Fire in Cypress Swamps in the Southeastern United States

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ABSTRACT

The apparent importance of fire to cypress swamps in the southeastern United States raises interesting evolutionary, ecological, and management questions. For instance, has fire frequency contributed to the divergence of the two forms of cypress, baldcypress (*Taxodium distichum* var. *distichum*) and pondcypress (*T. distichum* var. *nutans*)? The empirical evidence supporting the theory that these two forms are sibling species is that pondcypress often survives fires; it is particularly common where fire frequency is high; and its cone production may increase after a fire. However, there is conflicting evidence of the importance of fire to cypress reproduction and maintenance of dominance in a swamp, and the youth of most cypress swamps makes it difficult to interpret successional patterns. Cypress swamps are environmentally and economically valuable to society; thus, an understanding of the implications of using fire as a management tool is highly desirable. Prescribed burns in cypress swamps could remove shrubs and other understory vegetation and prevent more catastrophic fires in the future, but greater care would be necessary in swamps where regional water tables have been lowered. The increase in cone production after cutting large patches in a swamp suggests that clearcutting is a logical substitute for burning, but when logging is followed by burning, both cypress seedlings and coppice are destroyed, and species composition shifts dramatically. The suitability of planting baldcypress in pondcypress habitat, or vice-versa, for wetland creation or restoration must be resolved.

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INTRODUCTION

Swamps dominated by cypress (*Taxodium distichum*) in the southeastern United States are believed to be fire-climax ecosystems. Without fire, many of these swamps develop into mixed hardwood swamps, whereas very frequent fires lead to the formation of willow (*Salix* spp.) thickets or even marshes (e.g., Ewel and Mitsch 1978; Duever et al. 1984b; Hamilton 1984). But fire influences more than succession in cypress swamps, and understanding the full range of its effects is necessary for establishing appropriate management practices for these swamps.

Two forms of cypress are commonly found in the southeastern United States, and determining which form grows in a swamp can be an essential—but not necessarily easy—first step in evaluating the influence of fire in that swamp. Cypress is the most characteristic tree in southeastern United States wetlands, but, like many wetland species, its taxonomic status is confusing and poorly understood. The two forms are baldcypress (*Taxodium distichum* (L.) Rich. var. *distichum*) and pondcypress (*Taxodium distichum* var. *nutans* (Ait.) Sweet, or var. *imbricarium* (Nutt.) Croom, as suggested by Watson 1985); some (e.g., Wunderlin 1982; Clewell 1985; and Godfrey 1988) consider them separate species (*T. distichum* and *T. ascendens* Brongn., respectively). Sometimes they can be readily distinguished: pondcypress trees have gray, shaggy bark, often with characteristic red and white lichens; their leaves are closely appressed to the twig; and they are common in stillwater, acid, nutrient-poor ponds. Baldcypress bark, on the other hand, can be reddish-brown, and, although stringy, it is not shaggy; baldcypress leaves tend to be more splayed out from the twig; and baldcypress trees are more characteristic of nutrient-rich and species-diverse swamps such as lake margins, floodplain forests, and backwaters. Pondcypress trees at the Savannah River Plant in South Carolina are reported to have narrower crowns, to be taller at a given diameter, and to have a greater density of branchlets than baldcypress (Neufeld 1986). In many swamps, however, the transition in bark and leaf features from pondcypress to baldcypress is so gradual that many people prefer not to distinguish between the two trees, referring to both varieties simply as "cypress" (e.g., Duever et al. 1984a).

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Physiological differences between the two forms have also been described. Evapotranspiration rates per unit leaf area are lower in pondcypress than in baldcypress, perhaps as a result of their closely appressed leaves, sunken stomates, and other leaf characteristics (Brown 1981). An early observation that cypress trees produce mast seed crops every three to five years (Mattoon 1915) appears to be more appropriate for pondcypress, whereas baldcypress trees may produce seed more regularly; this difference is not yet well documented, however. Finally, baldcypress trees grow faster than pondcypress trees, presumably because of greater nutrient availability in the kinds of swamps where they are common (Brown 1981).

The physiological, morphological, and ecological similarities between pondcypress and baldcypress often overwhelm the differences in bark and leaf morphology described above and explain the reluctance of many (e.g., Duever et al. 1984a) to consider them as separate species. Both tolerate flooded conditions better than most trees, and both will develop pneumatophores (knees) that seem to grow slightly higher than ordinary high water level. Cypress seeds of neither form germinate under water, and under dry conditions the seedlings of neither form grow fast enough to withstand competition from other species.

