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Dendrochronological analysis of productivity and hydrology in two Louisiana swamps

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DENDROCHRONOLOGICAL ANALYSIS OF PRODUCTIVITY AND HYDROLOGY IN
TWO LOUISIANA SWAMPS

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree
Master of Science

In

The School of Renewable Natural Resources

by

John Blake Amos

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ABSTRACT

Modified river flows and land subsidence have subjected many coastal swamp forests in the delta of the Mississippi River to greatly altered flooding, sediment, and nutrient regimes. These areas have become inundated to greater depth, duration, and frequency and either are connected to the river and receive drastically increased sediment and nutrients (riverine swamps) or have become disconnected from riverine flooding (stagnant swamps) and receive little or no sediment and nutrient input. To better understand how these changes are affecting ecosystems, dendrochronological techniques for baldcypress (*Taxodium distichum* L. Rich.) were used at three sites in each of two contrasting swamps to compare how productivity has been historically related to climate and hydrology. The historical responses of baldcypress radial growth to 111 years of climatic variables and 51 years of hydrological data were analyzed by separate and simultaneous multiple linear regression analysis of effects. The effect of flooding on growth of baldcypress depended on the temporal scale and type of floodwater. Seasonal flooding increased growth in flood years for both stagnant and riverine swamps but decreased growth in the ensuing year. Long-term, riverine flooding was positively correlated to growth, but long-term, stagnant flooding was negatively correlated to growth. Growth in both swamps increased at onset of greater flooding, then decreased after several decades of continued frequent flooding. Climatic controls on growth depended upon interactions with hydrology but correlations between growth and flooding variables were consistent and much stronger than climate. When climate was analyzed separately, warm winters and cool, rainy growing seasons were important for higher growth. When hydrology was included in simultaneous analysis with climate, cool, dry fall weather of the previous year was also important. A model of baldcypress growth that only includes hydrologic regime is insufficient to understand growth. Climate, stand history,

hydrological regime and the interaction of these effects must be considered to accurately understand changes in growth.

INTRODUCTION

Swamps of the southeastern United States are dominated by cypress (*Taxodium* spp.) and tupelo (*Nyssa* spp.). Pondcypress (*T. ascendens* Brongn.) and swamp tupelo (*N. biflora* Walt.) are typically in shallow ponds and poorly drained areas of the Coastal Plain, and baldcypress (*T. distichum* (L.) Rich.) and water tupelo (*N. aquatica* L.) are typically in riverine wetlands (Wilhite and Toliver 1990). Ecosystem functions of these forested wetlands yield important services such as habitat, spawning and nursery grounds, commercial timber, floodwater storage, coastal storm abatement, aquifer recharge, improving water quality by uptake of nutrient and toxic compounds, erosion control, carbon storage, and nutrient cycling (Lugo and Brinson 1979; Brown et al. 1979; Gosselink et al. 1981; Ewel and Odom 1984; Mitsch and Gosselink 2000).

Many factors threaten cypress-tupelo swamps in coastal Louisiana. Although sediment input to deltaic forested wetlands was once sufficient to offset subsidence, large-scale and local hydrologic and geomorphic modifications have reduced or eliminated deposition of nutrient-laden sediment (Hatton et al. 1983). Therefore, levee construction and subsidence have caused the loss of much of Louisiana's cypress-tupelo forests (Salinas et al. 1986; Delaune et al. 1987; Conner and Brody 1989; Tye and Coleman 1989a). Hydrologic alterations have permanently impounded water in some areas, which has eliminated regeneration and may be reducing productivity of swamps by reducing growth of mature trees (Salinas et al. 1986; Delaune et al. 1987; Conner and Brody 1989; Chambers et al. 2005).

Baldcypress is the dominant species in the deltaic wetlands of Louisiana. Understanding the response of this species to changing hydrology is necessary because this is a major structural component of forested wetlands. However, its response to altered hydrology and climate is not clear (Stahle et al. 1985; Wilhite and Toliver 1990; Stahle et al. 1992; Stahle and Cleaveland

1992; Anderson et al. 1995; Young et al. 1995; Keeland and Young 1997). Laboratory studies have improved knowledge of baldcypress seedling germination, establishment, and growth response to hydrology and climate (Shanklin and Kozlowski 1985; Pezeshki 1990; Pezeshki 1994; Conner 1994; Kludze et al. 1994; Pezeshki et al. 1995; Anderson and Pezeshki 1999; Pezeshki et al. 1999; Souther and Shaffer 2000; Elcan and Pezeshki 2002) but a precise model of the response of mature trees to this combination of stressors is lacking.

Studies of growth response of mature baldcypress to changes in flooding have yielded equivocal results. Some studies have found declines in baldcypress radial growth upon introduction of permanent flooding to stands that previously experienced seasonal flooding (Beaven and Oosting 1932; Mitsch et al. 1979; Mitsch and Ewel 1979; Duever and McCollom 1987; Conner and Brody 1989; Conner and Day 1992b; Conner and Day 1992b; Keeland 1994; Megonigal et al. 1997) while other studies have found increases in growth (Eggler and Moore 1961; Conner and Day 1976; Conner et al. 1981; Keeland and Young 1997). Still other studies have found an initial increase in growth after onset of increased flooding followed by a long-term decline in growth (Stahle et al. 1992; Young et al. 1995).

These inconsistent conclusions may be the result of site-specific differences and/or limited temporal scales of measurement. Trees react to changing environmental conditions slowly (Kozlowski and Pallardy 1984) and short-term studies may not capture the delayed effects of chronic flooding. Long-term studies have been usually performed on single stands without replication of hydrologic condition. Neglecting site differences could drastically alter conclusions. Trees will respond to similar flooding conditions differently depending on age, acclimation to previous flooding, surrounding species composition, or any number of other

factors (Kozlowski et al. 1991). A long-term field study of mature baldcypress response to hydrology controlling for site conditions is needed.

Tree rings can provide long-term growth data with minimal field time while permitting annual resolution of growth. To better understand lasting and annual effects of changing hydrology on growth it is possible to relate tree growth to long-term hydrological data. Dendrochronological methods accurately assign ring width to the exact year of formation by the process of cross-dating (Fritts 1976). Without cross-dating, the year assigned to a particular tree ring can be inaccurate because of missing or false rings and result in invalid data (Fritts 1976; Fritts and Swetnam 1989). Several studies have used tree rings to assess the impacts of permanent flooding upon baldcypress (Eggler and Moore 1961; Mitsch and Ewel 1979; Duever and McCollom 1987; Klimas 1987; Young et al. 1995) but only three have explicitly stated use of cross-dating tree rings to relate growth to the effects of hydrology (Stahle et al. 1992; Young et al. 1995; Keeland and Young 1997). Previous studies have not used long-term hydrological data to assess effects on growth, but have instead simply analyzed the periods of growth before and after a known period of increased flooding. Statistical limitations of this Before-After-Control-Impact (BACI) approach can be severe because inaccurate results can be found up to 30% of the time (Murtaugh 2002). Thus, annual data is more appropriate for detecting a response. One study used dendrochronology to reconstruct summer streamflow (Cleaveland 2000) from long-term stream gauge data but did not include study sites in different hydrological regimes nor analyze climatic effects. No studies have used baldcypress tree rings to relate growth to long-term hydrological data on an annual basis while accounting for the influence of climate.

Objectives

The objective of this study is to better understand radial growth response of baldcypress to flooding under field conditions. Specifically, this study seeks to (1) understand response of baldcypress to long-term and short-term flooding; (2) understand response of baldcypress to climatic controls; (3) compare response of baldcypress to stagnant and flowing flood waters; and (4) assess the relative importance of all these factors on radial growth.

LITERATURE REVIEW

Baldcypress Responses to Flooding

Many studies of mature baldcypress have found a decrease in growth rate and increase in mortality following commencement of permanent inundation (Mitsch et al. 1979; Mitsch and Ewel 1979; Duever and McCollom 1987; Klimas 1987; Conner and Brody 1989; Conner and Day 1992b; Keeland 1994; Megonigal et al. 1997). In Maryland, Beaven and Oosting (1932) found mortality of baldcypress apparently caused by water stress over a one year period after a peat burn caused a site to begin to flood continually. A study of a Louisiana swamp permanently flooded for 18 years after creation of a lake found high mortality rates (50%) of mature baldcypress in response to chronic deepwater flooding (Egglar and Moore 1961). However, suggesting reduced competition as the cause, the annual growth of surviving trees was found to be greater after onset of flooding. A study of Lake Caddo created at the border of Louisiana and Texas suggested massive baldcypress mortality caused by permanent flooding would occur (Klimas 1987). Conversely, a later dendrochronological study of the same lake found no evidence to suggest such a decline, and growth rates within the historic range of variation (Keeland and Young 1997). A 5-year study of four similar Louisiana baldcypress-water tupelo swamps under varying hydrologic regimes found the lowest litterfall in an impounded area flooded continuously for 50 years, and highest in an area artificially managed to flood in the fall and drain in the summer (Conner and Day 1992b). Although baldcypress and water tupelo dominated the impounded area, the managed area was dominated by red maple (*Acer rubrum*, L.) and ash (*Fraxinus* spp.). Permanent flooding and resultant mortality of 20% of the less flood-tolerant hardwood species were inferred as the causes of low productivity at the impounded site and the high productivity at the managed area was attributed to pumped agricultural drainage

water containing high concentrations of nutrients and dissolved oxygen. Pondcypress has also showed both decreased biomass and growth over a period of up to 11 years caused by alteration to permanent flooding (Mitsch and Ewel 1979). Mitsch et al. (1979), using dendrochronological techniques (greater than 30 year period of analysis), found a dramatic decrease in pondcypress growth as caused by a rise in water level from beaver activity.

Other studies of baldcypress have found an increase in growth with increased flooding (Eggler and Moore 1961; Conner and Day 1976; Conner et al. 1981; Keeland and Young 1997). Diameter growth of impounded baldcypress is often greater than before initiation of permanent flooding because growth likely increases in response to reduced competition by mortality of less flood-tolerant species (Eggler and Moore 1961). A 1-year study of swamp productivity found baldcypress and water tupelo basal area increase was greater in an area of Louisiana impounded for 51 years than a nearby area that experienced seasonal flooding over that same time period (Gosselink et al. 1981). However, further studies at the same sites over a longer time frame (5 years) found progressively declining litterfall with permanently flooded conditions but diameter growth of the impounded area remained higher than a seasonally flooded riverine site and was equal to an area managed to flood seasonally (Conner and Day 1992a; Conner and Day 1992b). The authors inferred that surges in productivity after onset of greater flooding were caused by reduced competition from mortality of other species less tolerant to flooding. In reconstructing historical flow of the White River of Missouri and Arkansas, Cleaveland (2000) found a strong positive correlation of growth to summer (Jun-Aug) streamflow over a 55-year period. Increased soil moisture has been cited by some authors as a cause of greater growth after impoundment during the growing season for other bottomland hardwood species (Broadfoot 1967; Broadfoot and Williston 1973).

Several studies have found a short-term growth increase upon permanent flooding followed by a long-term decline (Stahle et al. 1992; Young et al. 1995). Using dendrochronological techniques, a surge in growth lasting 3 years followed by a period of 30 years of decreased growth was detected after an earthquake caused the creation of Reelfoot Lake in Tennessee and resulted in permanent flooding of the swamp (Stahle et al. 1992). These authors suggested the observed decline may have been a result of the standardization process but suggested that the surge was likely a result of increased soil moisture. A study in South Carolina of an area experiencing increased water levels from road construction also found a temporary increase in growth of baldcypress lasting three years followed by a depressed period of growth of greater than 16 years (Young et al. 1995). This study cited reduced competition or increased nutrient input as the likely cause of the short-term growth surge and inferred the growth depression was caused by prolonged deep flooding.

Mechanisms of Flooding Effects

Generally, research has found declining growth and increasing mortality with increased depth, duration, and altered seasonality of flooding. Mechanisms of these effects are not well understood for mature trees, but laboratory research on seedlings has found increased inundation during the growing season reduces growth by reducing root uptake and causing stomatal closure (Pezeshki et al. 1986; Pezeshki and Chambers 1986; Pezeshki and Delaune 1998).

Wetland plants, including baldcypress, are adapted for episodic soil saturation and associated chemical changes. However, even flood-tolerant species experience detrimental effects from prolonged flooding (Pezeshki and Santos 1998). Although knowledge of the complex biogeochemical interactions that occur in plants in response to flooding is limited, it is clear that the biotic activity after inundation that quickly depletes soil oxygen can affect root

systems (Richardson and Vepraskas 2001). A root system subjected to hypoxia or anoxia experiences diffusion of oxygen from roots to soil, inhibition of root uptake, chemical conversion of available nutrients to inaccessible forms, increased exposure to phytotoxins, and mortality (Ponnamperuma 1984; Kludze et al. 1994, 1997; Pezeshki 1994; Pezeshki and Delaune 1998; Anderson and Pezeshki 1999; Pezeshki et al. 1999).

Limited available oxygen in the rhizosphere stresses the root system, which affects uptake pathways and decreases net photosynthesis (Kludze et al. 1994; Pezeshki 1994; Anderson and Pezeshki 1999; Pezeshki et al. 1999). Low oxygen in the rhizosphere decreases stomatal conductance, transpiration, and net photosynthesis even in flood-tolerant species (Pezeshki et al. 1986; Kludze et al. 1994; Pezeshki and Delaune 1998; Pezeshki and Santos 1998). The primary cause of lower photosynthesis under flooded conditions is stomatal closure (Kozlowski and Pallardy 1984; Sojka 1992). However, the decrease in stomatal conductance is temporary so that it increases after extended flooding (Pezeshki et al. 1986; Pezeshki and Delaune 1998; Pezeshki and Santos 1998).

Many factors disrupt photosynthetic activities under flooded conditions. Decreased root growth of baldcypress leads to an inability to support shoot growth (Pezeshki and Delaune 1998) and inhibits the carbohydrate sink function of roots (Carmi 1993). Flooding lessens the number and type of mycorrhizal associations with kerri (*Eucalyptus diversicolor* F. Meull.) (Bougher and Malajczuk 1990), Virginia pine (*Pinus virginiana* Mill) (Worley and Hacskeylo 1959) Monterey pine (*Pinus radiata* D. Don), and Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) (Gadgil 1972), which diminishes nutrient uptake (Bougher et al. 1990). Loss of baldcypress productivity under flooded conditions has also been attributed to loss of photosynthetic enzymes (Pezeshki

1994), growth regulator imbalances, decreased translocation of photosynthates to roots, and lowered ability of root system to utilize photosynthates (Pezeshki and Santos 1998).

Accumulation of phytotoxic ions that are soluble during reducing conditions has been hypothesized to decrease growth and even cause death for some species, and is a feasible cause of reduced growth in baldcypress as well (Jones and Etherington 1970; Jackson and Drew 1984; Ponnampertuma 1984, 1997; Pezeshki and Delaune 1998). Reduced forms of iron, manganese, and sulfur can be passively absorbed into roots and then transported to the shoot (Jones and Etherington 1970). Even though flood-tolerant species such as water tupelo can immobilize these ions within the root system (McKevlin et al. 1995) and baldcypress can partially exclude them (Pezeshki et al. 1999), phytotoxins can damage the tissue of the roots, disrupt transport processes, and reduce overall root area (Crawford 1989).

Secondary effects of flooding, such as decreased oxygen and nutrient availability, rather than flooding itself may be to blame for detrimental effects on growth. Thus, flowing (riverine) water is less detrimental than standing, stagnant water for many species because it contains higher concentrations of nutrients and dissolved oxygen (Sabo et al. 1999a). Baldcypress and water tupelo seedlings grow better in aerobic floodwaters than in anaerobic conditions (Dickson and Broyer 1972). One-year old baldcypress saplings fertilized while flooded for two years showed higher growth than those that were not flooded and unfertilized (Effler and Goyer 2006). Seedlings of swamp tupelo and water tupelo subjected to flowing water flooding showed almost twice the height growth of seedlings flooded with stagnant water (Hook et al. 1970). Another study found highest net primary productivity in a permanently flooded riverine stand of baldcypress (Carter et al. 1973 as cited by Conner and Day 1976). Baldcypress of cypress-hardwood associations in seasonally flooded flowing water systems is more productive than

perennially flooded or rarely flooded cypress stands (Mitsch and Ewel 1979). However, flooded swamp tupelo seedlings fertilized with phosphorus did not show no significantly different height growth, root length, or dry weight than that of a control (Hook et al. 1983).

Application of wastewater (typically rich in nitrogen and phosphorus) on forested wetlands can ameliorate the adverse effects of flooding or even increase growth. Wastewater application on baldcypress and pondcypress forests has increased growth and productivity for over 40 years (Mitsch and Ewel 1979; Brown 1981; Nessel et al. 1982; Lemlich and Ewel 1984; Hesse et al. 1998). Mitsch and Ewel (1979) found an increase in productivity of baldcypress in a continually flooded wastewater site after a year of treatment. Wastewater application enhanced tree productivity in a seasonally drained littoral site over a period of at least 10 years (Lemlich and Ewel 1984). Tree growth rates of seasonally flooded pondcypress more than doubled in response to wastewater treatment application over a 41-year period (Nessel et al. 1982). Baldcypress in Louisiana showed enhanced growth over a 40-year period of wastewater application relative to a nearby stand (Hesse et al. 1998). Pondcypress flooded continuously showed a large biomass increase the year following effluent application (Brown 1981). However, nutrient additions have not always increased growth in forested wetlands. A 5-year study of wastewater additions to mature pondcypress normally flooded year-round found no noticeable effect (Straub 1984). Mortality rates were higher and growth rates were slower for baldcypress seedlings subjected to wastewater application but effects of the same treatment were negligible for pondcypress seedlings in another study (Deghi 1984).

Effects of Climate on Trees

Baldcypress growth is generally sensitive to climatic variability, especially spring precipitation and summer drought. Several studies have used baldcypress tree rings to

reconstruct climate or hydrological history. (Stahle and Cleaveland 1992; Stahle and Cleaveland 1994) found tree ring width of baldcypress in South Carolina, North Carolina and Georgia was positively correlated with spring (ranging from March to June) precipitation (as high as $r = 0.84$). Summer (June to August) Palmer's Drought Severity Index (PDSI) was positively correlated with baldcypress growth (Stahle et al. 1988; Fye et al. 2003). However, no such strong climatic associations with baldcypress growth have been found in southern Louisiana. Reams and Van Deusen (Reams and Van Deusen 1998) found the strongest correlation of baldcypress ring width to any monthly PDSI value during June ($r = 0.10$) and concluded that hurricane events and lack of summer droughts degraded climatic correlation compared to inland sites. All of these studies have only investigated climatic effects and have not investigated the role of hydrology in controlling growth.

Temperature and precipitation greatly influence the environmental and physiological processes dictating tree growth, and are usually highly correlated to growth and to each other because of the inverse relationship between cloud cover and solar radiation (Fritts 1976; Stahle et al. 1991). Warm summers often occur with lower precipitation, so that little soil water is available to satisfy high evaporative demand in uplands. Hot and dry conditions increase stress on the tree because they increase evaporative demand by increasing water vapor pressure deficit, plant temperatures, and respiration (Kozlowski et al. 1991). Water stress in wetlands can also occur because of prolonged flooding, so that climate and hydrology interact to increase water stress (Brown 1981; Jean and A. Bouchard 1996). The relationship of baldcypress growth to climate and hydrology in these swamps is not easily delineated.

Temperature influences initiation of cambial growth in the spring and affects the duration of the growing season (Kramer and Kozlowski 1979). Baldcypress productivity is greatest for

30-year average daily mean temperature of 19°C in the southeast U.S., and is less for higher and lower temperatures (Middleton and McKee 2004). Increases of temperatures above 35°C rapidly decrease physiological processes associated with growth (Kramer and Kozlowski 1979) and brief exposure to high temperatures decreases photosynthesis for several days while respiration continues unhindered (Larcher 1969).

Precipitation might increase growth of wetland plants by oxygenating floodwater and reducing vapor pressure deficit of the leaf to the atmosphere. Precipitation cannot increase growth of baldcypress and water tupelo by increasing soil moisture in permanently flooded conditions. However, precipitation may oxygenate flood waters both because it is high in dissolved oxygen concentration and by mechanical aeration (Broadfoot 1967; Brown 1988). Increased frequency and duration of rain events lowers the water vapor pressure deficit of the surrounding atmosphere (Larcher 1969) because of the associated high humidity.

