

SOME EFFECTS OF SOIL TYPE AND WATER REGIME ON GROWTH OF TUPELO SEEDLINGS¹

WILLIAM R. HARMS

*Southeastern Forest Experiment Station, Forest Service
U. S. Department of Agriculture, Charleston, South Carolina 29403*

Abstract. Two-year-old swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.) and water tupelo (*N. aquatica* L.) grown in large tanks in a silty clay loam soil from a river swamp or a sandy loam soil from a non-alluvial headwater swamp were subjected to continuous flooding at depths of 20 cm above the soil surface with moving water, 20 cm above the soil surface with stagnant water, or at the soil surface with moving water. Height growth of water tupelo averaged 1.8 times greater and dry weight 2 to 3 times greater in the more fertile soil from the river swamp than in soil from the headwater swamp. Soil type had no effect on growth of swamp tupelo. Growth and dry weight of both tupelos were poorest in the regime with stagnant water, which also had the highest CO₂ and lowest O₂ contents. Swamp tupelo grew 50 cm more in height in the surface-flooded regime with moving water than in either deep-flooded regime. Water tupelo in both regimes with moving water grew 37 cm taller than those in the stagnant regime.

INTRODUCTION

Swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.) and water tupelo (*N. aquatica* L.) are dominant tree species of the hardwood swamp forests of the Atlantic and Gulf Coastal Plains, with the range of water tupelo extending up the Mississippi valley as far as southern Illinois (Fowells 1965). The ability of these species to survive and grow under the variety of flooded conditions found in different swamps has long intrigued ecologists and physiologists, but relatively little research effort has been expended on the problems that must be solved before plant-environmental relations in these ecosystems can be accurately described.

The physiological problem that has received the most attention is that of the mechanisms that enable these species to grow in continuously saturated or flooded soils. Most upland species soon die when subjected to the same conditions. Flooding affects plant growth directly by reducing soil aeration. The lack of oxygen and the buildup of carbon dioxide in the soil lead to reduced growth by interfering with the physiological processes in the roots, such as water and mineral absorption. Indirect effects of flooding are related to the increased solubility of certain elements, notably iron and manganese, which may build up to toxic quantities under anaerobic conditions.

The physiological basis for the ability of swamp tupelo to thrive under flooded conditions has been partially explained by Hook et al. (1971). They showed that roots of swamp tupelo seedlings that developed in flooded soil were able to oxidize their rhizosphere, the oxygen diffusing down to the roots via the stem lenticels and cortex or phloem. Further, they found that these roots were also capable of ac-

celerated anaerobic respiration in the absence of external oxygen. In contrast, tupelo roots developed in well-drained soil had neither of these properties. Roots of tupelo seedlings grown hydroponically were found to tolerate concentrations of CO₂ as high as 31% for a 15-day experimental period. Seedlings of sweetgum (*Liquidambar styraciflua* L.), a non-swamp species, died after 10 days in 31% CO₂ and within 15 days in 10% CO₂. They concluded that the combination of accelerated anaerobic respiration in the absence of oxygen, oxidation of the rhizosphere, and tolerance of high concentrations of carbon dioxide is sufficient to account for the flood tolerance of swamp tupelo.

Although this work helps explain how swamp tupelo, and probably water tupelo, are able to grow in flooded soil, there remains the question of why the amount of growth often varies with type of swamp. Studies of seedling growth have shown that while these species survive and develop under a wide range of flooded conditions, the type of flooding is critical. Hook et al. (1970) found that height growth under moving water regimes was about double that under stagnant water regimes and that total dry weight growth was more than 2 times greater. Dickson (1968) reported that water tupelo seedlings in pots grew best when air was bubbled continuously through flooded soil and that growth was poorest in pots with drained soil. Kennedy (1970) studied growth of water tupelo in flooded plots on which stagnant water was maintained at depths of from 8 to 25 cm above the soil surface for various lengths of time during the growing season. He found that survival was little affected by depth of water but that height growth decreased as both depth and duration of flooding increased.

These studies suggest that seedlings of swamp and

¹ Manuscript received November 5, 1971; accepted August 7, 1972.

water tupelo will grow and develop best in soil that is flooded or saturated with water, provided that the water is not stagnant. It is not known, however, why stagnant water depresses growth. Hook et al. (1970) suggested that the concentration of dissolved O_2 and CO_2 in the soil water may be involved.

