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RESPONSE OF WOODY SWAMP SEEDLINGS TO FLOODING AND INCREASED WATER TEMPERATURES. I. GROWTH, BIOMASS, AND SURVIVORSHIP¹

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ABSTRACT

Growth, biomass, and survival of bald cypress (*Taxodium distichum* [L.] Richard), water tupelo (*Nyssa aquatica* L.), black willow (*Salix nigra* Marshall), and button bush (*Cephalanthus occidentalis* L.) were examined in a 3 × 3 factorial experiment varying water temperatures (AMBIENT, MID, and HIGH [~40 C]) and water levels (DRAINED, SATURATED, and FLOODED). Stem diameter and height, biomass, and survivorship for water tupelo and bald cypress were all reduced by the HIGH/FLOODED treatment. Black willow growth had the greatest variability among nonlethal flooding and temperature treatments, and achieved the greatest biomass of the four species. In the HIGH/FLOODED treatment, however, only 47% of the black willow seedlings survived and stem diameter, height, and biomass of survivors were greatly reduced. Button bush had intermediate variability of growth to the nonlethal treatments as compared to the other study species. Survival of button bush seedlings in the HIGH/FLOODED treatment was high (87%), but root biomass of the survivors was reduced. Interspecific differences in growth, biomass, survivorship, and morphological characteristics existed among these swamp species to experimental conditions. These responses may help explain vegetation patterns in a thermally impacted swamp.

A BALDCYPRESS-WATER TUPELO riverine swamp (*Taxodium distichum* [L.] Richard and *Nyssa aquatica* L.) is located on the United States Department of Energy's Savannah River Plant (SRP), near Aiken, South Carolina. The nuclear production facility has discharged thermal effluents since 1954 into tributaries which enter the swamp. Introduction of these effluents changed water levels, water temperatures, and sedimentation patterns in the tributaries and adjacent swamp areas, causing instantaneous and continuing mortality of the swamp forest (Sharitz, Gibbons, and Gause, 1974; Sharitz, Irwin, and Christy, 1974). Some of the impacted areas have been colonized by black willow (*Salix nigra* Marshall) and button bush (*Cephalanthus occidentalis* L.) (Sharitz, Irwin, and Christy, 1974). Interspecific differences in the tolerance to thermal effluents may

explain the observed patterns of mortality and revegetation.

In the southeastern United States, swamps often support a bald cypress-water tupelo forest. Black willow and button bush are often found in very wet, but usually early successional habitats. All of these species are rated as "most tolerant" to waterlogging (Hook, 1984a). Soil waterlogging, synonymous with soil flooding, is not in itself a stress since saturation of a cell with water is not injurious, but prolonged flooding can lead to the secondary physiochemical stress of oxygen deficiency (Levitt, 1972).

High temperatures can affect plant tissue by direct or indirect injuries (Levitt, 1972). Extreme temperature increases (>45 C) can cause direct injury of membranes and chemical decomposition (Ingram and Buchanan, 1984). Less extreme temperature can result in indirect injuries (biochemical lesions, toxicity, protein loss and starvation; Levitt, 1972). The initial discharges of thermal effluents on the SRP were reported to have temperatures of >70 C at the outfall (Christensen et al., 1984) and temperatures of impacted swamp areas currently reach 42 C (McLeod and Sherrod, 1981; Scott, Sharitz, and Lee, 1985). Mortality initially observed after the onset of effluent release probably resulted from direct injury, with indirect

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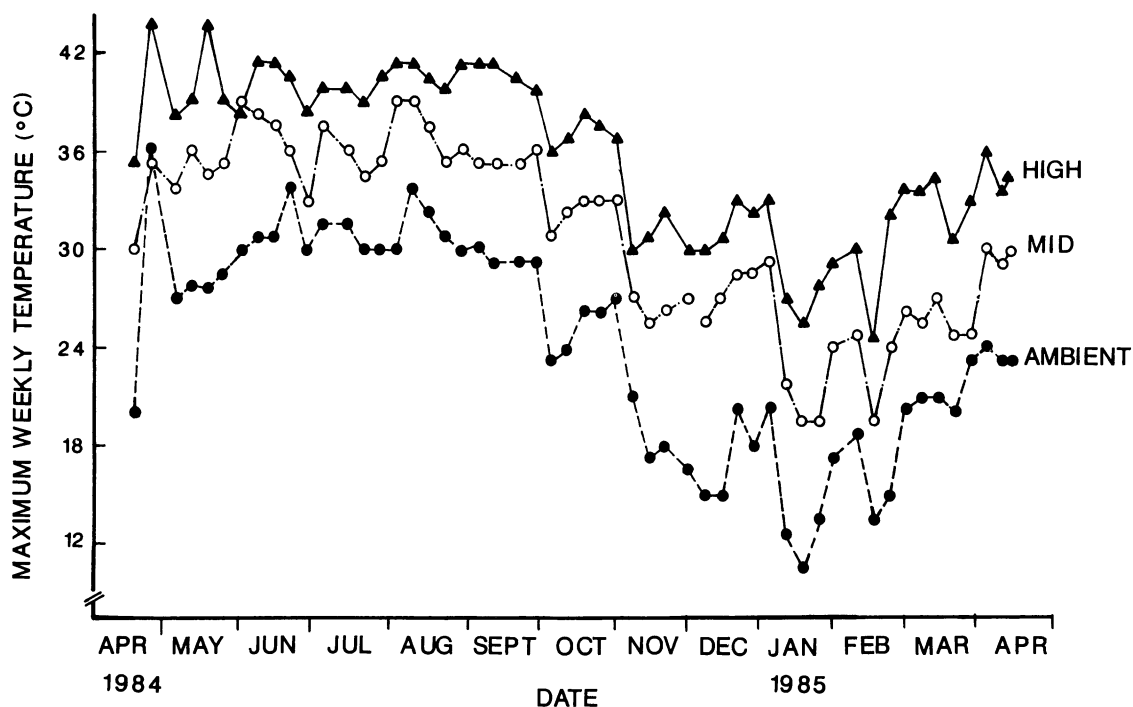


