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Ecophysiological implications of tree architecture for two cypress taxa, *Taxodium distichum* (L.) Rich. and *T. ascendens* Brongn.¹

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NEUFELD, H. S. (Botany Department, University of Georgia, Athens, Georgia 30602). Ecophysiological implications of tree architecture for two cypress taxa, *Taxodium distichum* (L.) Rich. and *T. ascendens* Brongn. Bull Torrey Bot. Club 113:118–124, 1986.—There are two widely-recognized cypress taxa in the southeastern United States, baldcypress (*Taxodium distichum* (L.) Rich.) and pondcypress (*T. ascendens* Brongn.). From measurements made on trees growing on the Savannah River Plant in South Carolina, morphological differences between the two types of cypress were found. Pondcypress have narrower crowns and are taller at a given diameter than baldcypress. In the distal 15 cm of branches, pondcypress have approximately twice as many branchlets as baldcypress. These branchlets average 63% longer and weigh cumulatively three times as much as those of baldcypress. Pondcypress allocate a lower per cent of aboveground biomass to branches, resulting in a more open crown. This, in turn, permits greater light penetration through the crown. They also retain a relatively greater proportion of their total foliar biomass in the interior portions of the crown. Pondcypress also have a higher leaf area ratio than baldcypress (2.60 versus 1.60 m²/kgdw), due primarily to the greater density of branchlets along the branches. The morphological differences exhibited by the pondcypress taxon, which is thought to be derived from the baldcypress taxon, are suggested as evolutionary adaptations resulting from climatically induced habitat changes.

Key words: cypress, *Taxodium*, tree architecture, ecophysiology

The architecture of woody plants is of interest to ecologists and morphologists (Norman and Jarvis 1974, 1975; Brunig 1976; Fisher and Honda 1979a, b; White 1983, Mooney and Chiarello 1984) because of its influence on energy and gas exchange processes, and the role it plays in determining growth and competitive capabilities. It has been suggested (White 1983) that changes in allometry and tree architecture may evolve independently of one another in response to changes in selection pressures. The ability to discern these selection pressures may be enhanced when closely related species are compared, because phylogenetic influences are minimized, and subsequent differences can be attributed largely to environmental effects.

The manner in which trees allocate biomass to photosynthetic and support tissues has been studied the most. Foliage orientation (Medina et al. 1978), distribution (Oker-Blom et al. 1983; Nicola and Pickett 1983) and amount (Nicola and Pickett 1983) have been shown to be important because of their effects on radiation absorption within the crown. While microclimatic effects on leaf energy budgets and gas exchange have been relatively well studied, further progress in plant ecophysiology now depends, in part, on the integration of leaf level processes with those of the whole plant (Mooney and Chiarello 1984) and will require more detailed investigations of plant architecture.

Previous work comparing the field water relations of two cypress taxa (baldcypress, *Taxodium distichum* (L.) Rich. and pondcypress, *T. ascendens* Brongn.) showed that they exhibited morphological differences which potentially could influence gas exchange patterns at the whole plant level (Neufeld 1984). The present study was done to quantify various aspects of the architecture of field-grown trees that might affect gas exchange and water relations of the entire tree.

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Methods. Morphological measurements were obtained for open-grown trees of both taxa at four study sites on the Savannah River Plant near Aiken, South Carolina (see Neufeld 1984 for site descriptions). There were two sites for each taxon, one chronically flooded and one seasonally flooded. The two taxa do not often co-occur naturally. None of the sites were currently receiving thermal effluents. Diameter (dbh) was measured with a diameter tape at 1.37 m and tree height estimated with a clinometer. Trees ranged in height from 3.51 m to 18.59 m. Mean maximum crown width was assessed visually using a vertically aligned pole and stakes placed in the ground at the edges of the crown. Two perpendicular sightings per tree were done and distances between stakes averaged to obtain mean crown width. All available trees at each site were measured, with a minimum at any site of at least 10. A total of 31 baldcypress and 28 pondcypress were measured.

Vertical orientation of the deciduous branchlets was determined for the distal 15 cm of a branch for three trees per site. Trees with branches at breast height, a southeastern exposure, and no evidence of shading were selected for sampling. Branchlets were assigned to one of twelve 30° classes, starting clockwise from the top vertical (sector 1 = 0–29°). Numbers of branchlets in each class, leaf length, cumulative leaf dry weight and branch dry weight were recorded.