Climate effects on growth can persist into the next growing season. Stored food reserves from the previous year directly affect growth early in the growing season. This is especially true in the stem, base, and root system (Fritts 1976) because the expanding crown uses photosynthates produced early in the growing season and there is minimal translocation of early photosynthates downward to the stem and roots. Thus, the stem is one of the parts of the tree most dependent on stored photosynthates and is most correlated to growth in the prior year (Fritts 1976; Bouriaud et al. 2005). Low reserves from poor growth years also cause the tree to form fewer and smaller leaves, buds, and roots for growth in the next year that in turn support less cambial growth later in the growing season.

Hurricanes greatly affect growth of coastal baldcypress by winds causing loss of branches, defoliation, and breakage (Reams and Van Deusen 1998). However, hurricane damage

is more prevalent in older trees (>300 years) (Duever et al. 1984; Francis and Gillespie 1989; Reams and Van Deusen 1998), so that growth rings in second-growth baldcypress may not record hurricanes as well (Reams and Van Deusen 1998). For this reason, the effects of hurricanes will not be analyzed in this study. It is more likely that growth will be affected the year after a hurricane, because the hurricane season for the North Atlantic Ocean falls at the end of the growing season (June 1-November 30 with peak activity between mid-August and mid-October). Several studies have found small ring widths in the year of or after a hurricane (Doyle and Gorham 1996; Reams and Van Deusen 1998).

Description of the Study Area

The lower Mississippi alluvial plain was formed as a result of sedimentation by the Mississippi River over the past several thousand years. The lower Mississippi alluvial valley was incised during the Pleistocene and alluviation of this entrenched valley has occurred during the Holocene (Tye and Coleman 1989b). Prior to hydrologic manipulation, major Holocene avulsion and realignment of the main Mississippi River channel in the deltaic plain occurred approximately every 1000-2000 years (Coleman 1988; Coleman et al. 1998). This channel shifting, as well as meander scrolling in the non-deltaic valley, created broad areas of nearly flat land near sea level (Kolb and Van Lopik 1958). However, a levee system now causes much of the sediment load of the Mississippi River to be deposited off the continental shelf in the Gulf of Mexico instead of being distributed among swamps and associated distributaries.

Backswamps in the Mississippi River delta are floodplain depressions situated between river meander belts and contain freshwater swamps, crevasse-splay complexes, small streams, and freshwater lakes closer to the ocean (Tye and Coleman 1989b; Aslan and Autin 1999). Fluvial geomorphology controls the structure of swamp habitat. Natural levees, which are coarse

sediments deposited during overbank flow, form ridges adjacent to channels, and fine-grained, low-lying backswamps form farther away from the channel (Fisk 1944, 1947; Frazier 1967; Tye and Coleman 1989a). These natural levees are the highest elevations in the delta of the Mississippi River and backswamps are the lowest (Frazier 1967; Tye and Coleman 1989a; Aslan and Autin 1999). The natural levees are only flooded during extreme flood events while the backswamps are, under natural conditions, generally flooded each spring (Conner and Day 1976; Brody et al. 1989). The fine-grained soils of these backswamps are the result of recurring large-scale overbank deposition (Fisk 1944, 1947) as well as input of sediment, including some sand, during periods of crevassing and avulsion (Kraus and Aslan 1993; Aslan and Autin 1999). The depth of these surficial fine-grained deposits are of varying thickness (Fisk 1944, 1947; Fisk 1947; Saucier 1994; Aslan and Autin 1999). It is in these backswamps that cypress-tupelo swamps typically are found.

Soils of backswamps vary depending on local hydrology as well as other factors. Low velocity flooding in backswamps causes hypoxic conditions that limit decomposition (Richardson and Vepraskas 2001). The slowly decaying organic material then forms a dark-colored muck over the mineral sediment. Organic matter accumulation in depressions that remain inundated for much of the year varies from a thin overlying layer to a layer deep enough to encompass most of the rooting zone (Frazier 1967; Tye and Coleman 1989a; Aslan and Autin 1999).

The most important human alteration of the natural processes of the Lower Mississippi River alluvial plain has been the construction of levees. Until the major flood of 1927, the levee system was an irregular composite of private and public installations of varying sizes, but the subsequent consolidation and completion of a full levee system has since completely encased the

lower river. Levee construction has reduced flooding and consequently disrupted hydrologic, sediment, and nutrient regimes for swamps (Conner and Day 1976; Conner et al. 1981; Hatton et al. 1983; Kemp et al. 1985; Slater et al. 1985; Conner et al. 1986; Salinas et al. 1986; Delaune et al. 1987; Brody et al. 1989; Conner and Brody 1989; Conner and Day 1992a; Conner and Day 1992b; Delaune et al. 2003). Generally speaking, anthropogenic flood-control measures have resulted in two suites of swamp ecosystems in the deltaic plain: systems that are excluded from riverine flooding by levees and systems within the Atchafalaya flood control levees that are connected to riverine flooding.

Systems Excluded from Riverine Flooding

Because of the levee system now present, some interdistributary basins in the deltaic plain receive little riverine input and, as a result, little sedimentation and nutrient input (Conner and Day 1976; Delaune et al. 1978; Delaune et al. 1981; Hatton et al. 1983). However, these swamps are experiencing an increase in water levels (Delaune et al. 1987). Without the sediment-rich floodwaters of the Mississippi River to counteract the subsidence (net loss of elevation) caused by consolidation of recent alluvium, much of the cypress-tupelo forest in the delta of the Mississippi River now experiences flooding more frequently, for longer durations, and at different periods of the year than before levee construction (Conner et al. 1981; Delaune et al. 1987). Basins now excluded from riverine flood waters are influenced primarily by subsidence, sea-level rise, and local modifications to hydrology (e.g., highways, railroads, canals, and spoil banks), so hydrologic budgets are driven by rainfall, upland runoff, and backwater flooding (Conner and Day 1988).

Sea Level Rise and Subsidence

Water levels in swamps of the Mississippi River delta are increasing from both eustatic sea-level rise and subsidence. Estimates of eustatic sea-level rise caused by climate change range from 1.2-3.0 mm/yr for the 20th century (Emery 1980; Gornitz et al. 1982; Robock et al. 1983; Clark 1986; Delaune et al. 1987). The most likely rate of current eustatic sea-level rise is 1.8 mm/yr (White et al. 2005). Rising surface air temperature causes increased sea levels primarily by thermal expansion of the upper layers of the ocean and melting of continental ice sheets. Clark (1986) found historic sea level rise to be 1 mm/yr for the past 3000 years in New York, but found gauge records show a sea level rise of 3 mm since 1930. This rise has caused a 0.5-1.0 m/yr landward movement of the coastline as well as an uphill, landward migration of coastal forest in response to changing soil conditions (Clark 1986). Analogous upward migration is impossible for many coastal cypress-tupelo forests in coastal Louisiana because levees limit landward expansion (Salinas et al. 1986).

Locally in Louisiana, subsidence of deltaic sediments is an even greater source of water level rise. Land subsidence in the Mississippi River delta has resulted from the consolidation of recently deposited sediments, fluid withdrawal and associated fault reactivation, and changes in sedimentation patterns (Salinas et al. 1986; Morton et al. 2003). The resulting general increase in flooding has been influential on the ecosystem in south Louisiana (Salinas et al. 1986; Delaune et al. 1987; Conner and Day 1988). Delaune et al. (1987) found net subsidence of 0.86 cm per year since 1963 in Lake Verret, with 90% of subsidence caused by hydrological alteration that eliminated historical sediment deposition. Conner and Day (1988) found net subsidence of 0.49 cm per year in Lake Verret and 0.25 cm per year in the nearby Barataria basin. Since the mid

1970s, subsidence rates seem to have slowed paralleling decreases in fluid withdrawal of subsurface hydrocarbons and water (Morton et al. 2002; Morton et al. 2003).

Lake Verret

An example floodplain which has been excluded from its associated river is the Lake Verret interdistributary basin. The Lake Verret basin was originally part of the Atchafalaya interdistributary basin before levee construction but now the protection levee of the Atchafalaya Floodway forms the western border of the basin and the natural and constructed levees of Bayou Lafourche and the Mississippi River form the east and north borders. Prior to construction of levees, the basin received floodwaters from the Mississippi/Atchafalaya system each spring (Fisk 1944) but now receives little sediment and, therefore, subsidence is causing rising water levels (Conner and Brody 1989). As is typical of subsiding systems with no riverine connection, the major hydrological input for this basin is precipitation (Conner et al. 1986). An estimated 48% of the basin is either cypress-tupelo swamps or seasonally flooded bottomland hardwood forests with most of the cypress-tupelo found in the southern portion (SCS 1978a as cited by Conner and Brody 1989).

Since the late 1960s, water levels in Lake Verret have almost always been sufficient to flood the surrounding forests throughout the year (Conner and Day 1988; Conner and Brody 1989). Gauge readings at the lake rose at a rate of 1.37 cm/yr from 1956-1986 because of subsidence (Conner and Day 1988; Conner and Brody 1989). Delaune et al. (1987) suggested that forests surrounding Lake Verret are currently undergoing changes in inundation predicted for other deltaic forests in the future and used this basin as a model. They found accretion in the swamp surrounding Lake Verret averaged 0.63 ± 0.35 cm/yr but water levels increased $1.49 \pm .32$ cm/yr for an accretion deficit of 0.86 cm/yr needed to maintain elevation. The increase in

water levels resulted in a sharp increase in the number of days flooded per year since the mid-1970s (Conner and Day 1988).

Forest growth in Lake Verret has been predicted to decline as flooding continues. A forest succession model predicted no swamp regeneration, decreased rate of average growth, and a conversion of forest to open water over a future period of fifty years (Conner and Brody 1989). As lower-elevation stands die, the higher elevation bottomland species are expected to be replaced by cypress-tupelo (Clark 1986; Conner and Brody 1989). However, it is expected that the migration of forest up the elevation gradient will be restricted by levees that protect agricultural fields from backswamp flooding (Salinas et al. 1986; Conner and Day 1988).

Systems in the Atchafalaya Basin Connected to Riverine Flooding

In contrast to most deltaic swamps, within the Atchafalaya Basin there are swamps that are experiencing increased flooding and associated sediments and nutrients from the Red River and a diversion of a portion of the Mississippi River (Tye and Coleman 1989b). The formation of the Atchafalaya River began by crevassing of the combined Red and Mississippi Rivers early in the 18th century and was well established by the middle of that century (Fisk 1952; Aslan et al. 2005). Historically, the Atchafalaya Basin received little water from the Mississippi River but dredging between 1880s and 1930s and clearing of a log jam by the 1880s enlarged the channel (Aslan et al. 2005). Infilling of Upper Old River, the meander bend that connected the Red River to the Mississippi River, caused the entire flow of the Red River to follow down the Atchafalaya River (Aslan et al. 2005). With the subsequent enlargement of the Atchafalaya River, an increasing proportion of the Mississippi River began to flow through the lower part of the old meander bend that formerly connected it to the Red River – Lower Old River. By 1950, when 25% of the Mississippi's flow followed the Atchafalaya, it was obvious that the Mississippi

River was in the process of avulsing to flow down the Atchafalaya River (Aslan et al. 2005). At that time, construction of the Old River Control Structure arrested the process. Since 1954, the Atchafalaya Basin has served as a major distributary that is managed by law to carry 30% of the combined flow of the Mississippi and Red Rivers. As a result of the increased flow and sediment over the past two centuries, the sediment grain size, sedimentation patterns, and geomorphology of the Atchafalaya have been greatly altered (Fisk 1952; Smith et al. 1985). Both the volume and size of sediment has increased.

Grand Lake

Grand Lake was once the largest lake in the lower Atchafalaya Basin, but has decreased in size greatly and become shallower (2-3 m average depth) because of sedimentation since the increase in flow of the Atchafalaya River (Fisk 1952; Tye and Coleman 1989b). The original area of 600 km² is now a series of smaller lakes with a combined area of 130 km², including Lake Fausse Point and Six Mile Lake (Tye and Coleman 1989b). As a result of high sedimentation rates, the species composition of forests in the Atchafalaya Basin is changing. The creation of new land has favored early-successional and invasive species such as black willow (*Salix nigra* Marsh.) and Chinese tallow (*Triadica sebifera* (L.) Small).

Not only is the Atchafalaya Basin experiencing heavy sediment accumulation, the water and sediments also carry high nutrient loads (Goolsby et al. 1999; Lane et al. 2002; Perez et al. 2003). The high nutrient load moving through the Atchafalaya Basin contributes to algal blooms and resulting hypoxia in the Gulf of Mexico (Goolsby et al. 1999). However, some of the nutrient input is removed before flowing into the Gulf because of the capacity of swamps to remove nutrients from floodwaters (Xu 2006). It is unclear what effect the increases in nutrients have had on forested wetlands.

Sediment and nutrient loads vary spatially within the Atchafalaya Basin. As a result of dredging and levees on the main channel of the northern Atchafalaya River, flow in the northern portion of the basin is mainly restricted to the channel (Sabo et al. 1999b). In the southern portion, distributaries carry flow from the main channel to backswamps before converging once again to flow out to one of two outlets of the basin (Sabo et al. 1999a). Within the basin, relatively higher concentrations of dissolved oxygen are associated with turbulent-water channels and lakes than in slow-moving channels (Sabo et al. 1999a). Thus there are pockets of swamp subjected to high sediment and nutrient loads as a result of increased flow near the main channel and lakes while other sections of the basin experience more stagnant flooding and little sedimentation and nutrient loading (Sabo et al. 1999a, 1999b).

Dendrochronology

Dendrochronology, or tree ring dating, measures the growth patterns common to a defined stand of trees and can address many different ecological questions. Historically, baldcypress was considered unreliable in dendrochronologic studies because of problems with missing or false rings and complacency (Fritts 1976; Duever and McCollom 1987; Young et al. 1993). However, several studies by Stahle as well as others have found this long-lived species (at least 1,600 years) is useful if proper crossdating is performed to account for the missing and false rings (Stahle et al. 1985, 1992; Stahle and Cleaveland 1992). Dendrochronology has been used to study climatic (Stahle et al. 1985) and hydrologic (Cleaveland 2000) influences on growth (Stahle et al. 1992; Stahle and Cleaveland 1992; Young et al. 1995; Keeland and Young 1997).

Previous wetland ecology studies have used dendrochronology to date specific ecological events, understand and date past forest disturbances, and reconstruct past climatic and hydrologic conditions. Dendrochronology revealed that hydrology is influential but not as important as

climate in growth of red maple and tamarack (*Larix laricina* (Du Roi) K. Koch) in the upper St. Lawrence River (Jean and A. Bouchard 1996). A transformation of baldcypress tree rings had a strong relationship ($r^2 = 0.68$) to total summer stream flow in Arkansas (Cleaveland 2000).

Ring width can be used to estimate total stand productivity. Basal area increment, a simple transformation of ring-width, is strongly correlated to volume and annual biomass production (Bouriaud et al. 2005). Net primary production (NPP) of a site is the sum of annual biomass increment (increment of standing woody and herbaceous plants), annual litterfall, mortality, and loss to grazing (Grier and Logan 1977). Cypress-tupelo swamps typically have little understory (Conner and Day 1976) and the role of herbaceous vegetation in NPP is negligible. When litterfall is assumed constant (Grier and Logan 1977), NPP of individual trees can be estimated readily from tree ring data of both living trees and downed snags (Graumlich et al. 1989).

Grazing has been considered negligible for baldcypress (Conner and Day 1976; Grier and Logan 1977; Conner and Day 1992b), although the recent emergence of the baldcypress leaf roller (*Archips goyerana* Kruse) may change this (Braun et al. 1990). The baldcypress leaf roller (BCLR) occurs in the southern Atchafalaya Basin including nearby Lake Verret. Historically, baldcypress was renowned for its resistance to insect problems (Brown and Montz 1986) but irregular occurrences of BCLR since its discovery in 1983 have locally damaged stands (Braun et al. 1990). Significant and repeated defoliation can occur when larvae emerge and consume new foliage each spring (Goyer and Chambers 1997 as cited by Chambers et al. 2005). Although defoliation by BCLR can reduce annual growth, no attempt was made in this study to account for it in models of ring width because of limited data.

METHODS AND MATERIALS

Study Sites

Two study areas, Lake Verret and Grand Lake, were selected to contrast blackwater, stagnant swamps with brownwater, riverine swamps. The swamps surrounding Lake Verret have been excluded from riverine inputs so that there is little velocity of flow and little sedimentation and nutrient input (Delaune et al. 1987; Sabo et al. 1999b). Swamps like those at Lake Verret are often referred to as “black water” swamps because there is little sediment in the water to hide the dark-colored organic tannins. The riverine swamps bordering Grand Lake along the Atchafalaya River in the lower Atchafalaya Basin receive large amounts of sediment and nutrients from higher velocity flows (Sabo et al. 1999a; Xu 2006). Swamps like those at Grand Lake are often referred to as “brownwater” swamps because of the color of the sediment-laden floodwaters.

Three sites were selected within each study area for a total of six baldcypress stands. Study sites are all in close hydrologic connection to a body of water with a water level gauge having long-term daily records (stage) of least 50 years. It was critical that sites have hydrologic connectivity, because site-specific water level for each site was extrapolated from gauge data.

The three sites in the stagnant, blackwater system of Lake Verret were Attakapas Landing (AT), Elm Hall Wildlife Management Area (EH), and Godchaux Canal (GC) (Figure 1, Table 1). All sites are on the eastern shore of the lake. There was surface accumulation of organic matter at each site (> 5 cm). Stand density was similar at AT and EH and both had closed canopies, but canopy gaps were common at GC. Individual tree age was calculated from cross-dated tree rings to get pith age (age of tree at 3 m) then 5 years was added to account for tree to grow to a height of 3 m (Williston et al. 1980; Keeland and Conner 1999). One tree at AT was a remnant (360 yrs old) but the remainder of trees were all between 87 and 105 years old. At EH, six trees were

greater than 500 years old but all others were between the ages of 108 and 128. One remnant was at GC, one >500 years old and another older one 199, but all other trees were between the ages of 106 and 94. Approximate year of stand establishment (estimated by age of second-growth trees and growth releases of remnant trees) was 1895-1896 for all Lake Verret stands. Tree species composition at AT and EH was baldcypress-water tupelo with some red maple on hummocks or downed snags. Baldcypress-water tupelo was the dominant association at GC but red maple, black willow, and buttonbush (*Cephalanthus occidentalis* L.) were present on hummocks and downed snags. Understory vegetation at AT and EH was sparse and limited to *Salvinia* spp. and *Iris* spp. Understory was dense at GC with a floating marsh mat containing *Hydrocotyle* spp., lizard's tail (*Saururus cernuus* L.), alligatorweed (*Alternanthera philoxeroides* (Mart.) Griseb.) and wild rice (*Zizania* spp.).

