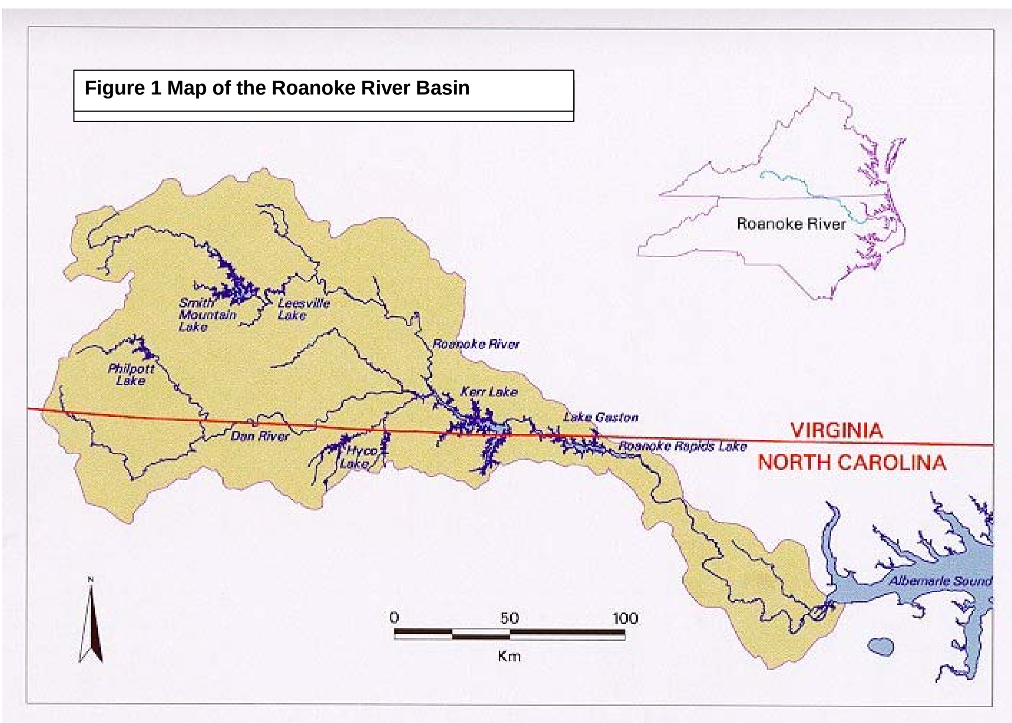

Figure 1 Map of the Roanoke River Basin

Perhaps the most important characteristic of managed flows on the LRR is increased return intervals of long duration flooding (>3 weeks) specifically during the early-growing-season (February – early May) (Pearsall 1998) (Figures 2 and 3). In addition, flood peaks and minima have been attenuated; for instance, prior to dam construction flow peaks of over 70,000 cfs were not uncommon; whereas, post-dam peaks never exceed 35,000 cfs. These fundamental changes in the hydrologic regime are likely to be exerting changes in the structure and functioning of floodplain forests on the LRR. In fact, analysis of regeneration patterns in LRR floodplain forests determined that the composition of the understory does not represent that of the overstory in some forest communities, suggesting that forest structure is changing in response to altered hydroperiod (Rice and Peet 1997, Townsend 1997). Simply, as seedlings and saplings favored by post-dam environmental conditions grow into the canopy, forest composition will change to reflect managed hydroperiods. There is little question that many additional responses to altered hydrology in the form of forest regeneration and growth remain unknown.

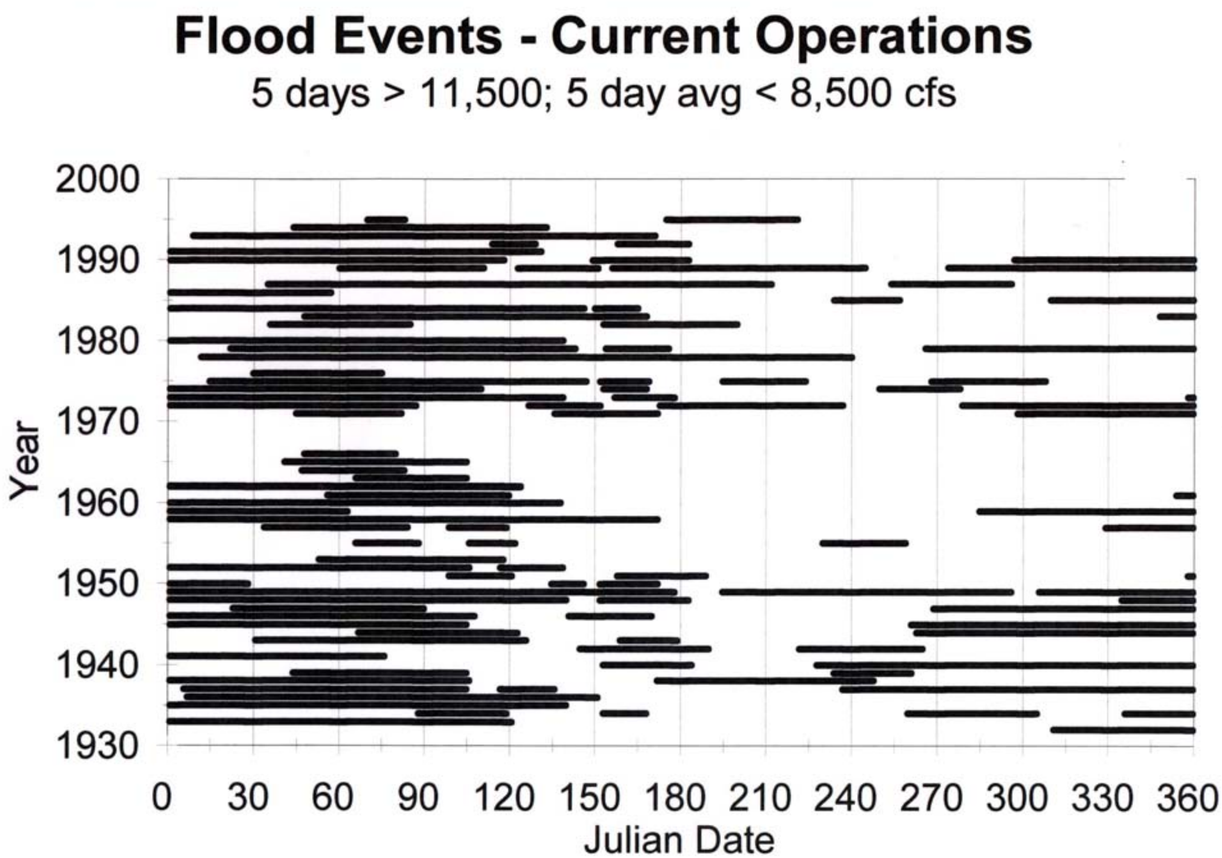

Figure 2

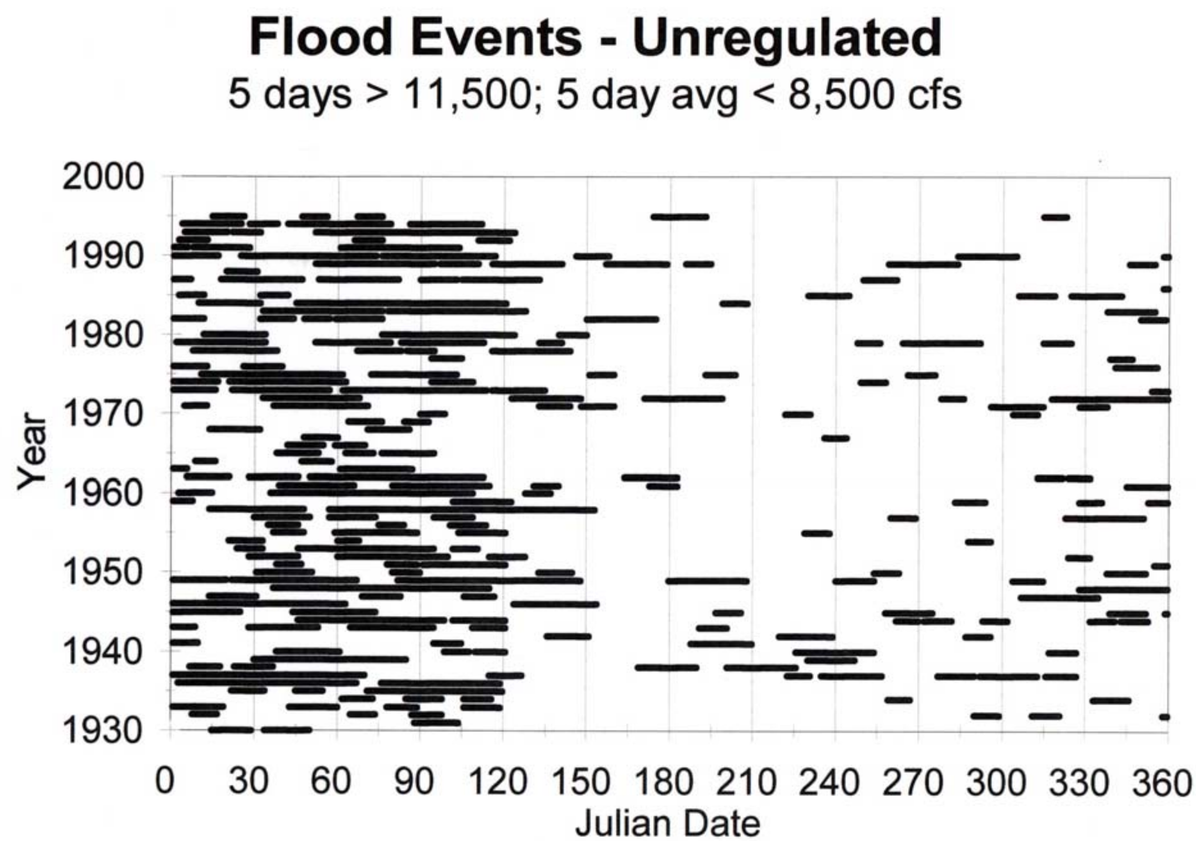

Figure 3

Like many other dams across the country, the Roanoke Rapids Dam is under examination for re-licensing. Re-licensing provides the opportunity for re-structuring of flow management protocols to meet conservation goals. However, in order to provide appropriate input to the dam re-licensing process it is necessary to understand 1) what changes have taken place in LRR forests as a result of altered hydrology 2) what aspects of altered hydrology have induced changes to LRR forests and 3) what alterations to reservoir operating procedures would be compatible with ecosystem management objectives. Adaptive management and basic research are the tools necessary to answer these questions. However, the first step in the development of any management program, is a detailed investigation of extant knowledge regarding the system, its component species, and environmental forcing variables. The purpose of this document is to do just that for floodplain forests on the LRR. Specifically, this document examines what is known regarding hydroperiod (depth, return interval, duration, seasonality) effects on bottomland hardwood growth and regeneration. Using this information hypotheses are generated regarding how managed flow regimes might have affected and continue to affect LRR floodplain forests.