Various soils were used in the studies cited, but none were true swamp soils. Because both soil type and water regime vary with type of swamp, tree growth differences observed among swamps may be related to both of these factors. The study reported here tested the growth of 2-year-old swamp and water tupelo seedlings under three water regimes in soil from two swamps.

EXPERIMENTAL METHODS

The study was conducted in a series of six concrete soil tanks at the Santee Experimental Forest, Berkeley County, South Carolina. These tanks, described by Hook and Stubbs (1967) and Hook et al. (1970), provide large growing compartments in which water regimes comparable to those found in swamps can be imposed. Each of the tanks is a box $180 \times 180 \times 180$ cm and has its own water control system. Water used in the tanks is obtained from a well. The storage sump was filled at the start of the study, and, except for natural rainfall, no more water was added during the study.

The experimental design was a split-split plot with two replications of two species, two soils, and three water regimes. Each tank was divided into two $90 \times 180 \times 180$ cm compartments by a plywood partition. Soil from the surface 15 cm of Bluebird swamp was placed in one compartment of each tank to a depth of 152 cm, and surface soil from the Santee swamp was placed in the other to the same depth.

Bluebird is a non-alluvial headwater swamp on the Francis Marion National Forest in coastal South Carolina. The soil is a fine sandy loam of the Portsmouth series and contains about 18% organic matter. The Santee swamp is an alluvial river swamp bordering the lower Santee River in South Carolina. The soil is a silty clay loam of the Wehadkee series and contains about 22% organic matter. Priester and Harms (1971) give a more complete description of the physical and chemical properties of both soils.

Seedlings of swamp and water tupelo were grown in flats in the greenhouse for 2 months. The swamp tupelo seed were collected from Bluebird swamp and the water tupelo seed from the Santee swamp. The effect of seed source on growth was reported by Hook and Stubbs (1967) and was not considered in this study. In early March, 1968, when the seedlings were 15 to 20 cm tall, they were out-planted in the soil tanks. In one-half of each soil compartment, 16 swamp tupelo were planted 23 cm apart in four rows in a plot 90 cm square; the same number of

water tupelo were planted in the other half. The seedlings were grown in the tanks the rest of the year with the soil maintained at a moisture content between saturation and field capacity.

In February of the second growing season, three water regimes were imposed. The water level in two tanks was maintained at the soil surface, with the water moving slowly across the plots in response to an hydraulic head differential of about 20 cm. In the second pair of tanks, the water level was maintained at a depth of 20 cm above the soil surface in a stagnant condition. In the third pair of tanks, the water level was also maintained at a depth of 20 cm above the surface, but the water was kept flowing across the soil compartment at a rate of about 30 cm per second. These water regimes were maintained from February through October.

At 2- to 3-week intervals, four water samples were taken from each plot from a depth of 8 cm below the soil surface. The water was withdrawn from within open-ended screen-wire cylinders, 2 cm in diameter and 30 cm long, that had been placed in the soil. The partial pressure of dissolved O_2 and CO_2 in the samples was measured with potentiometric membrane electrodes: a Beckman No. 39066 clinical oxygen sensor and a Beckman No. 39028 clinical carbon dioxide sensor.²

The height of all trees was measured at 1- to 2-week intervals from April through mid-October. At the end of the second growing season, 11 randomly selected trees were removed from each plot. Total dry weight of each tree was determined by oven-drying at $72^\circ C$ to a constant weight.

Treatment effects were analyzed in terms of total height, height growth, total dry weight, and relative growth rate. Relative growth rate (R) is the mean rate of weekly height growth per unit of height. It was calculated from height at the beginning and end of a measurement period by the formula:

$$R(\%) = \frac{\log_e H_1 - \log_e H_0}{t_1 - t_0} \times 100$$

where H_0 is the beginning height, H_1 is the ending height, and $t_1 - t_0$ is the length of the period in weeks (Fisher 1921). Treatment differences were tested by analysis of variance and Duncan's multiple-range test.