The three sites in the riverine system of the Atchafalaya Basin bordering Grand Lake were Six Mile Lake North (SM), Gray Horse Island (GH), and Verdunville Landing (VU) (Figure 1, Table 1). All sites are on the western shore of the part of Grand Lake that is now known as Six Mile Lake, just above the Wax Lake outlet of the Atchafalaya Basin. There was little surface organic accumulation at any of the Grand Lake sites. Stand density was similar at VU and GH and both had closed canopies, but SM was an open stand with lower stand density. All trees at SM were between the ages of 109 and 121 except one that was 143 and one that was 67. Trees at GH were between 147 and 197 years old except one that was 229. Trees at VU were between 67 and 92 years old. Species composition at SM and VU was pure baldcypress-water tupelo and there was no understory vegetation. Baldcypress and water tupelo were the dominant trees at GH but black willow, ash (*Fraxinus* spp.), buttonbush, and baldcypress seedlings < 1

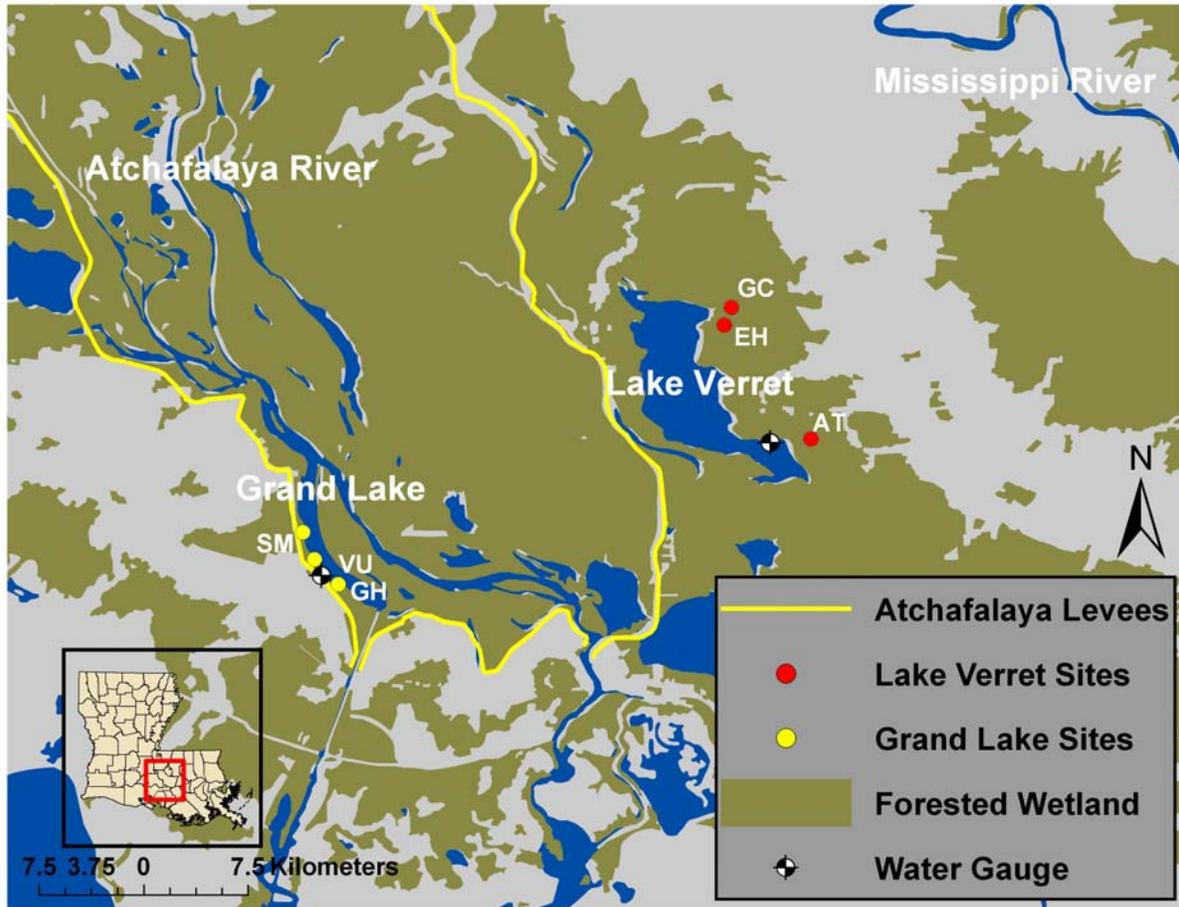


Figure 1. Study sites locations.

Table 1. Dendrochronological summary statistics for the six study sites and the measurement trees used in this study.

	Site					
	Lake Verret			Grand Lake		
	AT	EH	GC	SM	GH	VU
Number of Trees	10	10	10	10	11	11
Period of Ring Width Data	1895-2004	1887-2005	1890-2005	1885-2005	1877-2005	1916-2004
Series Intercorrelation	0.574	0.547	0.542	0.541	0.544	0.638
Average Mean Sensitivity	0.501	0.602	0.495	0.550	0.543	0.474
Average Diameter at 3m (cm)	41.0	60.8	50.7	47.4	39.5	34.5
Stand Initiation [†]	1895	1895	1896	1879	1803	1907
Number of Remnants (>250 yrs)	1	6	1	0	0	0
Height of Dominant Trees (m)	§	24.5	24.4	18.9	23.8	§
Date of Coring	04FEB05	18JUL05	09AUG05	26JUL05	01AUG05	24JAN05
Stand Density (m ² /ha)	§	23	25	§	30	§

§ = Unmeasured

[†] = As estimated from the oldest second growth tree; assumes 5 years for tree to grow to 3 m tall

year old were in the understory. Annual herbaceous vegetation was dense at GH and dominated by lizard's tail, alligatorweed, and *Iris* spp.

Climate Data

Climatic data were obtained from the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center (NCDC) database (NCDC, 2006b). Although there are likely some biases in this database (Keim et al. 2003), it is the best available historical data for the area and is commonly used in retrospective climate analysis of tree rings (e.g., Stahle et al. 1988; Stahle and Cleaveland 1992). All sites are found in Louisiana Region 8 as defined by NCDC, the values of which are calculated based on divisional weighting from statewide averages (Karl and Koss 1984) with data are available from 1895. Climate variables examined for correlation with ring width included monthly temperature, monthly precipitation, monthly Palmer's Drought Severity Index (PDSI), and monthly Palmer's Hydrological Drought Index (PHDI) (Fritts 1976; Fritts and Swetnam 1989). Drought indices measure the intensity of cumulative moisture conditions based upon precipitation, evapotranspiration and predicted runoff. The PDSI is designed to model soil moisture droughts, while the PHDI is designed to model longer-term drought in groundwater, stream, and lakes.

Hydrological Data

A water level gauge near the sites in each of the two basins had daily stage records for more than 50 years. Hydrologic data for the three sites within the Lake Verret basin were taken from the US Army Corps of Engineers (USACE) Lake Verret at Attakapas Landing gauge (52720) from 22 August 1955 to 31 December 2005, and hydrologic data for the three sites within the Grand Lake Basin were taken from the USACE Six Mile Lake near Verdunville gauge

(03645) from 1 January 1955 to 31 December 2005. The data from both gauges contained multiple short gaps and there was one prolonged gap for each gauge.

Linear regressions from nearby water level gauges were used to reconstruct missing periods (Figure 2, Table 2). The Attakapas Landing gauge was reconstructed mainly from the USACE Pierre Pass near Pierre Part gauge (52680). This gauge is on an inlet to Lake Verret about 16 km away from the Attakapas Landing gauge. From 1 January 1956 to 31 December 1958, neither the Attakapas Landing nor Pierre Part gauges collected data. For this period, the USACE Bayou Bouff at Amelia gauge (52800) was used. This gauge is on an outlet of the Verret Basin and about 20 km away through Fourmile Bayou, Grassy Lake, Simon Pass, and Lake Palourde. Although the hydrologic connection is remote, the Amelia gauge was highly correlated with Attakapas Landing. Regressions between Attakapas Landing and its two proxy gauges were temporally stationary.

Missing data at the Verdunville gauge were reconstructed primarily from the USACE/USGS (US Geological Survey) Lower Atchafalaya River at Morgan City gauge (03780) (Table 3). Relationships between all gauges in the Atchafalaya Basin changed through time, most likely because of canal or levee construction, sedimentation, and/or natural channel development. Therefore, a series of local linear regressions over homogeneous periods of 3 to 13 years were used to reconstruct data gaps. The Morgan City gauge is 22 km away and connected through another arm of Grand Lake. Correlations with closer nearby gauges (USACE/USGS Wax Lake at Callumet (03720), and USACE/USGS Chicot Pass near Myete Point (03450)) were not as high. An extended period of missing observations from 20 February 1963 to 11 March 1966 required correlation with the USACE Grand Lake at Charento (03555) because the relationship with the Morgan City gauge was nonstationary across the gap.

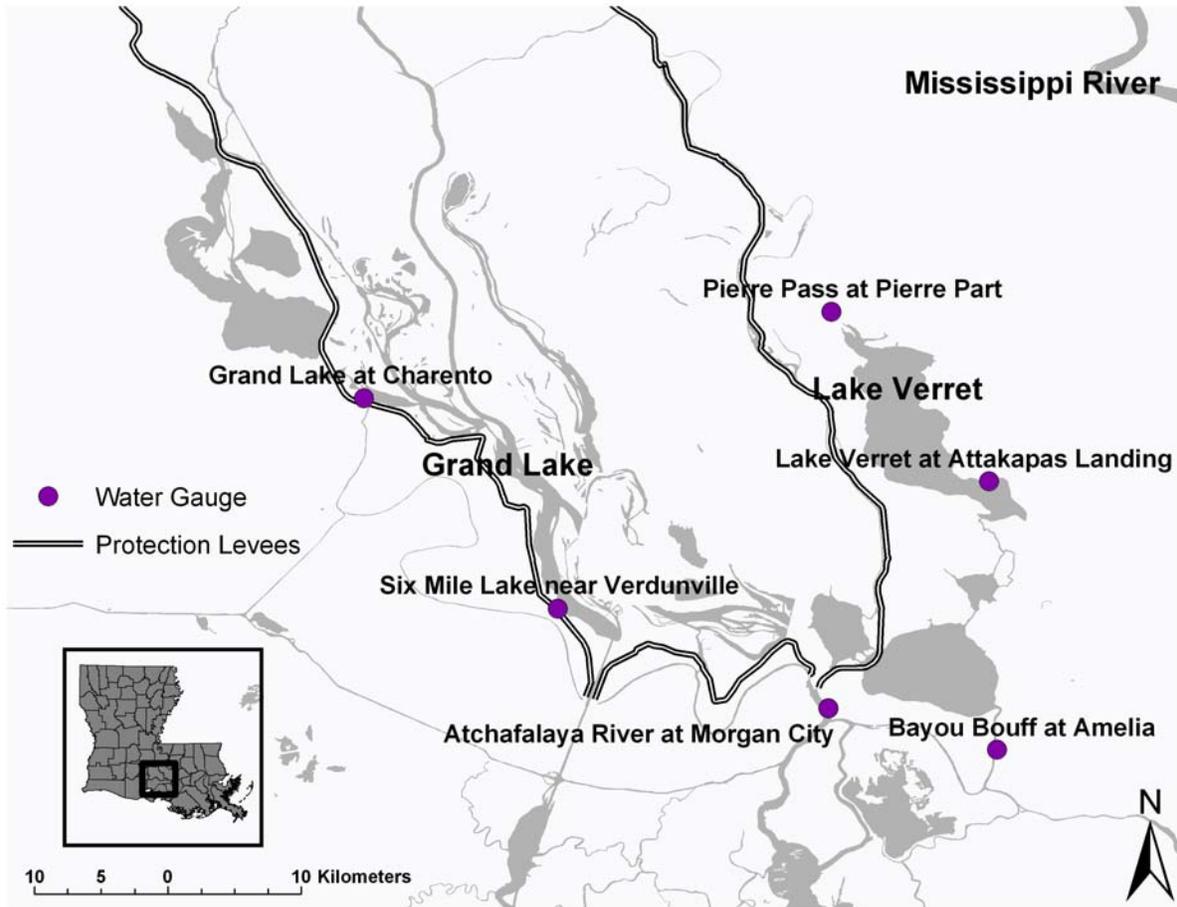


Figure 2. Location of USACE water level gauges used in water level data reconstruction.

Table 2. Lake Verret gauge (USACE gauge 52720 Lake Verret at Attakapas Landing (LV)) reconstruction periods and regressions using nearby data from USACE gauge 52680 Pierre Pass near Pierre Part (PP) and USACE gauge 52800 Bayou Bouff at Amelia gauge (BB).

Period of Reconstruction	Regression Equations	r^2
01/01/1959-12/31/2005	$LV = PP + (-0.0491*PP + 0.3054)$	0.93
01/01/1955-12/31/1958	$LV = BB + (0.0308*BB + 0.2178)$	0.97

Table 3. Grand Lake (GL) gauge (USACE gauge 03645 Six Mile Lake near Verdunville) reconstruction periods and formulae using nearby data from USACE/USGS gauge 03780 Lower Atchafalaya River at Morgan City (MC) and USACE gauge 03555 Grand Lake at Charento (CH).

Period of Reconstruction	Relationship	r^2
01/01/1995-01/01/2005	$GL = MC + (0.4627*MC - 0.2296)$	0.96
05/01/1988-12/31/1994	$GL = MC + (0.1577*MC - 0.5023)$	0.95
07/01/1975-04/30/1988	$GL = MC + (0.5263*MC + 0.3744)$	0.89
10/01/1972-06/30/1975	$GL = MC + (0.4551*MC + 1.0885)$	0.96
03/11/1966-09/30/1972	$GL = MC + (0.5048*MC + 0.6152)$	0.80
02/21/1963-03/10/1966	$GL = CH + (0.3795*CH + 0.4764)$	0.83

Hydrological information for each study site was extrapolated from gauge data by assuming the difference between stage readings and mean water depth at the site observed during data collection did not vary for the entire period (1955-2005). Subsidence and accretion have taken place during the period of record in both basins. Subsidence may have been greater at the study sites in the backswamp at Lake Verret than at the gauge because of possible differences in vertical accretion (Conner and Day 1991), so that historical flooding may be overestimated. In contrast, the sites at Grand Lake are on the edge of a lake that has not changed appreciably since at least 1917 (Reuss 2004) so that extrapolations are less likely to be subject to error.

Dendrochronological Methods

At least 10 dominant or codominant trees were selected per site for sampling. Dominant trees most accurately reflect growth dynamics of the whole stand instead of being dominated by local competition effects (Fritts 1976), so that their growth rates are most closely correlated to climatic and hydrologic variability. Trees with significant bole or crown damage were not included. Measurements taken at each tree included tree height, tree diameter at 3 m, and water depth.

Trees were cored with a clean, Teflon-coated 5.15 mm diameter increment borer. Two cores per tree were extracted at either 90° or 180° to account for within-tree variance in ring width and aid in crossdating and identifying false and missing rings. Each tree was cored at 3

meters above the ground to avoid ring malformations in the buttressed base (Parresol and Hotvedt 1990; Young et al. 1995; Keeland and Young 1997). Cores were then stored immediately in labeled plastic straws with ends sealed and placed within a hardshell sample holder.

In the lab, tree cores were dehydrated, mounted, and sanded to prepare for the process of cross-dating and measuring rings. All cores were placed in a dehydration oven for approximately two weeks at 40 C°. The slow and cool dehydration process prevented deformation of the cores. Once dehydration was complete, samples were secured onto grooved wooden holders by water-based glue to allow for realignment if necessary. Cores were sanded several times with progressively finer grit sandpaper (100-600 grit) to prepare the surface for reading (Stokes and Smiley 1968). Fine sanding of the surface is necessary for proper dating to make visible the cellular structure of the earlywood and latewood formation of each ring.

Tree rings from bark to pith and, if possible, those rings past the pith were measured from each core and then cross-dated with others from the same site. Ring width was measured and recorded to the nearest 0.01 mm on a Velmex sliding stage (model A60, Bloomfield, New York). Cross-dating to assign exact calendar year to each ring and identify missing rings and was performed using the skeleton plot method (Douglass 1941a, 1941b, 1943, 1947) and by marker rings of unusually good or poor growth years from existing baldcypress chronologies from the area (T. Doyle, USGS Wetlands Research Center, personal communication). After individual time series were cross-dated, replicate measurements of yearly ring widths within each tree were averaged to obtain final time series of measured ring widths (Fritts 1976).

Cross-dating and ring measurement were verified using the cross-dating software COFECHA (Holmes 1983; Grissino-Mayer 2001). The program COFECHA assesses correlation

of tree-ring series in overlapping segmented time series and also helps detect outlier ring measurements. To test for correlation across tree ring segments, the software first transforms the tree ring time series by applying a rigid spline to remove the low-frequency trends caused by biological or site factors, and then removes the autocorrelation of a series and log-transforms the data (these issues discussed in detail below).

The program COFECHA calculates several descriptive statistics to validate the accuracy of cross-dating and sensitivity of ring width series (relative change in ring width size). The series intercorrelation of the entire chronology is the mean of correlations of each individual tree-ring series to the chronology composed of the mean of all other series (range -1 to +1), and is considered a measure of crossdating accuracy that quantifies the strength of the common signal in the chronology. An acceptable value for mean series intercorrelation typically varies from 0.400 to 0.900 with species, geographic area, site homogeneity, competition factors, and disturbances (Grissino-Mayer 2001; NOAA 2005). Generally a series intercorrelation value of 0.500 or greater signifies a properly cross-dated chronology. The average mean sensitivity is the mean percentage change from each yearly ring width value to the next in a ring width series (Douglass 1936 as cited by Fritts 1976). Although values of this statistic vary by species and geographic area, low values indicating complacency to environmental controls range from 0.10-0.19 (little variation in ring width) and high values indicating sensitivity to environmental controls are greater than 0.30 (large variation in ring width) (Grissino-Mayer 2001). Tree age at 3 m was either observed directly in cores or, if pith was not contained in any cores, the number of rings prior to visible rings was estimated by dividing the pre-core radius (as estimated by geometry of visible rings) by the long-term average width of visible rings.

Statistical Methods

Modeling Ring Width

Change in tree ring width for trees in a stand is the result of several factors. A modified version of the conceptual linear aggregate model for ring width growth of an individual tree (Cook 1990) was used:

$$R(t) = f(A, C, D, \varepsilon) , \quad (1)$$

where $R(t)$ is the observed ring-width, $A(t)$ is the age-size-related trend in ring width, $C(t)$ is the climatically related environmental signal common to all trees in the stand, $D(t)$ is the disturbance signal common to all trees created by standwide and exogenous disturbance, and ε is lumped error associated with the unexplained variability unrelated to other signals, tree-specific disturbances, and measurement errors (assumed completely random).

Standwide exogenous disturbances, D , are events aside from climate that affect all trees within a particular stand. Examples include long-term stand dynamics that uniformly affect all residual trees, catastrophic single climatic events, or release of remaining trees after some event that removes trees throughout the stand. Effects of hydrology can be viewed as a standwide exogenous disturbance. In this research, the short-term, DS , and long-term, DL , effects of hydrology were modeled explicitly.

Sources of unexplained variability, ε , include microsite differences within the stand, gradients in soil characteristics and hydrology, and measurement error and are assumed to be completely random (Cook and Kairiukstis 1990). Also included in ε are local endogenous disturbances that affect individual trees instead of the entire stand. This signal is typically a disturbance in tree growth and generally results from, for example, a canopy gap or injury. Poor low-frequency correlation between tree cores would result from local endogenous disturbances.

Analysis was performed in two general ways: separate analysis of effects (those effects in Eq 1) and simultaneous analysis of effects. Separate analysis of effects was done to create a detailed model of long-term, DL , and short-term, DS , results of flooding by accounting for all other known influences on growth but hydrology. Simultaneous analysis was done in order to understand the relative importance of effects.

Separate Analysis of Effects

To study any one component of growth separately, the effects of variables were taken into account sequentially. Analysis proceeded by first modeling the age-related growth trend, A . The residuals of this model in predicting R are denoted R_A to indicate a time series of ring widths adjusted for the effects of age. Then the climatic signal in R_A was modeled, and the residuals of this model with R_A are denoted R_{AC} to indicate a time series of ring widths adjusted for the effects of age and climate (Table 4). The remaining variance is assumed to originate in D , which contains the effects of hydrology and error, ϵ .

Table 4. Description of terms used in modeling ring width.

Term	Description
A	Effects of age-related growth on ring width
C	Effects of climate on ring width
D	Exogenous disturbances, contains DL and DS
DL	Long-term disturbances (hydrology and stand dynamics) signal
DS	Effects of short-term disturbances (hydrology) signal
R	Raw ring width series
R_A	Ring width series adjusted for the effects of age-related growth (normalized)
R_{AW}	Ring width series adjusted for the effects of age-related growth and autocorrelation (normalized and prewhitened)
R_{AWC}	Ring width series adjusted for the effects of age-related growth, autocorrelation, and climate
R_{AC}	Ring width series adjusted for the effects of age-related growth and climate (reddened)
R_{ACD}	Ring width series adjusted for the effects of age-related growth, climate, and disturbance

Modeling Biological Growth (A)

The age-related trend results primarily from the geometrical limitation of adding a given volume of wood to an increasingly larger stem (Fritts 1976). This results in a progressive decrease in ring width with age that is expected to be approximately the same for all trees of a

given species in a given geographic area (Esper et al. 2003). A typical curve for modeling the biological growth trend, A , is the negative exponential equation (Fritts 1976)

$$A(t) = ae^{-bt} + k, \quad (2)$$

where a , b , and k are fitted parameters, e is the base of natural logarithms and $A(t)$ is the expected growth at year t . Parameters for Eq 2 were identified using Regional Curve Standardization (RCS) (Esper et al. 2003; Cook and Esper 2002) which aligns ring widths from all trees from all sites in a given region by cambial age then fits a single model (Eq 2) to all trees simultaneously. This method has been proven to retain significantly greater low frequency information (such as would be expected with exogenous disturbances), without loss of high frequency signal (Bunn et al. 2004), than does the more-traditional method of fitting each ring width series individually (Esper et al. 2003). Once a regional curve for A is established, the residual series is calculated is

$$R_A = \frac{Obs}{A}, \quad (3)$$

where R_A is the age-normalized ring width and, $Obs(t)$ is the time series of observed ring widths. A mean R_A for each stand was computed by averaging ring widths across all trees in that stand. A mean for each basin was computed by averaging the three stand averages within that basin.

Modeling Climatic Effects (C)

Prewhitening

The values of C include the collective influence of all climatic variables to which trees are exposed. All trees in a stand and basin are exposed to similar climate so it is assumed that they share a common climatic signal (Fritts 1976; Cook and Kairiukstis 1990). Thus, the climate model was fitted to basin-average R_A growth indices.