Lower Roanoke River Floodplain

The Roanoke River drainage basin covers 25,035 km^2 originating in the Blue Ridge Mountains of south-central Virginia (VA) and ending in the Albemarle Sound of North Carolina (NC) meandering 209 km from its beginnings in VA (Townsend 1997). The Roanoke is considered a brown-water river, because it carries a heavy clay sediment load derived from upstream sources in the Blue Ridge, Piedmont and Coastal Plain.

The LRR floodplain begins at the fall-line (geologic boundary between the Piedmont and Coastal Plain regions) where the Roanoke Rapids Dam now regulates flow to the LRR. The LRR floodplain downstream from the Roanoke Rapids Dam, represents the largest area of mature bottomland forest in the Mid-Atlantic region. Thus the Nature Conservancy (TNC), North Carolina Wildlife Resources Commission (NCWRC), Georgia-Pacific Roanoke Ecosystem Partnership (GREP) and U.S. Fish and Wildlife Service (USFWS) actively protect nearly 52,000 ha of the LRR floodplain.

Flooding Effects

The Rooting Environment During Flooding

The rooting environment is radically different during waterlogging than during mesic or dry conditions. During flooding substantial chemical changes occur that alter the capacity of soils to support plant growth: 1) oxygen is depleted, 2) concentrations of available forms of essential nutrients decrease and 3) toxins become bioavailable (Kozlowski 1986, Ponnamperuma 1984a, Ponnamperuma 1984b, Turner and Patrick 1968). Once flood waters cover the soil, oxygen diffuses into the soil solution at a rate so slow as to effectively not diffuse at all (Schlesinger 1997). Any oxygen present following flooding is rapidly consumed by soil fauna, microbes, and plant roots. Anaerobic organisms tolerate the subsequent depletion of oxygen by reducing nitrate [NO_3^-], manganese [Mn^{+4}], iron [Fe^{+3}], and sulfate [SO_4^{-2}] rather than oxygen in respiration (Turner and Patrick 1968). These biological pathways can result in a loss of basic nutrients. For example, denitrification ($NO_3^- \rightarrow N_2$) by denitrifying bacteria results in the loss of NO_3^- to the atmosphere as nitrogen gas (Schlesinger 1997). Not only are some nutrients lost, but nutrient cycling (90-95% of essential nutrients may be supplied by intra-system recycling), may also be inhibited due to a decrease in decomposition of organic matter (Kozlowski 1986, Schlesinger 1997). Under flooded conditions, roots must maintain uptake of essential nutrients and avoid uptake of bioavailable toxins such as reduced iron, manganese and sulfate (Armstrong et al. 1994, Turner and Patrick 1968).

The rapidity with which oxygen is depleted and the amount of change in biochemical reactions in the soil depends on the duration and season of flooding, and the velocity of flood waters. Shorter durations of flooding result in shorter periods of anoxia and consequently less change in other chemical reactions in the soil. During winter flooding, waterlogged conditions may be less of a problem for plants, because temperatures are low (gases are more soluble at colder temperatures) and biological oxygen demand is significantly lower than during the growing season. Turbulence associated with higher velocity floodwaters results in more oxygen mixing into the soil solution, thus allowing a shallow aerobic zone at the soil surface layer.

Plant Responses to Flooding

Flooding during the dormant season has little effect on most seedlings and trees. However, during the growing season, less tolerant trees such as American beech (*Fagus grandifolia*) (see Table 1) may succumb to waterlogging after 4 or 5 days, whereas seedlings of more tolerant trees such as green ash (*Fraxinus pennsylvanica*) will show decreased photosynthesis but will not die unless saturated soils and/or submergence persist for 17 days or more (Hosner 1960, Hosner and Boyce 1962).

Immediate responses of trees to waterlogging during the growing season include root die-back, stomatal closure, and decreases in water uptake, photosynthesis and translocation of photosynthate to roots (Baker 1977, Hook 1984b, Hook and Brown 1973, Hook et al. 1971, Hook et al. 1983, Hosner 1958). Both intolerant and tolerant species may also show a reduction in leaf chlorophyll content, and decreased shoot elongation and leaf expansion (Angelov et al. 1996, Gravatt and Kirby 1998, McKevlin et al. 1998, Newsome et al. 1982). Thus, bottomland hardwood species must manifest multiple strategies to survive, grow and reproduce during flooding (Angelov et al. 1996, Gravatt and Kirby 1998, McKevlin et al. 1998, Newsome et al. 1982). The response time and type of strategies vary with 1.) plant characteristics: species, genotype, age, life-history stage, and pre-conditioning to flooding; and 2.) hydroperiod characteristics: duration, velocity of flood waters, return interval and season of waterlogging. Consequently, the major determinant of plant distribution on the floodplain is the interaction between hydrologic regime and the ability of trees at various life-history stages to tolerate flooding.

Roots and Shoots: Effects of Flooding. Hypoxic conditions result in more than chemical modifications to the rooting environment; they also alter the carbon and water budgets of plants. Flooding can drastically reduce the energy status of the plant through increased catabolism of stored reserves and decreased photosynthesis, storage, and nutrient and water uptake. (Kludze et al. 1994, Kozlowski 1984, Kozlowski 1986, Kozlowski 1997, Kozlowski and Pallardy 1984, Pezeshki 1991, Pezeshki 1993, Pezeshki and Chambers 1986, Pezeshki et al. 1996).

Flooded conditions require roots to respire anaerobically unless other internal mechanisms are present to aerate the root. When roots respire anaerobically they use 16-18 times more carbohydrates to create the same amount of energy as created when respiring aerobically (Campbell 1993). Thus, long periods of anaerobiosis during the growing season can deplete carbohydrates stored in the roots of floodplain trees.

Further shifts in energy supply take place as photosynthesis is decreased. Photosynthesis requires water uptake. However, despite plentiful water, shoots and leaves of flooded seedlings may dessicate because water uptake requires energy and as discussed above, the energy status of root cells may be decreased by anaerobic conditions. Decreased water uptake eventually results in even greater energy loss as stomates close to prevent transpiration. When stomates close, the uptake of CO_2, which is also necessary for photosynthesis, is decreased, thus reducing photosynthetic rates (Newsome et al. 1982, Pezeshki 1987, Pezeshki 1993, Pezeshki and Chambers 1986, Pezeshki et al. 1996, Sojka 1992, Tang and Kozlowski 1982). Not surprisingly, flood-tolerant species acclimate to flooding and often return to near pre-flood levels of water uptake and photosynthesis (Pezeshki 1993, Pezeshki and Chambers 1986, Pezeshki et al. 1996, Sojka 1992, Tang and Kozlowski 1982). However, less tolerant species, may not be able to recover photosynthetic rates after floodwaters recede and seedlings of even the most tolerant species have a flooding duration threshold after which restoration of pre-flooding photosynthetic rate will not occur.

Stomatal closure is not the only process that decreases photosynthesis. Leaf chlorophyll content and leaf size may decrease in flooded plants, lowering photosynthetic rates and reducing energy supplies (Angelov et al. 1996, Gravatt and Kirby 1998).

Decreased energy presents significant issues for plant survivorship. Lowered photosynthetic rates and increased carbon allocation to roots results in lower shoot and leaf growth rates and nutrient uptake (an energy requiring process) during the growing season and consequently decreased storage of reserves for respiration during the dormant season (Crawford 1992). Roots weakened by anaerobic conditions are more susceptible to fungal rot (Dunson 1999, Kozlowski 1997). In addition roots growing in anaerobic soils often lack the carbohydrate reserves to support mycorrhizal associations and the anaerobic, reducing conditions are not conducive to mycorrhizal growth (Cantelmo and Ehrenfeld 1999). Despite these facts mycorrhizal associations are considered important for wetland trees (Cantelmo and Ehrenfeld 1999). Each of these symptoms of flooding decreases the volume of roots in the soil. These decreased root volumes may make seedlings and mature trees more susceptible to wind-throw, summer moisture stress or death during the dormant season when survivorship and spring bud-break is dependent on stored reserves (Angelov et al. 1996, Dunson 1999, Keeley 1979, Kozlowski 1997, Megonigal and Day 1992, Newsome et al. 1982, Siebel et al. 1998).

Because the flooded soil environment poses such significant problems for plant growth and survivorship, floodplain trees must possess adaptations that allow them to survive the stresses of waterlogged conditions.