Fig. 1. Weekly maximum water temperatures (C) for AMBIENT, MID, and HIGH treatments.

effects responsible for continuing the long-term canopy decline.

The study objective was to determine the impact of increased water level and water temperature on stem diameter and height growth, biomass, survival, and development of selected morphological characteristics (adventitious roots, lenticels, and numbers of basal stems) of bald cypress, water tupelo, black willow, and button bush seedlings.

MATERIALS AND METHODS—Experimental design was a complete factorial with three water levels and three water temperatures. An outdoor concrete channel, lined with plastic, was divided into three $6.7 \times 1.6 \times 0.2$ m pools, each maintained at a different temperature. Water level treatments were DRAINED = water 6 cm below soil surface with the pot in approximately 3 cm of water; SATURATED = water level at soil surface; and FLOODED = water 6 cm above the soil surface. Seedlings were placed on shelves submerged at different depths in the pools to achieve the relative water level treatments. The AMBIENT temperature pool simulated natural swamp temperatures, and the MID and HIGH pools were approximately 5 and 10 C above AMBIENT, respectively, and simulated water temperatures of impacted areas. Maximum and minimum water temperatures were recorded daily

throughout the growing season, with daily fluctuations averaging 6 C. Maximum weekly temperatures for the pools are shown in Fig. 1. Each pool contained half strength Hoagland's solution (Hoagland and Arnon, 1950), which was circulated by a pump to a separate heating chamber and returned to the pool by a gravity-fed drip system to aerate the solution. Dissolved oxygen of this solution was measured with an Orion oxygen probe, and was saturated with regard to temperature.

Bald cypress, water tupelo, and button bush seeds were collected from a thermally unimpacted area of the Savannah River swamp in the fall of 1983. These seeds were damp stratified (4 C) for several months. During January, bald cypress and water tupelo were germinated in flats of Metro-Mix 220 (cut sphagnum, pine bark, perlite, and vermiculite), while button bush seeds were germinated on damp filter paper in petri dishes. After germination, seedlings were transferred to 15.5 cm square pots of Metro-Mix 220. Black willow cuttings were taken from a Carolina Bay on the Savannah River Plant in March of 1984, rooted in aerated water baths, and then transferred to pots of Metro-Mix.

For each species, 35 seedlings per treatment were placed in the pools on 16 April 1984. Temperature alterations began on 19 April. At that time, height and basal stem diameter were

measured. The FLOODED treatment did not inundate more than 50% of the stem.

Height and basal stem diameter were measured every two weeks throughout the growing season for a subset of 15 seedlings per species/treatment. The November measurements (postsenescence) were analyzed for treatment differences. Eight to ten seedlings per treatment were harvested (postsenescence harvest, 15–16 January 1985), for each species. Due to high plant mortality, all water tupelo, bald cypress, and black willow survivors in the HIGH/FLOODED treatment (4, 12, and 10 replicates, respectively) were harvested in January. Preceding harvest, seedlings were measured for height and basal stem diameter, and the presence of adventitious roots and stem lenticels was noted. Leaf, stem, adventitious root and belowground root dry weights were determined (60 C until constant weight).

A secondary soil temperature gradient was created within each pool, due to differing water level treatments. In the MID and HIGH temperature pools, soil temperature was controlled by the pool temperature, with highest temperatures in the FLOODED treatment and lowest in the DRAINED. In the AMBIENT pool, solar heating of the soil created the opposite temperature gradient among water level treatments; here FLOODED was the coolest and DRAINED was the warmest. The nine treatments were arranged in order of increasing soil temperature from left to right on the X axis of some figures. This resulted in the reversal of the ordering of water level treatments in the AMBIENT treatment.