In order to model climate, C , an intermediate step is required because growth is serially correlated up to a 10 year lag or longer with correlations up to 0.65 (Fritts 1976; Guiot 1986; Cook and Kairiukstis 1990). In contrast climate variables are normally not serially correlated and are normally assumed to be white noise annual series (Jean and A. Bouchard 1996). Thus, autocorrelation unaccounted for in R_A can produce spurious results in modeling C . To remove autocorrelation in R_A and obtain a white-noise series for correlating with climate, a first difference ($R_A(t) - R_A(t-1)$) to the ring width index can be applied if the variance of the first differenced series is smaller than that of the original series followed by an autoregressive-moving average (ARMA) model (Box and Jenkins 1970). This process is known as “prewhitening” because it removes all variance but serially uncorrelated white noise prior to further analysis of the ring width time series. The ARMA model with autoregressive order a and moving-average order m is

$$\begin{aligned} \text{ARMA}(a, m) = \varphi_1 R_A(t-1) + \varphi_2 R_A(t-2) + \dots + \varphi_a R_A(t-a) + Z(t) + \theta_1 Z(t-1) \dots \\ + \theta_2 Z(t-2) \dots \theta_m Z(t-m) , \end{aligned} \quad (4)$$

where φ_a are the autoregressive coefficients, θ_m are the moving-average coefficients, and $Z(t)$ is mean zero white noise. The residuals of the regression between the $\text{ARMA}(a,m)$ model and the R_A model for each stand compose the prewhitened signal, R_{AW} , needed for correlation with climate variables.

The characteristics of the data dictated the appropriate ARMA model to apply to each growth-normalized basin-average R_A series (Figure 3, Table 5). A first difference of the series was not applied to either Lake Verret or Grand Lake series because the variance of the original chronologies had a smaller variance than did the first differenced chronology (Guiot 1986). To identify if autocorrelation was present, the simple and partial autocorrelation was tested with a

chi-square test for statistical difference from $\varphi_a = 0$ for $a \leq 6$ (Guiot 1986). If significant autocorrelations were present an ARMA model was fitted. Using PROC ARIMA (SAS 2003), both sites showed significant first-order autocorrelation (Lake Verret $\varphi_1 = 0.413$, $p < 0.0001$; Grand Lake $\varphi_1 = 0.346$, $p = 0.0002$) and a rejection of the hypothesis $\varphi_a = 0$ for $a \leq 6$ (Lake Verret $\chi^2 = 122.56$, $p < 0.0001$; Grand Lake $\chi^2 = 23.63$, $p = 0.0006$) (Figure 3). The appropriate ARMA model, ARMA(a, m), was identified by fitting candidate models up to ARMA(3,3) then selecting the appropriate process by lowest Akaike's Information Criterion, (AIC) (Guiot 1986). The best model according to AIC for Lake Verret R_A was ARMA(1,2) and for Grand Lake R_A was ARMA(1,0).

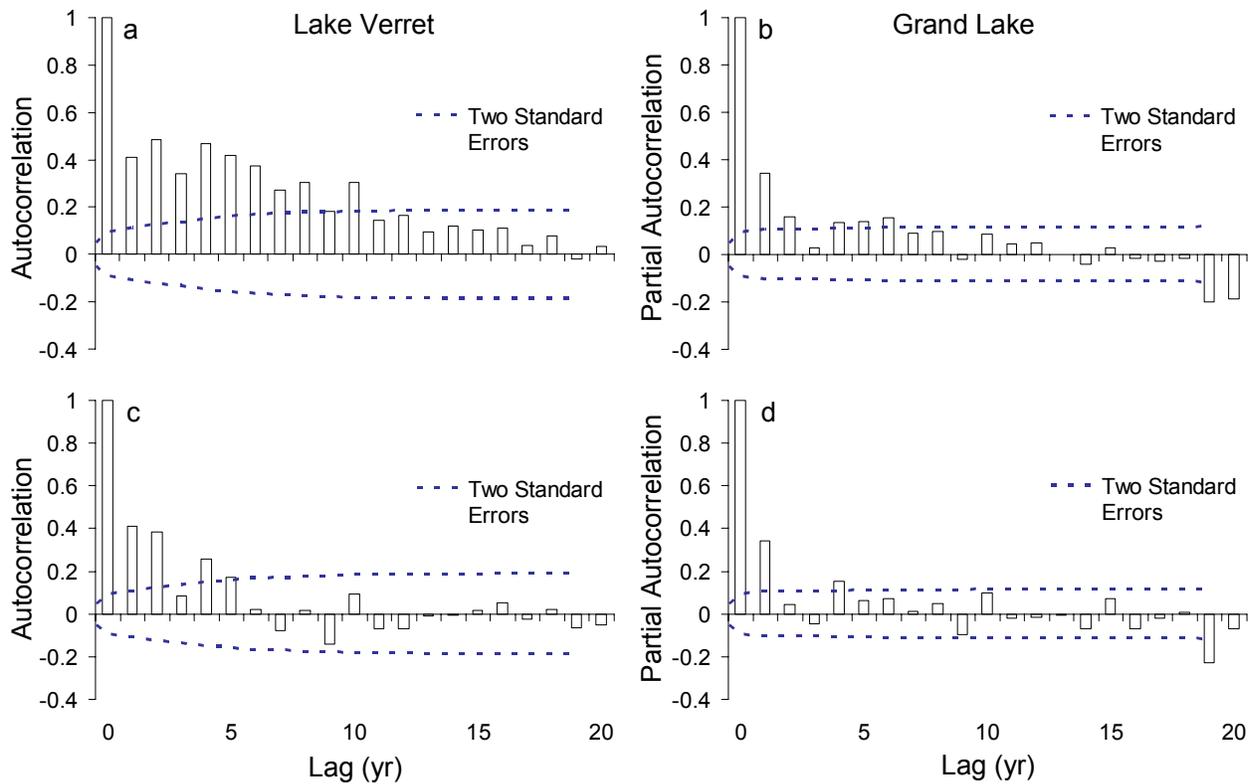


Figure 3. Autocorrelation and partial autocorrelation of the basin-average, age-normalized ring widths, R_A , at Lake Verret (a and c) and Grand Lake (b and d).

Table 5. Autoregressive-moving average model coefficients of age-normalized basin average series, R_A . Statistically significant coefficients at $p < 0.05$ are indicated by an asterisk.

Basin	Mean	ϕ_1	θ_1	θ_2
Lake Verret	0.39446	0.99399*	0.92409*	-0.15181
Grand Lake	0.92830*	0.34646*	-	-

Climate Variables

Simple exploratory correlations between normalized and prewhitened growth, R_{AW} , and all monthly climatic variables (temperature, precipitation, PDSI, and PHDI) were calculated using PROC CORR (SAS 2003). After completing analyses, results were grouped according to periods of the year with like signs of correlation to investigate seasonal correlations between climate and growth. Trees respond to climate over periods of longer than one year, so dendroclimatic investigations commonly use a “dendroclimatic” year that stretches over periods of both the year of growth as well as periods of the previous year (Fritts 1976). The growing season in south Louisiana for baldcypress begins in March after bud break in mid-February and ends in September (Eggler 1955). Thus, for these trees a 19-month dendroclimatic year showing seasonal patterns was defined, beginning in March Y-1 (March of the year preceding ring growth) and ending in September of the year of growth (Table 6). For all climate variables, these group analyses generally showed like signs in correlations between R_{AW} and variables in (1) March Y-1 through May Y-1; (2) June Y-1 through September Y-1; (3) October Y-1 and November Y-1; (4) December Y-1 through February; (5) March through May; and (6) June through September. Variables were therefore lumped into these divisions.

The PDSI and PHDI variables were highly correlated (>0.90) and PHDI was less correlated to R_{AW} , so all PHDI variables were removed from analyses. Also, removal of PHDI from the climate model was justified because it quantifies groundwater, stream, and lake

hydrology, which is modeled separately as part of disturbance effects, D . No other seasonal climate variables were highly intercorrelated.

Table 6. Climate and water depth variables included in analysis. All yearly average variables are based on a dendroclimatic year of March (Y-1) to September.

Variable Type	Variable	Description
Temperature	Winter Temp	Avg Mean-Monthly Temp (Dec(Y-1)-Feb)
	Spring Temp	Avg Mean-Monthly Temp (Mar-May)
	Summer Temp	Avg Mean-Monthly Temp (Jun-Sep)
	Spring Temp Y-1	Avg Mean-Monthly Temp (Mar-May) Y-1
	Summer Temp Y-1	Avg Mean-Monthly Temp (Jun-Sep) Y-1
	Fall Temp Y-1	Avg Mean-Monthly Temp (Oct-Nov) Y-1
Precipitation	Winter Precip	Total Precip (Dec(Y-1)-Feb)
	Spring Precip	Total Precip (Mar-May)
	Summer Precip	Total Precip (Jun-Aug)
	Spring Precip Y-1	Total Precip (Mar-May) Y-1
	Summer Precip Y-1	Avg Mean-Monthly P (Jun-Sep) Y-1
	Fall Precip Y-1	Avg Mean-Monthly Precip (Oct-Nov) Y-1
Palmer's Drought Severity Index (PDSI)	Winter PDSI	Avg Mean-Monthly PDSI (Dec(Y-1)-Feb)
	Spring PDSI	Avg Mean-Monthly PDSI (Mar-May)
	Summer PDSI	Avg Mean-Monthly PDSI (Jun-Sep)
	Spring PDSI Y-1	Avg Mean-Monthly PDSI (Mar-May) Y-1
	Summer PDSI Y-1	Avg Mean-Monthly PDSI (Jun-Sep)
	Fall PDSI Y-1	Avg Mean-Monthly PDSI (Oct-Nov) Y-1
Water Depth	Growing Season Flooded Days	Flooded Days (Mar-Sept)
	Growing Season Flooded Days Y-1	Flooded Days (Mar-Sept) Y-1
	Winter Water Depth	Avg Mean-Monthly Water Depth (Dec(Y-1)-Feb)
	Spring Water Depth	Avg Mean-Monthly Water Depth (Mar-May)
	Summer Water Depth	Avg Mean-Monthly Water Depth (Jun-Sep)
	Spring Water Depth Y-1	Avg Mean-Monthly Water Depth (Mar-May) Y-1
	Summer Water Depth Y-1	Avg Mean-Monthly Water Depth (Jun-Sep)
	Fall Water Depth Y-1	Avg Mean-Monthly Water Depth (Oct-Nov) Y-1
	10-Year Avg Water depth	10-Year Avg Water depth

Multiple Linear Regressions to Model Climate

Multiple linear regressions were performed using PROC REG (SAS 2003) between the seasonal climate variables and age-normalized and prewhitened basin-average growth, R_{AW} , to estimate the effects of climate, C , and produce a white-noise, zero-mean residual series, R_{AWC} . With such a large number of predictor variables (>40), a process to reduce the number of candidate variables was first performed. When a pair of strongly correlated ($r > 0.90$) predictor variables were found, the variable of lower simple correlation to the dependent variable was

removed to avoid multicollinearity. After this process, 24 candidate predictor variables remained. Also, growth year 1927 was removed from the analysis because it was an outlier (studentized residual Lake Verret 4.45, Grand Lake 5.14) most likely caused by the major flood during the spring of that year instead of climate.

A stepwise method was then used to select the best combination of variables for predicting growth using PROC GLMSELECT (SAS 2003). The stepwise selection began with no variables in the model, added the variable with the largest F statistic first, then recalculated F for all variables, whether already in the model or not, and removed those variables with $p > 0.8$. This process was reiterated until all variables in the model had $p < 0.10$ or the candidate variable to be added to the model was the one just deleted. Then, those variables entered through a stepwise process were used to find the appropriate model by minimum AIC and highest r^2 . The selected model was then fit using PROC REG (SAS 2003).

Model assumptions of climate models were checked by analysis of the studentized residuals (Johnson and Wichern 2002). The Variance Inflation Factor (VIF) statistic was calculated using PROC REG to check for multicollinearity; all VIF values were less than 1.005 compared to an acceptable maximum value of 10 (Freund and Wilson 1997). Normality of studentized residuals was not rejected by the Shapiro-Wilk test (Verret $p = 0.1324$; Grand $p = 0.1266$). Studentized residuals were not autocorrelated, as tested by the Durbin-Watson and ACF (autocorrelation function) statistics, nor were they correlated with the predictor or predicted values. To confirm that the effects of these climate variables remained stationary over time and did not interact with hydrological changes, the selected models were fit to data from 1895-1954 and to data from 1955-2004 as hydrologically contrasting periods.

The models of R_{AWC} for each of the two basins were then extrapolated to the stand level. To accomplish this, the basin-level model of R_{AWC} was re-trended (“reddened”) back to the original autocorrelated, normalized index to create the basin-level R_{AC} by adding the ARMA model to the white-noise climate model, R_{AWC} : $R_{AC} = R_{AWC} + \text{ARMA}$ (Guiot 1986). Once the predicted values of each basin-scale climate model, C , were reddened, each of the three associated stand average normalized chronologies, R_A , were divided by the reddened C series to produce residuals. These residuals are the R_{AC} stand dynamic signals free from biological (A) and climatic (C) influences.

Modeling Exogenous Factors (D)

The six, stand-level stand dynamic signals, R_{AC} , were assumed to contain (1) measurement errors, ϵ , that were assumed to be random; and (2) exogenous disturbances, D , composed of stand-level disturbances including hydrological effects (Eq 1). Therefore each R_{AC} was analyzed to estimate the relative effect of hydrological processes on stand growth.

Hydrologic Variables

Site-specific stage data extrapolated from U.S. Geologic Survey and Army Corps of Engineers gauge data were used to calculate monthly averages of water depth. The number of flooded days per month was estimated for each site by summing the number of days with water depth greater than zero. Growing season (March through September) flooded days per year and previous year were then calculated. Ten-year annual average water depth (Oct Y-1 to Sept) was also computed.

Analysis of Effects of Hydrology

To model and analyze both long-term and annual effects of flooding on growth, a cubic smoothing spline was used to extract the low-frequency variation, DL , and residuals from this

model remained as high frequency variation, DS (Cook 1985; Stahle et al. 1988; Cleaveland and Duvick 1992). Using program ARSTAN (Cook 1985), a spline was fitted to each site-level R_{AC} to remove 50% of the variance at the 20-year timescale at AT, GH, SM, and VU, and at the 10-year timescale at EH and GC. To estimate how the long-term variance modeled by the spline, or DL , related to the effects of long-term hydrological variations, correlations of the spline with the seasonal, mean yearly, days flooded, and mean multi-year flooding variables were calculated for each stand. Monthly-mean water depth data were grouped in the same seasons as climate data for these correlations.

To estimate the relationship between the high-frequency residuals of the spline, DS , and the annual effects of hydrology, correlations were calculated between DS and the monthly flooding variables and lags of monthly flooding variables to a length of five years. Periods of the year with like signs of correlation were then grouped together. Patterns of seasonal variables were similar to C , and typically extended for 19 months through to September of the year of growth. The seasonal divisions were generally like those in the climate analysis but several stands showed different seasons and were adjusted to contain months with like signs of correlation accordingly.

Multiple linear regressions between the seasonal hydrology variables and each stand-level short-term disturbance signal, DS , were performed using PROC REG (SAS 2003) to estimate the short-term effects of hydrology. A stepwise selection method was again used to select appropriate variables using PROC GLMSELECT (SAS 2003) and threshold to remain of $p < 0.15$. With the exception of the models of the EH and GH sites, residuals of all models were normally distributed and not autocorrelated. Residuals of the model of EH were autocorrelated (Durbin-Watson test; $p = 0.0164$), and residuals of the model of GH were nonnormal (Shapiro-

Wilk test; $p = 0.0376$) so the natural logarithm was taken of the GH *DS* signal and the regression was fit again. However, the parameter estimates of log-transformed model of GH was similar to the untransformed model (β_1 from 0.00409 to 0.00482; β_2 from -0.07347 to -0.07050; unlogged and logged, respectively) so the models were fit to untransformed data for best comparison across sites. Estimates using ordinary least squares regression such as with PROC REG are unbiased when autocorrelation is present (Ellner et al. 2002).

The *DS* signals were also analyzed for patterns matching years in which floods occurred. Growth in flood years (Trotter et al. 1998) and non-flood years were grouped and tested for statistical difference of means assuming unequal variances using PROC TTEST (SAS 2003). Flood years for the lower Mississippi River were 1903, 1907, 1908, 1912, 1913, 1916, 1920, 1922, 1923, 1927, 1929, 1932, 1937, 1945, 1950, 1957, 1958, 1973, 1974, 1975, 1979, 1983, 1984, 1993, and 1997.

Simultaneous Analysis

To estimate the effects of all environmental effects on ring width simultaneously, multiple linear regressions were performed using PROC REG (SAS 2003) between the each stand-level and both basin average age-normalized signal, R_A , and climate and hydrology variables. The value of R_A of the previous year was included as an independent variable to account for serial correlation. Stepwise selection was again used to select appropriate variables using PROC GLMSELECT (SAS 2003) and threshold to remain of $p < 0.10$. Residuals of EH and Lake Verret average were non-normal and autocorrelated ($p = 0.0272$ and 0.0370 , 0.0420 and 0.0174 ; EH and Lake Verret, respectively) and residuals of AT were autocorrelated ($p = 0.0025$). A natural logarithm was applied at EH and Lake Verret average that normalized the residuals but parameter estimates changed little (EH: β_1 from -0.07212 to -0.07949; β_2 from

0.00526 to 0.00515; β_3 from -0.01260 to -0.01640; β_4 from 1.28930 to 1.53984; β_5 from -2.25064 to -2.42990; Lake Verret average β_1 from -0.00604 to -0.00635; β_2 from 1.05420 to 1.29467; β_3 from 0.69230 to 0.57163; β_4 from -1.78153 to -2.08005; β_5 from -1.05556 to -0.72656; β_6 from 0.49970 to 0.59316; non-logged to logged, respectively) so the models were fit to untransformed data for best comparison across sites. A natural logarithm was also applied for the Lake Verret average model and normalized the residuals as well but parameter estimates Interaction terms of climate and hydrology were originally considered but later removed to improve interpretability because their inclusion did not increase model fit greatly and variables selected were similar.

RESULTS

Chronologies

Six baldcypress chronologies were developed dating from 1877 to 2005 (Table 1). Statistical analyses using COFECHA (Grissino-Mayer 2001) showed that all six were accurately cross-dated and all were valuable for dendroclimatic studies because of adequate series intercorrelation (>0.54) and high average mean sensitivity (>0.47 , Table 1) (Grissino-Mayer 2001).

Hydrology at the Study Sites

Flooding has increased since 1955 in Lake Verret, while flooding at Grand Lake has remained stationary since 1955 (Figure 4). Grand Lake experienced an increase in flow beginning in the 1880s and continuing until 1963 (Fisk 1952; Aslan et al. 2005) but it is unknown how these changes affected water levels (Aslan et al. 2005).

Separate Analysis of Effects

Age Effects (A)

The long-term average radial growth rate for all trees was 1.08 mm/yr, and the single largest ring was 11.36 mm/yr (Figures 5, 6). Ring width approached the long-term mean by age 150. The shape of the Regional Curve Standardization growth model, A , was dominated by the young trees. To estimate the effect of inaccurate estimation of the ages of old trees (>250), new models were fit for estimated ages double and half the original estimate at AT, EH, and GC. The parameters were $a = 1.87$, $b = 0.019$, $k = 1.08$ when the ages were halved, and $a = 1.85$, $b = 0.018$, $k = 1.08$ when the ages were doubled. The asymptote to which the model approaches does not change as might have been expected because of a strong influence of estimated age of remnant trees.