Roots and Shoots: Adaptations. Plants tolerant of flood events must be able to sustain root respiration in an oxygen-deficient environment, maintain selective nutrient acquisition (i.e. root uptake of essential nutrients in appropriate quantities), and tolerate or avoid the toxic products of the reduced environment (Drew and Lynch 1980). Thus, flood tolerant plants require adaptations that allow them to acclimate to the flooded environment. Plants able to adapt to waterlogging initiate a series of physiological and morphological changes depending on the characteristics of the flood, the species of plant and the relative tolerance of the individual:

1. production of greater concentrations of alcohol dehydrogenase (crucial for energy/ATP production during anaerobic respiration) (Armstrong et al. 1994)
2. development of secondary and adventitious roots,
3. development of aerenchyma,
4. stem and lenticel hypertrophy,
5. cambial permeability,
6. shallow rooting to exploit aerobic conditions at the soil surface. (Armstrong et al. 1994, Hook 1984a, Hook and Brown 1973, McKevlin et al. 1998)

The primary function of these adaptations is to allow respiration to occur in the absence of an aerobic soil medium. Physiological adaptations such as increased production of alcohol dehydrogenase (number 1 above) increase the rate of anaerobic respiration thus maintaining the energy status of the root. Morphological adaptations (numbers 2-4 above) provide oxygen to the root system. Once oxygen is brought to the root and diffused to the rhizosphere, most of the problems associated with anaerobiosis are mitigated (Armstrong et al. 1994, Kozlowski 1986); root cells may respire aerobically decreasing the likelihood of an energy debt, and oxygenation of the rhizosphere favors oxidation of toxic compounds to non-toxic forms and increased absorption of essential nutrients.

At the physiological level, waterlogging can induce production of higher concentrations of alcohol dehydrogenase. This enzyme is very important because it permits the production of ATP under anaerobic conditions through alcoholic fermentation of glucose. During ATP production (both anaerobic and aerobic respiration), NAD+ (a molecule that is crucial in ATP production) is

reduced to NADH. In order for ATP production to continue, NADH must be **oxidized** back to NAD+. During the final steps of aerobic respiration the presence of oxygen permits NADH to be oxidized/recycled to NAD+. However, under anaerobic conditions oxygen is not available but alcohol dehydrogenase can catalyze the oxidation of NADH→NAD+. Increased concentrations of alcohol dehydrogenase increase the rate of NADH oxidation and thus anaerobic respiration. Therefore, increased production of alcohol dehydrogenase can be a mechanism for acclimating to anaerobic conditions prior to the induction of morphological adaptations which allow oxygenation of root systems (Batzli and Dawson 1997, Keeley 1979), especially since morphological adaptations may take two weeks or more to develop.

Secondary water roots and adventitious roots may be the primary morphological adaptations that compensate for anoxia and low redox conditions. Several studies have shown that species tolerant of flooding produce new secondary roots and/or adventitious roots within a week to two weeks of waterlogging (Hook 1984a, Hook and Brown 1973, Hosner 1960, Hosner and Boyce 1962, Newsome et al. 1982, Sena-Gomes and Kozlowski 1980). Secondary and adventitious roots are more succulent and contain more aerenchymous tissue than roots developed under aerobic conditions (Hook et al. 1971, Keeley 1979). Production of adventitious roots is associated with re-opening of stomates and increased water absorption in waterlogged individuals (Gill 1970, Sena-Gomes and Kozlowski 1980). In addition, secondary roots and adventitious roots oxidize their rhizosphere, thus enhancing nutrient uptake and transforming toxic, reduced ions to their oxidized counterparts.

Secondary water roots and adventitious water roots work in conjunction with large intercellular spaces or aerenchyma running from the shoot to roots. This aerenchyma tissue (usually formed by a collapsing of cells) allows efficient gas transport from shoots to roots and vice versa. Aerenchyma facilitates gas transport in two manners: 1.) large intercellular spaces reduce diffusive resistance to O_2 transport from the shoot to root and of toxic gases (e.g. ethanol, a product of anaerobic metabolism) from root to shoot and 2.) since fewer cells are present, there is a reduction in oxygen demand per unit volume of tissue (Armstrong et al. 1994).

Hypertrophied stems and lenticels are an important part of this aeration system. Hypertrophy is the enlargement of an organ without an increase in the number of cells that make up that organ. Hypertrophy along with aerenchyma tissue increases the air space and thus movement of gases within the plant. Lenticels are small pores on the stems of woody plants (commonly seen as small protuberances on the stems of hackberry and sugarberry). They are major sites of gas exchange aiding in oxygen transport into shoots and serving as excretory sites for the toxic products of anaerobic metabolism (Hook 1984a, Hook et al. 1971). Stem hypertrophy or buttressing is commonly observed in floodplain tree species such as baldcypress (*Taxodium distichum*), green ash, and water tupelo (*Nyssa aquatica*). Stem hypertrophy also increases intercellular space in the shoot allowing transport of oxygen to roots.

An additional adaptation for increased gas transfer is greater cambial permeability; thus, the bark of flood tolerant trees often allows oxygen to diffuse into intercellular spaces and may also allow excretion of the toxic products of anaerobic metabolism. Flood tolerant seedlings such as water tupelo and green ash have greater cambial permeability than in the less flood-tolerant sycamore (*Platanus occidentalis*), tulip tree (*Liriodendron tulipifera*), sweetgum *Liquidambar styraciflua* (Hook and Brown 1973).

Aerobic conditions may be present just at the surface of a waterlogged soil depending on the amount of mixing and biological and chemical oxygen demand (Armstrong et al. 1994). A shallow rooting habit allows plants to exploit this zone and confers some flood tolerance as long as surface soils remain slightly oxygenated. Evidence of this adaptation has been found by many researchers: rooting depth is consistently related to flooding frequency in swamp forests (Armstrong et al. 1976, Lieffers and Rothwell 1987, Megonigal and Day 1992). For instance, continuously flooded bald cypress seedlings produced only 6% of their roots below 30 cm in depth, whereas periodically flooded seedlings produced on average 30% of their roots below 39 cm in depth and some up to 100 cm deep (Megonigal and Day 1992). However, shallow rooting may be a function of root death in soil horizons that have lower redox potentials and not an adaptive mechanism per se.

Tolerance Versus. Intolerance

Waterlogging tolerance describes a species' ability to tolerate soil saturation or partial inundation (flooding above the root collar but not submergence of foliage) during the growing season (Hook 1984b). Tolerance varies with species age and life-history stage. For example, mature baldcypress and water tupelo can survive and thrive under continuously saturated or flooded conditions; however, their seeds will not germinate under water, nor will their seedlings survive continuous submergence during the growing season. Mature trees and established seedlings (under 50cm height, surviving a second or third growing season) of baldcypress and water tupelo are considered most tolerant of flooding (sensu (Hook 1984b), see table 1) whereas a species such as American beech is considered least tolerant, surviving only 7-10 days of flooding as a mature tree during the growing season (Hall and Smith 1955, Hook 1984b).

Implications

Given what is known regarding hydroperiod and the tolerances of various life-history stages of woody species, what are the implications of regulated hydrology for 1.) regeneration, and 2) mature tree growth? The following sections provide descriptions of the interaction of hydroperiod with regeneration and growth. Bulleted paragraphs are crucial issues that require further investigation. The effects of altered hydrology on forest composition and diversity will be discussed in the section on regeneration. The effects of altered hydrology on forest productivity will be discussed with mature tree growth.

Regeneration

The composition of the advanced regeneration pool, i.e. the available seedling bank, in bottomland hardwood forests is dependent upon the interaction of environmental factors with several demographic processes:

1. seed production
2. seed dispersal
3. seedling emergence
4. seedling survivorship
5. seedling growth (Grubb 1977)

Table1. Waterlogging Tolerance of Selected Southern Bottomland Hardwood Species.*
These tolerances are general metrics regarding the survivorship of species under particular lengths of time of waterlogging. They are not meant to prescribe hydroperiod regimes for particular species. These tolerance categories concern already established seedlings and trees and do not consider the seed germination or seedling establishment phase. These tolerances consider only saturated soils or partial inundation, not submergence. Tolerances at juvenile life history stages are crucial for estimating regeneration, composition and diversity under various hydroperiod scenarios; however, tolerances at early life-history stages have been difficult to determine and what little data is available has not been previously compiled. The compilation of tolerances at juvenile life history stages will be completed in the second phase of this study, but it is important to note that there is not very much information available and what is available is from laboratory studies.

Species	Common Name	Tolerance
Fraxinus carolineana	Carolina Ash	Most Tolerant[a]
Nyssa aquatica	Water Tupelo	Most Tolerant
Salix nigra	Black Willow	Most Tolerant
Taxodium distichum	Bald-Cypress	Most Tolerant
Carya aquatica	Water Hickory	Highly Tolerant[b]
Fraxinus profunda	Pumpkin Ash	Highly Tolerant
Quercus lyrata	Overcup Oak	Highly Tolerant
Acer negundo	Box Elder	Moderately Tolerant[c]
Acer rubrum	Red Maple	Moderately Tolerant
Acer saccharinum	Silver Maple	Moderately Tolerant
Betula nigra	River Birch	Moderately Tolerant
Diospyros virginiana	Persimmon	Moderately Tolerant
Fraxinus pennsylvanica	Green Ash	Moderately Tolerant
Ilex decidua	Deciduous Holly	Moderately Tolerant
Liquidambar styraciflua	Sweetgum	Moderately Tolerant
Platanus occidentalis	American Sycamore	Moderately Tolerant
Populus deltoides	Eastern Cottonwood	Moderately Tolerant
Quercus phellos	Willow Oak	Moderately Tolerant
Quercus laurifolia	Laurel Oak	Moderately Tolerant
Ulmus americana	American Elm	Moderately Tolerant
Carpinus carolinina	Ironwood	Moderately Tolerant
Celtis laevigata	Sugarberry	Weakly Tolerant[d]
Quercus michauxii	Swamp Chestnut Oak	Weakly Tolerant
Quercus shumardii	Swamp Red Oak	Weakly Tolerant
Asimina triloba	Pawpaw	Weakly Tolerant
Quercus pagota	Cherrybark Oak	Least Tolerant[e]
Ulmus rubra	Slippery Elm	Least Tolerant
Fagus grandifolia	American Beech	Intolerant