RESULTS AND DISCUSSION

Soil

Response of swamp and water tupelo to soil type was similar, but the magnitude of the effects differed. Total height, height growth, growth rate, and dry

² Beckman Instruments Co., Fullerton, California. Mention of trade names is for identification only and does not constitute endorsement by the U. S. Department of Agriculture.

TABLE 1. The effect of soil type and water regime on total height, height growth, relative growth rate, and total dry weight of 2-year-old swamp and water tupelo seedlings^a

Treatment variable	Swamp tupelo				Water tupelo			
	Total height (cm)	Height growth (cm)	Growth rate (%)	Dry weight (g)	Total height (cm)	Height growth (cm)	Growth rate (%)	Dry weight (g)
Bluebird soil	131 ₁	75 ₁	3.04 ₁	47.4 ₁	142	67	2.34	92.5
Santee soil	144 ₁	83 ₁	3.07 ₁	46.5 ₁	214	122	3.13	176.6
Deep flooding, stagnant water	114 _a	54 _a	2.32 _a	45.7 _a	148	70	2.25 _a	100.5 _a
Deep flooding, moving water	130 _{ab}	70 _a	2.88 _a	44.7 _a	197 _a	105 _a	2.77 _{ab}	163.7 _b
Surface flooding, moving water	170 _b	112	3.98	65.7 _a	189 _a	110 _a	3.18 _b	139.4 _{ab}
Average ^b	138	79	3.06	52.0	178	95	2.73	134.5

^a Within a species, the values for soil having the same subscript number, or the values for water regime having the same subscript letter, are not significantly different at the 5% level.

^b Species averages are significantly different at the 5% level.

weight of water tupelo were significantly affected by soil type (Table 1). On the average, the water tupelo seedlings grew 55 cm more on the Santee than on the Bluebird soil, and the average relative growth rate was 0.79% greater. Dry weight differences in water tupelo were also impressive. In the stagnant water regime where the difference among soils was largest, there was almost 3 times as much dry matter on the Santee soil as on the Bluebird soil.

Swamp tupelo was little affected by soil regardless of water regime. Differences were consistently in favor of the Santee soil, but they were small and nonsignificant (Table 1).

The soil effect was probably nutritional. Santee is higher than Bluebird in all of the nutrient elements except phosphorus (Priester and Harms 1971). These data suggest that nutrient requirements may be greater for water tupelo than for swamp tupelo. Further evidence of nutrient deficiencies of water tupelo seedlings on Bluebird soil was the lighter green color of their leaves as compared with those on Santee soil. Swamp tupelo leaves, on the other hand, did not show any noticeable differences in color on the two soils.

The interaction of soil and water regime was not significant, but the data suggest that the depressing effects of stagnant water on growth were partially overcome on the Santee soil. On that soil, water tupelo seedlings in the stagnant regime exceeded the growth of those on the Bluebird soil in all three water regimes and approached the growth of those on the Santee soil in the two regimes with moving water (Fig. 1).

Water regime

Neither species did well under stagnant conditions, but swamp tupelo did not do well in deep, moving water either. Height growth and relative growth rate of swamp tupelo were significantly depressed in both

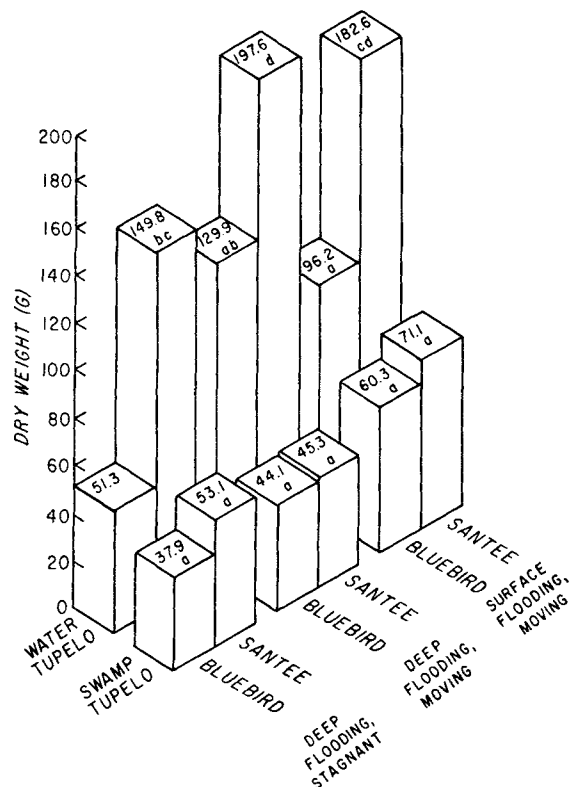


FIG. 1. The effect of water regime and soil on dry weight of 2-year-old swamp and water tupelo seedlings. Values within species followed by the same subscript are not significantly different at the 5% level.