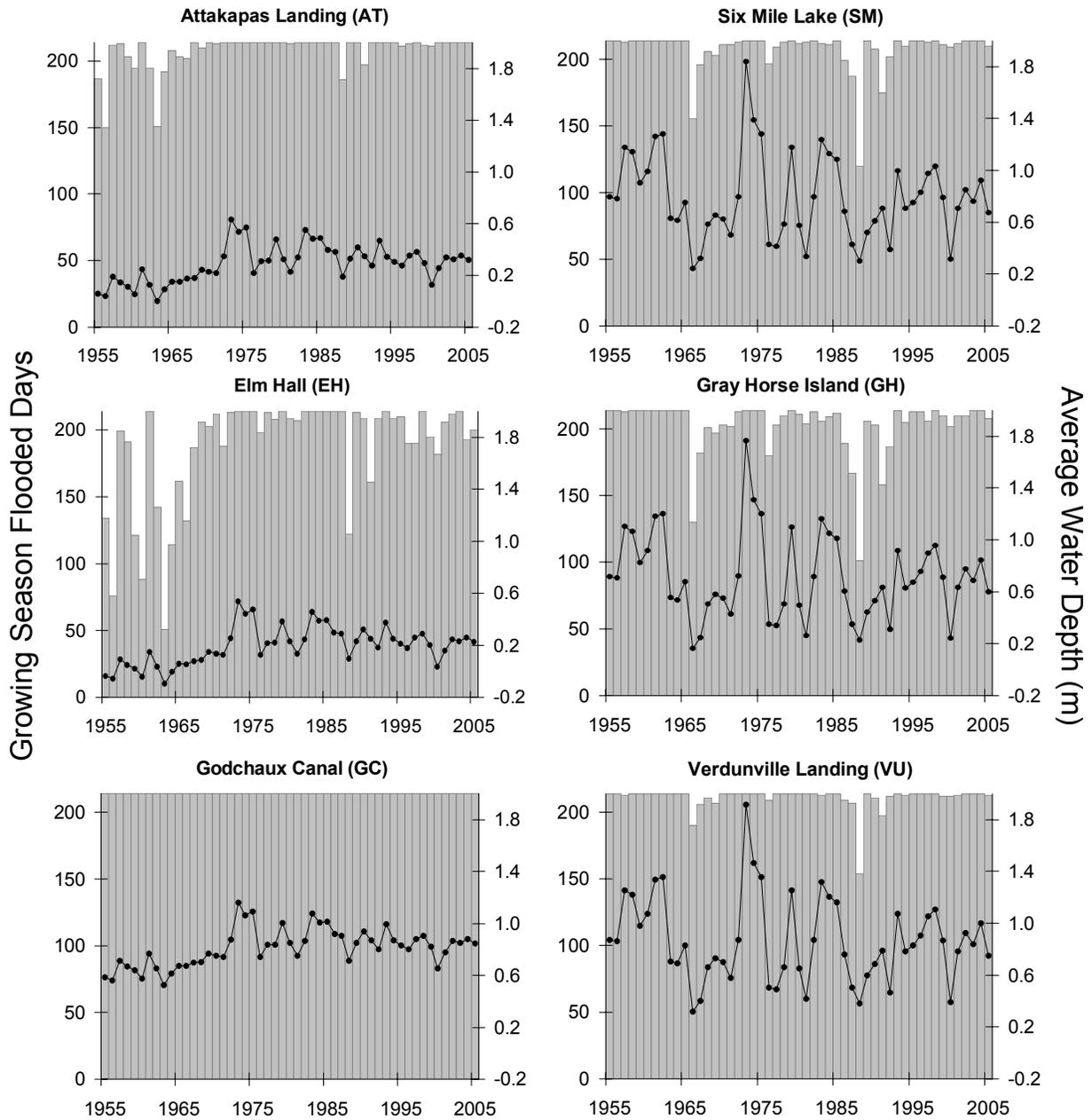


Figure 4. Growing season flooded days (bars) and average water depth (lines) by hydrologic year (Oct-Sept) for each study site.

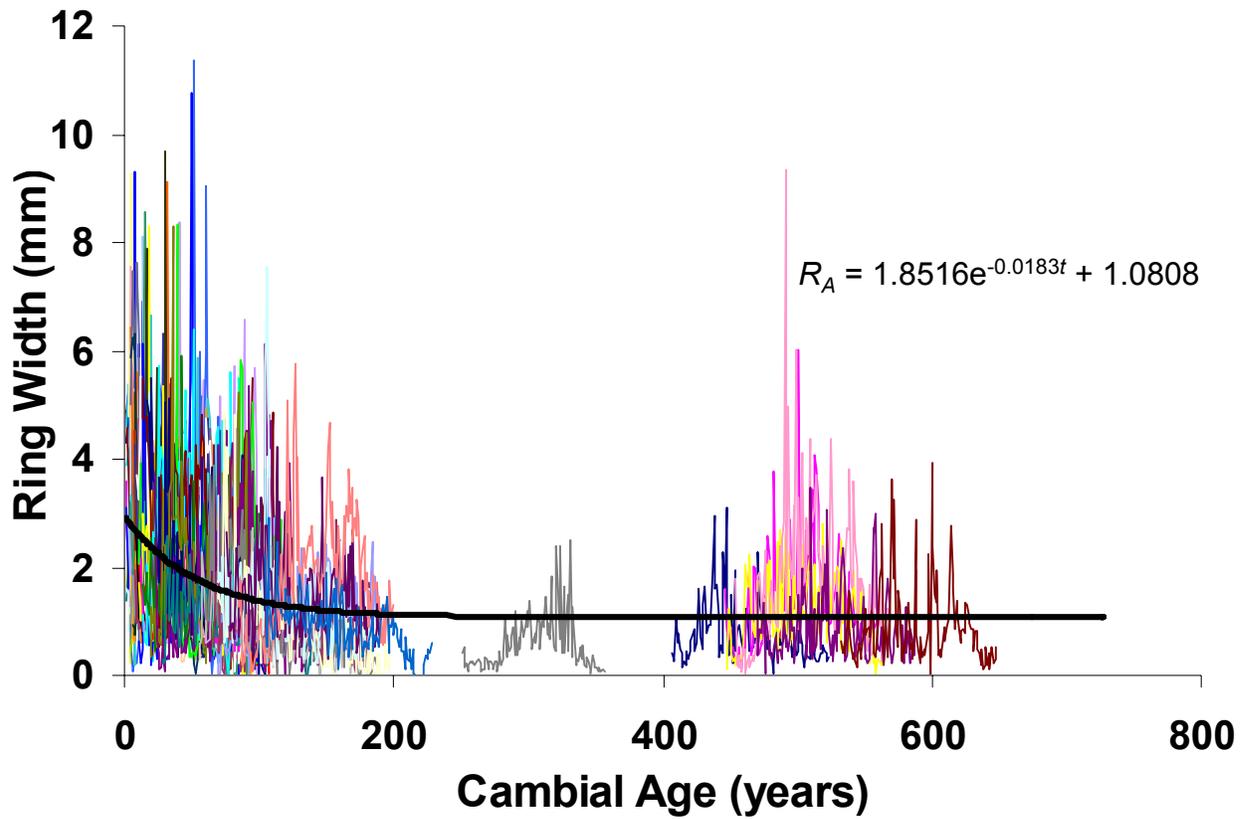


Figure 5. Regional Curve Standardization (RCS) model of age-related growth, A , in ring widths. All sites are plotted; each tree is a different color ($n = 62$).

Climate Effects (C)

Correlation analyses of climate variables with age-normalized and prewhitened site and basin average chronologies, R_{AW} (Figure 7), were significantly correlated to several seasonal temperature variables and spring precipitation (Table 7). Correlations were similar across sites and basins. One variable, spring temperature Y-1, was more highly correlated in the Grand Lake basin than in the Lake Verret basin.

Winter temperature was the climatic variable most correlated to growth, and was positively correlated at all six sites ($p < 0.001$ to $p < 0.05$, $r = 0.23$ to 0.38). Summer temperature was negatively correlated to growth at two sites (AT and SM) but not significantly correlated at any other site. Spring temperature of the previous year (Y-1) was negatively correlated with growth at five sites but was more highly correlated at the Grand Lake sites. Spring precipitation was positively correlated with growth at all six sites ($p < 0.01$ to $p < 0.05$, $r = 0.19$ to 0.30), but no other precipitation variable was significantly correlated. Several other variables were less correlated to growth at up to two sites but showed no consistent patterns across sites.

Correlations of climatic variables to basin-average R_{AW} chronologies followed the same patterns as for the individual-site R_{AW} chronologies except for spring temperature Y-1 (Table 7). Winter temperature was significantly positively correlated to growth in both basins. Summer temperature was negatively correlated to growth at both basins. Spring temperature Y-1 was significant only at the Grand Lake basin and was negatively correlated to growth. Spring precipitation was positively correlated to both basin averages.

Multiple Linear Regression to Model Climate Effects

A three-variable model was selected to model the effects of climate, C , in the normalized and prewhitened Lake Verret basin-average R_{AW} , and a four-variable model was selected to

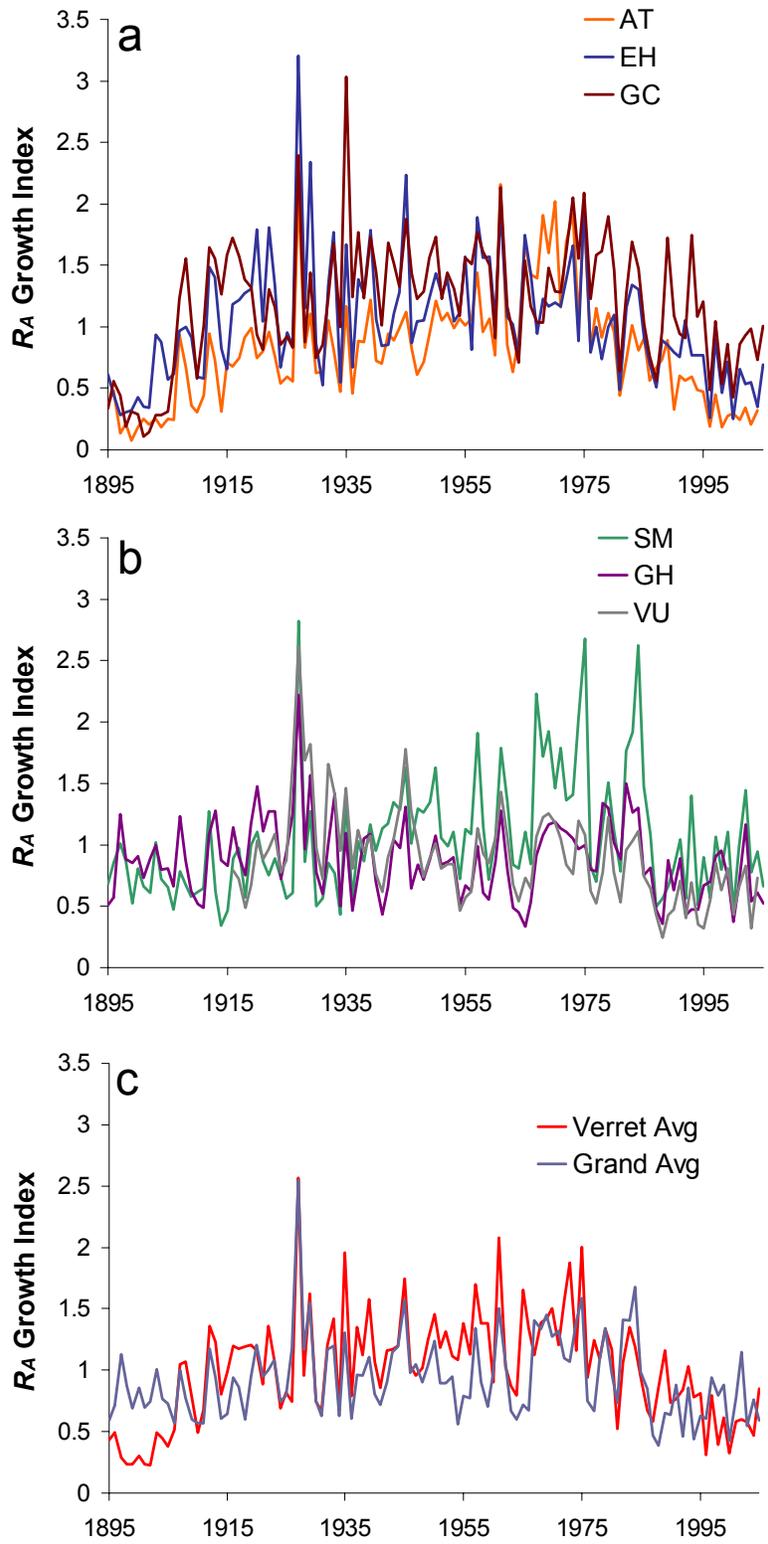


Figure 6. Age-normalized growth indices, R_A , for Lake Verret sites (a), Grand Lake sites (b), and basin averages (c).

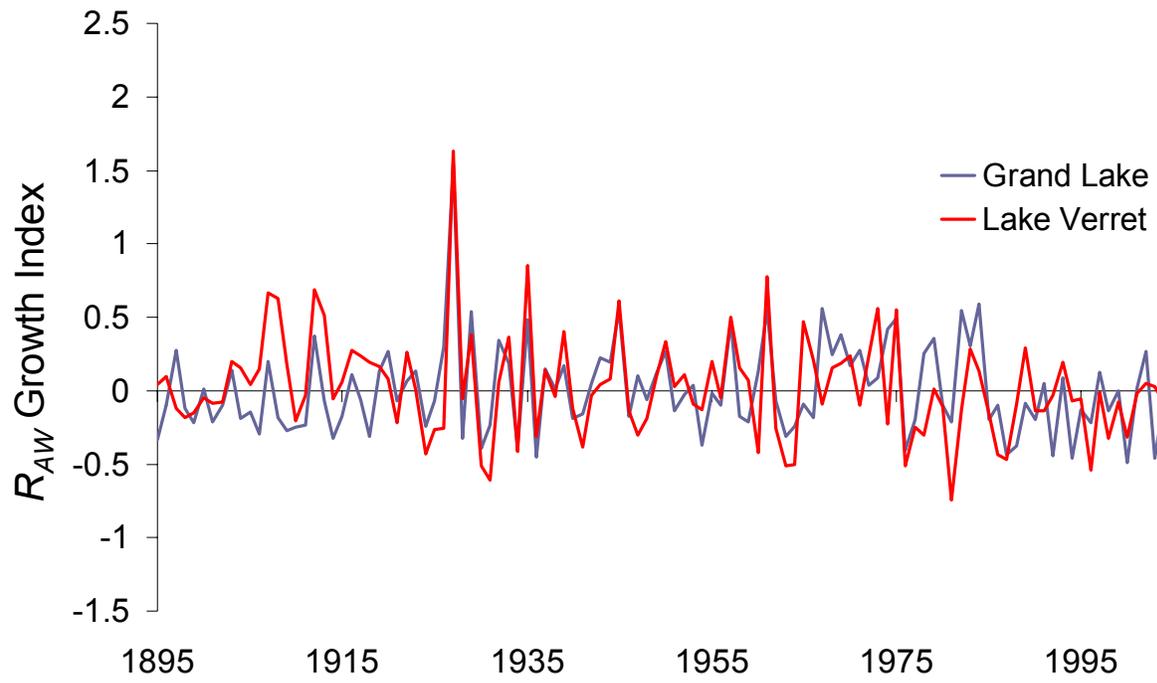


Figure 7. Age-normalized and prewhitened chronologies, R_{AW} , of each basin average.

Table 7. Correlation coefficients, r , between climatic variables and age-normalized and prewhitened growth indices, R_{AW} .

Variable	Site						Verret	Grand
	Lake Verret			Grand Lake				
	AT	EH	GC	SM	GH	VU		
Winter Temp*	0.29 ^b	0.38 ^a	0.30 ^b	0.23 ^c	0.24 ^c	0.32 ^b	0.33 ^a	0.28 ^b
Spring Temp	0.10	0.14	0.13	0.07	0.12	0.02	0.18 ^d	0.09
Summer Temp*	-0.22 ^c	-0.14	-0.16	-0.24 ^c	-0.14	-0.12	-0.19 ^c	-0.19 ^c
Spring Temp Y-1 [†]	-0.15	-0.18 ^d	-0.16 ^d	-0.18 ^d	-0.26 ^b	-0.28 ^b	-0.13	-0.25 ^b
Summer Temp Y-1	0.02	0.10	0.06	-0.05	0.11	0.11	0.02	0.06
Fall Temp Y-1	-0.01	0.00	0.02	0.11	0.08	0.23 ^c	0.01	0.14
Winter Precip	0.00	0.06	-0.04	-0.05	-0.02	-0.05	-0.03	-0.04
Spring Precip*	0.19 ^c	0.22 ^c	0.30 ^b	0.25 ^b	0.23 ^c	0.23 ^c	0.24 ^c	0.28 ^b
Summer Precip	0.07	0.05	0.11	0.02	-0.04	0.01	0.09	-0.02
Spring Precip Y-1	-0.05	0.06	-0.01	0.04	0.04	-0.07	0.04	0.00
Summer Precip Y-1	-0.16	-0.11	0.08	0.09	-0.04	0.05	-0.04	0.03
Fall Precip Y-1	-0.16 ^d	-0.05	-0.01	-0.01	-0.02	-0.01	-0.12	-0.02
Winter PDSI	-0.14	-0.07	0.00	0.03	-0.06	-0.03	-0.12	-0.02
Spring PDSI	0.04	0.11	0.16 ^d	0.15	0.05	0.10	0.08	0.13
Summer PDSI	0.14	0.11	0.18 ^d	0.14	0.05	0.12	0.15	0.11
Spring PDSI Y-1	0.00	0.09	0.10	0.16 ^d	0.02	0.04	0.05	0.09
Summer PDSI Y-1	0.05	0.06	0.17 ^d	0.18 ^d	0.01	0.11	0.12	0.09
Fall PDSI Y-1	-0.15	-0.08	0.08	0.07	-0.03	0.07	-0.08	0.03

* = Variable used in both basin average climate effects multiple regression models

[†] = Variable used only in Grand Lake basin average climate effects multiple regression model

^a $p < 0.001$

^b $p < 0.01$

^c $p < 0.05$

^d $p < 0.10$

model the effects of climate in the Grand Lake basin-average R_{AW} (Table 8, Figure 8). The variables selected for both basins were winter temperature Y-1, summer temperature, and spring precipitation. Spring temperature Y-1 was originally included in the Lake Verret model but later removed because the model coefficients were found to change sign over the period of data.

Lake Verret Climate Model

The three-variable multiple linear model of C in the Lake Verret basin ($r^2 = 0.18$) was:

$$R_{AWC} = 3.61427 + 0.05231*\beta_1 - 0.16459*\beta_2 + 0.00548*\beta_3, \quad (5)$$

where

β_1 is average monthly-mean temperature (C°) of winter Y-1,
 β_2 is average monthly-mean temperature (C°) of current summer, and
 β_3 is total precipitation (cm) of current spring.

Grand Lake Climate Model

The climate model for Grand Lake ($r^2 = 0.23$), was:

$$R_{AWC} = 4.89277 + 0.03060*\beta_1 - 0.15118*\beta_2 - 0.07148*\beta_3 + 0.00642*\beta_4, \quad (6)$$

where

β_1 is average monthly-mean temperature (C°) of winter Y-1,
 β_2 is average monthly-mean temperature (C°) of current summer,
 β_3 is average monthly-mean temperature (C°) of spring Y-1, and
 β_4 is total precipitation (cm) of current spring.

Exogenous Disturbance (D) Effects

Correlation analysis of hydrological variables and the stand-level exogenous disturbance signals, D , showed contrasting long-term effects but similar short-term effects.

Long-term Hydrology and Stand Dynamics Effects (DL)

There was a sharp contrast between basins in their responses to long-term hydrology and stand dynamics signal DL . The 20-year spline used to model the long-term variation in R_{AC}

Table 8. Standardized coefficients for the overall model applied to the climatic effects on Lake Verret and Grand Lake age-normalized and prewhitened basin average, R_{AW} , with standardized coefficients of two periods of that overall model to show stationarity.