Significant interactions between water level and water temperature in the two-way analysis of variance dictated that statistical differences be based on one-way analyses of variance. Tukey's Studentized Range was used to test for differences among individual means of treatments at $\alpha = 0.05$ (Kirk, 1968; SAS, 1982). Data cited in text are $\bar{x} \pm 1$ SE, unless otherwise noted.

Two potential problems limited the data analysis. First was the problem imposed by mortality in the HIGH/FLOODED treatment. Since zeros were not entered for dead seedlings, calculated means were biased, underestimating the stress effect. A second problem was the increased variance associated with extremely stressful treatments, also noted by Odum, Finn, and Franz (1979). Both problems decreased the power of statistical analyses and led to more conservative interpretations.

RESULTS—Growth—Among species, height increased in the order of bald cypress, water

tupelo, button bush, and black willow (tallest). The opposite order was generally seen for stem diameter, with water tupelo being largest. Bald cypress, water tupelo, and button bush in the AMBIENT and MID temperature treatments completed ~90% of their seasonal height growth by mid-July. Black willow reached 75% of maximum height by mid-July and increased in height throughout the season. Basal diameters, for all four species, were 75% of maximum by mid-July.

In the AMBIENT temperature treatments, which simulated natural swamp temperatures, water tupelo and bald cypress showed little difference in stem heights (Fig. 2A, B) due to flooding, but had significantly larger basal diameters (Fig. 3A, B) under SATURATED and FLOODED conditions. Growth in the MID temperature treatments closely resembled that in the respective AMBIENT treatments. Heights and diameters in the HIGH/DRAINED treatment were similar to those in the AMBIENT/DRAINED treatment. While water tupelo in the HIGH/SATURATED treatment had significantly smaller heights and stem diameters than at the lower temperatures, bald cypress did not show this response. The HIGH/FLOODED treatment produced seedlings with the smallest height and basal diameters for both species.

Black willow growth in the AMBIENT and MID temperature treatments was not significantly different (Fig. 2C, 3C). In the HIGH temperature treatment, however, black willow grew similarly to the other species in that it did not show the late growing season increase in height that was evident for black willow seedlings in corresponding AMBIENT and MID treatments. Heights and stem diameters in the HIGH/SATURATED treatment were significantly smaller than in the corresponding lower temperature treatments, with the HIGH/FLOODED treatment producing further significant reductions.

Button bush differed from the other species in that heights and diameters generally increased in response to the 5 C temperature elevation of the MID treatment (Fig. 2D, 3D). Within the SATURATED and FLOODED treatments, button bush growth at HIGH temperature was not different from that at AMBIENT, but both were significantly less than in the MID temperature treatment. Button bush had less reduction in stem diameter and height in the HIGH/FLOODED treatment than the other three species examined in this study.