Many other species of plants have similar pairs of varieties, with the two members found in different kinds of wetlands, or in a wetland and an upland. Evolutionary causes of the differences between the two members of such pairs are not always well understood. For many species (such as *Nyssa sylvatica* Marsh. and *N. sylvatica* var. *biflora* (Walt.) Sarg.: Keeley 1979), differences in exposure to flooding may be responsible for different tolerances to flooding in adult individuals. Greater incidence of drought and nutrient impoverishment in habitats where pondcypress grows may have favored changes in crown size, height, and number of branchlets that reduce water loss (Neufeld 1986). The presence or absence of fire may have had a more dramatic effect, however, and was suggested by Harper (1927) as a major factor separating the two kinds. Because of the apparent importance of fire to cypress trees, understanding its effects on cypress swamps is essential to determining what role it should play in swamp management.

DIFFERENCES BETWEEN PONDCYPRESS AND BALDCYPRESS SWAMPS

Pondcypress and baldcypress usually grow in very different types of swamps, suggesting that ecotypic differentiation between the two species may in fact be profound. Pondcypress is usually the dominant species in stillwater ponds that are often called "domes," because the trees are generally shorter on the edges and taller in the middle. These swamps are moderately productive and in north Florida are approximately equivalent in both net and gross primary productivity to plantations of slash pine (*Pinus elliottii*) at the same latitude (Ewel 1990a). A dwarfed form of pondcypress (also called "hatrack" cypress) is found in nutrient-poor shrub bogs such as Tate's Hell in Florida's panhandle and in shallow-soil savannas throughout the Big Cypress and Everglades in south Florida, and productivity in these swamps is very low. In baldcypress swamps on the other hand, where pH is higher and nutrient limitation is less marked, productivity may be as high as in any terrestrial ecosystem at the same latitude.

In some swamps, such as strands, where water may flow very slowly during the wet season, pondcypress is more common on the fringes, baldcypress dominates the interior, and many individuals are likely to be difficult to assign to either type. Such ambiguous individuals may also be found in large cypress domes that merge with others in wet years to form temporary strands.

FREQUENCY AND CONSEQUENCES OF BURNING IN CYPRESS SWAMPS

Cypress domes and strands, where pondcypress is most common, are often surrounded by either pine savannas (especially in north Florida and other sites to the north and west in the Atlantic and Gulf coastal plains) or marshes (especially in south Florida). Both pine savannas and many types of marshes sustain frequent wildfires and are considered fire climax ecosystems (Wade et al. 1980, Abrahamson and Hartnett, 1990). Because cypress domes, with their slowly decomposing litter, may be dry for 3–6 months each year (Marois and Ewel 1983; Duever et al. 1984b), fire may burn into them often enough to be an important ecological factor.

Deepwater swamps where baldcypress grows, on the other hand, are less likely to burn. Floodplain forests may contain baldcypress swamps in oxbows and backwaters where deep peat deposits are kept moist by long contact with the water table (Duever et al. 1984a). Other areas are periodically cleared of litter by floods. Fires started by lightning strikes in these swamps may therefore have a local effect, and fire is less likely to penetrate from the uplands except during prolonged droughts.

The ranges of pondcypress and baldcypress overlap, although the latter is more restricted, extending west along the Coastal Plain only into southeastern Louisiana and north into southeastern Virginia (Figure 1a). Pondcypress is particularly common where lightning fires are most frequent [from 15–25 fires per million hectares per

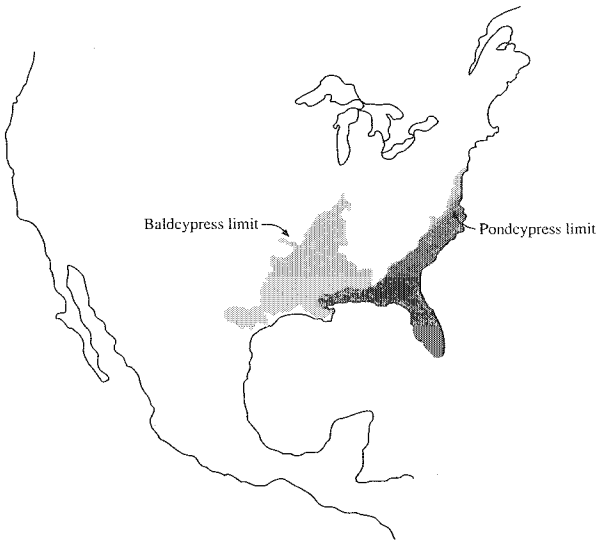

Fig. 1a. Distributions of baldcypress and pondcypress in the southeastern United States (after Little 1971)

