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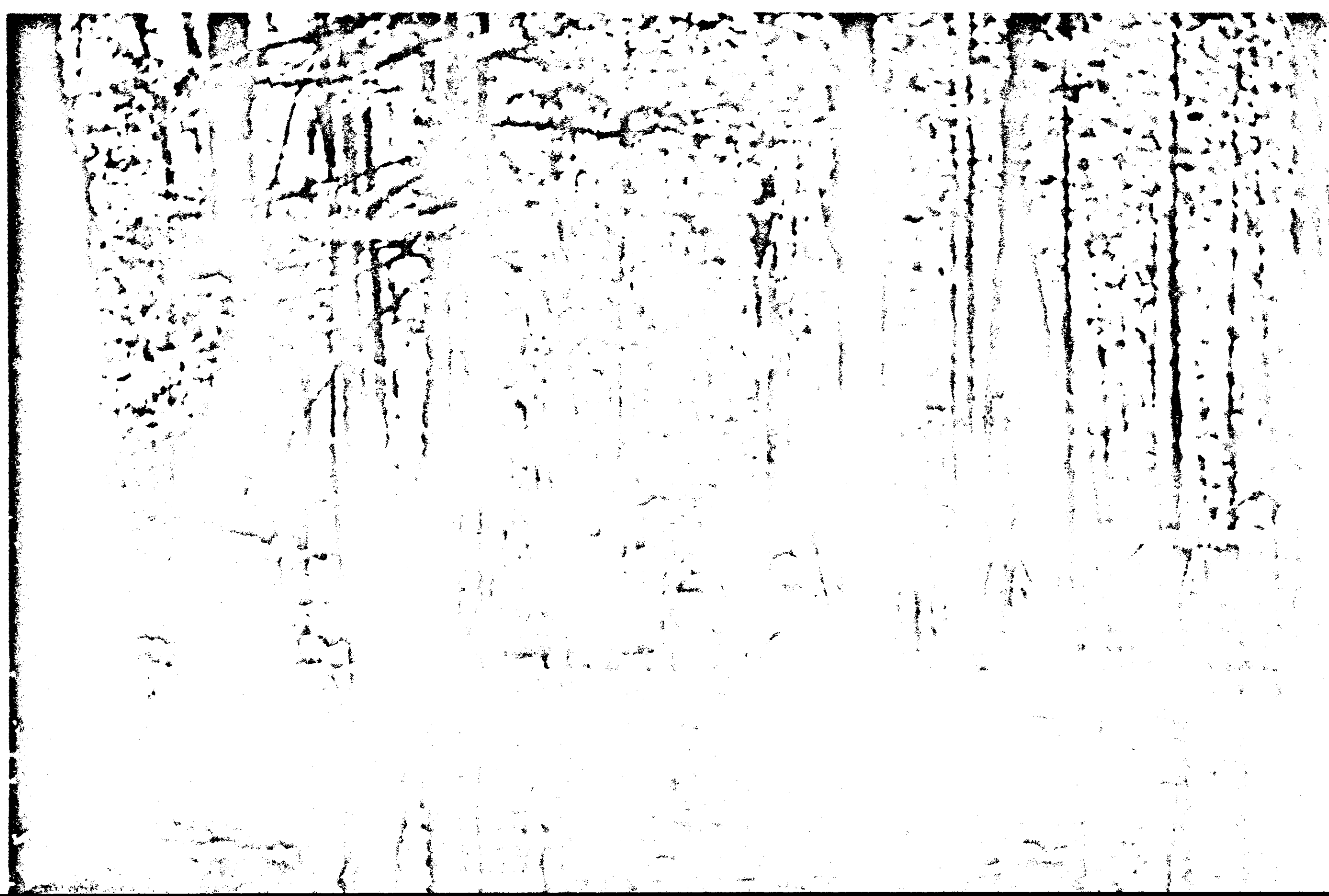
THE SWAMP and its Water Nymph

by Donal D. Hook, O. Gordon Langdon, and W. A. Hamilton*

Above: Wateree River Swamp, South Carolina

This gadget, devised to research growth of trees in water, is called "hydroedaphytron"

A 30-year-old stand of water tupelos that originated from stump sprouts after logging



ENVIRONMENTAL CONCERN has brought a raft of "ecologists" and "environmentalists" to our door, and they are chock full of questions about the future of our swampland ecosystem. To most of them, swamps are "water, snakes, muck, brush, alligators, and mosquitoes." But to the forester and land manager, the swamp is a beautiful habitat for wildlife and an important source of veneer logs for the "fruitwood" furniture industry.