Model	Winter Temp	Summer Temp	Spring Temp Y-1	Spring Precip	r^2
Lake Verret					
Overall	0.27 ^b	-0.24 ^b	§	0.24 ^b	0.18
1895-1954	0.21	-0.21	0.40 ^a	0.17	0.12
1955-2005	0.30 ^b	-0.27 ^b	-0.18	0.30 ^b	0.25
Grand Lake					
Overall	0.17 ^c	-0.25 ^b	-0.23 ^c	0.32 ^b	0.23
1895-1954	0.30 ^b	-0.13	-0.25 ^c	0.38 ^b	0.28
1955-2005	0.08	-0.30 ^c	-0.18	0.28 ^c	0.20

§ = variable not included

^a $p < 0.001$

^b $p < 0.01$

^c $p < 0.05$

^d $p < 0.10$

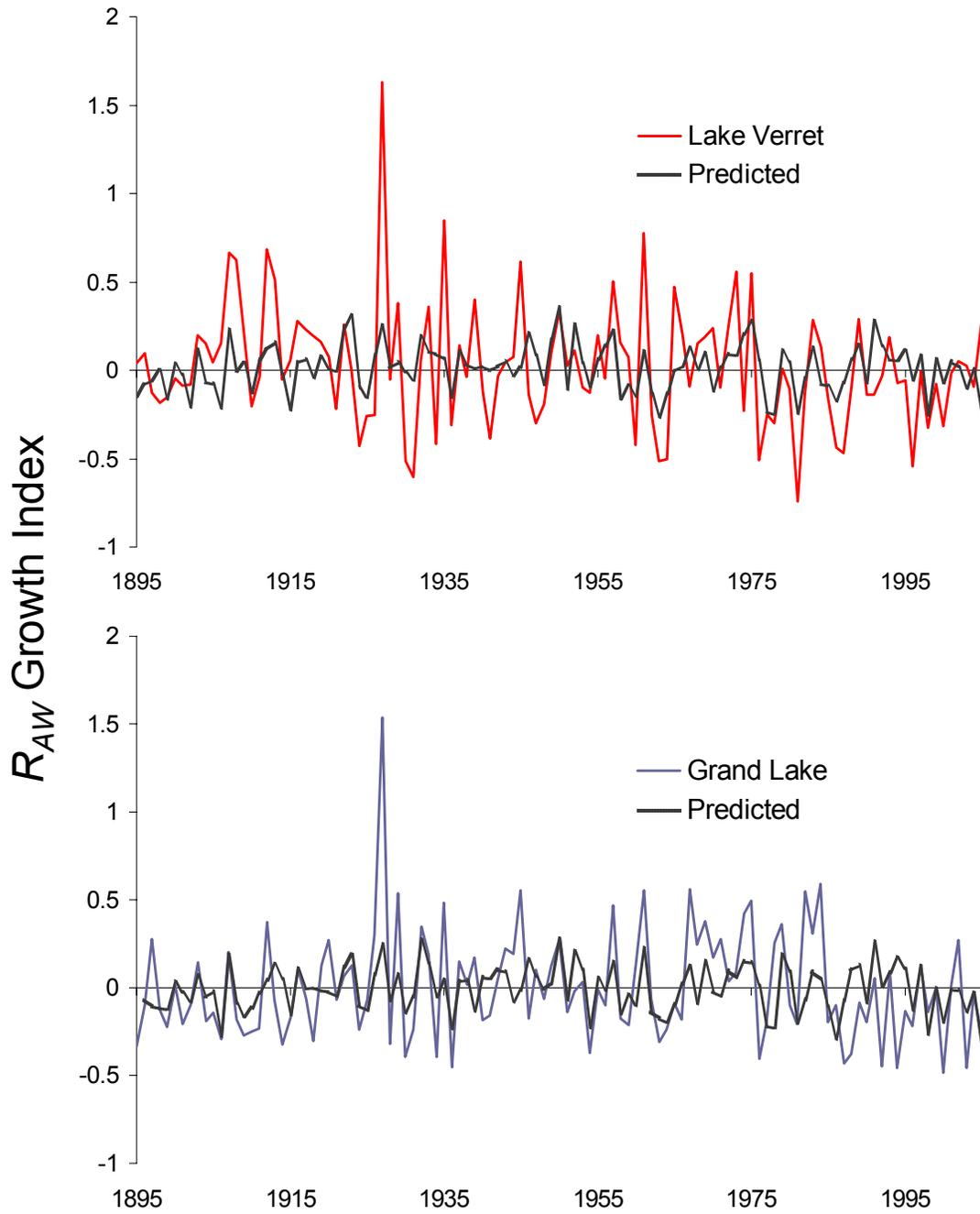


Figure 8. Ring width normalized for age-related growth and serial correlation (prewhitened) R_{AW} (colored lines) as modeled by multiple regressions (stippled lines; climate models, C) with climatic variables.

(Figure 9) correlated to hydrological variables similarly to sites within basins (with one exception) but differently to sites between basins (Table 9).

In the Lake Verret basin, there was strong, negative correlation between *DL* and ten-year average water depth for AT and EH but no correlation with flooding at GC. All seasonal averages of flooding also were negatively correlated to growth at AT and EH as high as $r = -0.46$ ($p < 0.001$), but not correlated at GC.

In the Grand Lake basin, there was positive correlation between *DL* and ten-year average water depth for all sites in the Grand Lake basin. Seasonal average or monthly water depth was also positively correlated to *DL* at Grand Lake sites, except at SM.

Stand Dynamics

In separate analyses, all sites recorded suppression/release events in the stand dynamic signal (*D*) (Figures 9, 10) although the events occur at different times. It is likely that harvesting and stand dynamics resulting from harvesting caused the patterns observed in the early 1900s at sites AT, EH, and GC in the Lake Verret basin. Most of these trees are second-growth germinating after the harvest around the turn of the century. However, a few trees were remnant individuals not harvested. For those remnant trees, this pattern appears to be in response to suppression and release. Although harvesting at two of the Grand Lake sites (SM and VU) also occurred around this same time the age of these trees suggest they were not present at harvest but regenerated as a result of harvest; thus, no release occurred in these sites.

There was a recent increase in the long-term hydrology and stand dynamics signal, *DL*, at all sites (particularly strong in EH and GC) (Figures 9, 10) that must be understood in terms of climate modeling and the typical distribution of radial growth. The separate-effects climate model for both basins predicted extremely poor growth from the early 1990s to 2005 but

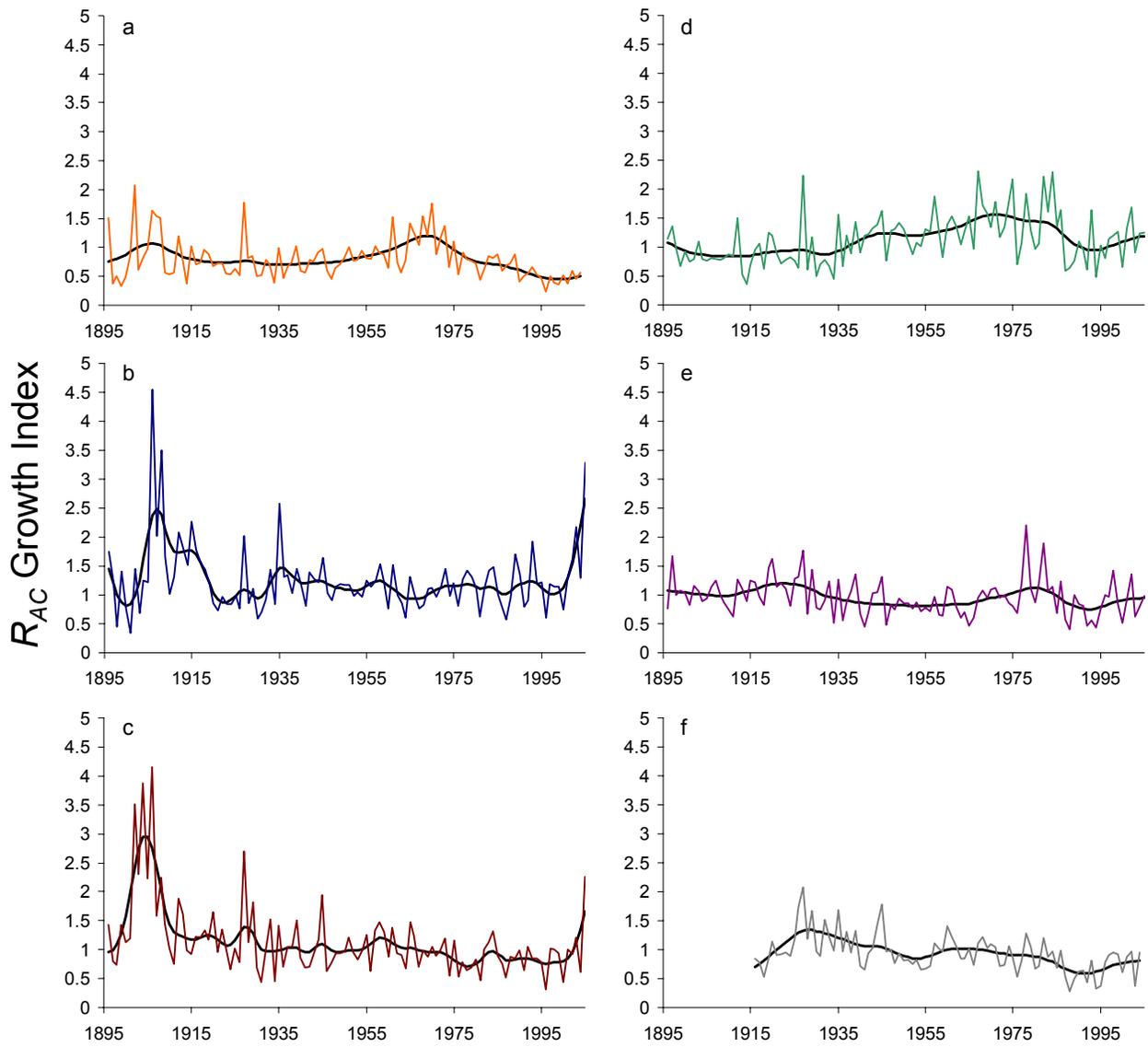


Figure 9. Spline fits of long-term hydrology and stand dynamics signal (DL ; black lines) to colored ring width series adjusted for the effects of age-related growth and climate (R_{AC} ; colored lines) at AT (a), EH (b), GC (c), SM (d), GH (e), and VU (f).

Table 9. Correlation coefficients, r , between water depth variables and long-term hydrology and stand dynamics signal, DL .

Variable	Site					
	Lake Verret			Grand Lake		
	AT	EH	GC	SM	GH	VU
Year	-0.85 ^a	-0.24 ^d	0.44 ^b	-0.61 ^a	0.02	-0.78 ^a
January Water depth Y-1	-0.21	-0.38 ^b	-0.02	0.06	0.06	-0.04
February Water depth Y-1	-0.27 ^d	-0.36 ^c	-0.01	-0.05	0.01	-0.04
March Water depth Y-1	-0.39 ^b	-0.37 ^b	0.07	-0.11	0.06	-0.14
April Water depth Y-1	-0.35 ^c	-0.46 ^a	-0.01	0.13	0.24 ^d	0.08
May Water depth Y-1	-0.29 ^c	-0.36 ^c	0.06	0.16	0.18	0.14
June Water depth Y-1	-0.43 ^b	-0.20	0.23	0.03	0.12	0.06
July Water depth Y-1	-0.38 ^b	-0.18	0.26	0.01	-0.04	0.23
August Water depth Y-1	-0.24	-0.35 ^c	0.01	0.07	-0.22	0.45 ^b
September Water depth Y-1	-0.05	-0.27 ^d	0.03	0.17	-0.14	0.53 ^a
October Water depth Y-1	-0.21	-0.06	0.22	0.12	-0.13	0.40 ^b
November Water depth Y-1	-0.28 ^d	-0.16	0.18	0.10	-0.02	0.19
December Water depth Y-1	-0.13	-0.16	0.14	0.11	0.16	0.03
January Water depth	-0.15	-0.19	0.14	0.08	0.09	-0.01
February Water depth	-0.21	-0.11	0.23	-0.05	0.02	-0.05
March Water depth	-0.33 ^c	-0.30 ^c	0.11	-0.08	0.08	-0.14
April Water depth	-0.27	-0.46 ^a	-0.02	0.15	0.22	0.09
May Water depth	-0.23	-0.38 ^b	0.02	0.16	0.14	0.13
June Water depth	-0.39 ^b	-0.28 ^c	0.15	0.03	0.10	0.04
July Water depth	-0.35 ^c	-0.26 ^d	0.17	-0.02	-0.07	0.17
August Water depth	-0.17	-0.34 ^c	-0.01	0.01	-0.26 ^d	0.38 ^b
September Water depth	0.01	-0.14	0.13	0.11	-0.16	0.47 ^a
Growing Season Flooded Days	-0.22	-0.32 ^c	*	0.08	0.15	0.19
Growing Season Flooded Days Y-1	-0.26 ^d	-0.32 ^c	*	0.12	0.19	0.23
Winter Water depth Y-1	-0.18	-0.17	0.18	0.06	0.10	-0.01
Spring Water depth	-0.30 ^c	-0.41 ^b	0.04	0.10	0.17	0.05
Summer Water depth	-0.30 ^c	-0.30 ^c	0.14	0.04	-0.08	0.28 ^c
Spring Water depth Y-1	-0.37 ^b	-0.43 ^b	0.04	0.08	0.19	0.04
Summer Water depth Y-1	-0.35	-0.27 ^d	0.18	0.08	-0.05	0.33 ^c
Fall Water depth Y-1	-0.26 ^d	-0.12	0.20	0.11	-0.07	0.30 ^c
Ten-Year Average Water depth	-0.77 ^a	-0.38 ^c	0.14	0.39 ^b	0.44 ^b	0.45 ^b

* GC was flooded continuously

^a $p < 0.001$

^b $p < 0.01$

^c $p < 0.05$

^d $p < 0.10$

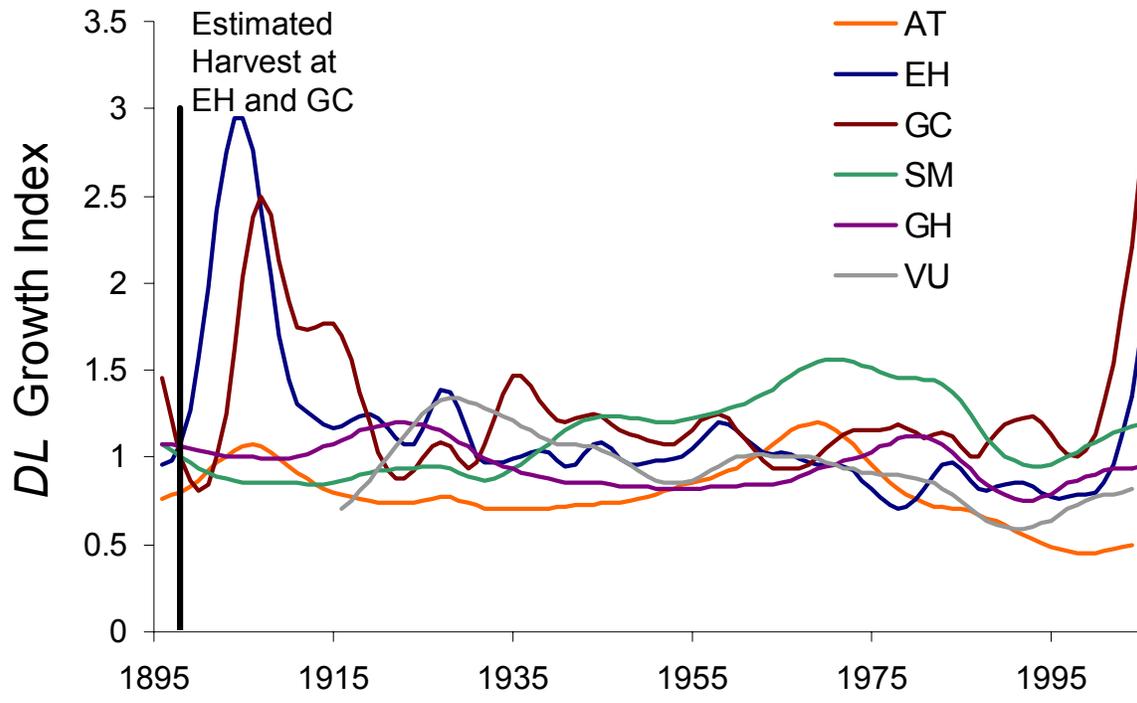


Figure 10. Long-term hydrology and stand dynamics signal *DL*.

observed growth was not as poor. The residuals of this model (R_{AC}) are exaggerated during this period because the predicted growth was so small that the actual growth was proportionally much larger. Thus, the inferred effect of hydrological processes (DL) was large and positive during this time.

Short-term Hydrology Effects (DS)

The contrast in the responses to long-term hydrology between the Lake Verret and Grand Lake sites did not extend to their responses to short-term hydrological fluctuation. The DS signal at all six sites in both basins was positively correlated to annual water depth and flooding variables (Table 10). Higher water depth during the spring months correlated to increased growth at EH, GC, in the Lake Verret basin and SM in the Grand Lake basin. Greater water depth in the summer months was positively correlated to growth at all six sites. Growing season flooded days was positively correlated to growth at AT in the Lake Verret basin and all sites in the Grand Lake basin.

The short-term disturbance signal, DS , correlated negatively to flooding in the previous year at four sites in both basins. Water depth during the months of April through June of the previous year was negatively correlated to DS at AT in the Lake Verret basin while GC in the Lake Verret basin and GH and VU in the Grand Lake basin showed significant correlation to individual months throughout the previous year. There were significant negative correlations between DS and mean-monthly water depth at greater than one year lag at GC in the Lake Verret basin and GH and VU in the Grand Lake basin.

Multiple Linear Regression to Model DS

The multiple regression models for each stand-level DS followed the same patterns as for the simple correlation analysis (Figure 11, Table 10). Water depth in the previous year was

Table 10. Correlation coefficients, r , between water depth variables and short-term hydrology and disturbance signal, DS.

	Site					
	Lake Verret			Grand Lake		
	AT	EH	GC	SM	GH	VU
Year	0.02	-0.01	-0.02	-0.01	0.01	-0.02
October Water depth Y-2	-0.08	-0.15	-0.33 ^c	-0.14	-0.29 ^c	-0.21
November Water depth Y-2	-0.04	-0.13	-0.20	-0.22	-0.32 ^c	-0.20
December Water depth Y-2	0.00	-0.01	-0.01	-0.16	-0.34	-0.29 ^c
January Water depth Y-1	-0.02	0.14	0.02	-0.15	-0.32 ^c	-0.24 ^d
February Water depth Y-1	0.05	0.15	-0.01	-0.17	-0.27 ^d	-0.21
March Water depth Y-1	-0.12	-0.03	-0.16	-0.07	-0.07	-0.09
April Water depth Y-1	-0.26 ^d	-0.10	-0.13	-0.19	-0.20	-0.21
May Water depth Y-1	-0.25 ^d	-0.03	-0.21	-0.09	-0.26 ^d	-0.11
June Water depth Y-1	-0.26 ^d	-0.08	-0.25 ^d	0.08	-0.14	0.12
July Water depth Y-1	-0.21	-0.03	-0.14	0.04	-0.14	0.16
August Water depth Y-1	-0.12	-0.13	-0.05	-0.08	-0.19	0.06
September Water depth Y-1	-0.18	-0.14	-0.05	-0.07	-0.18	0.01
October Water depth Y-1	0.04	0.04	0.03	-0.07	-0.20	0.03
November Water depth Y-1	0.01	0.01	-0.06	0.09	-0.13	0.10
December Water depth Y-1	0.19	0.12	0.11	0.20	-0.09	0.15
January Water depth	0.15	0.16	0.16	0.15	-0.09	0.10
February Water depth	0.06	0.20	0.20	0.27 ^d	0.09	0.29 ^c
March Water depth	0.18	0.29 ^c	0.28 ^d	0.12	-0.05	0.06
April Water depth	0.22	0.28 ^c	0.31 ^c	0.29 ^c	0.15	0.24 ^d
May Water depth	0.23	0.21	0.29 ^c	0.31 ^c	0.17	0.24 ^d
June Water depth	0.20	0.18	0.27 ^d	0.43 ^b	0.29 ^c	0.31 ^c
July Water depth	0.20	0.14	0.27 ^d	0.35 ^c	0.18	0.28 ^c
August Water depth	0.29 ^c	0.28 ^d	0.34 ^c	0.25 ^d	0.01	0.21
September Water depth	0.38 ^b	0.35 ^c	0.39 ^b	0.18	-0.04	0.17
Growing Season Flooded Days	0.30 ^c	0.23	*	0.30 ^c	0.28 ^c	0.33 ^c
Growing Season Flooded Days Y-1	-0.08	-0.01	*	0.08	-0.04	0.13
Ten-Year Average Water depth	-0.14	-0.01	-0.01	0.02	-0.05	0.03

* GC was flooded continuously

^a $p < 0.001$

^b $p < 0.01$

^c $p < 0.05$

^d $p < 0.10$

negatively correlated with *DS* and water depth in the year of growth ring formation was positively correlated with *DS*. The two-variable multiple linear model of short-term hydrology at AT ($r^2 = 0.28$) was:

$$R_{ACD} = 0.94519 - 0.14581*\beta_1 + 0.32690*\beta_2 , \quad (7)$$

and with standardized coefficients, was:

$$R_{ACD} = - 0 .39644*\beta_1 + 0.49146*\beta_2 , \quad (8)$$

where

β_1 is average monthly-mean water depth (m) of Mar(Y-1)-Jun(Y-1), and
 β_2 is average monthly-mean water depth (m) of Aug-Sep.

