

are more susceptible to winter freezing (Mattoon, 1915). Water levels are not likely to be low in summer in many places. Summer is Florida's rainy season, and swamps may be dry for a long enough time to allow germination only once or twice in a decade. In the deeper swamps of North Carolina's Coastal Plain, water levels fall to the soil surface only once every 10 to 20 years (Wells, 1942). Louisiana cypress swamps, on the other hand, are usually flooded only during winter and spring (Applequist, 1959).

## Seedling Survival

Seedlings are more likely to survive brief periods of inundation under clear, cool water than under warm, turbid water (Putnam et al., 1960). However, there is disagreement about the effects of inundation during the growing season on survival of first- and second-year seedlings. Demaree (1932) and Williston et al. (1980) reported that seedlings cannot tolerate any flooding. In Louisiana, cypress seedlings were killed by more than 2 weeks of flooding in the spring and summer and by more than 3 weeks of flooding after leaf-drop in the fall (Rathborne, 1951). Putnam (1951) found that submergence during the dormant period of flood-tolerant tree species, including cypress, is not detrimental; continued submergence into the growing season simply prolongs dormancy, but the trees will resume growth after water levels subside. Once buds have opened, however, no species except willow can survive more than a few days underwater.

Others have observed that cypress seedlings can survive flooding after they have leafed out. In a study of planted 1-year-old seedlings, 67% survived 20 days of submergence at the beginning of the growing season; 55% survived 20 to 29 days; and 31% survived 30 to 45 days (Bull, 1949). Baldcypress seedlings put out new leaves in August following several months of complete submergence after they had leafed out in the spring (Krinard, 1959).

One-year-old baldcypress seedlings survived after being covered with 0.6 meter (2 feet) of oxygenated (average 7 ppm O<sub>2</sub>) water for periods up to 4 weeks, but growth rates varied during the 5 months following their release from flooding (Loucks and Keen, 1973). Best growth was measured on seedlings that had been under water for 2 weeks.

At the other extreme of water stress, cypress seedlings are apparently sensitive to drought. Although wilted cypress seedlings may recover quickly when watered (Mattoon, 1916), 4- to 6-week-old baldcypress seedlings exposed to drought were irreversibly damaged within 3 to 4 hours (Dickson and Broyer, 1972). In the Okefenokee Swamp, cypress trees are more likely to become established during droughts

(Schlesinger, 1978; Duever and Riopelle, 1984), and there is evidence of a 25- to 30-year cycle of drought and fire (Izlar, 1984a).

When drainage causes prolonged drought, cypress may be outcompeted by shrubs and hardwoods. Swamp hardwoods are replacing cypress in southwest Florida where the water table is receding (Craighead, 1971). Densities of hardwood and shrub species increased in drained pondcypress domes in north Florida (Marois and Ewel, 1983).

The optimal soil conditions for cypress seedlings appear to include adequate aeration and abundant soil moisture. In greenhouse experiments with 4- to 6-week-old baldcypress seedlings, those in flooded, aerated soil grew about twice as much in 3 months as those in unsaturated, but moist, soil (Dickson and Broyer, 1972). In experiments on nutrient uptake, 2-month-old baldcypress seedlings in saturated, aerobic soil absorbed more nutrients than did seedlings in saturated, anaerobic soil or in unsaturated soil (Dickson et al., 1972).

Seedlings grown in the wild commonly reach heights of 20 to 25 centimeters (8 to 10 inches) in the first growing season and 40 to 50 centimeters (16 to 20 inches) in the second season (Mattoon, 1916). They can reach 1.2 meters (4 feet) in 4 years (Betts, 1938). Such rapid early growth may be an evolved response to the risk of inundation by rising water levels (Mattoon, 1916). However, mortality can be high; 66% of a group of wild seedlings died after two growing seasons, probably because they were inundated (Deghi, 1984). Deghi found the survival rate of planted baldcypress and pondcypress seedlings to be much higher than that of seedlings that had germinated in situ.

Assessments of the light requirements of cypress seedlings range from very intolerant (Zon and Graves, 1911) to intolerant (Hamilton, 1984) to moderately tolerant (Mattoon, 1915; Stubbs, 1973; Williston et al., 1980) to tolerant (Putnam, 1951). In shade-house experiments, the increase in biomass of baldcypress seedlings was greatest under 80% of full sunlight, while the increase in height was greatest under 32% of full sunlight (Browder et al., 1974). Seeds often sprout under heavy shade but do not survive into the second year (Demaree, 1932). Crowding or shading may interfere with pondcypress regeneration; the density of pondcypress seedlings in north Florida domes is inversely related to the density of herbs, shrubs, and other trees (Terwilliger and Ewel, 1986).

Uprooting or clipping of seedlings by herbivores destroyed more than 90% of planted 1-year-old seedlings in a Louisiana study (Blair and Langlinais, 1960). Further studies showed that nutria (*Myocaster coypus*) and swamp rabbits (*Sylvilagus aquaticus*) were responsible.