stagnant and moving water in the deep-flooded regimes as compared with surface flooding (Table 1). Total height of this species in moving water of the deep-flooded regime did not, however, differ from that in either of the other regimes.

Water tupelo grew equally well in both regimes with moving water, but the seedlings in the stagnant regime grew significantly less by 36 cm (Table 1).

Relative growth rate also was significantly lower in the stagnant regime.

Water regime had no statistically significant effect on total dry weight of swamp tupelo. Some of the differences, especially between the stagnant and surface-flooded regimes, were quite large, however, and possibly would have been judged real had the study design been more sensitive. Dry weight of water tupelo was significantly affected by water regime, although the effect was not as great as that due to soil (Fig. 1). Weight was greatest in the deep- and surface-flooded regimes with moving water and least in the stagnant regime.

The different responses of these two species to water regime are consistent with the environmental conditions under which they grow (Klawitter 1962). Swamp tupelo is found most often in non-alluvial swamps and ponds where the free water is commonly shallow and slow moving. Rainfall is the only

source of water for these swamps; consequently, water levels may drop below the soil surface during the growing season. Water tupelo is rarely found in great numbers on such sites. It is largely confined to the river swamps, which are subject to frequent and deep inundation by flood water. Swamp tupelo does not normally occur in the deeper parts of river swamps but rather along the margins where the water is shallow.

The periodic height measurements taken during the growing season are plotted in Fig. 2 as weekly relative growth rate. These curves show that growth rate was little influenced by water regime until after the first growth peak. In the moving water regimes, growth of both species recovered somewhat following the decline after the first peak and reached a second, lower peak in early June. A second period of declining growth was followed by a third and lowest peak in late July, after which growth fell steadily to the end of the season.

In the stagnant regime, neither species recovered after the first peak but rather showed a more or less continuous decline through the rest of the season. Swamp tupelo seedlings in the deep-flooded regime with moving water did not grow much faster than those in the stagnant regime, but there were periods of increased activity in the deep-flooded regime corresponding to the peaks observed in the surface-flooded regime.

The curves in Fig. 2 are similar to those shown in Hook et al. (1970). There are two important differences, however. First, in Fig. 2 growth is shown to have continued to the end of the season in all regimes, while Hook et al. (1970) showed that, after the first rapid flush, height growth under stagnant conditions fell to a very low level in water tupelo and ceased by early August in swamp tupelo. Their seedlings were transplants that had grown for a year in an unflooded nursery soil. When they were placed in the tanks in flooded soil, the initial root system died and new roots, acclimated to saturated conditions, developed. Possibly the trees in the stagnant water never developed fully effective roots. In the present study, the seedlings grew in the tanks in wet soils for a year prior to treatment and had well-developed roots at the time treatment began.

The second major difference is in the response of swamp tupelo to the deep-flooded regime with moving water. Contrary to the data of the present study, Hook et al. (1970) showed that swamp tupelo grew as well in the deep-flooded as in the surface-flooded regime. The reason for the difference is not evident from the data. However, the differences in the experimental material (1-year-old transplants versus tank-grown seedlings) and soil type (pine stand versus swamp) may have influenced the response to water regime.

