Effects of Light on Growth, Morphology, and Photosynthesis in Baldcypress (Taxodium distichum (L.) Rich.) and Pondcypress (T. ascendens Brongn.) Seedlings

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NEUFELD, HOWARD S. (Dept. Bot., Univ. Georgia, Athens, GA 30602). Effects of light on growth, morphology, and photosynthesis in Baldcypress (*Taxodium distichum* (L.) Rich.) and Pondcypress (*T. ascendens* Brongn.) seedlings. Bull. Torrey Bot. Club 110: 43–54 1983.— Growth patterns of baldcypress (*Taxodium distichum* (L.) Rich.) and pondcypress (*T. ascendens* Brongn.) seedlings were examined under light levels ranging from 5–100% full sunlight. Leaf arrangement on baldcypress branchlets remained distichous under all light conditions. However, leaf arrangement on pondcypress branchlets changed from radial when grown in high light to distichous when grown in low light. Leaves of pondcypress were consistently narrower and thicker than those of baldcypress. Pondcypress branchlets became more vertically oriented when plants were grown in high light, but assumed a similar orientation to baldcypress ones when grown in low light. Baldcypress produced greater biomass, leaf area, height, and diameter growth in most light treatments than pondcypress. Maximum photosynthetic rates were higher for pondcypress on a unit leaf area basis, but not different when expressed on a leaf dry weight basis. Higher specific leaf weights, resulting in greater internal leaf surface area available for CO_2 uptake may have accounted for the differences in photosynthetic rates per unit leaf area. The present study confirms field observations by previous investigators concerning the growth habits of these two taxa, but in addition, suggests that some of these differences are under genetic rather than environmental control.

Key words: baldcypress, pondcypress; *Taxodium*; growth; photosynthesis; light effects.

Bald and pondcypress (*Taxodium distichum* (L.) Rich. and *T. ascendens* Brongn. have been recognized as distinct entities in the southeastern U.S. since the time of Nuttall (1818). These taxa differ in both habitat preference and appearance. Baldcypress is more common along rivers and lake margins, where water flows freely and flooding levels fluctuate only moderately over the year. Pondcypress occurs more frequently in areas that are flooded by stagnant water and which have a more pronounced seasonal fluctuation in water level (Harper 1902; Mattoon 1915; Langdon 1965; Walker 1967). However, either can be found in habitats considered typical of the other (Harper 1905; personal observation).

Baldcypress has been suggested to grow faster than pondcypress (Harper 1902; Langdon 1965). Deghi (1978) observed greater height growth in baldcypress seedlings transplanted to a slope in Gainesville, Florida but Murphy (1974) obtained the opposite results with plants growing in a greenhouse. These conflicting reports constitute the only known direct comparisons of growth between the taxa.

Marked variation occurs between the taxa in the orientation and placement of leaves about the branchlets, and in the anatomy and morphology of individual leaves (Harper 1902; Detwiler 1916; Henry and McIntyre 1926). Deciduous branchlets of baldcypress bear distichously placed leaves while those of pondcypress bear smaller scale-like leaves that are appressed to the branchlet and distributed radially around it. Branchlets are generally more vertically oriented in pondcypress than baldcypress. Henry and McIntyre (1926) and Brooker and Lucansky (personal communication) have shown that leaves of baldcypress are elliptical in cross-section, and thinner and wider than the triangularly-shaped pondcypress leaves.

There is some confusion in the litera-

ture regarding the biological and ecological distinctness of the two taxa because some trees can be found with both leaf types and arrangements, or with foliar characteristics intermediate between the two forms already described (Elliott 1821–1824; Sargent 1896; Mohr 1901; Harper 1902; Kurz and Godfrey 1962; Radford *et al.* 1968). Most common perhaps is the occurrence of baldcypress-like branchlets on what appear to be pondcypress trees (Harper 1902). These branchlets are found mainly on older and shaded branches of adult trees, or on saplings growing in the shade of larger trees, suggesting that light may influence leaf and branchlet characteristics. Porcher (1966) remarked that in certain Carolina Bays in South Carolina adult pondcypress trees were readily identifiable as such whereas all young trees resembled baldcypress trees. Upper canopy branchlets on baldcypress bear smaller leaves than lower ones, and may superficially resemble shaded pondcypress branchlets (pers. obs.). Watson (pers. comm.) has recently revised the genus and suggests that the two taxa are more properly classified as varieties rather than as species.

The objectives of this study were to compare growth, physiology, and leaf characteristics between the taxa under various light levels, and to determine if the differences in morphology and growth observed in the field were environmentally controlled.