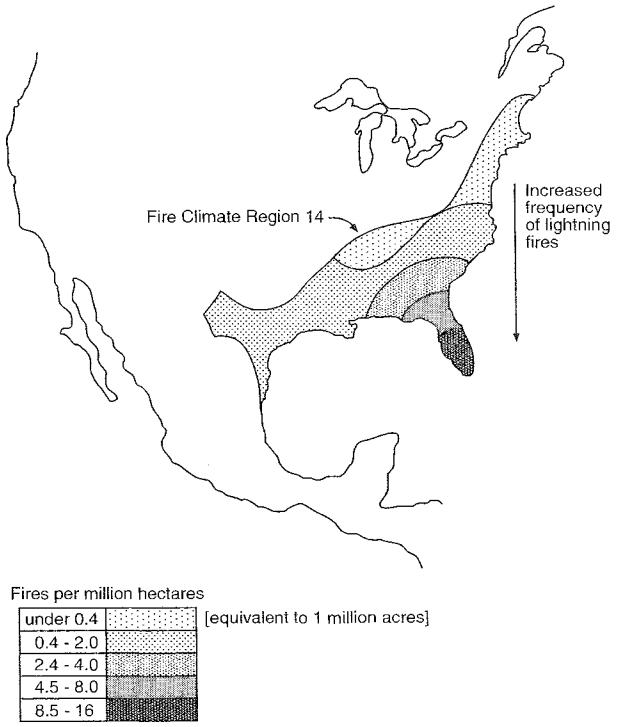

Fig. 1b. Frequency of lightning fires in Fire Climate Region 14 (after Schroeder and Buck 1970)

year through southern Alabama, central Georgia, and southern South Carolina to 50–100 fires per million hectares per year in Florida south of Orlando (Schroeder and Buck 1970) (Figure 1b)].

Fire frequency in the Okefenokee Swamp, where pondcypress is common, averaged one every 28 years between 1844 and 1955 (Hamilton 1984). Fire frequency may have been one every 20 years in north Florida before European settlement (Ewel 1990a) and was probably much higher in south Florida (Wade et al. 1980). It is possible, therefore, that pondcypress and baldcypress are sibling species, with exposure to fire as an important evolutionary force (Harper 1927).

Once fire burns into a cypress dome or strand, most trees that are killed are usually in the center, where the root system of a tree is more likely to be girdled by burning, particularly in a long-burning peat fire (Ewel and Mitsch 1978). Roots of trees around the edge of the swamp may extend beneath the relatively shallow peat layer into the mineral soil below and thus are more protected from slowly intensifying peat fires. Doughnut-shaped cypress ponds and open sloughs in the middle of cypress strands probably result from this phenomenon. Burned interior areas become ponds, eventually becoming marshes that are gradually invaded by shrubby species and then by cypress once again, as well as by typical subdominant hardwoods (e.g., Hamilton 1984).

Although it is tempting to attribute the domed outline formed by cypress trees in a pond to fire (e.g., Kurz and Wagner 1953), this is probably not the case. Faster growth rates in the center, perhaps because of deeper peat deposits or less competition, are more likely than age of trees to explain the presence of shorter trees on the edge and taller trees in the middle of these swamps (Brown 1981; Ewel and Wickenheiser 1988). A confounding factor is that most cypress domes in the Southeast today are relatively young second-growth swamps. Virtually every swamp in Florida–and perhaps in the entire Atlantic and Gulf Coastal Plains–has been harvested (at least partially) within the last two hundred years (e.g., Terwilliger and Ewel 1986), so shapes may reflect anthropogenic activity.

Fire may stimulate seed production by pondcypress. Fire scarring, like other forms of physical damage, induces seed production in conifers in general (Owens and Blake 1985), and several people have reported seeing severely burned (but still living) cypress trees laden with cones. Furthermore, cone production is more likely to be highest on the edge of a newly opened area than in an undisturbed swamp (Ewel, unpubl. data). Although seedlings are more likely to survive and grow well in sunlight than under shade (summarized in Brandt and Ewel 1989), no seedlings were found in burned swamps in one study in north Florida (Cook and Ewel 1992). The relationship between fire and reproduction in pondcypress needs additional study.

Pondcypress has several adaptations that help it survive fire (summarized in Ewel and Mitsch 1978). In particular, when the crown is burned, adventitious branches are produced that enable the tree to begin photosynthesizing once again. If the entire top is destroyed, the tree produces root sprouts. Observations of this ability to survive burning, particularly in the older literature,

do not always indicate whether the tree that has burned is baldcypress or pondcypress. It is likely, however, that baldcypress' response to fire is similar to that of pondcypress. Among 14 southern trees that were tested for fire resistance, baldcypress ranked behind only longleaf pine (*Pinus palustris*), slash pine (*P. elliottii*), and loblolly pine (*P. taeda*) (Hare 1965); pondcypress was not tested. It is possible that both varieties are fire resistant, but pondcypress' shaggier bark may afford it more insulation from fire than baldcypress.