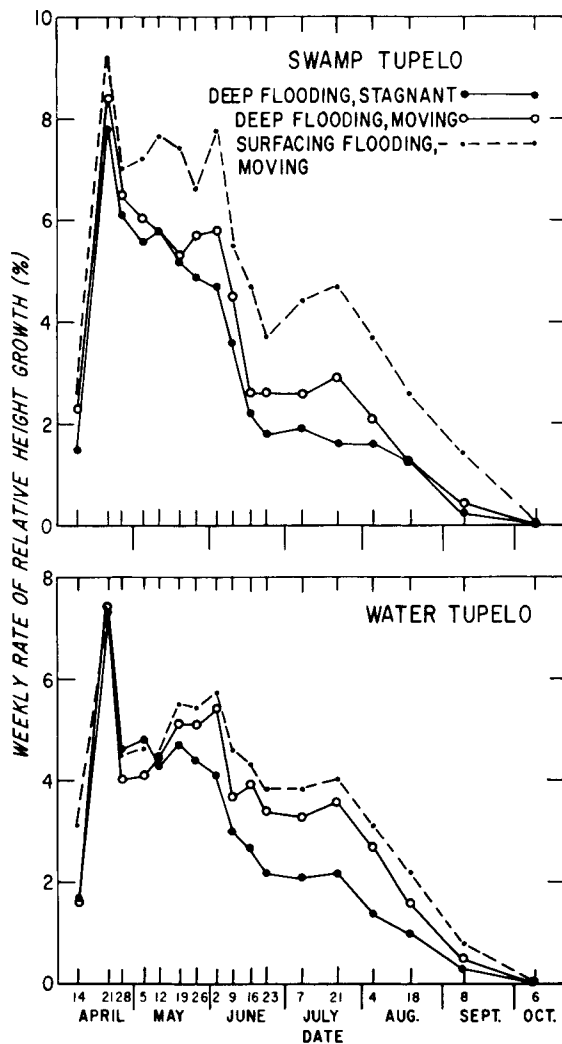


FIG. 2. Weekly mean rate of relative height growth of 2-year-old swamp and water tupelo in three water regimes.

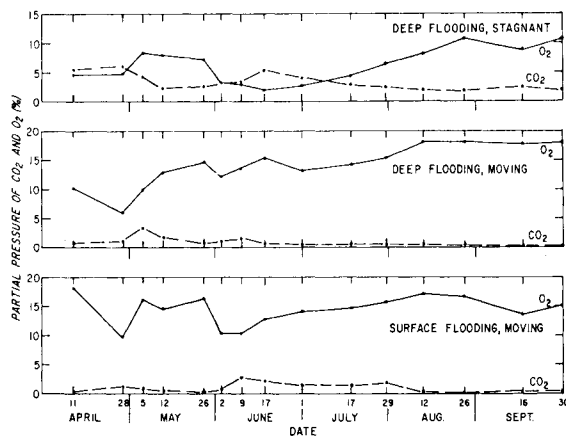


FIG. 3. Seasonal trends in CO_2 and O_2 in water 8 cm below the soil surface in three water regimes.

TABLE 2. Average partial pressure of dissolved CO_2 and O_2 in water 8 cm below the soil surface in three water regimes^a

Water regime	CO_2 (%)	O_2 (%)
Deep flooding, stagnant	3.3	6.1
Deep flooding, moving	.9 _a	13.9 _a
Surface flooding, moving	.9 _a	14.4 _a

^a Within each column, values not followed by the same subscript are significantly different at the 5% level.

Effects of carbon dioxide

The average partial pressures of CO_2 and O_2 are expressed as a percentage of the total atmospheric pressure after correction for water vapor pressure. Early in the year, there was considerable fluctuation in both CO_2 and O_2 (Fig. 3). In June, CO_2 peaked in all three water regimes and then declined over the rest of the year. An O_2 minimum was measured at about the time of the CO_2 maximum in June, after which O_2 showed a fairly steady increase to a maximum in August. Variance analysis of the seasonal averages showed that, in the stagnant regime, CO_2 was significantly higher and O_2 was significantly lower than in either regime with moving water (Table 2).

The high CO_2 and the low O_2 in the stagnant water attest to the anaerobic conditions under this regime. These conditions are also reflected in the poor seedling growth in this regime. The low CO_2 and high O_2 in the two regimes with moving water, and the lack of significant differences between the two, also correlate well with the growth of water tupelo in these regimes. The relatively poor growth of swamp tupelo in both deep-flooded regimes could have resulted from a lack of O_2 . Swamp tupelo may be more dependent than water tupelo on internal diffusion or transport of atmospheric O_2 to the roots. Deep flooding reduces the stem surface exposed to

the air and therefore lessens the number of lenticels through which atmospheric O_2 can diffuse.