Penetration through the crown of photosynthetically active radiation for three trees of each taxon was estimated using a Li-Cor 191s line quantum sensor (Li-Cor Inc., Lincoln, NE). Because this 1 m sensor was too long for the type of measurements needed, the outer 7.5 cm were covered with aluminum foil, leaving just a 25 cm segment uncovered in the middle. Light readings were taken between 1100 and 1400 hours solar time in the southeastern quadrant of each crown. The quantum sensor was held parallel to the ground at a height of 2 m and positioned perpendicular to a radius from the bole. Readings were taken from the outer edge of the crown inward to the bole in 15 cm intervals. Individual readings were expressed as a per cent of full sun, and the location of those readings expressed as a per cent of the distance from the crown edge to the bole. Representative branches were then removed and the distribution of foliage by weight assessed for equal increments from the crown edge to the bole. These equal increments were then expressed as a per cent of the distance from the crown edge to the bole.

Biomass allocation patterns were determined by harvesting five trees of each taxon prior to leaf fall in September 1982. Care was taken to harvest trees which were similar in size, since allometric relationships change as trees become larger (Mitsch and Ewel 1979). Sample trees ranged in height from 3.28 m to 7.65 m. Site conditions limited harvesting of baldcypress to the seasonally-flooded site and pondcypress to the chronically-flooded site. Trees were cut at water or ground level, whichever was higher, and then separated into bole, branch (dead and alive) and foliage. Roots were not harvested. Diameters at 0.1 and 0.5 m above buttswell were measured in the field. Biomass was oven-dried at 60°C to constant weight and weighed to the nearest 0.2 g. Leaf areas were calculated by multiplying foliage dry weight by specific leaf area data of the previous year (Neufeld 1984).

Nomenclature follows that of Radford, Ahles and Bell (1968).

Results. Linear regression analyses of crown width and height against dbh (Fig. 1) each produce lines with significantly different intercepts between the taxa (p < 0.001) but similar slopes (p > 0.05, t-test, Zar 1974). Reanalysis of the regressions using Bartlett’s method for calculating a Model II regression (Sokal and Rohlf 1969), which is more appropriate when the independent variable has an error variance associated with it, did not significantly change the results. The error of measurement associated with dbh is generally small anyway (around 0.2 cm). These data show that baldcypress are consistently shorter and have wider crowns than pondcypress of similar diameter.

The distal 15 cm of pondcypress branches have 2× as many branchlets, which average 1.6× longer and weigh cumulatively 3× as much as those of baldcypress (Table 1). Dry weight of pondcypress branches is higher, as is the ratio of branchlet to branch dry weight.

Orientation of branchlets about the branches is shown in Fig. 2. Over 63% of pondcypress branchlets are found within 30° of top vertical compared to only 26% for baldcypress branchlets. Chi-square analyses
show that these distributions are significantly different \((p < 0.001)\). Baldcypress branchlets are more evenly distributed across the upper hemispheric portion of the branch than those of pondcypress.

Baldcypress allocate about 15% more aboveground biomass to branches than do pondcypress (Fig. 3), apparently at the expense of bole wood, as no differences occur in the proportion of biomass in foliage. Differences for branches and boles are significant at \(p < 0.05\) as determined by Student's t-test. The greater branch development in baldcypress occurs partly as a result of higher branch densities along the bole. Branches are spaced much farther apart on pondcypress than baldcypress (pers. obs.). Leaf area ratio, the ratio of leaf area to total tree dry weight, is significantly higher in pondcypress than baldcypress \(2.60 + 0.26 \text{ m}^2/\text{kgdw} \text{ and } 1.60 + 0.18 \text{ m}^2/\text{kgdw} \text{ respectively, } p < 0.02; \text{ values are means } \pm \text{ standard error}\). The greatest proportion of baldcypress foliage is located at the outer portions of the crown, whereas for pondcypress this occurs midway through the crown toward the bole (Fig. 4a). Less light penetrates through the more closely spaced branches of baldcypress than of pondcypress (Fig. 4b). These data indicate less self-shading in pondcypress than in baldcypress crowns.

**Discussion.** In the following discussion, I speculate about the implications of tree architecture on the ecophysiology of the two cypress taxa. I start by relating aspects of structure to function at the leaf and shoot level, and then work up to effects at the stand or community level.