The characteristic mosaic of pine-and-cypress communities in Florida probably appeared only 11 thousand years ago, as water tables rose in a terrain that had been dry and sandy, and fire became more common (summarized by Webb 1990). It is possible that baldcypress could not have moved southward into the Southeast had it not been fire resistant. The close relationship between the two forms may reflect the relatively short time not only for development of the complex mosaic of fire-climax ecosystems that exists in the Coastal Plain and particularly Florida, but also for the concurrent speciation of pondcypress from baldcypress in the absence of complete reproductive isolation between the two forms.

MANAGEMENT AND FIRE IN CYPRESS SWAMPS

Pondcypress swamps provide several benefits to society (Ewel 1990b). When left undisturbed, these wetlands afford wildlife habitat, provide at least some groundwater recharge because of their low evapotranspiration rates, and serve as detention basins that delay overland water flow as a landscape becomes saturated. They can be manipulated to serve as stormwater drainage systems, to yield wood, and to filter nutrients from secondarily treated wastewater. Baldcypress swamps (large strands, backwater swamps, and lake margins) also provide wildlife habitat and timber; in addition, they damp flood surges and function as a nutrient filter for agricultural runoff. Both kinds of swamps are often inadvertently drained, flooded, and allowed to burn too frequently or too infrequently. Discussion of the role of fire in management of these swamps therefore requires considering not only the benefit for which the swamp is being managed, but also the impact of prospective management on other values. The previous history of the swamp may also play a role in determining what types or intensity of management it can sustain.

Should pondcypress swamps be burned periodically? If fire is as important a factor as has been suggested above, regular prescribed burning is necessary. Allowing a prescribed burn in a pine plantation to move into a swamp may be the only management decision that is needed. Although the shrubs and hardwoods that invade in the absence of fire do not appear to affect cypress growth significantly, the accumulation of fuel may increase the probability of cypress tree mortality when the swamp finally does burn (Marois and Ewel 1983). The major disadvantage of burning a swamp may be the likelihood of starting a peat fire that may be difficult to monitor or control. A peat fire may also burn around the base of a cypress tree, providing ready access to fungi that cause heartrot. This could increase wildlife habitat by contributing to the formation of hollow snags, but it could decrease the future commercial value of the wood.

Should drained pondcypress swamps be burned periodically as well? When hydroperiods are shortened by regional drainage systems, the possibility increases that a fire will become too hot and burn away peat to significant depths, killing more trees. If the intensity and duration of a fire in such a swamp can be controlled, however, more frequent light fires may be both desirable and feasible.

Does clearcutting replace fire? Both thinning and cutting in large patches or strips stimulate cone production (Ewel, unpubl. data), although the response may not be so dramatic as with fire. Pondcypress seedlings grow more slowly under shade than in full sunlight (Neufeld 1983), and recovery from clearcutting through both coppice and seedlings has been demonstrated for some swamps in central Florida (Ewel et al. 1989), but low seedling survival rates have been reported for pondcypress seedlings in clearcut sites in south Florida (Gunderson 1984). Competition with rapidly growing herbaceous vegetation may be a more important factor in a clearcut site than in a burned site.

Should logging therefore be followed by burning? Because reproduction in the relatively young second-growth cypress swamps that dominate the coastal plain today seems to depend heavily on stem and seed production by coppice (Ewel et al. 1989), it is essential that fire be kept from freshly logged sites. Several accounts (many of them summarized in Gunderson 1984) indicate that cypress is eliminated when logged sites are burned, perhaps because burned stumps will not sprout, and freshly deposited seeds are destroyed; willow and tupelo gum (*Nyssa* spp.) are likely to be successful invaders.

Might baldcypress be planted in pondcypress habitats? When cypress seeds or seedlings are planted for reforestation or mitigation, does it matter which variety is planted? Have anthropogenic changes in water quality, water turnover rates, and fire frequencies made the differences between the two academic? This important question should be addressed because of growing interest in restoring and even creating wetlands, particularly in urban areas.

Increased exploitation of cypress swamps for wastewater disposal and fiber production (primarily as chips for horticultural use), together with long-term changes in hydroperiod caused by regional drainage patterns, indicate that cypress swamps may have to be managed more intensively in order to maintain them in a landscape. Studying the results of carefully planned burn programs and documenting the susceptibility and response of each kind of tree to fire can contribute substantially to our understanding of evolutionary, ecological, and management-induced relationships in cypress swamps.

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