About ten years ago we began research efforts in swamps of the South Carolina Coastal Plain. We wanted to know how trees were able to live and thrive in water and why their growth was so much better in some swamps than in others. We were primarily interested in two species: swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.) and water tupelo (*Nyssa aquatica* L.). Because the swamp habitat is unique, we knew far less about the site requirements and consequently the management of tupelos than we knew about most other commercial forest species. For instance, no one has been able to reliably determine the age of tupelos. Because of the "false ring" phenomenon, efforts to count annual rings have yielded confused and confounded results. Even so, these trees live so well in water they commonly reach heights of 80 to 100 feet and diameters of 3 to 4 feet.

Before we begin our story, let us tell you something about the nature of swamps. They are either nonalluvial (occurring in uplands) or alluvial (in river bottoms). Their waters vary in depth from 7 feet or more during flooding to below the surface during droughts, and they flow among the trees up to three miles an hour or they become stagnant. The moving waters have a very important job in the regeneration of water tupelos—they carry the floating seed through the swamp to places where they can germinate.

Harmless little green snakes as well as copperheads and cottonmouth water moccasins share this habitat with deer, squirrels, turkeys, buzzards, bluebirds, robins, darts, and lizards. In upland swamps robins do the same job that water does in river swamps—they transport seed of swamp tupelo away from trees and deposit them in places where they will germinate.

The "brush" found in the swamp is composed of many individual species: buttonbush, swamp-privet, planertree, bayberry, dahoon, swamp cyrilla, redbay, supplejack, wild rose, poison-sumac, and viburnum. Baldcypress (*Taxodium distichum* (L.) Rich.) is the only other commercially important tree species sharing the swamps with tupelos. On the swamps' edges but not in them can be found pine, black willow, swamp cottonwood, red maple, locust, overcup oak, water oak, water hickory, sweetgum, elm, ash, sweetbay, and dogwood growing in various mixtures.

Soil in upland swamps is coarser, drier, and less fertile than the saturated silts and clays in the more productive river swamps. Annual rainfall averages 53 inches, temperature averages 65 degrees, and the growing season is about 240 days in this area of the Southeast. In such climate, fire is not a problem, nor is plant disease a serious problem in tupelo swamps. The incidence of "damping off" of water tupelo seedlings—an occasional disease problem—would be reduced if more sunlight could reach and warm the water early in the cool, damp growing season.

With this background of the drowned home of the tupelos, let us try to answer the question: How are these trees able to grow where others cannot?

For a plant to survive and grow in a flooded soil, it must be capable of offsetting the lack of oxygen around its roots by some special adaption it has retained or acquired in the process of natural selection. Some plants circumvent this problem by developing an abnormal root system near the water surface, others transport oxygen from the atmosphere to the roots through the stem, and others may be capable of carrying on anaerobic respiration (conversion of carbohydrates to energy in the total absence of oxygen). Furthermore, roots must develop tolerance to poisonous compounds which may occur in flooded soils.

Our answers to these anomalies about the tupelos are our research story, written in a series of experiments. First, observations were made in field studies of growth and survival under different swamp conditions. From this we progressed to controlled studies where we measured growth and survival in relation to levels of oxygen and carbon dioxide in soil flooded in different ways. Finally, we verified the minute anatomical and physiological adaptations of tupelos by laboratory tests.