The most striking differences in crown architecture between the two taxa are in al-

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Total Number of Branchlets</th>
<th>Individual Branchlet Length (cm)</th>
<th>Cumulative Branchlet Dry Weight (g)</th>
<th>Branch Dry Weight (g)</th>
<th>Branchlet/Branch Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bald</td>
<td>44.2 ± 3.5</td>
<td>4.58 ± 0.27</td>
<td>0.98 ± 0.10</td>
<td>0.36 ± 0.05</td>
<td>2.57 ± 0.41</td>
</tr>
<tr>
<td>Pond</td>
<td>104.2 ± 8.2</td>
<td>7.32 ± 1.05</td>
<td>3.10 ± 0.96</td>
<td>0.54 ± 0.08</td>
<td>6.06 ± 2.02</td>
</tr>
</tbody>
</table>

Data are \(\bar{X} \pm SE\) with \(N = 6\). Student's t-test used to detect differences between taxa.

\(* = p < 0.01\).
Fig. 3. Percentage distribution for biomass in bole, branch, and foliage for pondcypress and baldcypress saplings (n = 5). Vertical bars are 95% confidence intervals.

lometric relationships, biomass allocation patterns, and branchlet densities and orientation. Pondcypress have narrower crowns, and are taller than baldcypress of the same diameter. These patterns result, in part, from a lower per cent allocation of biomass to branches. In addition, pondcypress branchlets are clustered more densely on branches and oriented more vertically.

Reorientation of branchlets to vertical positions can lead to lower photosynthesis because vertical branchlets receive lower daily total radiation amounts than horizontal ones (Gates 1980). In addition, higher branchlet densities, particularly along the distal 15 cm, may increase shading by neighboring branchlets (see Oker-Blom et al. 1983). However, if both the relative and absolute amounts of self-shading were less, then reductions in leaf photosynthesis would be lowered. Most of the foliage of baldcypress trees is found at the outer edge of the crown, whereas pondcypress foliage is found in greatest abundance midway between the crown edge and bole. The more closely spaced branches of baldcypress, with more horizontally oriented branchlets bearing distinctly placed leaves, result in much greater leaf overlap, and hence, light interception. Thus, light levels in the bottom, interior portions of their crowns are much lower. A similar pattern exists for Douglas-fir (Jensen and Long 1982). In contrast, pondcypress branches are far enough apart

that light easily penetrates to the bole. This may permit higher rates of photosynthesis to occur further into the crown than is possible for baldcypress trees, and result in the retention of foliage closer to the bole. Although one might expect that, as main branches subdivide into higher order branches, a greater percentage of foliage would always occur at the crown edge, in pondcypress there is greatly reduced branching of main branches (pers. obs.) and more foliage is closer to the bole. Since photosynthetic rates on a weight basis (determined in the lab on leaves held normal to the light) did not differ between the taxa (Neufeld 1984), their divergent canopy architectures must account for any differences in whole tree photosynthesis that occur.

Fig. 4. Percentage distribution of foliage (a) and light penetration (b) versus relative distance (%) from the crown edge for pondcypress (○) and baldcypress (●) saplings (n = 3). Vertical bars in (a) are 95% confidence intervals.
Vertically oriented branchlets receive more radiation early in the morning (Gates 1980), when both temperature and vapor pressure deficit are relatively lower. Presumably, this is more favorable for photosynthesis because temperatures at this time are often closer to the optimum and because cypress stomata close as the humidity goes down (Neufeld 1984). Although vertically oriented branchlets would again receive more radiation late in the day, temperatures and vapor pressure deficits are often still high enough to restrict photosynthesis. Vertical branchlet orientation may be important for pondcypress, which grow in habitats subject to seasonal drought stress. This orientation may maximize water use efficiency, particularly during periods of water stress, because CO₂ uptake would occur early in the day when transpiration is relatively low. With severe water stress, stomata of woody species tend to open for only a brief period in the morning and remain closed the rest of the day (Schulze et al. 1980). Vertical orientation may, in addition, reduce photoinhibition damage to water-stressed leaves by lowering radiation flux densities during critical times, such as midday (Powles 1984; Ludlow and Bjorkman 1984). More detailed studies on branchlet placement and patterns of radiation interception, coupled with ‘in situ’ measurements of gas exchange, are needed to develop canopy models of gas exchange for cypress.

Any benefit of altered branchlet orientation may be moderated by the presence of nearby trees. For example, during early morning, interception of light by adjacent trees in a stand is maximized (Thomas et al. 1972; Hutchison and Matt 1977), and the benefits of vertical branchlets are lessened. At this time, only foliage on trees growing in the open, or at the edges of stands, or foliated tops of dominant trees would receive appreciable direct light. During midday, light penetration to lower parts of the crown is greatest, but vertically oriented branchlets are disadvantageous. More effective light interception would occur if branchlets were more horizontally oriented. In fact, many branchlets of pondcypress on understory trees or on interior or lower branches are more horizontally oriented and have larger, more exerted leaves (Porcher 1966, pers. obs.). Withers (1979) reported similar foliar changes for an Acacia in Australia, and both Kinerson (1979) and Pickett and Kempf (1980) showed that upper leaves of some North American forest tree species were more vertically oriented than lower ones. McMillen and McClendon (1979) and Neufeld (1983) concluded that low light resulted in a more horizontal leaf orientation.

