Tree Physiology 15, 753–758

Growth and nutrient use efficiency of water tupelo seedlings in flooded and well-drained soil

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Received April 11, 1994

Summary Growth characteristics and nutrient utilization rate of *Nyssa aquatica* L. seedlings grown in pots containing flooded or well-drained soil were compared in a greenhouse study. For most of the growing season, relative height and diameter growth rates, and biomass accumulation rates were greater for seedlings in flooded soil than for seedlings in well-drained soil. The concentration of Fe in the roots of seedlings in flooded soil was almost tenfold greater than that of seedlings in well-drained soil. However, flooding had no effect on foliar Fe concentrations. The flooding treatment resulted in decreased concentrations of N in all component parts and increased concentrations of P in the roots and stem, but it had no effect on foliar P concentrations. In response to flooding, foliar K concentrations decreased, whereas the concentration of K in the roots increased. Flooding had no effect on the K concentration of the stem. Seedlings in flooded soil produced more total biomass per milligram of nutrient absorbed than seedlings in well-drained soil, suggesting that *N. aquatica* seedlings are more efficient at producing biomass and height growth under hydric conditions than under mesic conditions.

Keywords: hydric, mesic, nutrient uptake, Nyssa aquatica, rhizosphere oxidation, stem hypertrophy.

Introduction

Water tupelo (*Nyssa aquatica* L.) is an important tree species for wildlife habitat enhancement and forested wetland restoration projects because of its soft mast production and ability to grow well in wet conditions. Unlike most other bottomland species, growth of water tupelo can be better under shallow flooding or saturated soil conditions than under well-drained conditions (Hosner and Boyce 1962, Hosner and Leaf 1962). The best water tupelo sites are those that maintain a water table at or near the surface throughout most of the growing season (Johnson 1990); however, fertility of the soil and degree of aeration of the flood water are also important factors (Harms 1973).

Dicke and Toliver (1990) observed that water tupelo was less competitive than bald cypress (*Taxodium distichum* L. Rich.) in seasonally flooded stands but more competitive than bald cypress in continuously flooded stands and concluded that water tupelo is a poor competitor under mesic conditions. To obtain more detailed information on the seedling physiology of this wetland species, we compared growth, nutrient concentrations, nutrient utilization rate, and biomass allocation of water tupelo seedlings grown in flooded and well-drained soil under greenhouse conditions.

Materials and methods

Treatment conditions

Four-liter plastic pots (25-cm diameter) were lined with plastic bags to prevent loss of soil, water and nutrients. Each pot contained 4.1 kg (dry weight basis) of potting medium (1/2 mix of builder's sand and soil from the A1 horizon of a Bethera soil (clayey mixed thermic Typic Paleauults; Soil Survey Staff 1975)) plus 60 μg P g^{-1} soil (as CaH_2PO_4). Phosphorus was added because of the low concentration of available phosphorus in the potting medium.

In mid-March, water tupelo seeds obtained from a local seed source were germinated in the pots and thinned to three seedlings per pot. Pots were randomized on benches in a greenhouse as a factorial experiment with four replications. Each bench of 10 pots represented a replication.

An establishment period of 4 weeks was allowed before the treatments were imposed. During this time, water was applied daily to maintain 25% soil water by weight, and 35 ml of 0.1 strength Hoagland's solution was added once to each pot (Hoagland and Arnon 1950). In mid-April after the 4-week establishment period, treatments consisting of well-drained soil (25% water by weight, checked daily) and flooded soil (2 cm standing water above soil surface) were imposed on the pots with distilled water. The target weight for the pots in the well-drained treatment was increased during the course of the experiment to account for increases in seedling biomass. Benches were repositioned in the greenhouse and pots were relocated on each bench weekly to avoid positioning effects. No supplemental light was provided. A 50% neutral density shade cloth was placed over the greenhouse in midsummer to moderate high temperatures and was removed in early fall.

Harvests

During the first 12 weeks of treatment, one pot from each treatment and replication was harvested every 4 weeks starting in mid-May. Thereafter, four pots per treatment were harvested every 8 weeks for a total of five harvests during 28 weeks of treatment.