The three-variable multiple linear model of short-term hydrology at EH ($r^2 = 0.24$) was:

$$R_{ACD} = 0.90229 - 0.20923*\beta_1 + 0.13426*\beta_2 + 0.18820*\beta_3 , \quad (9)$$

and with standardized coefficients, was:

$$R_{ACD} = - 0 .36711*\beta_1 + 0.34314*\beta_2 + 0.26456*\beta_3 , \quad (10)$$

where

β_1 is average monthly-mean water depth (m) of Jun(Y-1)-Sep(Y-1),
 β_2 is average monthly-mean water depth (m) of Mar-May, and
 β_3 is average monthly-mean water depth (m) of Aug-Sep.

The two-variable multiple linear model of short-term hydrology at GC ($r^2 = 0.31$) was:

$$R_{ACD} = 0.88443 - 0.17350*\beta_1 + 0.21185*\beta_2 , \quad (11)$$

and with standardized coefficients, was:

$$R_{ACD} = - 0 .51777*\beta_1 + 0.57490*\beta_2 , \quad (12)$$

where

β_1 is average monthly-mean water depth (m) of May(Y-1)-Jun(Y-1), and
 β_2 is average monthly-mean water depth (m) of Mar-May.

The two-variable multiple linear model of short-term hydrology at SM ($r^2 = 0.20$) was:

$$R_{ACD} = 0.89147 - 0.03539*\beta_1 + 0.12297*\beta_2 , \quad (13)$$

and with standardized coefficients, was:

$$R_{ACD} = - 0 .19867*\beta_1 + 0.43226*\beta_2 , \quad (14)$$

where

β_1 is average monthly-mean water depth (m) of Mar(Y-1)-May(Y-1), and
 β_2 is average monthly-mean water depth (m) of Jun-Sep.

The two-variable multiple linear model of short-term hydrology at GH ($r^2 = 0.21$) was:

$$R_{ACD} = 0.32584 + 0.00409*\beta_1 - 0.07347*\beta_2 , \quad (15)$$

and with standardized coefficients, was:

$$R_{ACD} = + 0 .29017*\beta_1 - 0.36410*\beta_2 , \quad (16)$$

where

β_1 is number of growing season flood days, and
 β_2 is average monthly-mean water depth (m) of Dec(Y-2)-Feb(Y-1).

The three-variable multiple linear model of short-term hydrology at VU ($r^2 = 0.24$) was:

$$R_{ACD} = -1.07403 - 0.04663*\beta_1 + 0.05174*\beta_2 + 0.01018*\beta_3 , \quad (17)$$

and with standardized coefficients, was:

$$R_{ACD} = - 0 .31786*\beta_1 + 0.30914*\beta_2 + 0.37055*\beta_3 , \quad (18)$$

where

β_1 is average monthly-mean water depth (m) of Mar(Y-1)-May(Y-1),
 β_2 is average monthly-mean water depth (m) of Dec(Y-1)-Feb, and
 β_3 is number of growing season flood days.

Effect of Floods on Radial Growth

Analysis (t -tests) of growth in flood years versus non-flood years showed statistically significant differences in the short-term disturbance signal DS in all sites but GH (AT $p =$

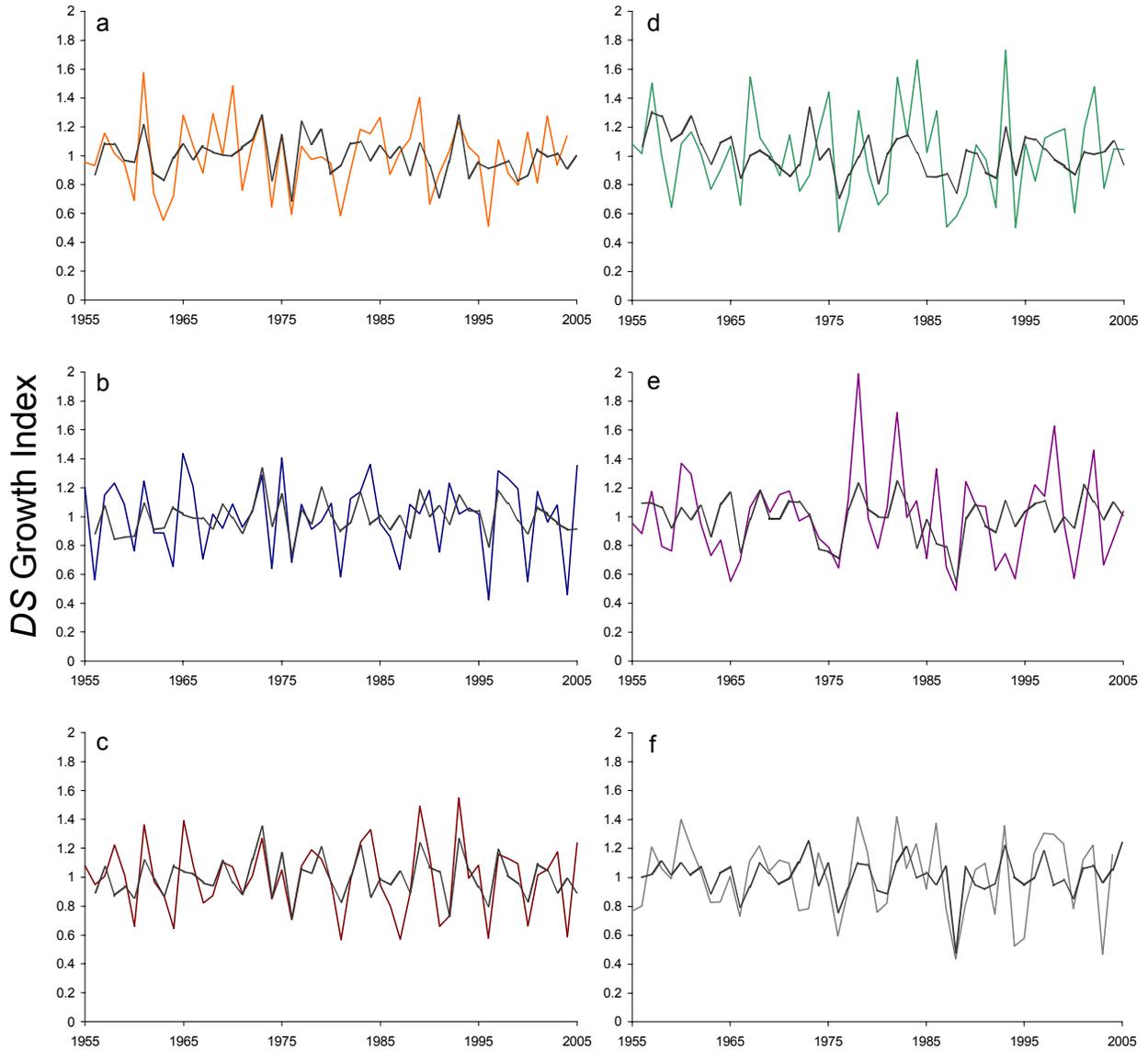


Figure 11. Short-term disturbance signal DS (colored lines) as modeled by multiple regressions (stippled lines) with seasonal water depth variables for AT (a), EH (b), GC (c), SM (d), GH (e), and VU (f).

0.0257; EH $p = 0.0008$; GC $p = 0.0215$; SM $p = 0.0094$; GH $p = 0.0522$; VU $p = 0.0033$).

Highlighting years in which flooding occurred in the Mississippi River (Trotter et al. 1998) on cumulative distribution functions of DS illustrates the strong relationship between flood years and good growth (Figure 12).

The largest floods occurred in conjunction with many of the years of greatest growth at both swamps. The seven greatest floods, as quantified by highest stage, greatest flow, and days in flood at Red River Landing, Louisiana from 1927-1997 were, in descending order 1997, 1927, 1983, 1945, 1979, 1973, and 1975 (Trotter et al. 1998). Several flood years did coincide with greater growth years in one or both basins (1908, 1913, 1922, 1923, 1936, 1958, 1979, and 1997). In all of these years at least one basin had above average growth.

Simultaneous Analysis

Multiple regression models of each stand-level R_A (Figure 13) by climate and hydrology variables generally showed similar results as separate analysis. Models accounted for 40% to 72% of variance. Growth of the previous year was selected for inclusion all models except EH. At all sites, climate variables were generally not as highly correlated to growth as were hydrological variables (Tables 11, 12). Growth at sites in both basins was negatively correlated with water depth of the previous year, and positively correlated with water depth of the winter preceding year of growth through the end of the growing season. Ten-year average stage was negatively correlated with growth at two sites in the Lake Verret basin (AT and EH) but at no other sites.

The four-variable multiple linear model at AT ($r^2 = 0.72$) was:

$$R_A = 0.79376 + 0.59267*\beta_1 - 1.27890*\beta_2 + 1.01097*\beta_3 - 1.67540*\beta_4 , \quad (19)$$

where

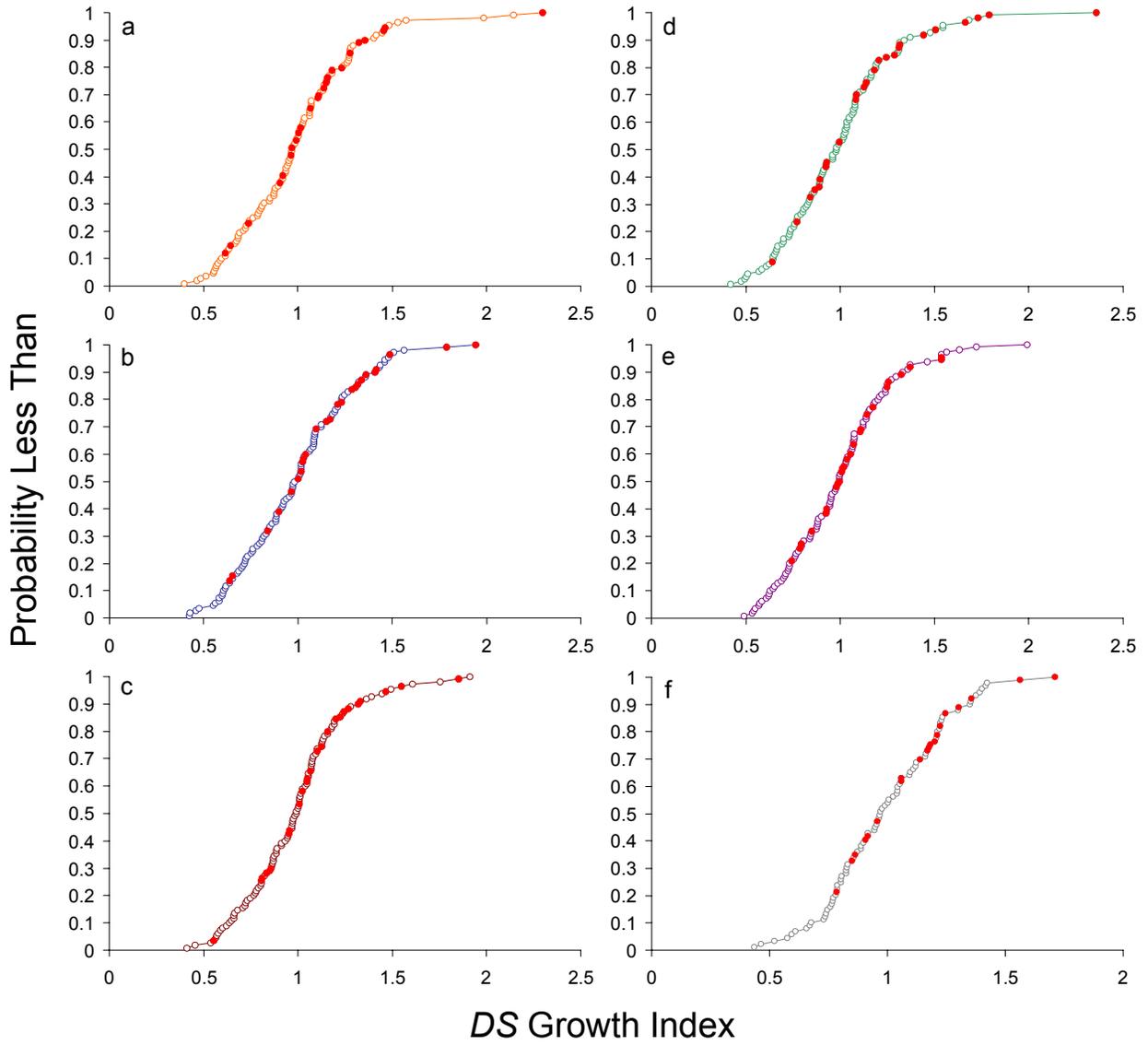


Figure 12. Cumulative distribution functions of the short-term disturbance signal DS highlighting flood years in red for AT (a), EH (b), GC (c), SM (d), GH (e), and VU (f).

β_1 is one-year lag of the R_A growth index,
 β_2 is average monthly-mean water depth (m) of summer Y-1,
 β_3 is average monthly-mean water depth (m) of spring,
 β_4 is 10-year average annual water depth (m).

The five-variable multiple linear model at EH ($r^2 = 0.52$) was:

$$R_A = 2.40458 - 0.07212*\beta_1 + 0.00526*\beta_2 - 0.01260*\beta_3 + 1.28930*\beta_4 - 2.25064*\beta_5, \quad (20)$$

where

β_1 is average monthly-mean temperature (C°) of fall Y-1,
 β_2 is total monthly-mean precipitation (cm) of summer,
 β_3 is total monthly-mean precipitation (cm) of fall Y-1,
 β_4 is average monthly-mean water depth (m) of winter, and
 β_5 is 10-year average annual water depth (m).

The four-variable multiple linear model at GC ($r^2 = 0.54$) was:

$$R_A = 0.26280 + 1.47110*\beta_1 + 0.00748*\beta_2 + 0.46699*\beta_3 - 1.13931*\beta_4, \quad (21)$$

where

β_1 is average monthly-mean water depth (m) of summer,
 β_2 is total monthly-mean precipitation (cm) of spring,
 β_3 is one-year lag of the R_A growth index, and
 β_4 is average monthly-mean water depth (m) of spring Y-1.

The four-variable multiple linear model at SM ($r^2 = 0.40$) was:

$$R_A = 0.65001 + 0.35903*\beta_1 + 0.63605*\beta_2 - 0.01356*\beta_3 + 0.09311*\beta_4, \quad (22)$$

where

β_1 is one-year lag of the R_A growth index,
 β_2 is average monthly-mean water depth (m) of summer,
 β_3 is total monthly-mean precipitation (cm) of fall Y-1, and
 β_4 is average monthly-mean PDSI of summer Y-1.

The four-variable multiple linear model at GH ($r^2 = 0.49$) was:

$$R_A = -0.14796 + 0.49340*\beta_1 - 0.01119*\beta_2 + 0.00402*\beta_3 + 0.04776*\beta_4, \quad (23)$$

where

β_1 is one-year lag of the R_A growth index,

β_2 is total monthly-mean precipitation (cm) of fall Y-1,
 β_3 is total growing season flooded days, and
 β_4 is average monthly-mean PDSI of summer.

The five-variable multiple linear model at VU ($r^2 = 0.58$) was:

$$R_A = 3.39108 + 0.58318*\beta_1 + 0.37784*\beta_2 - 0.11357*\beta_3 - 0.12590*\beta_4 - 0.00598*\beta_5, \quad (24)$$

where

β_1 is one-year lag of the R_A growth index,
 β_2 is average monthly-mean water depth (m) of summer,
 β_3 is average monthly-mean temperature (C°) of summer,
 β_4 is average monthly-mean water depth (m) of spring Y-1, and
 β_5 is total monthly-mean precipitation (cm) of fall Y-1.

The five-variable multiple linear model at Lake Verret Average ($r^2 = 0.67$) was:

$$R_A = 0.97081 - 0.00604*\beta_1 + 1.05420*\beta_2 + 0.69230*\beta_3 - 1.78153*\beta_4 - 1.05556*\beta_5 + 0.49970*\beta_6, \quad (24)$$

where

β_1 is total monthly-mean precipitation (cm) of winter,
 β_2 is average monthly-mean water depth (m) of winter,
 β_3 is average monthly-mean water depth (m) of spring,
 β_4 is average monthly-mean water depth (m) of summer Y-1,
 β_5 is 10-year average annual water depth (m), and
 β_6 is one-year lag of the R_A growth index.

The five-variable multiple linear model at Grand Lake Average ($r^2 = 0.52$) was:

$$R_A = 0.51194 - 0.01008*\beta_1 + 0.03841*\beta_2 + 0.41357*\beta_3 - 0.13682*\beta_4 + 0.55892*\beta_5, \quad (24)$$

where

β_1 is total monthly-mean precipitation (cm) of fall Y-1,
 β_2 is average monthly-mean PDSI of summer,
 β_3 is average monthly-mean water depth (m) of summer,
 β_4 is average monthly-mean water depth (m) of spring Y-1, and
 β_5 is one-year lag of the R_A growth index.

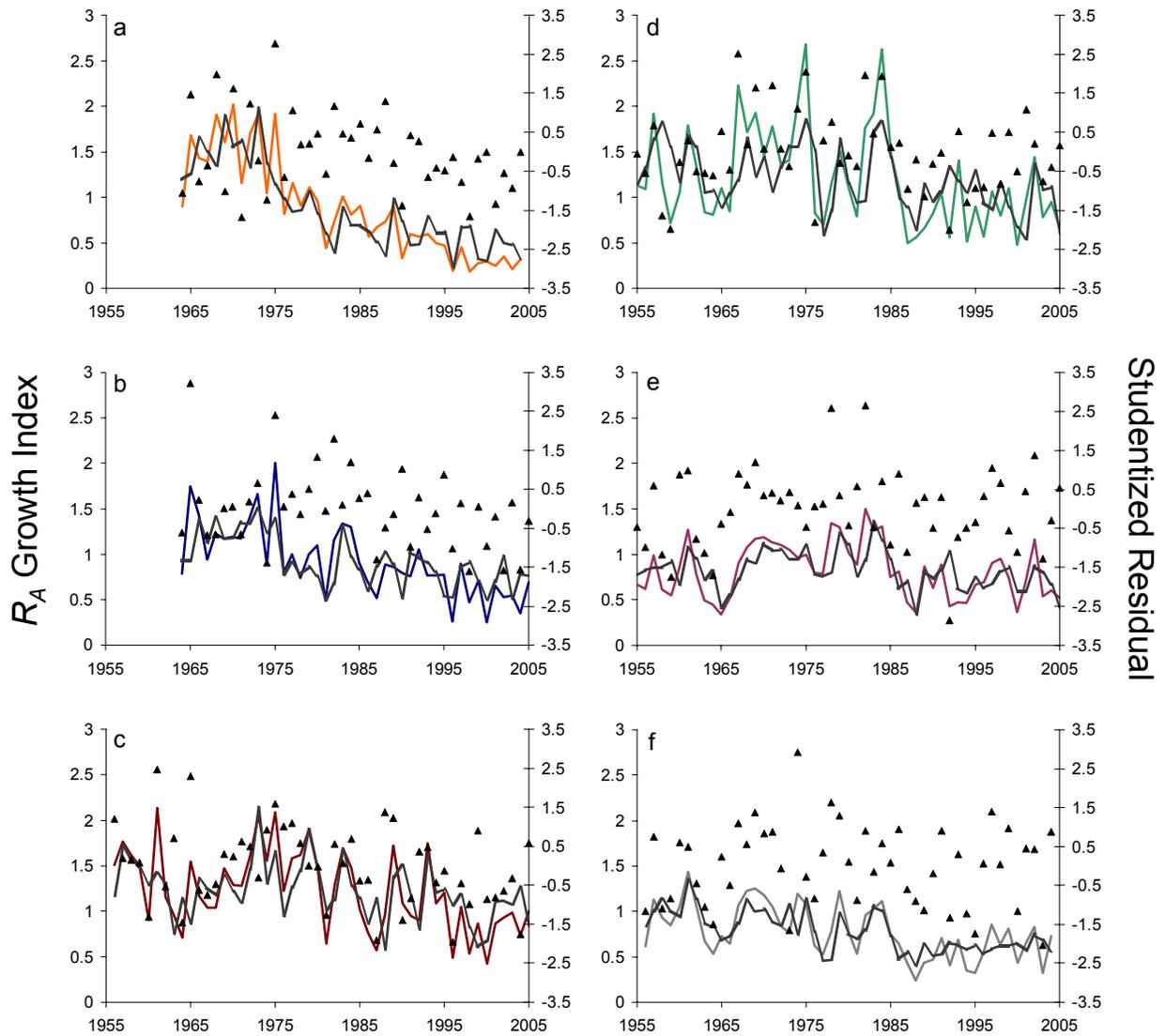


Figure 13. Ring width normalized for age-related growth R_A (colored lines) as modeled by multiple regressions (stippled lines) with all seasonal climate and flooding variables at AT (a), EH (b), GC (c), SM (d), GH (e), and VU (f). Triangles are the studentized residuals of the model.