Biomass—Root and shoot biomass of water tupelo was more constant among nonlethal

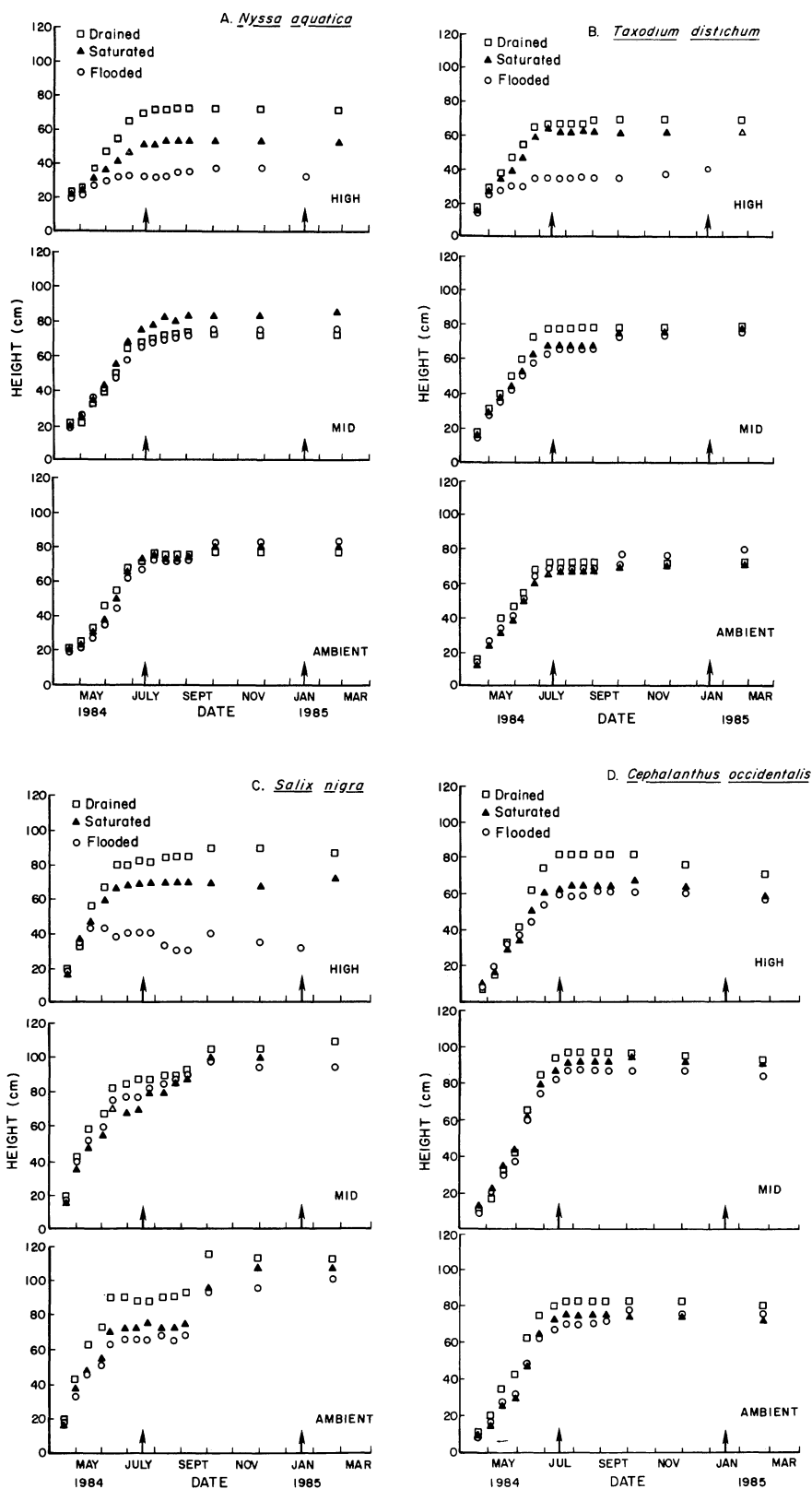


Fig. 2. Mean stem height (cm) of A) *Nyssa aquatica* (water tupelo), B) *Taxodium distichum* (bald cypress), C) *Salix nigra* (black willow), and D) *Cephalanthus occidentalis* (button bush) grown in DRAINED, SATURATED, and FLOOD-ED water level treatments at AMBIENT, MID, and HIGH temperature regimes. Arrows indicate dates of harvests.