Measurements

Before harvest, seedling heights and ground line diameters were measured. Soil redox potential (15 cm below soil surface) and pH (5 cm below soil surface) were measured for each pot. Redox potential measurements were adjusted to pH 7. At harvest, the soil was gently washed from the root systems, and the three seedlings from each pot were placed in plastic bags on ice until completion of the harvest later the same day. Seedlings were then separated into roots, stems and foliage, and dried in a forced air oven at 70 °C to obtain component dry weights. Leaf weight ratio (foliage wt/total wt), shoot/root weight ratio, (shoot wt/root wt), and root weight ratio (root wt/total wt) were computed from the dry weights. Relative height and diameter growth rates, and biomass accumulation rates for each component were computed for each interharvest period using the formula:

$$\text{Relative growth rate} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1} \qquad (1)$$

where W_2 and W_1 are the growth variables (height, diameter or dry weight) at the beginning and end of the time interval, and $t_2 - t_1$ is the time interval of interest (Beadle 1985).

Chlorophyll analysis

Fresh foliage samples were stored in plastic bags, in darkness, below 4 °C until analyzed. Chlorophyll content was determined by the method of Arnon (1949). The analysis was completed within 30 h of seedling harvest.

Nutrient analysis

Concentrations of N, P, K, Ca, Mg, Na, Mn, Zn and Fe per gram dry weight were determined for roots, stems and foliage after the tissues were ground to pass a 40-mesh screen. Nitrogen was determined by the salicylate-cyanurate method (Nelson and Sommers 1973). A separate sample was ashed, taken up in 0.3 M HNO_3 and analyzed for P by the molybdovanadate procedure (Jackson 1958) and for metals by atomic absorption spectrometry. Total uptake of individual nutrients in mg was also determined to enable the calculation of utilization rate (U) by the formula:

$$U = \frac{W_2 - W_1}{T_2 - T_1} \times \frac{\ln M_2 - \ln M_1}{M_2 - M_1}, \qquad (2)$$

where W_1 equals the first harvest total weight, W_2 equals the final harvest total weight, M_1 equals the first harvest nutrient content, M_2 equals the final harvest nutrient content, and $T_2 - T_1$ equals the time interval in weeks between the first and the final harvests (Hunt 1982).

Statistical analysis

The experiment was designed as a 2 × 5 factorial (two water regimes and five harvest dates). Seedling growth parameters and nutrient concentrations were analyzed as a two-way ANOVA using SAS statistical analysis software (SAS Institute Inc., Cary, NC; Neter et al. 1985). Nutrient utilization rate was analyzed as a 1-way ANOVA (Neter et al. 1985). Individual pots were treated as the experimental units, and dimensions of the three seedlings per pot were averaged to obtain pot means for each treatment. Statistical significance was determined at the 0.05 level. Simple correlations were used to determine relationships between growth and nutrient variables (Neter et al. 1985).

Results

Soil conditions

Flooded soil rapidly became anoxic. After 4 weeks of treatment, the redox potential of the flooded soil was 212 mV compared with 872 mV for the well-drained soil. In flooded soils, redox values were lowest (104 mV) after 12 weeks of treatment but increased to 227 and 179 mV after 20 and 28 weeks of treatment, respectively. Redox potentials of well-drained soil were lowest (417 mV) after 20 weeks of treatment. Flooding did not significantly alter soil pH which averaged 4.7 for the well-drained soil and 4.8 for the flooded soil throughout the growing season.

Growth

At Week 4, relative height growth rate of seedlings in well-drained soil was higher than that of seedlings in flooded soil (Figure 1). However, after 8 weeks of treatment, the relative height growth rate had more than doubled for seedlings in flooded soil whereas it had only increased by a factor of 1.5 for seedlings in well-drained soil. After 12 weeks of treatment,

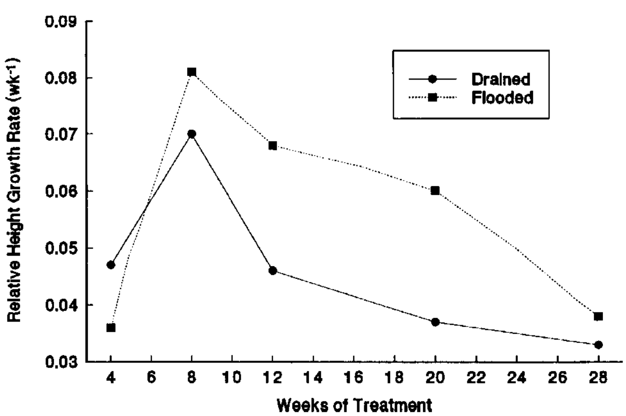

Figure 1. Relative height growth rate (week^{-1}) of water tupelo seedlings grown in flooded and well-drained soil for 4, 8, 12, 20 or 28 weeks from March 21 until October 31.

relative height growth rates of seedlings in both treatments declined, but the rates remained higher for seedlings in flooded soil. At the final harvest (Week 28), seedlings in the flooded and well-drained soil treatments were 67 and 55 cm tall, respectively.