A low allocation of biomass to branches was reported for pondcypress by Brown (1978) who calculated ratios of bole to branch surface area of 5.0 for pondcypress compared to only 1.5 for baldcypress. These morphological differences may result from diminished internodal elongation (Watson 1983; J. A. Jernstedt, pers. comm.). This altered development could be a simple evolutionary change, involving only rearrangements of allometric relationships caused by changes in hormonal physiology, and not by more complex changes in organogenesis.

A narrower crown might be an adaptation to maintain high tissue turgor pressure as soils dry. Shorter and less extensive branching may lower resistance to water flow (Zimmermann 1978; Whitehead et al. 1985), resulting in a higher water potential and turgor pressure. Since maximum crown widths differ by no more than 1 to 2 m for a given diameter, and greenhouse measurements (Neufeld, unpubl. data) show a minimum pressure gradient along a branch in xylem pressure potential of 0.2 MPa/m, theoretical differences in water potentials between the taxa can only be 0.1 to 0.2 MPa. Most likely this difference offers only a slight advantage to pondcypress in withstanding drought.

The taller habit of pondcypress at the same diameter compared with baldcypress might serve to compensate for its narrower crown. Slender conical crowns result in less daily radiation interception than broader, flat ones (Brunig 1976), unless offset by greater height growth (Jahnke and Lawrence 1965). Increased height growth would minimally change water potentials, since hydraulic conductances are high longitudinally (Zimmermann and Brown 1971; Zimmermann 1978): only for very tall trees would the gravimetric component be appreciable. There is evidence from field measurements of transpiration and water potential that pondcypress may have a higher hydraulic conductivity to flow of liquid water than baldcypress (Neufeld 1984). Taller trees may actually be
a compromise growth response to sustain adequate foliage for additional growth, and to allocate that foliage to minimize water stress. Even though pondcypress have foliar and crown characteristics which appear to be adaptations for greater drought tolerance, they have a high leaf area ratio, in part because of their increased height and greater branchlet densities, and potential leaf surface area available for CO₂ uptake is not reduced.

Both pondcypress and baldcypress at the Savannah River Plant allocate 15% of their aboveground biomass to foliage when they are open-grown (Fig. 3). This apportionment to foliar biomass is much higher than that for either taxon in Florida. Allocations there ranged from 0.60% to 13.3% (mean = 3.9%) with older tress partitioning smaller percentages to foliage than younger trees (Brown 1978, Mitsch and Ewel 1979). However, trees in Florida were not necessarily open-grown and stand development may lower the percentage of biomass devoted to foliage. Similar trends in biomass allocation were found by van Buijtenen (1978) for plantation-grown loblolly and slash pines.

The close grouping of trees in stands reduces the amount of solar radiation striking the swamp soil or water surface, thereby lowering the amount of water lost by purely evaporative processes. Brown (1981) noted a high albedo for cypress, and much incident radiation was reflected, never reaching the swamp floor. Prolonged retention of soil water occurs within these stands compared with less dense stands, where relatively more water is evaporated and unavailable for uptake by trees (Brown 1981). Walker (1967) stated that pondcypress often develop denser stands than baldcypress, perhaps because their narrower crowns allow for more trees per unit ground area than baldcypress. Habitats supporting pondcypress generally exhibit very high water use efficiencies compared to other ecosystems (Brown 1981), suggesting that stand structure is important for the water balance of cypress communities.

Finally, I wish to speculate on the selective forces responsible for the evolution of these taxa. Pondcypress probably evolved from baldcypress (Watson 1983) in response to climatic changes which occurred around 11,000 years ago (Davis 1983, Webb 1981). Presumably it was hotter and drier then (Watts and Stuiver 1980), and the more upland populations of cypress may have become reproductively isolated from those nearer to rivers and creeks. Drought and nutrient deficiencies were probably more acute in the upland areas (Watson 1983, Monk and Brown 1965) and the major differences between the morphology of pondcypress and baldcypress (reduced internodal elongation and slower growth rates for pondcypress) are consistent with evolutionary theory concerning adaptation of plants to relatively more drought prone and nutrient impoverished habitats (Grime 1979, Neufeld 1983).

Literature Cited