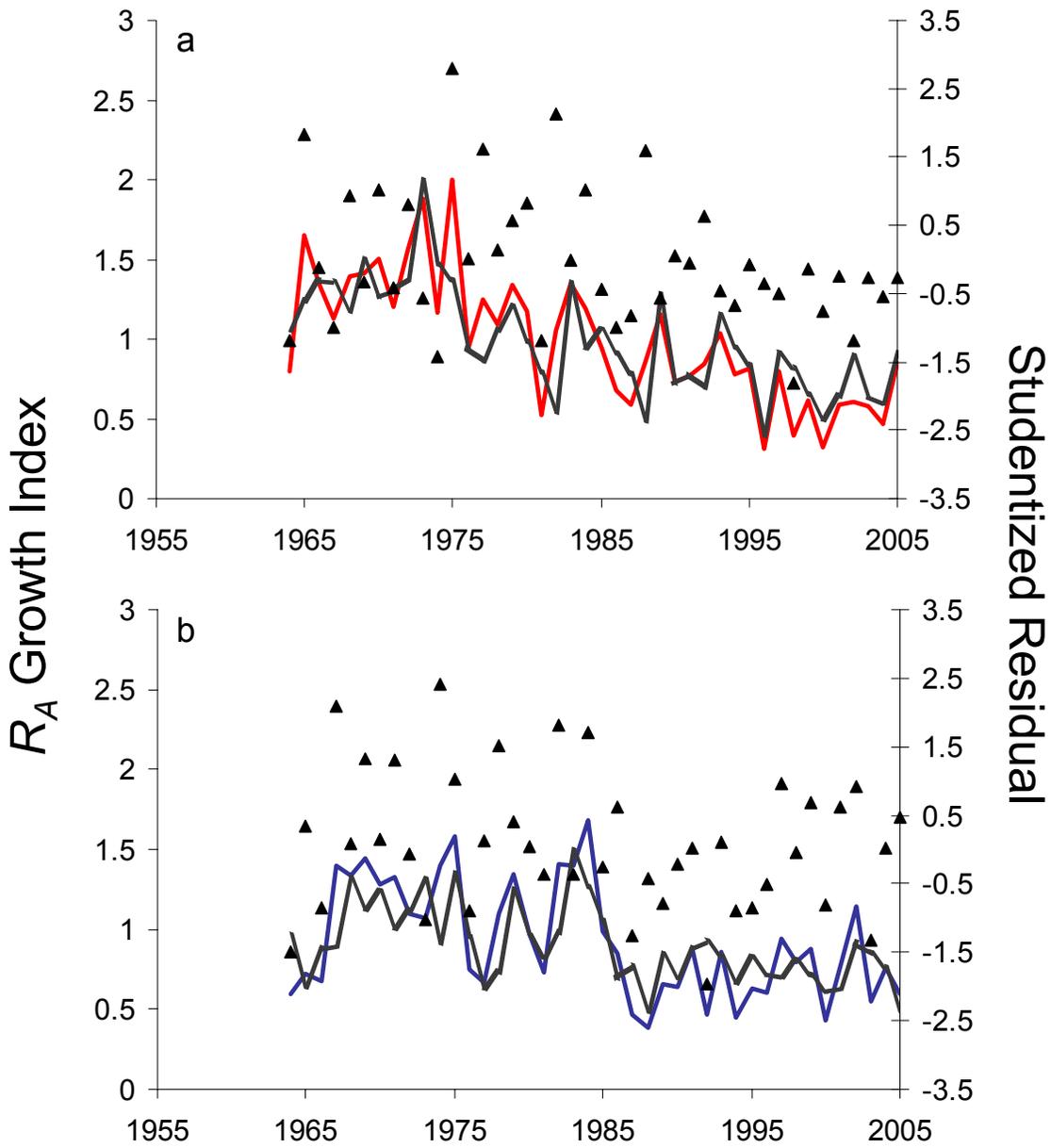


Figure 14. Ring width normalized for age-related growth R_A (colored lines) as modeled by multiple regressions (stippled lines) with all seasonal climate and flooding variables for Lake Verret (a), and Grand Lake (b). Triangles are the studentized residuals of the model.

Table 11. Standardized multiple regression coefficients of simultaneous analysis of R_A using all seasonal climate and flooding variables.

	Site						Verret	Grand
	Lake Verret			Grand Lake				
	AT	EH	GC	SM	GH	VU		
Lag one-year R_A	0.59 ^a		0.47 ^a	0.36 ^a	0.49 ^a	0.59 ^a	0.50 ^a	0.55 ^a
Spring water depth Y-1			-0.53 ^a			-0.23 ^c		-0.21 ^d
Summer water depth Y-1	-0.32 ^c						-0.58 ^a	
Winter water depth		0.61 ^a					0.47 ^b	
Spring water depth	0.35 ^b						0.32 ^c	
Summer water depth			0.47 ^a	0.39 ^a		0.44 ^a		0.40 ^a
Growing season flooded days					0.29 ^c			
10-Yr Avg water depth	-0.31 ^c	-0.57 ^a					0.25 ^d	
Fall temp Y-1		-0.25 ^c						
Summer temp						-0.20 ^d		
Fall precip Y-1		-0.32 ^c		-0.24 ^c	-0.35 ^b	-0.19 ^d		-0.28 ^c
Winter precip							-0.21 ^d	
Spring precip			0.26 ^c					
Summer precip		0.21 ^d						
Summer PDSI Y-1				0.25 ^c				
Summer PDSI					0.31 ^d			0.22

^a $p < 0.001$

^b $p < 0.01$

^c $p < 0.05$

^d $p < 0.10$

Table 12. Standardized multiple regression coefficients of R_A forcing seasonal climate and flooding variables selected for inclusion in simultaneous models to show similarities and differences between stands.

	Site						Verret	Grand
	Lake Verret			Grand Lake				
	AT	EH	GC	SM	GH	VU		
Lag one-year R_A	0.41 ^b	0.07	0.56 ^b	0.33 ^d	0.52 ^b	0.54 ^b	0.45 ^b	0.50 ^b
Spring water depth Y-1	-0.08	0.08	-0.31	-0.26	-0.23	-0.43 ^c	-0.17	-0.34 ^d
Summer water depth Y-1	-0.18	-0.24	-0.48 ^d	0.11	-0.08	0.15	-0.31	0.08
Winter water depth	0.42 ^c	0.58 ^c	0.71 ^b	0.32	-0.03	0.32	0.60 ^b	0.17
Spring water depth	-0.13	0.06	-0.15	0.15	0.49 ^d	-0.01	-0.10	0.23
Summer water depth	0.11	0.08	0.21	0.29	0.07	0.20	0.10	0.31 ^d
Growing season flooded days	0.01	-0.03	*	0.07	0.10	0.16	§	§
10-Yr Avg water depth	-0.42 ^c	-0.50 ^c	0.04	0.13	0.09	0.07	-0.25	0.10
Fall temp Y-1	-0.09	-0.19	-0.10	-0.14	0.03	0.03	-0.09	-0.04
Summer temp	-0.02	-0.13	-0.12	0.00	0.30	-0.13	-0.06	0.11
Fall precip Y-1	-0.19	-0.20	-0.04	-0.42 ^b	-0.52 ^b	-0.26	-0.13	-0.44 ^c
Winter precip	-0.04	-0.01	-0.27 ^d	-0.29	-0.38 ^c	-0.13	-0.12	-0.32 ^d
Spring precip	0.27	0.21	0.42	-0.25	-0.47 ^d	-0.07	0.40 ^d	-0.29
Summer precip	0.40	0.37	0.28	-0.27	-0.53	-0.20	0.49 ^d	-0.35
Summer PDSI Y-1	0.12	0.08	0.13	0.09	-0.29	-0.02	0.18	-0.04
Summer PDSI	-0.43	-0.38	-0.44	0.43	0.42 ^c	0.18	-0.57	0.64

* GC was flooded continuously

§ Flooded days not included for basin average model

^a $p < 0.001$

^b $p < 0.01$

^c $p < 0.05$

^d $p < 0.10$

DISCUSSION

Effects of Climatic (C) on Growth

Separate analyses of climate and disturbance indicated climate influenced growth similarly for all sites in both basins, although the combined effects of climate accounted for only a small portion of the variance in growth ($r^2 = 0.18$ and 0.23 ; Lake Verret and Grand Lake, respectively). Reams and Van Deusen (1998) also found low association of climate to tree-ring growth in Louisiana. However, studies of baldcypress in other regions have found ring width growth highly correlated to climatic variables such as summer PDSI ($r^2 = 0.47$) (Stahle et al. 1988).

Temperature was an important variable in separate analysis at all six sites when climate was analyzed separately from disturbance. The consistent positive correlation between winter temperature and growth could be linked to the warming of flood waters, which would allow root systems to become physiologically active earlier in the spring (Babalola et al. 1968; Kozlowski et al. 1991). The negative correlation between summer temperature and growth at three sites (AT, EH, and SM) and the inverse relationship between summer temperature and precipitation ($r = -0.38$, $p < 0.0001$) likely indicate increased stress on the tree by increasing water vapor pressure deficit. The negative correlation between spring temperature of the year prior to growth and growth may indicate decreased stored food reserves that affected growth early in the successive growing season.

Spring precipitation was positively correlated with growth when climate was analyzed separately from disturbance. Although high spring precipitation in some climates occurs with lower spring temperatures, that was not the case for these data ($r = -0.03$, $p = 0.83$) because spring precipitation originates in Gulf of Mexico moisture and occurs with warm southerly winds

(Keim 1996). The study sites were typically flooded during the spring, so it is unlikely that higher spring precipitation increased growth by increasing soil moisture. It is possible that rainwater oxygenates flood waters or that precipitation reduces water stress because it coincides with high humidity that lowers vapor pressure deficit. Fall precipitation Y-1 was included in four of six simultaneous models. Relationships of ring width to climate of fall Y-1 are not unusual (Fritts 1976; Tardif and Stevenson 2001), but the cause of a negative relationship between growth and fall Y-1 precipitation and temperature is unclear. It is possible that storage of photosynthates in the fall of the previous year is impeded by wet conditions for some reason.

Climatic variables included in simultaneous analysis of effects differed from those included in separate analysis and were less consistent in strength and correlation than those included separate analysis. For example, fall precipitation Y-1 was included in four of six simultaneous models but showed no significant correlation in independent analysis. Winter and summer temperature were strongly correlated to growth in separate analyses but not included in any simultaneous models except one (summer temperature at GH).

Effects of Flooding and Other Disturbances (*D*) on Growth

The effect of flooding on growth of baldcypress depended on the temporal scale and type of floodwater. In the short term (seasonal), flooding increased growth in both stagnant, blackwater and flowing, brownwater swamps. However, long-term, chronic flooding (greater than 10 years) affected baldcypress differently depending upon site, and, by inference, the nature of floodwater. Growth in two of the three stands in stagnant, blackwater systems was negatively correlated to prolonged flooding while all sites in flowing, brownwater systems were positively correlated to prolonged increase in flooding and water depth. The third blackwater site was uncorrelated with long-term variability in flooding.

Although it is unclear exactly which climatic time periods and variables are important for baldcypress growth, it is clear that hydrology is the driving effect of baldcypress growth in these swamps. Hydrological variables were of similar sign and strength of correlation in both separate and simultaneous analyses but climatic variables were of weaker correlation and inconsistent between analyses. When climate was analyzed separately, warm winters and cool, rainy growing seasons were important for higher growth. But when hydrology was considered in simultaneous analysis, cool, dry falls of the previous year were important as well as the important variables found in separate analysis. Including climate in models did improve predictions, which indicates it acts in conjunction with hydrology to influence growth. Other studies including both climatic and hydrological effects on wetland tree growth have found hydrology as a significant effect but not dominant over climate (Jean and Bouchard 1996). Climate, stand history, hydrology and the interaction of these effects must be considered. This may be the reason other studies of baldcypress growth in Louisiana have found poor correlations with climate variables.

Lake Verret

The decreases in growth at Lake Verret sites with increases in long-term flooding and water depth are typical of other studies of baldcypress growth in swamps subjected to chronic flooding by stagnant, non-flowing water (Beaven and Oosting 1932; Mitsch et al. 1979; Mitsch and Ewel 1979; Conner and Day 1992b; Keeland 1994). The productivity has decreased and ecosystem services and functions have been altered by the rise in flooding by stagnant water. Decreased growth reduces carbon sequestration (Felzer et al. 2004). Lower radial growth is correlated with lower primary productivity (Grier and Logan 1977), and this effect on the major structural component of the sites will cascade through the ecosystem. In addition to lower stand

productivity, increased flooding reduces regeneration (Keim et al. in press; Conner et al. 1986). Baldcypress cannot regenerate under flooded conditions (Demaree 1932) and seedlings cannot survive complete immersion for prolonged periods of time (Souther and Shaffer 2000). Thus, mortality of standing trees will cause the swamp to eventually convert to marsh or open water.

It is unclear why growth at GC (Lake Verret) showed no correlations to long-term flooding. The cause of a lack of detectable response is unclear and contrary to virtually all studies of baldcypress growth in response to stagnant water flooding. Most likely, there are important processes controlling growth at the GC that were not analyzed in this study. For example, stand dynamics may have masked the effects of hydrological changes in the middle portion of the twentieth century. Canopy gaps were common at this site and it is possible that this stand was once mixed cypress-tupelo and bottomland hardwoods. Flooding might have caused mortality of bottomland hardwoods and the reduced competition allowed the remaining baldcypress to grow at a sustained high rate. There was an increase in growth in the 1960s common to all Lake Verret sites that also occurred at GC, and from that point to 2005, growth at GC was much greater than the other two Lake Verret sites. It may be that agricultural runoff from fields 3 km away delivers sediment, nutrients, and flowing water via Godchaux Canal adjacent to the site to help offset the negative effects of flooding (Conner and Day 1992b). Other Lake Verret sites were not situated near bayous or canals draining agricultural land.

Grand Lake

All sites at the brownwater, riverine swamp showed increased growth with long-term increased flooding when effects of climate and disturbance were analyzed separately. Although long-term average water depth was not significant in any simultaneous model of climate and disturbance at Grand Lake, it was positively correlated and a strong candidate for inclusion. The

effects of riverine flood waters with high nutrient concentrations in the Atchafalaya Basin may play a role in increased growth rates with deeper, longer, and more frequent flooding.

The response of baldcypress to flooding at these sites is likely not typical of the entire Atchafalaya Basin. Nutrients and sediment concentrations decrease with distance from the source of input at the main channel. Nutrients in overbank flow are quickly taken up by vegetation. Concentrations of N and P in forested wetlands can return to background concentrations within 1200 m of enriched input (Brantley 2005). Sediment is also deposited near source flow, so that large areas of the Atchafalaya Basin are stagnant swamps (Sabo et al. 1999a; Sabo et al. 1999b). Thus, sites in the Atchafalaya Basin further away from the main channel would likely experience reduced growth with long-term flooding, similar to the stagnant Lake Verret sites.

Stand Dynamics

The long-term effects of hydrology are difficult to distinguish from stand dynamics because stand dynamics may actually have its origins in long-term alterations to hydrology. A competition release effect on radial growth after initiation of increased flooding has been noted previously in baldcypress. One study of baldcypress flooded continually for 18 years found that mortality was 50%, but annual growth of remaining trees was greater than before the mortality and change in hydrology (Eggler and Moore 1961). Conner and Day (1992a) and Young et al. (1995) also inferred increases in growth after hydrological change was a possible result of decreased competition from adjacent trees as mortality occurred. Similar patterns have been found in a recent dendrochronological study of a flooded swamp (Izdepski, Keim, Amos, and Day, unpublished data). In that study, a long-term increase in growth was attributed to observed mortality of less flood-tolerant species when flooding increased then followed by a decrease in growth apparently caused by water stress. Low stand density and

apparent evidence of logging in the *DL* signal (Figure 10) indicates this may have occurred in several sites, and other stand disturbances are likely. These stand disturbance patterns alter the correlation of growth to hydrology because physical environment affects ecological relationships.

Seasonal Flooding (*DS*)

Both separate and simultaneous analyses showed that growth responded similarly to short-term (seasonal) flooding over all sites in both basins. Flood events are the main source of variation in *DS* because drought did not affect the study sites (Figure 4). Flooding at Grand Lake sites comes with nutrients and the relationship with growth is obvious. Although disconnected from riverine flooding, the Lake Verret sites may have responded positively to seasonal flooding in the year of growth because of increased flow velocities during floods. Floods convert Lake Verret into a temporary flowing water system instead of remaining stagnant. Increased flow also may flush phytotoxins and increase dissolved oxygen in the root zone. Positive correlation of growth to short-term high water also means reduced growth during low water flooded periods. Study sites in the Lake Verret basin were still flooded even at the very lowest stage, so that most periods of low stage are periods during which flood waters would be most stagnant, most hypoxic, most phytotoxic, and most depleted of nutrients.

Short-term (seasonal) flooding in the year prior to growth was negatively correlated to growth at all sites over both basins in both the separate and simultaneous model analyses. While it is unclear how this relationship functions, greater growth in the previous year may deplete carbohydrate stores for the following year.

Further development of this tool will be useful to infer historical hydrology in forests where hydrological data are unavailable. Flow reconstructions have been successful in other

areas (Cleaveland 2000), but seasonal stage has not been analyzed this way. Reconstructions are possible in these stands because hydrology is more nearly a simple effect on growth than is climate. Water level data are not available in most swamps even though it is an important ecological variable.

Flood Years

Flood years of the Lower Mississippi River Alluvial Valley coincided with good growth years at both Lake Verret and Grand Lake. High growth occurred in the same year as floods (rather than the year after), presumably because floods typically occurred in the spring of the year and can benefit growth immediately and throughout that growing season. Flood events deposit nutrients in the floodplain and flush hypoxic, phytotoxic water. Grand Lake receives floodwaters from the Mississippi River through the Atchafalaya River, but Lake Verret does not directly receive this flow. Backwater flooding from the lower Atchafalaya River does occur in the Lake Verret basin (Conner and Brody 1989) but it is unlikely that riverine water actually reaches the study sites. Therefore, it is more likely that this stagnant swamp is converted to a flowing system during flood events.

Management Implications

These results have implications for managing forested wetlands in Louisiana. There are several implications for managing baldcypress growth in green tree reservoirs or in other similar situations where flooding can be controlled. Previous studies have found seasonal flooding to be most beneficial (Conner and Day 1976) but the results of this study concur with other studies that show flooding by flowing water may be beneficial even during the growing season. Stagnant flood waters should be avoided, especially during the growing season. Flooding beginning in

October had little effect, but delaying impoundment until November or December would allow greater photosynthate storage (Fritts 1976).

Diversion of water from the Atchafalaya Floodway Basin into Lake Verret could be beneficial to tree growth in both swamps. Conner and Day (1991) proposed diversion of winter flood waters, which is the peak period of sediment delivery. The higher concentration of nutrients and dissolved oxygen of Atchafalaya waters also could be beneficial to forest growth in Lake Verret if diverted during the growing season. Maintaining flow velocities would be critical, although potentially difficult. Other swamps within the Atchafalaya Basin flooded by stagnant water may also benefit from a diversion that drains at least some of the excess water and sediments from stagnant backswamps. However, exacting planning would be necessary to make certain these diverted waters reach the backswamps and do not simply cause additional problems by creating lacustrine deltas and littoral edges as in the Atchafalaya basin (Tye and Coleman 1989b). To ensure flooding did not prevent regeneration at Lake Verret, a drawdown would be necessary from time to time.

CONCLUSIONS

Flooding was the dominant environmental control of growth at all study sites. Over a long-term period (greater than 10 years), flooding in the stagnant, blackwater Lake Verret swamp was negatively correlated to growth while flooding in the riverine, brownwater Grand Lake swamp was positively related to growth. In contrast, effects of short-term (seasonal) flooding were similar at all sites regardless of whether they were subject to blackwater or riverine flooding. Increased flooding was correlated to greater growth in the year of flooding but less growth in the following year.

Growth at all sites was more strongly related to flooding than to climatic variables. Results of separate and simultaneous analysis of climatic effects differed on which climatic time periods and variables are important for baldcypress growth. Separate analysis of climate effects suggested that cool, rainy growing seasons increased growth, but simultaneous analysis of climatic and hydrological effects suggested a cool, dry fall of the previous year also improved growth.

Models of baldcypress growth that solely included hydrologic or climatic variables were insufficient to understand changes in radial growth. Climate, stand dynamics, hydrology and the interaction of these effects must be considered.

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