Table 1. (cont.)
[a] Most Tolerant – These species are capable of tolerating flooding as seedlings as long as they are only partially inundated. They are capable of surviving in soils that are waterlogged almost continually and often have higher growth rates in flowing than stagnant water. These species produce soil water roots and adventitious roots, oxidize their rhizosphere, accelerate anaerobic metabolism and tolerate or avoid uptake of toxic compounds characteristic of anoxic, low redox conditions. (Hook 1984b)
[b] Highly Tolerant – These species can live as established seedlings through maturity in soils that are flooded for 50-75% of the year as long as most of that flooding is during the dormant season and not necessarily continuous. (Hook 1984b)
[c] Moderately Tolerant -- These species can live as established seedlings through maturity in soils that are flooded for up to 50% of the year, most being during the dormant season and not necessarily continuous. (Hook 1984b)
[d] Weakly Tolerant – These species can live as established seedlings through maturity in soils that are saturated or flooded for no more than 10% of the growing season, and for up to 4 weeks at a time during the dormant season. (Hook 1984b)
[e] Least Tolerant – These species can live in soils that are only infrequently flooded, for periods of less than 5 days, and for less than 2% of the growing season. (Hook 1984b)

* (Hook 1984b)

These processes are dependent upon species response to and tolerance of flooding regimes, light regimes, soil type, herbivory/predation, pathogens, and competition (Grubb 1977, Streng et al. 1989). Although these other environmental factors may be important, there is little question that variability in the form of hydrologic regime is a primary control on recruitment and establishment of different bottomland hardwood species at different times within the growing season and at different elevations on the floodplain. Particular plant species and life-form types are consistently associated with specific fluvial landforms and elevations (both relating to hydroperiod) on forested floodplains (Hupp 1983, Hupp and Osterkamp 1985, Lisle 1989). Tree growth rates and survivorship are distinctly related to variations in water availability from situations of moisture stress to waterlogging (Astrade and Begin 1997, Hall and Smith 1955, Jean and Bouchard 1996, Keeland and Sharitz 1995, Stromberg 1993, Stromberg and Patten 1990, Stromberg and Patten 1996, Yankosky 1982, Young et al. 1995). Variation in floodplain forest composition in northern taiga (Mann et al. 1995), western alluvial floodplains (McBride and Strahan 1983, Strahan 1983), and bottomland hardwood forests (Streng et al. 1989) is related to the interaction of species emergence and establishment phenology with 1) the timing and duration of flooding, soil saturation and moisture stress; and 2) the temporal availability of appropriate microsites with regards to soil moisture and alluvial deposits. While other factors such as light regimes, soil type, herbivory/predation, pathogens, and competition play an important role – hydrology is often the primary variable that determines species composition and diversity.

Seed Production and Dispersal. Growing season flooding poses four stresses to mature trees: 1.) an anoxic rhizosphere, 2) decreased nutrient availability, 3) increased bio-availability of toxic minerals, and 4) toxic products of anaerobic metabolism. Under managed flow regimes these stresses are present during a period when most species are flowering and/or fruit-ripening begins, the early-growing season. Because these stresses can result in increased carbon allocation to adaptations to flooding, and lower photosynthesis rates and nutrient uptake, less resources may be available to invest in reproduction. Consequently, a year with continuous early-growing-season flooding could potentially lower the viability and number of seeds produced. This phenomenon has been observed in sweetgum; it produces low percentages of sound seed if subjected to excessive soil moisture during the growing season (Burns and Honkala 1990).

- Continuous early-growing-season flooding can reduce the quality and quantity of seed production.

During the mid- to late- growing-season (July – October) flows are reduced under both managed and unregulated hydrologic regimes. This is the period of fruit ripening for many floodplain trees. Trees conditioned to continuous early-growing-season flooding under managed flow regimes are likely to have shallower rooting systems and may have poorer water use efficiency then those not subject to early-growing-season flooding (Kozlowski 1986, Kozlowski 1997, Megonigal and Day 1992). Thus, the combination of continuous early-growing-season flooding and mid- to late-growing-season decreases in flow can result in moisture stress to floodplain trees and potentially lower the viability and number of seeds produced under managed flow regimes. Again, sweetgum is known to display this phenomenon (Burns and Honkala 1990).

- The combination of continuous early-growing-season flooding (consistent with managed flow regimes) with low mid- to late-growing-season flows subjects floodplain trees to moisture stress, potentially compromising the quality and quantity of seed production for species.

Survivorship of seedlings is dependent upon seeds reaching appropriate microsites for germination (Battaglia et al. In prep., Huenneke and Sharitz 1986, Huenneke and Sharitz 1990, Jones et al. 1994, Jones et al. 1989, Streng et al. 1989). Seed dispersal through bottomland forests can occur by many means: wind, animals, gravity, water. In bottomland hardwood forests and swamp forests many seeds are dispersal by water(hydrochory) (Schneider and Sharitz 1988). Many bottomland species have buoyant seeds that retain viability when immersed. However, species do differ in their buoyancy and once submersed for long periods some may lose viability.

Seeds of most species disperse during the fall through early winter (except for maples and elms, dispersing in early spring) (Burns and Honkala 1990). Prior to managed flow regimes on the LRR, this period of dispersal was marked by short duration floods. Currently, floods of many months from fall to spring may alter dispersal patterns and compromise seed viability. In addition, longer periods of dispersal may prevent seeds from reaching appropriate microsites (Schneider and Sharitz 1988).

- Long floods of many months, typical of managed flow regimes on the LRR, during the period of seed dispersal, disperse bottomland hardwood seeds farther than during the short duration floods characteristic of unregulated flow regimes.

- Farther dispersal due to continuous flooding during seed fall may result in lowered probability of seeds coming to rest on microsites appropriate for germination.

- Longer periods of flooding during seed dispersal may compromise the viability of seeds.

Prior to managed flow regimes on the LRR, higher elevation environments (those flooded at >20,000-25,000 cfs) were also flooded much more frequently for durations of 7 days or more. Floods of this magnitude affect communities on the floodplain that support a diverse suite of bottomland hardwoods with varying levels of tolerance, from highly tolerant species such as overcup oak, to much less tolerant species such as cherrybark oak. Flooding during the growing season excludes proliferation of upland species such as beech (Hall and Smith 1955). Flooding under unregulated regimes maintained diversity in these communities by providing: 1.) an influx of seeds from upstream; and 2.) spatial and temporal variability in establishment microsites. Under unregulated regimes, species tolerant of flooding were maintained even at higher elevations on the floodplain; the complete lack of flooding associated with managed flow regimes allows upland species such as beech to proliferate and eliminates flood tolerant species from the advance regeneration pool (Rice and Peet 1997, Townsend 1997). Thus, diversity in the advance regeneration pool is compromised and canopy composition will eventually change as upland species replace bottomland hardwoods.

- Portions of the pre-dam floodplain are no longer flooded, these disconnected habitats no longer receive an influx of seeds from floodwaters, thus their species richness and diversity is compromised.

- Lack of upper-elevation floodplain inundation is driving species composition toward increased densities of less flood-tolerant species, thus potentially lowering diversity at these elevations and altering historic community composition.

Prior to managed flow regimes, low elevations on the floodplain, were exposed when flows were reduced to between 2000 cfs and 500 cfs for periods of 7 days of more. This exposure allowed seedlings to establishment on low elevation sand bars and banks. These areas of the floodplain were exposed up to 10 times a decade (McCrodden 1999). Currently, these elevations are rarely exposed (McCrodden 1999).

- Reduced incidence of short-duration flow levels reduce woody seedling establishment on low elevation sites such as point bars.

- Loss of this habitat from the LRR floodplain system results in an overall loss to diversity.

Seedling Emergence, Survivorship and Growth. Many floodplain forest seedlings emerge prior to canopy leaf-out, e.g.: green ash, deciduous holly, and ironwood (Streng et al. 1989, Wardle 1959). Early emerging seedlings germinate under relatively high-light conditions, thus they have higher relative growth rates early in the season, and can grow an order of magnitude larger than if emergence were to follow leaf-out (Jones and Sharitz 1989). Thus these seedlings are able to maintain a size advantage over later emerging species such as red maple and American elm (Streng et al. 1989), and over later emerging individuals of their own species (Jones and Sharitz 1989). This size advantage may allow them to be better competitors for light and below-ground resources. Additionally, larger size may confer higher survivorship during periodic spring flooding especially, if seedlings are taller than the depth of floodwaters (Streng et al. 1989). Early germination also seems to confer higher survivorship of other stresses (herbivory, pathogens, etc.) as well (Streng et al. 1989). Since managed flow regimes inundate the floodplain for long periods during the early-growing-season (lasting well past canopy leaf-out) and because most species do not germinate under water (a small percentage of red and silver maple seeds germinate under water in the laboratory) (Hosner 1957) the emergence of many species is likely to be delayed past canopy leafout – thus altering competitive and other interactions.

- Due to continuous early-growing-season flooding, those species that have germination windows during this period miss optimum germination conditions (temperature and light levels), resulting in fewer successful germination events when floodwaters recede.

- Because early emerging seedlings no longer have a competitive advantage over species that emerge later in the growing season, such as red maple and American elm, early emerging species may decrease in relative abundance.

- Low inter-annual variation in early-growing-season floods as characterized by the current managed flow regime, may consistently favor later-emerging species, thus reducing diversity in the advanced regeneration pool and eventually in the canopy.

Seedlings may have to contend with submergence during the early-growing-season. Seedlings encountered submergence during the pre-dam era and continue to encounter it post-dam. However, in the post-dam era the length of time that seedlings are submerged is likely to be much greater due to the longer durations of early-growing-season floods. Submerged seedlings lose terminal buds, their leaves turn chlorotic, plants are defoliated and some die-back to the root collar (Baker 1977, Hosner 1958, Hosner 1960). While seedlings that die back to the root collar may re-sprout, it can take up to 4 weeks (e.g. sycamore and sweetgum) (Baker 1977), and seedlings repeatedly killed back to the root collar in subsequent years are less likely to survive to maturity. Older seedlings, whether it be by days or years are more likely to survive complete submergence than younger seedlings. Seedlings that do survive growing-season submergence but are completely or partially defoliated or die back to the root collar require less stressful hydrologic conditions in order to recover and may take up to several weeks to recover or re-sprout (Baker 1977, Hosner 1958, Hosner 1960).