Methods. Baldcypress cones were collected along the shore of Lake Newnan near Gainesville, Florida in mid-November of 1979, and pondcypress cones from three nearby cypress domes. The cones were air dried for two weeks and the seeds manually extracted and soaked for five minutes in 85% ethyl alcohol (Bonner 1974). After washing in distilled water, seeds were stratified in flats of wet sand at 5 C in the dark for 6 weeks. The flats were then transferred to the greenhouse and seeds allowed to germinate *in situ*. When seedlings were approximately 20 cm tall (2 months) they were transplanted into 16 cm diameter plastic pots containing standard greenhouse soil. Plants were watered weekly with $\frac{1}{2}$ strength nutrient solution (Hoagland and Arnon 1950) supplemented by additional KNO_3.

Twenty seedlings of each taxon were randomly allocated to each of 5 levels of light (100% = full sun, 75%, 50%, 25%, 5%). Light levels were obtained by completely enclosing the seedlings within black plastic shade cloths of varied mesh size. Light irradiances (photosynthetically active photon flux density—PPFD) were determined using a quantum sensor (Li-Cor Inc., Lincoln, Nebraska) at noon on clear days. Air temperatures were monitored weekly with maximum-minimum thermometers, but varied among treatments by less than 3 C. The experiment was conducted outdoors in Athens, Georgia.

Height to the nearest mm (from the cotyledonary node) and diameter to the nearest 0.1 mm (from just above the cotyledonary node) were measured weekly beginning April 13. Seedlings were grown for 117 days, at which time 10 individuals of each taxon in each treatment were randomly harvested and leaf, stem, branch, and root biomass were determined. Tissues were oven-dried for at least 72 hours at 70 C before weighing. Prior to harvesting, leaf areas were obtained using a Li-Cor area meter. Specific leaf weights were calculated as the ratio of leaf dry weight to area. Also, leaves were subjectively rated on a scale from 1 for distichously arranged to 5 for radially arranged about the branchlet.

Branchlet angles were measured on day 109 with a protractor on 10 individuals per taxon per treatment as the angle between the adaxial surface of the 10th matured branchlet and the main stem. One leaf was sampled from each of 5 individuals per taxon per treatment on day 114 and chlorophyll determined using the method of Hiscox and Israelstam (1979). For determinations of leaf width and thickness single leaves were collected on day 90 from each of 4 individuals per taxon in the 100% and 5% treatments, then fixed and stained (Berlyn and Miksche 1976), and measured using a microscope fitted with an ocular micrometer.

Photosynthetic measurements were conducted on 3 seedlings per taxon per

treatment beginning August 27, after the completion of the growth portion of the experiment. Plants were brought in daily from the treatments and sealed into a 17 liter chamber so that approximately the terminal 20 cm of shoot was enclosed. Photosynthesis and respiration rates were measured in a system similar to that described by Bazzaz and Boyer (1972). Irradiation was provided by a metal halide lamp. Air temperatures were maintained at 27 C $\pm$ 1 C and relative humidity between 65–75% although transpiration was not measured. Carbon dioxide exchange rates were determined from the slope of the addition or depletion of CO_2 in the system within the range of 300–360 ppm. Each run began with a determination of the dark respiration rate, followed by progressive increases in PPFD up to near full sunlight (approximately 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$). Plants were equilibrated at each light level before progressing to the next one. After completing a run, leaf areas and weights were determined as previously described. Rates were calculated per unit area, unit dry weight, or per seedling. For the latter, rates per unit area for each seedling were multiplied by total seedling leaf area and adjusted for plants of equal total biomass using data from Fig. 1.

Due to the radial placement of leaves on pondcypress seedlings grown in high light, leaf areas of intact branchlets were severely underestimated. To correct for this, leaf areas were determined on intact branchlets and compared with those obtained by detaching the leaves of those branchlets so as to eliminate mutual shading. In the three highest light treatments leaf areas had been underestimated by approximately 21%. No difference was found for baldcypress branchlets grown in these same light levels, and because of the similar type of leaf placement in both taxa grown in the two lower light levels, no difference was assumed to occur there also. Hence leaf area data for the pondcypress seedlings grown in the three highest light treatments have been increased by 21%, including the seedlings harvested for biomass determinations.

All data were analyzed statistically using the General Linear Model programs in SAS (Barr *et al.* 1979). In order that adjustments could be made from differences in initial height and diameter, analysis of covariance was used to test for significant differences among treatments and between taxa. Percentage data were log or square root transformed prior to statistical analyses (Sokal and Rohlf 1969).

Results. Height growth for both taxa was least under 5% light (Table 1). For the other treatments, baldcypress height growth tended to increase as light intensity decreased, such that the greatest growth occurred in 25% light. Differences were significant among all treatments except 100% and 75% light. For pondcypress, height growth peaked in 25% light also, but did not differ from that in 100% light. Baldcypress consistently outgrew pondcypress in all light treatments except 100% light.

Diameter growth tended to decrease with decreasing light intensity for both taxa (Table 1). By the end of the growth period, baldcypress had achieved significantly greater diameter growth than pondcypress in all treatments. Analysis of covariance revealed no effect of initial height or diameter on subsequent growth patterns within or between taxa.