In a field study over a four-year period, both water tupelo and swamp tupelo survived better and grew more as the water table got higher and fluctuated. On some of the drier sites, survival was near zero—only one of 50 planted sites was acceptable for tupelo growth. In another five-year study, diameter growth of mature swamp tupelo increased as the water table became higher and fluctuated.

In a study along the Santee River, we found that past diameter growth was greatest when the river was above flood stage, when spring temperatures were warm, and when spring precipitation was normal or above.

These results indicated that growth of tupelos is poor in drier-than-flooded conditions and that in flooded conditions best growth is achieved under a fluctuating water table.

To clarify the results of our field studies we constructed the hydroedaphytron. This gadget with a fancy name is a complex, outdoor research instrument used to simulate various swamp conditions. In experiments with the hydroedaphytron we found that tupelos grew just half

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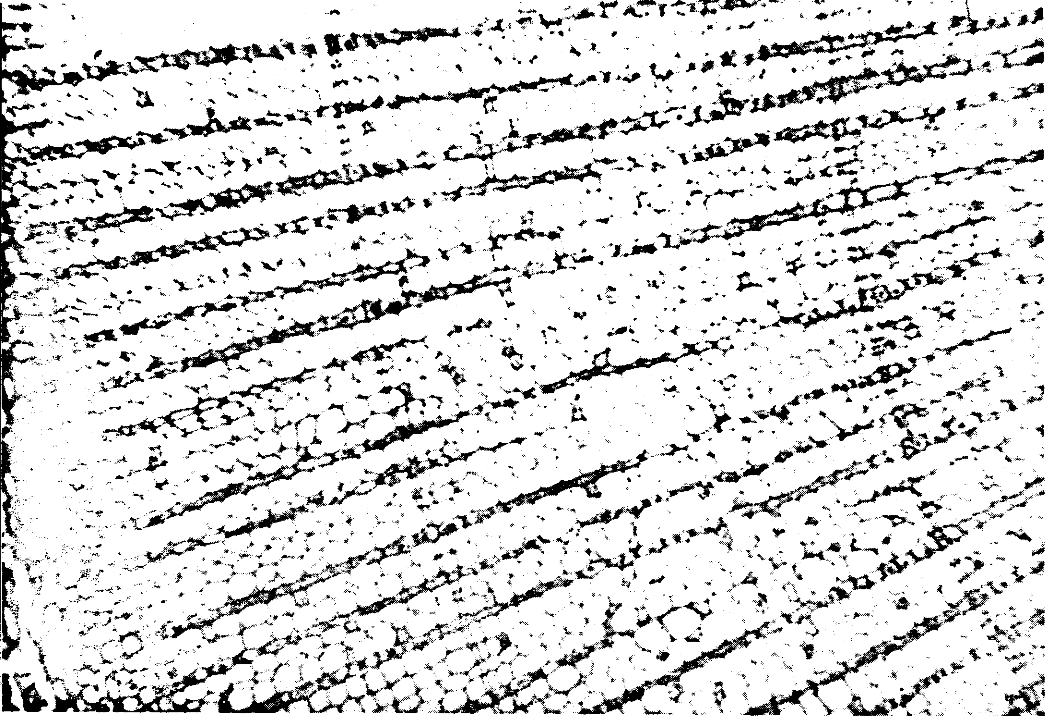
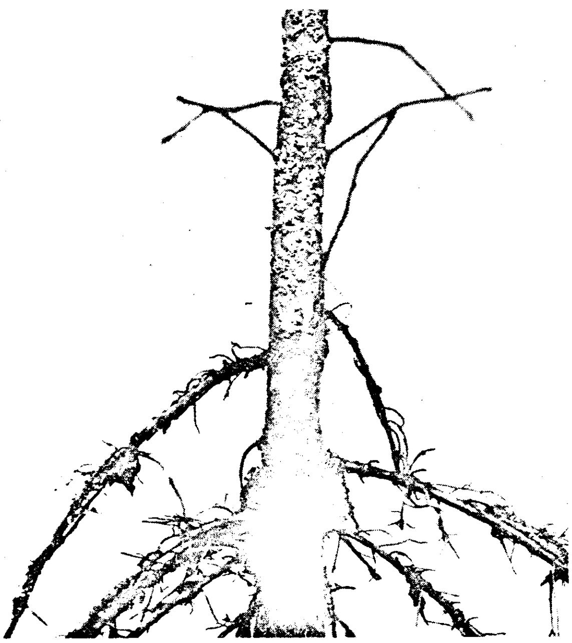
**Hook is Associate Professor, Department of Forestry, University of Kentucky; Langdon is Principal Silviculturist, Southeastern Forest Experiment Station, Charleston, S.C.; Hamilton is Station Technical Publications Editor. Hook was on the Station staff at Charleston when this paper was written.*