- It is likely that habitats which are subject to greater durations of continuous early-growing-season flooding at depths high enough to submerge seedlings are unable to support seedlings due to submergence death and/or repeated die-back to the root collar

Again growing-season floods pose significant stresses to seedlings, as a result of saturated soils, partial inundation and/or submergence. These stresses may reduce the quantity of carbohydrates available for storage at the end of the growing season. Adequate supplies of stored carbohydrates are crucial for survivorship through the winter and for spring growth. Maintenance respiration and winter root elongation require carbohydrates supplies. At the beginning of the growing season fine root development, bud-burst, leaf-out and stem elongation, require use of stored reserves from the previous growing-season. Stored reserves must be sufficient to support growth and survivorship until well after leaf-out and renewal of photosynthetic capacity. Managed flow regimes on the LRR may inundate the floodplain from as the beginning of October (late-growing-season) through June or July. Many questions arise regarding the ability of seedlings to survive repeated years of continuous winter and growing-season flooding. In fact Angelov (1996) found that death of both continuously (entire year for two years) flooded (at partial inundation) and only winter through early-growing-season flooded (at partial inundation) swamp chestnut and cherrybark oak seedlings occurred in phases. Death occurred after periods of major vegetative growth e.g. bud burst in the spring and summer stem elongation.

- Because anoxic conditions require that individuals place more carbohydrate reserves into anaerobic root metabolism and morphological adaptations to flooding, seedlings that are exposed to flooding from the late-growing-season through winter may not have sufficient reserves to survive the winter dormant season.

- Because anoxic conditions require that individuals place more carbohydrate reserves into anaerobic root metabolism and morphological adaptations to flooding, seedlings that are exposed to repeated years of winter through early-growing-season flooding may not have sufficient reserves to survive normal root development, bud-burst and stem elongation in the spring.

- Root growth may begin as early as February for species such as sugar maple (Richardson 1957). It is not known whether long-term, anoxic conditions during this initial growth period might inhibit growth.

Many of the adaptations to flooding appear to confer lower moisture stress tolerance later in the growing-season (Dickson and Broyer 1972, Dunson 1999, Jane and Green 1985, Jane and Green 1986, Keeley 1979, Kozlowski 1997, Megonigal and Day 1992, Newsome et al. 1982, Siebel et al. 1998, Sun et al. 1995, Townsend and Roberts 1973). In addition, plants are not able to harden off to moisture stress like conditions while subjected to continuous flooding early in the season. For instance: natural variation in spring flows allows cottonwoods in the plains states to gain moisture stress tolerance prior to natural flow reductions in the summer. Patterns of managed flow that result in continuous flooding prior to summer moisture stress prohibit development of moisture stress tolerance in this system, thus causing decline in cottonwood forests (Rood and Mahoney 1990). Managed flow regimes on the LRR often result in long-duration early-growing-season flooding followed by reduced floodplain inundation later in the growing-season (July, August, September). Although the pattern of reduced floodplain inundation later in the growing season is not significantly different from the unregulated scenario the combination with continuous early-growing-season flooding (uncommon in the unregulated system) sets seedlings and trees up for moisture stress.

- Seedlings that acclimate to the continuous early-growing-season flooding on the LRR are unlikely to survive late summer moisture stress, due to the fact that they are acclimated to waterlogged conditions.

Natural hydrologic regimes on the LRR were highly variable within and between years (McCrodden 1999, Richter et al. 1996, Richter et al. 1997), thus they favored survivorship and establishment of some species during particular years and portions of the growing season and others at other times. In this manner, inter-annual and intra-annual diversity in unregulated hydroperiods maintained diversity in the advanced regeneration pool and likely played a long-term role in maintaining canopy diversity (Streng et al. 1989). Managed flow regimes are much less variable. It is highly likely that reduced variability in hydroperiod results in lower diversity in the advanced regeneration pool and will result in an eventual decrease in canopy diversity.

Mature Tree Growth

Hydrologic regime often dictates above-ground productivity of bottomland hardwood and cypress-tupelo swamps. In general, flowing-water regimes (as opposed to stagnant), pulses of flooding (as opposed to continuous flooding), and shallower flooding (as opposed to deeper flooding) result in higher productivity (Brown and Peterson 1983, Conner and Day 1976, Conner and Day 1992, Keeland et al. 1997, Megonigal et al. 1997, Mitsch et al. 1991). While these findings may be of some import to management decisions, there is conflicting evidence that these generalities always hold (Young et al. 1995); in addition the studies that observed these phenomena compared different wetlands with different hydrologic regimes rather than the same wetland under an altered hydrologic regime. Few studies have attempted to determine the effect of an abrupt change from natural to managed hydrology (such as dam construction managed flow regimes or impoundment) on productivity and/or tree growth. Those that have, found obvious decreases in tree growth under altered hydrologic regimes (Johnson et al. 1976, Reily and Johnson 1982, Young et al. 1995).

Altered hydrology in the form of increased depth of flooding and increased duration of flooding can decrease diameter growth and productivity of bottomland hardwoods (Megonigal et al. 1997, Young et al. 1995). Megonigal et al. (1997) provide convincing evidence that a change from periodic flooding to near-continuous flooding in baldcypress swamp and mixed-hardwood stands (*Fraxinus* spp., sugarberry, and sweetgum) resulted in a significant decrease in productivity. Baldcypress trees subjected to consistently deeper flooding display an immediate surge in growth for the first few years, followed by a consistent decrease in growth over time with no recovery (Young et al. 1995).

It might seem counterintuitive that tolerant species such as baldcypress would succumb to waterlogging stress. However, individuals of these species develop root systems morphologically and physiologically tailored to specific hydrologic regimes (Hook et al. 1971, Megonigal and Day 1992). The succulent secondary water roots that develop under continuous and/or deep flooding maintain more efficient anaerobic metabolism and rhizosphere oxidation than those developed under periodic and/or shallow flooding (Keeley 1979). These root systems are quite plastic when individuals are seedlings, but are much less so as mature trees. It is unlikely that the large root system of a mature tree can allocate the carbon necessary to restructure such a large root system in response to altered hydrologic regime (Harms et al. 1980, Keeley 1979).

- It is highly likely that changes to hydrologic regime on the LRR floodplain that have resulted in deeper and more continuous flooding in various floodplain habitats (such as cypress-tupelo swamps and bottomland hardwood swamps) has decreased the productivity and probability of survivorship of canopy trees.

Bottomland hardwood species that do acclimate to continuous early-growing-season flooding under managed flow regimes may be more susceptible to moisture stress in the typical low flow period during the late summer.

- Continuous early-growing-season flooding due to managed flow regimes in conjunction with late summer moisture stress may result in growth declines because responses to continuous early-growing-season flooding (e.g. lowered root volume) will confer less tolerance of moisture stress.

Hydrology and Species Parameters: What we Need to Know

It is difficult to predict the effects of environmental disturbance on ecosystem health. However, it is obvious that significant alterations to the hydrologic regime of a riverine system can have deleterious effects on regeneration and tree growth. To predict those impacts and the extent to which those impacts might be mitigated by alteration of current release practices requires that we obtain more detailed information in two categories: 1) how discharge at the Roanoke Rapids Dam relates to hydrologic regime at specific topographic positions and within specific plant communities on the LRR floodplain; and 2) species specific tolerances to flooding in terms of days, season and saturation, partial inundation and submergence for each life-history stage: seed, seedling, sapling, mature tree. Coupling these sets of information in either a spatial database and/or a forest simulation model will give us greater power to 1) assess the effects of post-dam flow regimes and 2) predict the effects of potential flow regimes. Results should provide potential hydroperiods for adaptive management on the LRR.

Critical Data Needed

Three sets of critical data are needed to develop hydroperiod scenarios that promote forest ecosystem health on the LRR: 1.) statistical and graphical definitions of the differences in pre- and post-damming hydrologic regimes; 2.) spatial distribution of floodwater and water table heights based on discharge at the Roanoke Rapids Dam; and 3.) species parameters for tolerance of soil saturation, submergence, duration, return interval and seasonality of waterlogging and species response to various hydrologic scenarios in terms of growth and survivorship at each life-history stage.

1. Differences in Pre- and Post-Damming Hydrology, Definitions. Definitions of the differences between pre- and post-damming hydrology are necessary baseline information for conservation oriented flow management design. The task of relating forest parameters to hydrologic regime requires clearly defined explanations of differences in pre- and post- damming hydrologic regime in terms of peak and minimum flows, duration and depth of low and high flow periods, and seasonality of all aspects of the two regimes. Richter [, 1996 #12; , 1997 #48] has developed definitions of the differences between pre- and post- damming regimes based on a monthly time-step. Time-steps of days and weeks are more biologically relevant for tree seedlings thus, Brian McCrodden (Water Resources Management, Inc.) is currently developing definitions of differences between the pre- and post- damming regimes using smaller time-steps. These definitions will also be necessary when analyzing flow regimes effects on other aspects of riverine and floodplain ecosystem functioning (fish population dynamics, nutrient cycling, geomorphological change, etc.)

2. Spatial Distribution of Floodwater and Water Table Heights. Spatial distributions of floodwaters and water table heights provide better estimates of hydroperiod regime across the floodplain in specific plant community types. Researchers with University of Maryland and Water Resources Management, Inc. are involved in mapping the spatial distribution of floodwaters and water table heights on the LRR floodplain based on discharge at the Roanoke Rapids Dam.

3. Species Tolerances and Response to Hydrologic Regimes. Bottomland hardwood species specific tolerances to duration, depth and season of waterlogging and submergence can be found throughout the literature. Values are available for many species at various life-history stages. The literature is by no means complete, especially for juvenile life-history stages, however an organized review (which will be provided by the author in a second report to TNC) will provide the information needed to begin to develop initial management protocols for hydroperiods on the LRR.

In addition, conservation oriented flow management policies require an understanding of the effects of hydrology on species composition, survivorship and growth. Bottomland hardwood species responses to hydrologic regime in the form of seedling emergence, establishment, growth and survivorship, and sapling and mature tree growth and survivorship have been investigated under a multitude of experimental and natural conditions, as discussed above. However extrapolation from experimental studies and studies on other forested wetlands is difficult. It is more likely that a combination of well monitored (with hydrological and seedling establishment, growth and survivorship data) plots on the LRR floodplain and laboratory/wetland garden experiments could provide better estimates of seedling tolerances at different ages to various durations and timings of saturation, partial inundation and submergence on the LRR itself. Obtaining tolerance and response data from these and other studies will take time, thus an adaptive management plan for defining Roanoke River optimum hydroperiods is logical.