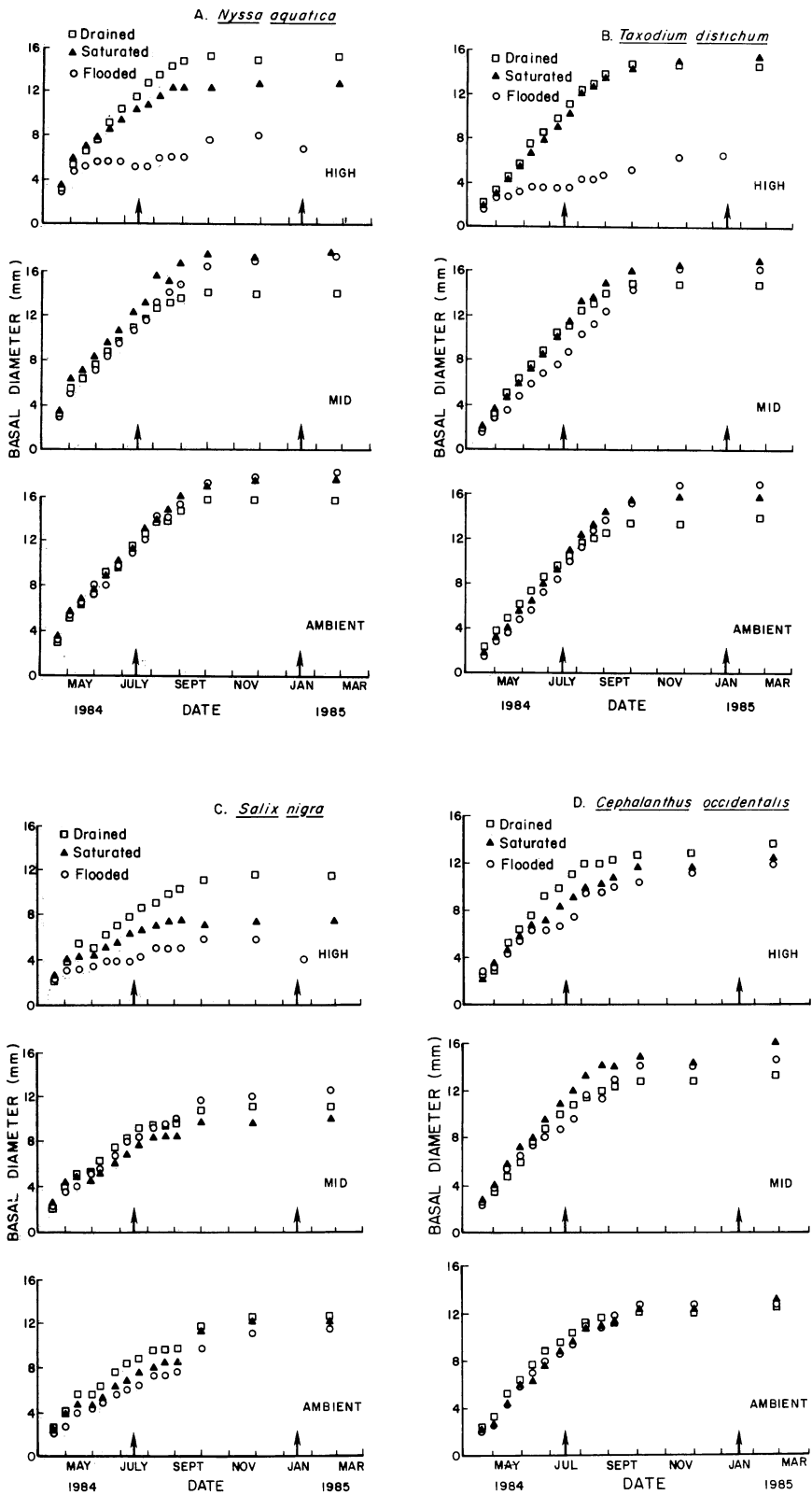


Fig. 3. Mean basal stem diameter (mm) of **A**) *Nyssa aquatica* (water tupelo), **B**) *Taxodium distichum* (bald cypress), **C**) *Salix nigra* (black willow), and **D**) *Cephalanthus occidentalis* (button bush) grown in DRAINED, SATURATED, and FLOODED water level treatments at AMBIENT, MID, and HIGH temperature regimes. Arrows indicate dates of harvests.

treatments than that of the other species (Fig. 4A). Root biomass varied more with flooding level than did shoot biomass, but neither was statistically different within the AMBIENT and MID treatments. The HIGH/SATURATED treatment reduced shoot and root biomass, which was consistent with the reduced stem height and diameter. Additional significant reductions in shoot and root biomass were caused by the HIGH/FLOODED treatment.

Biomass of bald cypress also showed little variability among the nonlethal treatments, particularly in the shoots. Root biomass was more variable in response to water level, with AMBIENT/DRAINED conditions promoting statistically greater root biomass. The HIGH/FLOODED treatment significantly reduced shoot and root biomass.

Black willow had more than twice the biomass of any other species (Fig. 4C). In addition, black willow had the greatest growth differences among water levels. The AMBIENT/DRAINED treatment produced the greatest biomass, and both increasing water level and/or increasing temperature resulted in decreased biomass. Although the HIGH/FLOODED treatment significantly reduced both shoot and root biomass, compared to AMBIENT/DRAINED, the large variability associated with the HIGH/FLOODED mean made it impossible to differentiate statistically from other less stressful treatments.

Button bush biomass in the MID temperature treatments was greater than that for the AMBIENT or HIGH temperatures. Biomass of button bush was more affected by flooding than water tupelo and bald cypress, but less than black willow. The HIGH/FLOODED treatment produced the least total biomass, with root biomass reduced and shoot biomass not differing from most of the other treatments.

Morphological characteristics—Water tupelo seedlings had hypertrophied lenticels on a single stem and no adventitious roots. Bald cypress seedlings also had only one basal stem, but did not have hypertrophied lenticels or adventitious roots in any treatment, except the HIGH/FLOODED treatment having three individuals with stem lenticels and one individual with small adventitious roots. Black willow seedlings had hypertrophied lenticels in all treatments and adventitious root production in the FLOODED treatments made up 71% (AMBIENT), 79% (MID), and 77% (HIGH) of the root biomass. In all treatments, black willow had numerous branchings high up on the stems, but never more than one basal stem. Button bush seedlings had hypertrophied len-

ticles in all FLOODED treatments and adventitious roots made up 12% (AMBIENT), 36% (MID), and 25% (HIGH) of the root biomass. All treatments had individuals with more than one basal stem, and the number of stems was greatest (3.5) in the HIGH/FLOODED treatment.