At Weeks 12 and 20, relative diameter growth rate of seedlings in flooded soil was higher than that of seedlings in well-drained soil (0.03 and 0.04 mm mm^{-1} $week^{-1}$ versus 0.00 and 0.02 mm mm^{-1} $week^{-1}$, respectively). At Week 28, relative diameter growth rate of seedlings in flooded soil declined sharply (< 0.01 mm mm^{-1} $week^{-1}$), whereas it increased to a maximum (0.04 mm mm^{-1} $week^{-1}$) in seedlings in well-drained soil; however, at the end of the study, stem diameters of seedlings in flooded soil were still larger than those of seedlings in well-drained soil (12 versus 10 mm).

Relative biomass accumulation rate ($week^{-1}$) differed between treatments during the growing season. Between Weeks 4 and 8 (May 16–June 13), there were no differences in biomass accumulation for any seedling component (foliage, stem, roots or total) (Figure 2). Between Weeks 8 and 12 (June 13–July 11), seedlings in flooded soil produced stem, root and total biomass at a faster relative rate than seedlings in well-drained soil (Figure 2). Foliage biomass accumulation rates were higher for seedlings in flooded soil than for seedlings in well-drained soil; however, the differences were not significant. Relative foliage, stem, root and total biomass accumulation rates of seedlings in well-drained soil were near zero between Weeks 8 and 12.

From Weeks 12 to 20 (July 11–September 6), the root biomass accumulation rate was significantly higher for seedlings in flooded soil than for seedlings in well-drained soil; however, the rate for seedlings in the well-drained soil increased over the period, whereas the rate for seedlings in the flooded soil declined (Figure 2). Accumulation rates for foliage, stem and total biomass did not differ significantly between treatments (Figure 2).

From Weeks 20 to 28 (September 6–October 31), relative biomass accumulation rates of all components except foliage increased in seedlings in well-drained soil, whereas the rates declined in seedlings in flooded soil (Figure 2). All biomass accumulation rates, including foliage, were significantly higher for seedlings in well-drained soil than for seedlings in