Synthesis of Critical Data: GIS/Simulation Modeling

Simulation modeling and GIS databases offer potentially powerful solutions to dealing with the complexity of data described above. Using these tools we can synthesize spatial diversity, species diversity, inter and intra-annual hydroperiod diversity and answer difficult questions regarding how floodplain forests on the LRR might respond to particular flow management regimes. In addition, these tools allow us to look at a diverse species component, rather than targeting one or two species, whose requirements may not be an appropriate standard for maintaining species diversity throughout the floodplain system.

Conclusions

In conclusion, there is little doubt that managed flow regimes have altered forest growth, composition, and diversity on the LRR. Dam-regulated hydrologic regimes have been implicated in forest decline, loss of habitat and decreased diversity in many river systems (Brooks and Brierley 1996, Dahm et al. 1995, Johnson 1992, Johnson 1994, Johnson et al. 1995, Nilsson et al. 1991, Nilsson and Jansson 1995, Reily and Johnson 1982). Seeds, seedlings and canopy trees are sensitive to the duration, seasonality, and return interval of flooding and moisture stress, and to the depth of flooding. Flooding and moisture stress pose significant stresses to plants, altering the carbon and water budget, and making plants more susceptible to pathogens and herbivory. Thus, altered hydroperiod regimes compromise 1) seed production, dispersal and viability; 2) seedling survival, emergence, establishment and growth 3) mature tree growth and survivorship; and 4) persistence of both low elevation and high elevation habitats that require very low minimum and very high peak flows at appropriate seasons to maintain community composition.

To what extent is it possible to combine hydroelectric power production at the Roanoke Rapids Dam with conservation of environmental values downstream on the LRR? An answer to this question is impending, however, it requires more detailed information regarding how discharge at the Roanoke Rapids Dam is spatially distributed across the floodplain and how species indigenous to the LRR floodplain respond to various hydroperiod parameters. Once these details are clarified they can be used to make predictions about forest, growth, composition, and diversity at various topographic positions on the floodplain. With these predictions in hand, environmental and forestry interests can make more comprehensive recommendations for adaptively managed flow regimes that support ecosystem health on the LRR

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Lower Roanoke River Hydroperiods, Part II. Approaches to Clarifying the Affects of Altered Hydrology on Forest Health and Species Specific Parameters

Introduction

This report consists of two comprehensive tables. The list of hypotheses that were generated in Part I of this report regarding implications of altered hydrology for forest ecosystem health is the basis for Table 1. The testability of these hypotheses, general suggestions on techniques for testing these hypotheses, and examples of species that might be most affected by the processes explained in the hypotheses are also discussed in Table 1. Table 2 is a list of tree species found on the lower Roanoke River (LRR) floodplain, their flowering, fruiting, dispersal and germination phenology; their tolerance of shading, and various levels of flooding from soil saturation to submergence at seed, seedling and mature tree stages. The purpose of Table 1 is to suggest how managed hydrology may affect forest ecosystem processes, which of these effects require further clarification and which species might be most affected by the processes discussed in each hypothesis. Clarification of managed flow affects on forest ecosystem processes is necessary so that interested parties can make educated recommendations during the dam re-licensing process for the Roanoke Rapids Dam and important if flows on the LRR will be managed adaptively. The purpose of Table 2 is to provide detailed information regarding phenology and tolerances of various levels of flooding for woody species found on the LRR floodplain. This information could be included in forest simulation models that might predict potential successional changes that could occur in LRR forests based on particular hydrologic regimes.

Table 1. A list of hypotheses regarding woody species response to altered hydroperiod regime on the floodplain of the Lower Roanoke River, North Carolina. The testability of these hypotheses is discussed. Particular species that are more likely to be effected by processes discussed in each hypothesis are listed.

SEED PRODUCTION AND DISPERSAL

Hypotheses	Testability	Species of Interest
1. Continuous early-growing-season flooding can reduce the quality and quantity of seed production.	May be testable by manipulating water levels in a series of green-tree reservoirs, in which mature trees are already established. Would require a long time-series.	Primarily species that are found at lower elevations on the floodplain and especially those whose submergence tolerance is not known, e.g.: *Quercus sp.* *Platanus occidentalis* *Ulmus americana* *Acer rubrum* *Acer saccharinum* *Liquidambar styraciflua*
2. The combination of continuous early-growing-season flooding (consistent with managed flow regimes) with low mid- to late-growing-season flows subjects floodplain trees to moisture stress, potentially compromising the quality and quantity of seed production for some species.	May be testable by manipulating water levels in a series of green-tree reservoirs, in which mature trees are already established.	Any species with fall fruit ripening. *Nyssa aquatica* *Carya aquatica* *Quercus sp.* *Fraxinus sp.* *Carpinus caroliniana* *Diospyros virginiana* *Ilea decide* *Liquidambar styraciflua* *Platanus occidentalis* *Celtis laevigata* *Asimina triloba*
3. Long floods of many months, typical of managed flow regimes on the LRR, during the period of seed dispersal, disperse bottomland hardwood seeds farther than during the short duration floods characteristic of unregulated flow regimes.	Testable see: Sharitz and Schneider, "Hydrochory and regeneration in a Bald Cypress-Water Tupelo Swamp Forest. [1]	Any species where a significant proportion of seeds are dispersed by hydrochory *Nyssa aquatica* *Taxodium distichum* *Quercus sp.* *Fraxinus sp.* *Salix nigra* *Platanus occidentalis* *Populus deltoides*

SEED PRODUCTION AND DISPERSAL (CONT.)		
Hypotheses	**Testability**	**Species of Interest**
4. Farther dispersal due to continuous flooding during seed fall may result in lowered probability of seeds coming to rest on microsites appropriate for germination.	Testable see Sharitz and Schneider, "Hydrochory and regeneration in a Bald Cypress-Water Tupelo Swamp Forest"[1] and "Seed bank dynamics in a southeastern riverine swamp."[2]	Any species where a significant proportion of seeds are dispersed by hydrochory *Nyssa aquatica* *Taxodium distichum* *Quercus sp.* *Fraxinus sp.* *Salix nigra* *Platanus occidentalis* *Populus deltoides*
5. Longer periods of flooding during seed dispersal may compromise the viability of seeds.	Testable: • Seed viability testing, float seeds in water for different lengths of time, determine germination rates. • Also determine how long seeds will float, an estimate of how long they may be dispersing.	Any species where a significant proportion of seeds are dispersed by hydrochory *Nyssa aquatica* *Taxodium distichum* *Quercus sp.* *Fraxinus sp.* *Salix nigra* *Platanus occidentalis* *Populus deltoides* Many species are viable after floating for 1 month, however data for many species are not available or do not extend past 1 month
6. Portions of the pre-dam floodplain are no longer flooded, these disconnected habitats no longer receive an influx of seeds from floodwaters, thus their species richness and diversity is compromised.	Testable but requires short duration high volume flows released on the LRR for comparison to base level. Schneider and Sharitz[1] results are suggestive of this phenomenon.	Any species where a significant proportion of seeds are dispersed by hydrochory *Nyssa aquatica* *Taxodium distichum* *Quercus sp.* *Fraxinus sp.* *Salix nigra* *Platanus occidentalis* *Populus deltoides*

Seed Production and Dispersal (cont.)		
Hypotheses	**Testability**	**Species of Interest**
7. Lack of upper-elevation floodplain inundation is driving species composition toward increased densities of less flood-tolerant species, thus potentially lowering diversity at these elevations and altering historic community composition.	Testable using tank studies or green-tree reservoirs where seeds and/or seedlings are subjected to various hydrological regimes, simulating water tables consistent with pre-dam and base-level hydrologic regimes. Forest simulation models3 might also be useful.	All species but those in the most and highly tolerant category e.g.: *Fagus grandifolia* *Quercus sp. Primarily: Q laurifolia, lyrata, michauxii* *Fraxinus pennsylvanica* *Asimina triloba* etc.
8. Reduced incidence of short-duration, low-flow levels reduce woody seedling establishment on low elevation sites such as point bars.	Testable in the field if a pattern of short-duration low-flow levels can be initiated on the LRR for experimental purposes.	*Salix nigra* There may be some herbaceous species that are of interest as well.

Seedling Emergence, Survivorship and Growth		
Hypotheses	**Testability**	**Species of Interest**
9. Due to continuous early-growing-season flooding, those species that have germination windows during this period miss optimum germination conditions (temperature and light levels), resulting in fewer successful germination events when floodwaters recede.	Testable in green house flats submerged to simulate various timings of spring flooding typical of pre-dam hydrology and base-level hydrology.	Primarily species that germinate prior to leaf-out and also those that germinate later in the spring. *Fraxinus sp.* *Acer rubrum* *Ulmus americana* *Liquidambar styraciflua* Quercus sp., except Q. michauxii germinates in fall. *Carpinus caroliniana* *Celtis laevitgata*
10. Because early emerging seedlings no longer have a competitive advantage over species that emerge later in the growing season, such as red maple and American elm, early emerging species may decrease in relative abundance.	Testable in tanks, using mixed species component and regulation of water levels based on germination timing.	Primarily species that germinate prior to leaf-out and also those that germinate later in the spring. *Fraxinus sp.* *Acer rubrum* *Ulmus americana* *Liquidambar styraciflua* *Quercus sp. not Q. michauxii, which germinates in the fall.* *Carpinus caroliniana* *Celtis laevitgata*