Although it is not known which factors in the stagnant regime were responsible for the poor seedling growth, research reported by Hook et al. (1970, 1971) indicates that high concentrations of CO_2 in the water may depress growth. However, the inhibiting CO_2 concentrations cited by these authors exceeded those measured in the present study (30% vs. 6%). Differences in soil, microbial populations, and in relative vigor of the root systems may account for some of the difference. In addition to CO_2 , other gases are also produced under anaerobic conditions: namely, CH_4 , H_2 , and H_2S . Of these, H_2S is known to be toxic to plant roots (van't Woudt and Hagan 1957). That one or more of these gases could have been present can be inferred from the data on O_2 and CO_2 in Table 2. Given that N_2 in the water was in equilibrium with atmospheric N_2 at the normal concentration of 79%, then N_2 plus CO_2 and O_2 accounted for about 94% of the total pressure in the two regimes with moving water and for only 88% in the stagnant regime. If we allow for some error in measurement of CO_2 and O_2 , possibly 5% of the total pressure in the regimes with moving water and 10% in the stagnant regime were due to some other gas or gases. It is entirely possible, therefore, that growth, especially in the stagnant regime, could have been restricted by gases other than CO_2 .

In conclusion, these results show that soil properties as well as type of flooding are critical to the growth and development of swamp and water tupelo. The data provide strong evidence that a fertile soil can moderate some of the depressing effects that stagnant water has on growth of water tupelo and, to a much lesser degree, of swamp tupelo. Water tupelo apparently was much more sensitive to soil or soil-related factors than swamp tupelo, but growth of water tupelo was better than that of swamp tupelo on all tested combinations of soil and water regime.

The poorer growth of both species under the stagnant regime than under the regimes with moving water can probably be attributed, at least in part, to low O_2 and to the high concentration of CO_2 and other gases in the stagnant water. Depth of flooding above the soil surface may also be an important factor. Its effect may be related to the internal aeration of the seedlings and the diffusion of O_2 through the stem. The apparent adverse effect of deep water on swamp tupelo may help to explain why this species is seldom found in swamps subject to frequent, deep flooding.

LITERATURE CITED

- Dickson, R. E. 1968. Effects of aeration, water supply, and mineral nutrition on growth and development of tupelo gum (*Nyssa aquatica* L.) and baldcypress (*Tax-*

- odium distichum* L. Rich.). Ph.D. thesis, Univ. of Calif., Berkeley, 138 p. Univ. Microfilms 69-10,276.
- Fisher, R. A. 1921. Some remarks on methods formulated in a recent article on "The quantitative analysis of plant growth." *Ann. Appl. Biol.* **7**: 367-372.
- Fowells, H. A. 1965. Silvics of forest trees of the United States. USDA Forest Serv. Agric. Handb. 271, 762 p.
- Hook, D. D., C. L. Brown, and P. Kormanik. 1971. Inductive flood tolerance in swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.). *J. Exp. Bot.* **22**: 78-89.
- , O. G. Langdon, J. Stubbs, and C. L. Brown. 1970. Effect of water regimes on the survival, growth, and morphology of tupelo seedlings. *Forest Sci.* **16**: 304-311.
- , and J. Stubbs. 1967. Physiographic seed source variation in tupelo gums grown in various water regimes. Ninth South. Conf. Forest Tree Impr. Proc. 1967: 61-64.
- Kennedy, H. E., Jr. 1970. Growth of newly planted water tupelo seedlings after flooding and siltation. *Forest Sci.* **16**: 250-256.
- Klawitter, R. A. 1962. Sweetgum, swamp tupelo and water tupelo sites in a South Carolina bottomland forest. D. F. thesis, Duke Univ., 176 p. Univ. Microfilms 63-4547. Ann Arbor, Mich.
- Priester, D. S., and W. R. Harms. 1971. Microbial populations in two swamp soils of South Carolina. Southeast. Forest Exp. Sta., USDA Forest Serv. Res. Note SE-150, 6 p.
- van't Woudt, B. D., and R. M. Hagan. 1957. Crop responses at excessively high soil moisture levels, p. 514-578. In J. N. Luthin, ed., *Drainage of agricultural lands*. Agronomy VII.