Cross-section of the stem of a two-year-old swamp tupelo shows false ring (center left)

Water roots and lenticels help this swamp tupelo to live in continuous flooding



as well under stagnant flooding as they did in flooding with moving water. And, continuous surface saturation with moving water gave better growth than flooding continuously 8 inches deep. The best growth of both tupelos was achieved under a flooding treatment where the water table was held either 9 or 18 inches below the surface for two weeks between week-long flooding 8 inches deep.

Both fertility and physical qualities of swamp soil appear to have a highly significant effect on growth of the trees. Regardless of how we adjusted the water levels, both tupelos grew better in a fertile river swamp soil than in a headwater swamp or pine upland soil.

Measurements in stagnant water showed that oxygen content was low and carbon dioxide content was high. But when we flooded with moving water, oxygen content of water in the soil increased and carbon dioxide decreased. These results suggested that carbon dioxide concentrations in stagnant water were probably high enough to be poisonous in the soil and that oxygen content was low enough to limit growth of most tree species; growth conditions were improved in moving water.

In our controlled flooding studies, tupelos developed numerous water roots and lenticels, or pores, on the flooded stems, as we expected them to do. These morphological structures, especially the lenticels, play a prominent role in flood tolerance of tupelo trees.

Lack of or absence of oxygen around the roots of swamp tupelo seedlings, caused by flooding, results in the deterioration of the original root system and the development of a new one. The new roots arise from the taproot and are more succulent and less branched than the original ones. In the absence of oxygen these new roots have a higher rate of anaerobic respiration than roots grown in a well-drained soil. In addition, the new roots create an oxygen environment around themselves. Oxygen enters the stem through lenticels and is transported to the roots through intercellular spaces in the cortex, phloem, and xylem. Tupelo seedlings grow equally well with their roots in water containing oxygen (aerated) and in water containing none (nonaerated). The new roots of swamp tupelo are quite tolerant of high concentrations of carbon dioxide. Root development, height growth, and respiration rate of roots were not reduced until concentrations of carbon dioxide reached 31 percent in laboratory experiments.

Tupelos live and thrive in the swamps because they are well adapted to conditions of their habitat. Lack of oxygen in the soil caused by flooding does not hinder their growth—they transport oxygen from the atmosphere to the roots through stem lenticels. In addition, their roots respire anaerobically. Furthermore, the flooded roots of tupelos are more tolerant to carbon dioxide than are roots of trees that grow on dry sites. Deep and prolonged flooding may reduce the growth of tupelos by blocking oxygen transport between the atmosphere and roots when stem lenticels are covered with water. When this happens the energy for root growth and active uptake of nutrients would largely depend upon anaerobic respiration.

The inability of tupelos to thrive outside of swamps is probably related to their inability to withstand low levels of moisture; our planting tests showed very poor survival on all but the wettest sites. Also, our laboratory research has shown that adaptations in these trees are for abundance of moisture not for lack of it. Even the wettest sites in many bottomlands suffer drought. It is possible that tupelos won't migrate out of the swamps because these sporadic periods without moisture occur in every forest habitat but a swamp.

Our research has identified some of the conditions that exist in the swampland ecosystem and has clarified how the tupelos are able to thrive in their environment. And, we still marvel at botanist Linnaeus's insight in choosing the generic name for tupelos—*Nyssa*—which means "water nymph." ■