A ratio of basal stem diameter-to-height was calculated to determine stem hypertrophy. Water tupelo and bald cypress in the MID/SATURATED and MID/FLOODED treatments and bald cypress in the AMBIENT/SATURATED and AMBIENT/FLOODED treatments had significantly greater diameter-to-height ratios than in the respective DRAINED treatments. In the HIGH temperature treatment, however, FLOODED water tupelo and bald cypress seedlings had smaller diameter-to-height ratios. Diameter-to-height ratios of black willow and button bush showed no trends due to water level treatments.

Survivorship—Long-term exposure to the HIGH/FLOODED treatment resulted in some mortality in each of the species (Fig. 5). Water tupelo was least tolerant of the HIGH/FLOODED treatment, while button bush was most tolerant. Bald cypress and black willow showed intermediate responses. Timing of mortality was different for each species. Mortality in the HIGH/FLOODED treatment started early in August for water tupelo and black willow, and continued into autumn for water tupelo. Bald cypress mortality appeared to begin in late August and continued into autumn. Button bush mortality occurred late in autumn.

DISCUSSION—Flooding response—While water tupelo growth has been inconsistently affected by saturation or flooding with moving water, stagnant conditions, either saturated or flooded, have consistently reduced water tupelo and bald cypress growth, probably as a consequence of altered dissolved carbon dioxide and oxygen concentrations in the flood water (Hook et al., 1970; Kennedy, 1970; Dickson and Broyer, 1972; Dickson, Broyer, and Johnson, 1972; Harms, 1973; Shanklin and Kozlowski, 1985).

In our study, with moving water, flooding did not reduce biomass or height of water tupelo but did reduce root biomass of bald cypress seedlings in the AMBIENT treatment. In a shorter-term study, a similar ambient flooding treatment did not reduce biomass (Donovan and McLeod, 1985). Thus, our findings for water tupelo and bald cypress are consistent with previous work indicating that these species