SEEDLING EMERGENCE, SURVIVORSHIP AND GROWTH (CONT.)		
Hypotheses	**Testability**	**Species of Interest**
11. It is likely that habitats which are subject to greater durations of continuous early-growing-season flooding at depths high enough to submerge seedlings are unable to support seedlings due to submergence death and/or repeated die-back to the root collar	Testable in tanks or green-tree reservoirs, requiring at least 5 years to obtain conclusive results.	Primarily species that are found at lower elevations on the floodplain and especially those whose submergence tolerance is not known, e.g.: *Quercus sp.* *Platanus occidentalis* *Ulmus americana* *Acer rubrum* *Acer saccharinum* *Liquidambar styraciflua* *Nyssa aquatica* *Taxodium distichum* *Populus deltoides*
12. Because anoxic conditions require that individuals place more carbohydrate reserves into anaerobic root metabolism and morphological adaptations to flooding, seedlings that are exposed to flooding from the late-growing-season through winter may not have sufficient reserves to survive the winter dormant season.	Testable in tanks, requires physiological measurements.	Primarily species that are found at lower elevations on the floodplain, e.g.: *Quercus sp.* *Platanus occidentalis* *Ulmus americana* *Acer rubrum* *Liquidambar styraciflua* *Nyssa aquatica* *Taxodium distichum* *Acer saccharinum* *Populus deltoides*
13. Because anoxic conditions require that individuals place more carbohydrate reserves into anaerobic root metabolism and morphological adaptations to flooding, seedlings that are exposed to repeated years of winter through early-growing-season flooding may not have sufficient reserves to survive normal root development, bud-burst and stem elongation in the spring.	Testable in tanks, requiring physiological measurements.	Primarily species that are found at lower elevations on the floodplain, e.g.: *Quercus sp.* *Platanus occidentalis* *Ulmus americana* *Acer rubrum* *Liquidambar styraciflua* *Nyssa aquatica* *Taxodium distichum* *Acer saccharinum* *Populus deltoides*

SEEDLING EMERGENCE, SURVIVORSHIP AND GROWTH (CONT.)		
Hypotheses	**Testability**	**Species of Interest**
14. Root growth may begin as early as February for species such as sugar maple [4]. It is not known whether long-term, anoxic conditions during this initial growth period might inhibit growth.	Testable in tanks with manipulated water levels, dissolved oxygen and redox measurements. Requiring enough individuals for destructive sampling or a rhizotron setup.	Primarily species that are found at lower elevations on the floodplain, e.g.: *Quercus sp.* *Platanus occidentalis* *Ulmus americana* *Acer rubrum* *Liquidambar styraciflua* *Nyssa aquatica* *Taxodium distichum* *Acer saccharinum* *Populus deltoides*
15. Seedlings that acclimate to the continuous early-growing-season flooding on the LRR are unlikely to survive late summer moisture stress, due to the fact that they are acclimated to waterlogged conditions.	Testable in tanks with manipulated water levels, redox potential and soil moisture measurements.	Primarily most tolerant and highly tolerant species, but also some moderately tolerant species.
MATURE TREE GROWTH		
16. It is highly likely that changes to hydrologic regime on the LRR floodplain that have resulted in deeper and more continuous flooding in various floodplain habitats (such as cypress-tupelo swamps and bottomland hardwood swamps) have decreased the productivity and probability of survivorship of canopy trees.	Testable through tree-ring studies. Look for correlations between climate, hydrology and ring widths.	*Nyssa aquatica* *Taxodium distichum* *Quercus sp.* *Fraxinus pennsylvanica* *Platanus occidentalis* *Populus deltoides* *Ulmus americana* *Carya aquatica*
17. Continuous early-growing-season flooding due to managed flow regimes in conjunction with late summer moisture stress may result in growth declines because responses to continuous early-growing-season flooding (e.g. lowered root volume) will confer less tolerance of moisture stress.	Possibly testable through tree-ring studies. Possibly in green-tree reservoirs with manipulated water regimes, but requiring many years of repeated measurements using dendrometer bands.	*Ulmus americana* *Fraxinus pennsylvanica* *Platanus occidentalis* *Populus deltoides* *Acer rubrum*

Table 2. Species specific phenology and tolerance values for bottomland hardwood trees of the lower Roanoke River.

MOST TOLERANT SPECIES

Species		Phenology				Seed/Seedling Tolerances						Mature Tolerance
Scientific Name	**Common Name**	**Flowering Fruit Ripening**[5]	**Seed Dormancy**[6]	**Dispersal**[6]	**Germination**[7]	**Shade**[7]	**Seed Viability in Water**[7]	**Germination in Water**	**Tolerance Soil Saturation**[A]	**Tolerance Submergence**[B, C]	**Primary Mode of Dispersal**[7]	**% Growing Season Inundated**[D]
Fraxinus caroliniana	Carolina Ash	May July-Oct.	Not Available (NA), but likely.	Oct.-Spring	Spring	NA	NA	Better under submerged than saturated soil.[8]	NA	NA	NA	41.6 (*Fraxinus sp.*)
Nyssa aquatica	Water Tupelo	April-May Sept.-Oct. Before Leaf-out.	Yes	Oct.-Nov.	Spring-Summer	Intolerant Requires flood-waters to recede.	14 months[7]	No[9]	No mortality in 60 days. Roots grow after saturated conditions removed. Significant increase in growth compared to control. 25% reduction in photosynthesis over 32 days flooding.[10] Established seedlings grow better in saturated conditions then undersaturated.[11]	***95% surviving 4 weeks SPRING flooding, however all leaves lost.***	Hydrochory	38.4
Salix nigra	Black Willow	March-April April-May	No	April-May	May	Very Intolerant	Up to 32 in water. But, only a few days dry.[9]	Yes[9]	No mortality in 60 days. Tips of 2° roots die, but a new root system develops. Roots grow immediately after saturated conditions removed.	Height growth halted. 87% survive 30 days flooding, 23% lose terminal buds. Rapid recovery.	Hydrochory	42.5
Taxodium distichum	Bald-Cypress	March-April	Yes	Oct.	Spring	Inter-mediate Tolerance	30 months	No. But, requiring saturated not submerged soils and adequate time to grow taller than typical water levels.[12]	Yes	Yes as long as not completely submerged. Complete submergence halts growth.[12] 1 year old seedlings: 100% survival of four weeks mid-growing-season flooding. Height growth reduced.[13]	Hydrochory	>75[8]

HIGHLY TOLERANT SPECIES												
Species		**Phenology**				**Seed/Seedling Tolerances**						**Mature Tolerance**
Scientific Name	**Common Name**	**Flowering Fruit Ripening**[5]	**Seed Dormancy**[6]	**Dispersal**[6]	**Germination**[7]	**Shade**[7]	**Seed Viability in Water**[7]	**Germination in Water**	**Tolerance Soil Saturation**[A]	**Tolerance Submergence**[B, C]	**Primary Mode of Dispersal**[7]	**% Growing Season Inundated**[D]
Carya aquatica	Water Hickory	April-May Oct.	Yes	Nov.-Dec.	April-early June	Inter-mediate	NA	No	Probably very tolerant, no data available.	NA	Hydrochory Zachary	NA
Fraxinus profunda	Pumpkin Ash	April-May Aug.-Oct.	Yes	Oct.-Dec.	Spring	Moderate	Several Months	Not likely (no experimental studies available)	No mortality in 60 days. Root growth immediately after saturated conditions removed. Significant increase in growth compared to control.	NA	Amenochory Hydrochory	41.6 (*Fraxinus sp.*)
Quercus lyrata	Overcup Oak	March-April Sept.-Oct.	Yes	Oct-Winter	Spring	Intolerant	NA	Not likely (no experimental studies available)	Probably very tolerant, no data available	NA	Hydrochory Zoochory	40.3 Longer duration flooding from Dec.-June may increase susceptibility to borers[7]

MODERATELY TOLERANT SPECIES

Species		**Phenology**				**Seed/Seedling Tolerances**						**Mature Tolerance**
Scientific Name	**Common Name**	**Flowering Fruit Ripening** 5	**Seed Dormancy**[6]	**Dispersal** 6	**Germination** 7	**Shade**[7]	**Seed Viability in Water**[7]	**Germination in Water**	**Tolerance Soil Saturation**[A, E]	**Tolerance Submergence**[B, C]	**Primary Mode of Dispersal**[7]	**% Growing Season Inundated**[D]
Acer negundo	Box Elder	March-April May-Oct.	Yes	Sept.-Mar.	Spring	Moderate	NA	Not likely (no experimental studies)	NA	Height growth halted. 93% survive 30 days, 28% lose terminal buds, medium recovery. 30 % survival of 1 year old seedlings. 13	Amenochory	NA
Acer rubrum	Red Maple	Jan.-March April-July	No	May-July	Immediately after ripening and reaching seedbed	Intolerant	Up to 32 days. 9	No. Immediately after soaked and removed from water.9	No mortality in 60 days. Roots are dormant but recover quickly. Roots systems take at least three weeks to redevelop after saturated conditions removed. ***8 day old seedlings are stunted by between 1-32 days of flooding. Seedlings flooded for at least 6 days do not show recovery to normal growth up to 48 days after flooding*.**	Height growth halted. 93% survive 10 days, 0% survive 20 days.	Amenochory	36.4
Acer saccharinum	Silver Maple	Feb.-April April-July	No	April-July	Soon after dispersal	Intolerant	Up to 32 days.9	No. Immediately after soaked and removed from water. 9	No mortality in 60 days. Roots are dormant with minor mortality. Roots systems take at least three weeks to redevelop after saturated conditions removed.	Height growth halted, but 100% survival up to 30 days	Amenochory	NA
Betula nigra	River Birch	March-April May-June	NA	May-June	Spring	Intolerant	NA	Not likely (no experimental studies)	***12 day old river birch seedlings are stunted under saturated conditions for 2-32 days. Growth response is stunted up to 52 days following saturated conditions.***	NA	Amenochory	23.2
Carpinus caroliniana	Ironwood	March-April Sept.-Oct.	Yes	Oct.-Spring	Spring	Very Tolerant	NA	Not likely (no experimental studies)	NA	NA	Zoochory	23.2