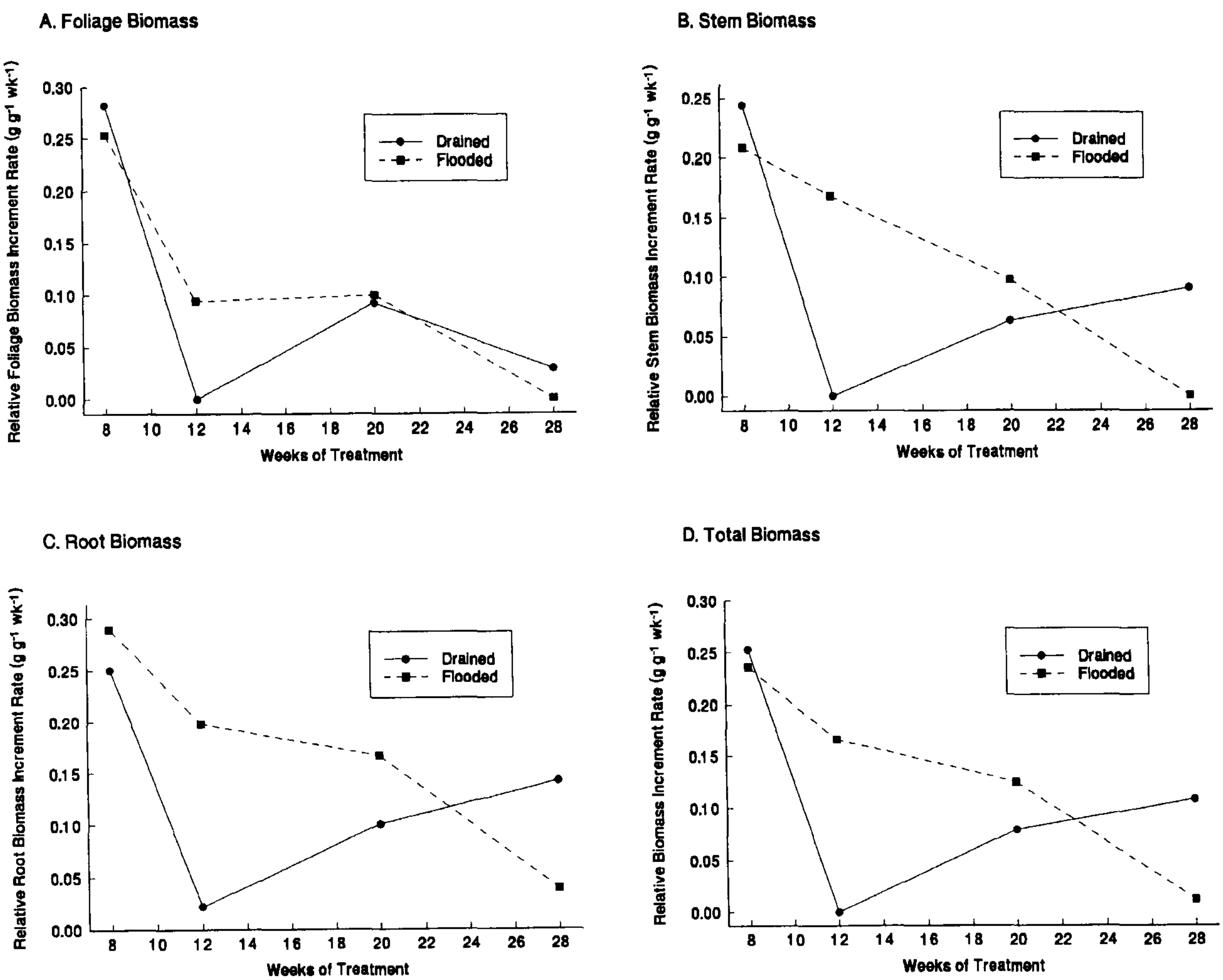

Figure 2. Relative biomass accumulation rates ($week^{-1}$) of water tupelo seedlings grown in flooded or well-drained soil for 8, 12, 20 or 28 weeks from March 21 until October 31.

flooded soil. However, at the final harvest (Week 28), total accumulated biomass was greater for seedlings in flooded soil than for seedlings in well-drained soil (Figure 3), even though foliage biomass of seedlings in flooded soil was less than that of seedlings in well-drained soil at Week 28, and was also less than that of seedlings in flooded soil at Week 20, indicating early foliage abscission in seedlings in flooded soil.

By Week 28, the flooding treatment had caused small but statistically significant changes in biomass allocation. Thus, in response to flooding, the leaf weight and shoot/root weight ratios decreased (0.05 versus 0.09 and 0.77 versus 0.84, respectively), whereas the root weight ratio increased slightly (0.57 versus 0.54).

Chlorophyll and nutrient concentrations

The flooding treatment resulted in decreased chlorophyll concentrations of foliage and N concentrations of all tissues (Table 1). Foliar P concentration was unaffected by flooding, whereas P concentrations in stem and roots were enhanced by the flooding treatment. Flooding decreased the K concentration of foliage, had no effect on the K concentration of stem tissue, and increased that of root tissue. Flooding had no effect on foliar Mg concentrations, but it decreased the concentrations of Mg in stem and root tissues. Other nutrients were either increased (foliage and stem Ca, and stem and root Fe) or unaffected by flooding.

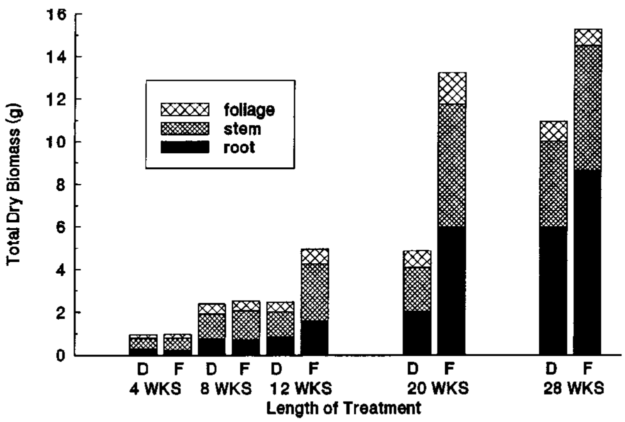

Figure 3. Total accumulations of biomass by component (foliage, stem or roots) for water tupelo seedlings grown in flooded (F) or well-drained (D) soil for 4, 8, 12, 20 or 28 weeks from March 21 until October 31.