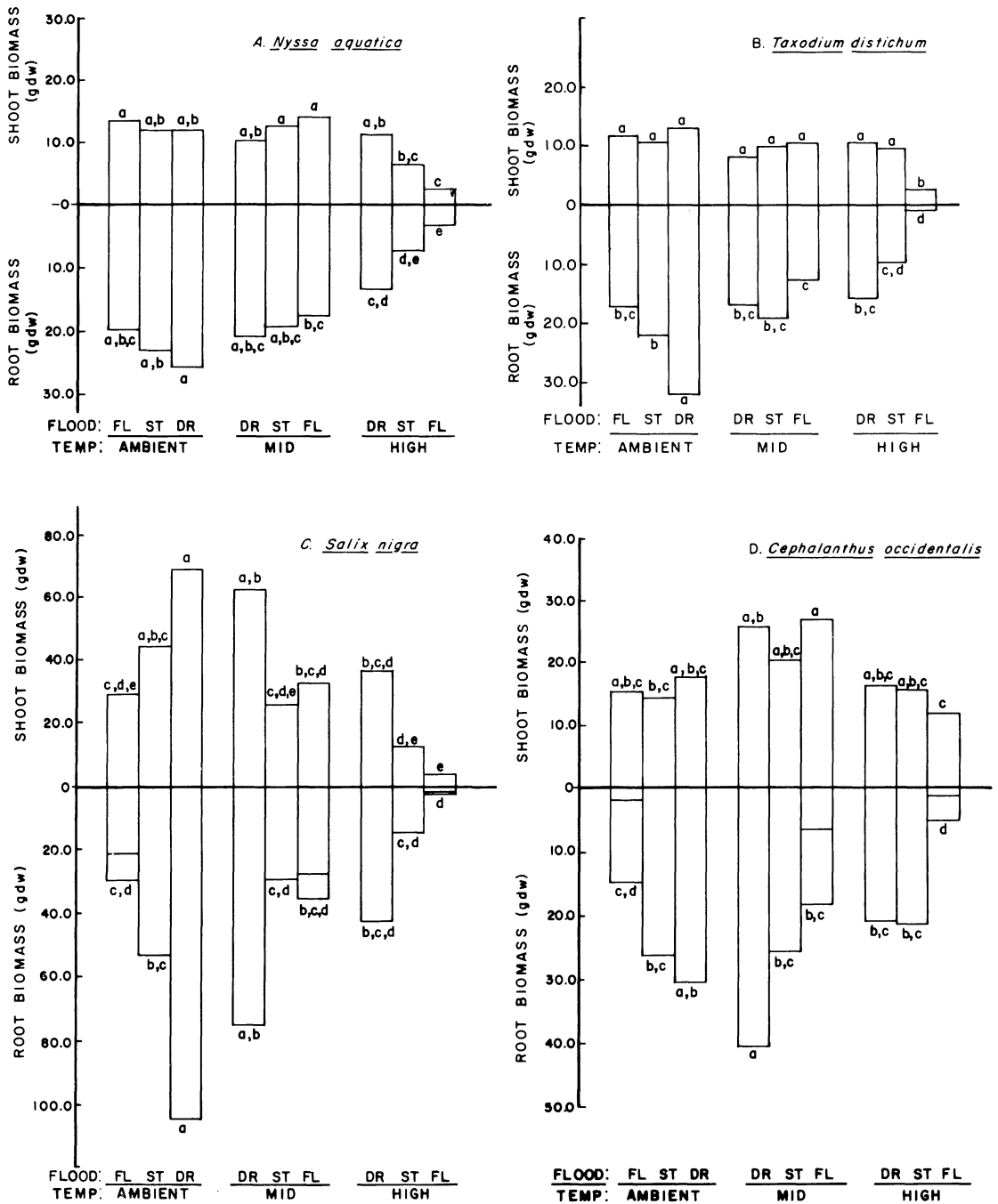


Fig. 4. Mean shoot and root biomass (gdw) of A) *Nyssa aquatica* (water tupelo), B) *Taxodium distichum* (bald cypress), C) *Salix nigra* (black willow), and D) *Cephalanthus occidentalis* (button bush) grown in DRAINED (DR), SATURATED (ST), and FLOODED (FL) water level treatments at AMBIENT, MID, and HIGH temperature regimes. When root biomass is indicated in two sections, the portion adjacent to the X axis represents adventitious roots. Different lower case letters for a parameter indicate statistical differences at alpha level = 0.05.

are the most flood-tolerant canopy components of southeastern swamp forests.

Black willow and button bush were both less flood-tolerant than water tupelo and bald cy-

press, since flooding reduced biomass at both AMBIENT and MID temperatures. There are many reports of black willow and button bush survival in hypoxic substrates (Chirkova and

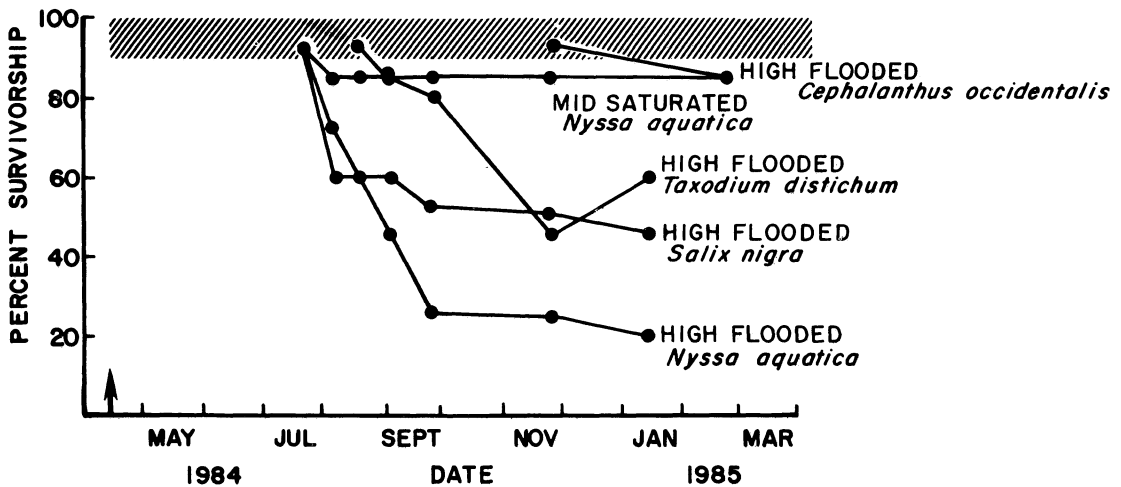


Fig. 5. Percent survivorship for *Nyssa aquatica* (water tupelo), *Taxodium distichum* (bald cypress), *Salix nigra* (black willow), and *Cephalanthus occidentalis* (button bush) grown in DRAINED, SATURATED, and FLOODED water level treatments at AMBIENT, MID, and HIGH temperature regimes. Survivorship in treatments not represented individually had greater than 90% survival (hatched bar). Increases in survivorship represent resprouting of seedlings that had previously been scored as dead.

Gutman, 1972; Pereira and Kozlowski, 1977; Martin, Christy, and McLeod, 1977; Dionigi, Mendelssohn, and Sullivan, 1985), but little information is available on the effects of water level on growth. McLeod and McPherson (1973) determined that the response of black willow to flooding was dependent on soil type and nutrient status. Growth characteristics such as plasticity of growth response, ability to accumulate a large biomass in one growing season and continuation of growth into the autumn reflect the pioneer role of these species in many communities.

Limited intraspecific variability or plasticity indicated by the more fixed growth pattern for water tupelo and bald cypress may be a disadvantage for species incapable of accelerated growth in a better environment. The plastic growth of colonizing species, such as black willow and button bush, may be potentially more strongly affected by stress, but may also impart a competitive advantage in less stressful sites.