MODERATELY TOLERANT SPECIES (CONT.)												
Species		**Phenology**				**Seed/Seedling Tolerances**						**Mature Tolerance**
Scientific Name	**Common Name**	**Flowering Fruit Ripening** 5	**Seed Dormancy**[6]	**Dispersal** 6	**Germination** 7	**Shade**[7]	**Seed Viability in Water**[7]	**Germination in Water**	**Tolerance Soil Saturation**[A]	**Tolerance Submergence**[B, C]	**Primary Mode of Dispersal**[7]	**% Growing Season Inundated**[D]
Diospyros virginiana	Persim-mon	May-June Sept.-Oct.	Yes	Oct.-Dec.	April-May	Tolerant	NA	NA	Relatively Tolerant[8]	NA	Zoochory	30.4
Fraxinus pennsylvanica	Green Ash	April Aug.-Oct.	Yes. Can be for several years.	Oct.-Spring	Spring	Tolerant	NA	Not likely (no experimental studies)	No mortality in 60 days. Some mortality of 2° root tips, but many new tips. Roots grow immediately after saturated conditions removed. Significant increase in growth compared to control. Photosynthesis is reduced during flooding [10].	Height growth halted. 73% survive 20 days. 20% survive 30 days but 66% lose terminal bud. ***91% surviving 4 weeks SPRING flooding, leaves remain. Most killed re-sprout from root collar.***	Amenochory Hydrochory	41.6 (*Fraxinus sp.*)
Ilex decidua	Deciduous Holly	April-May Sept.-Oct.	Yes	NA	Spring	NA	NA	NA	NA	NA	Zoochory	35.2
Liquidambar styraciflua	Sweet-gum	March-May April-Oct.	Yes	Oct.	Spring	Intolerant	NA	NA	No shoot mortality in 60 days. 2° roots die. Roots systems take three weeks to redevelop. Significant decrease in growth compared to control. 5 mo.-old seedlings survive 2 yr. continuous flooding. Smaller than seedlings grown under periodically flooded conditions. [19]	Height growth halted. 75% survive 10 days. None survived 20 days. ***68% surviving 4 weeks SPRING flooding, leaves remain. Many killed re-sprout from root collar.***	Gravity Amenochory	34.3
Platanus occidentalis	American Sycamore	April-May Oct.	No	Feb.-Apr.	Soon after Dispersal	Intolerant	Up to 32 days. Higher viability after soaking.[9]	No. Immediately after soaked and removed from water.[9]	74%survive 60 days. All 2° and lower 1° roots die; surviving roots are dormant. Roots systems take at least three weeks to redevelop after saturated conditions removed. ***17 day old sycamore is stunted by 32 days saturation, 20 days after saturation growth is still stunted.***	Height growth halted. 100% survive 10 days, but do not recover quickly. None survived 20 days. ***52% surviving 4 weeks SPRING flooding, all leaves lost. Most killed re-sprout from root collar.***	Amenochory Hydrochory Zoochory	23.9

MODERATELY TOLERANT SPECIES (CONT.)

Species		Phenology				Seed/Seedling Tolerances						Mature Tolerance
Scientific Name	**Common Name**	**Flowering Fruit Ripening** [5]	**Seed Dormancy**[6]	**Dispersal** [6]	**Germination** [7]	**Shade**[7]	**Seed Viability in Water**[7]	**Germination in Water**	**Tolerance Soil Saturation**[A]	**Tolerance Submergence**[B, C]	**Primary Mode of Dispersal**[7]	**% Growing Season Inundated**[D]
Populus deltoides	Eastern Cotton-wood	March-April	No	May-Aug.	Soon after falling unless floating or immersed in water	Intolerant	Up to 32 days. [9]	Yes [9]	93 % survive 60 days. All roots but 1^{o} die. Roots systems take at least three weeks to redevelop after saturated conditions removed. 65% of 1 yr. seedlings survive 30 days during the mid-growing season.[13]	Height growth halted. 93% survive 10 days, recover rapidly; 73% survive 20 days, recover slowly; 47% survive 30 days but 29% lose terminal buds. ***24% surviving 4 weeks SPRING flooding, all leaves lost. Most killed re-sprout from root collar.***	Amenochory Hydrochory	34.5
Quercus laurifolia	Laurel Oak	March-April Sept.-Nov.	Require 2 years on tree to mature. Dormant after Dispersal	Sept.-Oct.	Spring	Tolerant	At least 30 days	Not likely (no experimental studies)	NA	NA	Hydrochory Zoochory Gravity	NA
Quercus phellos	Willow Oak	March-April 2nd yr. after flowering Sept.-Nov.	Yes	Oct.-Winter	Spring	In-tolerant	Prolonged submersion can reduce viability, but not significantly	NA	No shoot mortality in 60 days. Roots are dormant but only some 2^{o} roots die. Roots systems take at least three weeks to redevelop after saturated conditions removed. Significant decrease in growth compared to control.	NA	Gravity Hydrochory Zoochory	30.6
Ulmus americana	American Elm	Feb.-March March-April	No	March-April	Spring	Inter-mediate	Up to 32 days. Higher viability after soaking. [9]	No. Immediately after soaked and removed from water. [9]	93% survive 60 days, but all 2^{o} roots die. Roots systems take three weeks to redevelop after saturated conditions removed. Significant increase in growth compared to control. ***11 day old seedlings severely stunted by 8-16 days even up to 46 days after saturation.***	Height growth halted. 100% survive 10 days, but 50% lose terminal buds. 26% survive 20 days.	Amenochory	24.6

Weakly Tolerant Species

Species		**Phenology**				**Seed/Seedling Tolerances**						**Mature Tolerance**
Scientific Name	**Common Name**	**Flowering Fruit Ripening** [5]	**Seed Dormancy** [6]	**Dispersal** [6]	**Germination** [7]	**Shade**[7]	**Seed Viability in Water**[7]	**Germination in Water**	**Tolerance Soil Saturation**[A]	**Tolerance Submergence**[B, C]	**Primary Mode of Dispersal**[7]	**% Growing Season Inundated**[D]
Celtis laevigata	Sugar-berry	April-May Aug.-Oct.	NA	Oct.-Dec.	Spring	NA	NA	NA	93% survive 60 days but all but primary roots die! Roots systems take at least three weeks to redevelop after saturated conditions removed.	NA	NA	NA
Quercus michauxii	Swamp Chestnut Oak	April-May Sept.-Oct.	No	Sept.-Oct.	Sept.-Oct.	Intolerant	NA	NA	Intolerant[8].	NA	Zoochory Hydrochory	28.6
Quercus shumardii	Swamp Red Oak	April Sept.-Oct.	Yes	Mid-Winter-Late Winter	Spring	Intolerant	NA	NA	67% survive 60 days. Roots go dormant and some 2^o roots die. Roots systems take at least three weeks to redevelop after saturated conditions removed.	Height growth halted does not resume within 2 months after flooding. 93% survive 10 days.	Hydrochory Zoochory	Damaged by 2 months of flooding in the spring[8].
Asimina triloba	Pawpaw	March-May Aug.-Oct.	Yes	Late Fall-Winter	Spring	NA	NA	NA	NA	NA	NA	11.6

LEAST TOLERANT SPECIES												
Species		**Phenology**				**Seed/Seedling Tolerances**						**Mature Tolerance**
Scientific Name	**Common Name**	**Flowering Fruit Ripening** 5	**Seed Dormancy** 6	**Dispersal** 6	**Germination** 7	**Shade**[7]	**Seed Viability in Water**[7]	**Germination in Water**	**Tolerance Soil Saturation**[A]	**Tolerance Submergence**[B, C]	**Primary Mode of Dispersal**[7]	**% Growing Season Inundated**[D]
Quercus pagota	Cherry-bark Oak	April Sept.-Nov.	Dormant	Fall-Winter	Spring	Intolerant			11% die after 15 days, 47% die after 30 days. Roots go dormant. At 60 days 87% mortality and all roots died. Roots systems take at least three weeks to redevelop after saturated conditions removed. 50% survival of 1 yr. old seedlings flooded from Nov.-May. Most mortality late May-mid-June. [19]	Height growth halted. 86% survive 5 days but recover slowly. 6% survive 10 days.	Hydrochory Zoochory	NA
Ulmus rubra	Slippery Elm	Feb.-March March-April	No	March-April	March-April	Tolerant	NA	NA	NA	NA	Amenochory	NA

INTOLERANT SPECIES												
Species		**Phenology**				**Seed/Seedling Tolerances**						**Mature Tolerance**
Scientific Name	**Common Name**	**Flowering Fruit Ripening** 5	**Seed Dormancy** 6	**Dispersal** 6	**Germination** 7	**Shade** 7	**Seed Viability in Water**[7]	**Germination in Water**	**Tolerance Soil Saturation**[A]	**Tolerance Submergence**[B, C]	**Primary Mode of Dispersal**[7]	**% Growing Season Inundated**[D]
Fagus grandifolia	American Beech	March-April Sept.-Oct.	Yes	After First Frost	Spring	Very Tolerant	NA	NA	Likely to have very little tolerance as a seedling. “Few tree species are less tolerant of flooding during the growing season than American beech.” [7]	Likely to have very little tolerance as a seedling. “Few tree species are less tolerant of flooding during the growing season than American beech.” [7]	Zoochory Gravity	3.2

Footnotes

[A] Hosner[14] inundated seedlings submerged seedlings approximately two months after germination; seedlings were well past the cotelydon stage and were not subjected to any flooding stresses prior to soil saturation for up to 60 days.
[B] Hosner[15] submerged seedlings approximately two months after germination, seedlings were well past the cotelydon stage and were not subjected to any flooding stresses prior to submergence for up to 30 days.
[C] Notes in ***bold-italics*** in this column are results from Baker's 1977 study[16]. One year seedlings (nursery stock, no prior stressors) were subjected to one month of submergence following leaf-out in early May. Results from this study mimic natural conditions better than other studies, however, there was no control.
[D] These estimates are based on Hall and Smith's[17] observations of trees in the Kentucky Reservoir on the Tennessee River. These bottomlands were subjected to growing season flooding every year for 8 years.
[E] Notations in ***bold italics*** are from McDermott's [18] studies on recently germinated seedlings.

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