Nutrient utilization rate

Flooding increased the amount of dry matter produced per week per mg of all nutrients absorbed except Fe (Table 2). This increase corresponded with the increase in biomass accumulation rate associated with flooding.

Discussion

The increases in height growth and biomass accumulation of water tupelo seedlings in response to flooding were similar to those previously reported (Hosner and Boyce 1962, Hosner and Leaf 1962, Hosner et al. 1965, Dickson et al. 1965, Hook et al. 1970, Kennedy 1970, Dickson and Broyer 1972, Harms 1973). The poor performance of water tupelo seedlings grown in well-drained conditions was similar to that reported by Hosner et al. (1965), Dickson et al. (1965), and Harrington (1965). The effects of flooding on tissue nutrient concentrations were similar to those reported by Hosner et al. (1965), who concluded that the flood-induced decreases in foliar N and K concentrations were due to a dilution effect as a result of the enhanced growth of the seedlings. We found that water tupelo seedlings in flooded soil grew more rapidly and utilized nutrients more efficiently by producing more biomass per week per milligram of every nutrient absorbed (except Fe) than seedlings in well-drained soil. Although flooding caused a decrease in the chlorophyll concentration of the foliage, the decrease was not correlated with Mg concentration suggesting that the decline in chlorophyll concentration was not the result of Mg deficiency. Low chlorophyll concentrations were, however, correlated with decreases in N concentration in foliage and stems.

The sharper decline in biomass accumulation rates of seedlings in well-drained soil compared with seedlings in flooded soil between June 13 and July 11 was attributed to their greater sensitivity to drought stress associated with the high air temperatures (mean maximum of 38 °C) and low relative humidities (mean maximum of 34% RH) recorded in the greenhouse during the period. Between July 18 and September 20, a shade

Table 1. Effects of flooding on chlorophyll and nutrient concentrations[1] of the foliage, stem and roots of water tupelo seedlings.

Concentration	Foliage		Stem		Roots	
	Well-drained	Flooded	Well-drained	Flooded	Well-drained	Flooded
Chlorophyll (mg g^{-1})	0.76 a[2]	0.61 b	–	–	–	–
N (mg g^{-1})	2.53 a	1.87 b	0.56 a	0.37 b	1.08 a	0.73 b
P (mg g^{-1})	0.135 a	0.125 a	0.064 b	0.073 a	0.118 b	0.239 a
K (mg g^{-1})	0.71 a	0.60 b	0.21 a	0.20 a	0.26 b	0.32 a
Mg (mg g^{-1})	0.35 a	0.31 a	0.14 a	0.11 b	0.16 a	0.11 b
Ca (mg g^{-1})	0.55 b	0.68 a	0.25 b	0.30 a	0.13 a	0.13 a
Fe (µg g^{-1})	88 a	110 a	28 b	45 a	379 b	2295 a

[1] Values are the means of five harvests.
[2] Values for each component followed by the same letter do not differ significantly at $P = 0.05$.

Table 2. Nutrient utilization rate[1] of selected nutrients for water tupelo seedlings grown in flooded and well-drained soil.

Nutrient	Nutrient utilization rate (g mg^{-1} $week^{-1}$)	
	Well-drained soil	Flooded soil
N	0.120 a[2]	0.479 a
P	1.067 b	2.191 a
K	0.362 b	1.205 a
Mg	0.634 b	3.045 a
Ca	0.531 b	1.602 a
Na	1.06×10^{-4} b	4.32×10^{-4} a
Mn	1.71×10^{-3} b	8.38×10^{-3} a
Zn	3.95×10^{-3} b	2.05×10^{-2} a
Fe	4.85×10^{-4} a	3.60×10^{-4} a

[1] Nutrient utilization rate is defined as the grams of total biomass produced by the seedling per milligram of nutrient taken up per week.