Bald cypress and water tupelo often show stem hypertrophy as a result of flooding (Mattoon, 1915; Kurz and Demaree, 1934; Penfound, 1934; Langdon, DeBell, and Hook, 1978), as was seen for seedlings in this study in the AMBIENT and MID temperatures. Adventitious roots were not initiated by either species. Black willow and button bush, which are both well known for formation of adventitious roots (Yeager, 1949; Pereira and Kozlowski, 1977; Hook, 1984b), did so prolifically in the AMBIENT/ and MID/FLOODED treatments. Black willow adventitious roots in

the AMBIENT/and MID/FLOODED treatments created large root mats floating above the soil. Though many woody species develop adventitious roots when inundated, their adaptive significance may vary among species (Hook and Sholtens, 1978; Wample and Reid, 1979; Kozlowski, 1984). While Gill (1975) found adventitious roots to be of minor significance to flood tolerance of *Alnus glutinosa*, Tsukahara and Kozlowski (1985) recently demonstrated significantly reduced growth when adventitious roots were severed from flooded *Platanus occidentalis*. Adventitious roots do not seem to be a necessary part of the flood tolerance capacity of water tupelo and bald cypress. In addition to being associated with flooding responses of black willow and button bush, adventitious roots may allow them to persist in early successional environments characterized by fluctuating water and sediment levels.

Flood tolerant woody species lose their original root system within several weeks of soil waterlogging, and subsequently develop succulent soil water roots (Hook, 1984b). In the present study, roots were not divided into original roots and secondary soil water roots. However, in AMBIENT and MID temperature treatments, secondary roots of SATURATED and FLOODED seedlings were more succulent than those of DRAINED seedlings. These may have been soil water roots developed due to waterlogging. Also, more roots were initiated at or near the soil surface.

Hypertrophied lenticels were prolific on the

stems of water tupelo, black willow and button bush. This study did not score lenticels for the degree of hypertrophy, but their presence indicates the capacity for partial oxygen stress avoidance (Hook, Brown, and Kormanik, 1970; Chirkova and Gutman, 1972; Pereira and Kozlowski, 1977; Kozlowski, 1984).

These morphological and biomass responses are all indicative of the very flood tolerant nature of water tupelo, bald cypress, button bush, and black willow.

High temperature interaction—The HIGH treatments in this study, simulating reactor coolant effluent temperatures, introduced a thermal stress to which swamp species are not usually exposed. Bald cypress, water tupelo and black willow seedlings were less able than button bush to tolerate the HIGH/FLOODED conditions as indicated by low seedling survival and reduced biomass, height and basal stem diameter of survivors. Reduction of biomass in response to similar conditions has previously been observed for field introductions of bald cypress (Sherrod, Somers, and McLeod, 1980) and water tupelo (Martin and McLeod, unpublished data).

HIGH temperature treatment also altered morphological responses to flooding. The HIGH/FLOODED treatment did not induce stem hypertrophy in seedlings of water tupelo and bald cypress, but a few adventitious roots and stem lenticels were produced. Water tupelo and bald cypress had severely reduced root biomass in the HIGH/FLOODED treatment. Black willow also had reduced root biomass, 77% of which was adventitious. Succulent soil roots initiated near the soil surface, which were produced by all species in the flooded treatments at AMBIENT temperature, did not develop in the HIGH/FLOODED treatment. Button bush produced the largest number of basal stems in the HIGH/FLOODED treatment. Since these morphological characteristics have been correlated with increased ethylene production, it suggests that the increased temperature may have altered the hormonal response normally associated with flooding in these species. Conversion of ACC (1-aminocyclopropane-1-carboxylic acid) to ethylene is temperature sensitive; none occurs above 35–40 C (Abeles, 1973; Yu, Adams, and Yang, 1980). Root temperatures of 40 C have also been reported to affect cytokinin concentrations in roots and leaves of apple trees (Gur, Bravdo, and Mizrahi, 1972). Therefore, altered hormonal response may be responsible for the lack of lenticel and stem hypertrophy and adventitious root development, which could af-

fect oxygen availability and compound the effects of temperature-induced increases in metabolic rate.

The differential responses of the four species may partially account for their success or failure in thermally impacted areas of the SRP swamp. High temperatures interacted with flooding to greatly reduce biomass, survival, and morphological acclimation of water tupelo, bald cypress and black willow. Thus, the success of water tupelo and bald cypress seedlings in thermally impacted areas may be reduced by their lower thermal tolerance. Button bush was most tolerant of the thermal flooded conditions accounting for its abundance in the thermally impacted SRP swamp. While black willow was not thermally tolerant, it demonstrated growth plasticity which may allow it to take advantage of appropriate microsites and thereby avoid thermal stress.

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