[2] Values for each nutrient followed by the same letter do not differ significantly at $P = 0.05$.

cloth (50% shade neutral density) was in place over the roof of the greenhouse to moderate temperatures to a mean daily maximum of 35 °C. The finding that biomass accumulation rates for seedlings in well-drained soil increased after the placement of the shade cloth and continued to increase after its removal supports the suggestion that temperature and humidity extremes contributed to the early decline in height growth and biomass accumulation rates of seedlings in well-drained soil. Growth and nutrient accumulation in water tupelo seedlings are more sensitive to water stress than in other flood-tolerant species (Hosner et al. 1965, Dickson et al. 1965). Dickson et al. (1965) reported that the upper leaves of water tupelo seedlings grown in soil watered to field capacity wilted on hot afternoons.

Water tupelo is well adapted to flooded soil conditions and maintains root growth and function, processes that require oxygen transport from the shoot to the root. Fisher and Stone (1990) showed that K uptake in slash pine (*Pinus elliottii* Engelm.) roots was dependent on the atmosphere surrounding the shoot. Stems exposed to ambient air exhibited a net influx of K, whereas stems exposed to nitrogen gas exhibited a net efflux of K. We found that the flooding treatment caused an increase in K concentrations of root tissues, suggesting that seedlings in flooded soil maintained a level of aerobic respiration that was sufficient to provide energy for K uptake. Stem hypertrophy, exhibited by the seedlings in flooded soil, increases shoot surface area and in conjunction with lenticel hypertrophy improves gas exchange within the shoot (Hook et al. 1970). Roots of water tupelo develop extensive zones of aerenchyma within the root cortex (McKevlin, unpublished observations), and water tupelo is able to oxidize its rhizosphere (Hook et al. 1970).

Of particular interest in terms of waterlogging tolerance is the ability of water tupelo to regulate Fe accumulation in the shoot. Excess Fe in foliage tissue is toxic to some species (Jones 1971*a*, 1971*b*, Sanderson and Armstrong 1978, Hendry and Brocklebank 1985, Wheeler et al. 1985). Foliage and stem Fe concentrations in water tupelo did not increase with flooding. Root Fe concentrations increased markedly, but the Fe in the root appeared to be in the free space (McKevlin, unpublished observations).

Rapid height growth of water tupelo seedlings is probably an adaptation allowing seedlings to become established during occasional dry spells on sites that are normally completely inundated. Because water tupelo seeds do not germinate under water, germination in nature tends to occur in mid to late growing season (Shunk 1939) or only in years of low water. The late timing of germination in water tupelo necessitates that initial height growth be rapid because there is little time for sufficient height growth to insure that the terminal shoot is above the winter flood waters. We found that seedlings in flooded soil increased in height, diameter and biomass at a faster rate than seedlings in well-drained soil early in the growing season. By September, seedlings in flooded soil exhibited little growth, whereas seedlings in well-drained soil continued to increase in diameter and biomass at a moderate rate. The reason for the early cessation of shoot growth under flooded conditions is not known but may be indicative of changes in photosynthate sink strength and carbon allocation brought about by flooding in preparation for winter dormancy (cf. Hook et al. 1970). Carbon allocation shifts from height growth to diameter growth and root production late in the growing season (Scarascia-Mugnozza 1991, Friend et al. 1991).

In summary, water tupelo seedlings exhibited higher relative growth rates and nutrient utilization rates in flooded soil than in well-drained soil in this greenhouse pot study. The flooded seedlings also exhibited rapid early shoot growth and appeared to shift carbon allocation to root growth earlier in the fall than seedlings in well-drained soil. This phenological pattern may be an adaptation to the late timing of germination under natural conditions. The relatively low shoot/root biomass ratio of seedlings growing in well-drained soil and their apparent sensitivity to temperature and humidity extremes suggest that water tupelo has a high requirement for water and requires a large root system to support its aboveground biomass under mesic conditions. We conclude that successful establishment of water tupelo on wetland restoration sites will depend on the presence of adequate soil water during the planting phase, the time when water levels are often lowered to facilitate planting.

Acknowledgments

We thank R.E. Dickson, K.W. McLeod, R.H. Jones and W.H. Conner for helpful comments on the manuscript. Technical assistance was provided by Raymond R. McKevlin, Jr., Teresa Fox and Martha Singletary.

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