Biomass accumulation in both taxa was greatly reduced in 5% light, but only slightly affected by the other treatments (Fig. 1). Accumulation was significantly greater (nearly double) for baldcypress than pondcypress in all treatments. When total biomass was broken down into its component parts (Fig. 1), similar trends were observed among the fractions. Leaf and stem biomass for both taxa were little affected by the four higher light treatments, but baldcypress leaf and stem biomass were approximately 2X those of pondcypress. Branch production was small and variable across treatments for both taxa, and neither produced any branches in 5% light. Branch biomass generally was greater in baldcypress. Root biomass was clearly more sensitive to light than any of the other biomass fractions and steadily declined in the three lower light treatments. Baldcypress root biomass was ap-
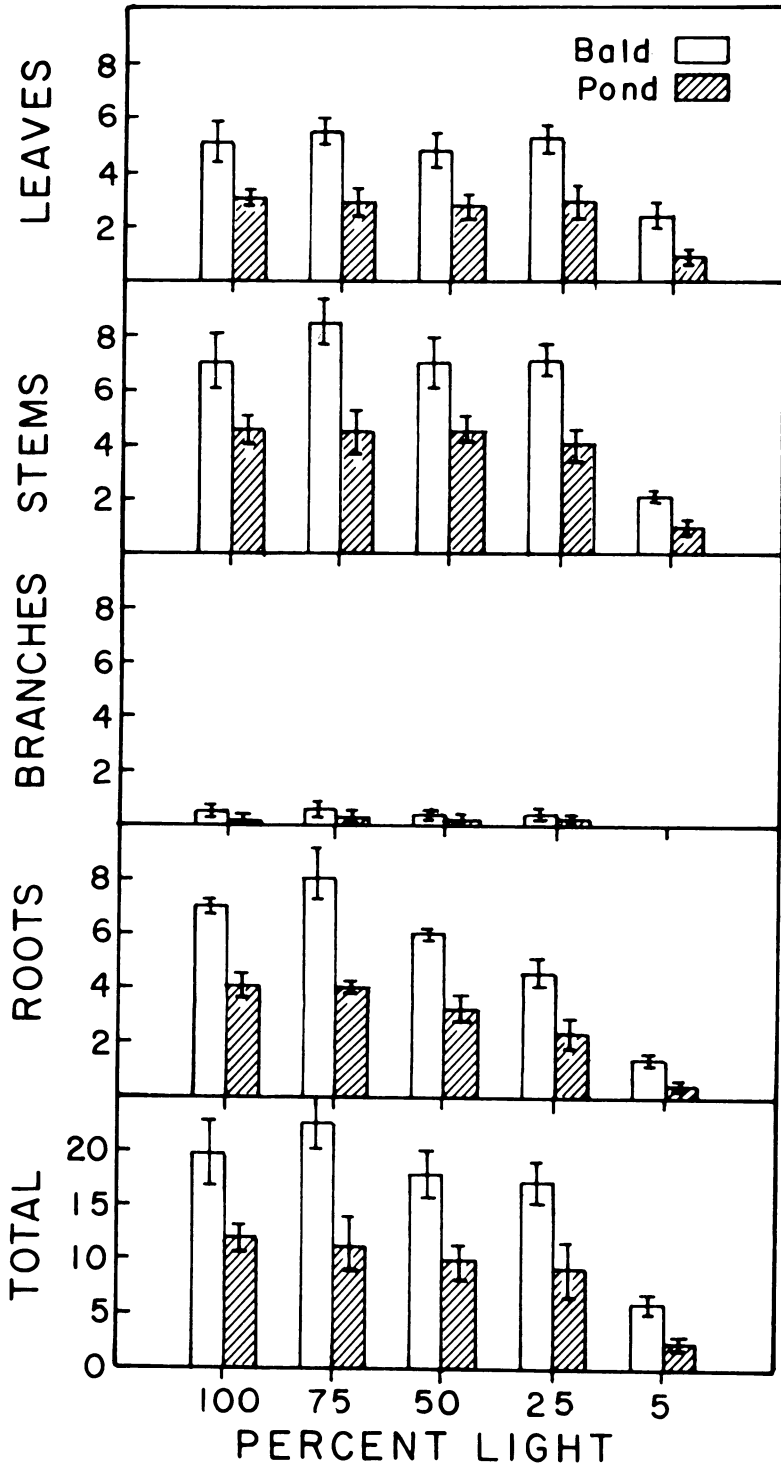
Fig. 1. Biomass accumulation (grams dry weight) in cypress seedlings grown in 5 levels of light for 117 days. Error bars indicate mean ± 95% confidence in interval. N = 10 except for pondcypress in 50% and 5% light where N = 9. Light levels expressed as percent of full sunlight.

Table 1. Growth, branchlet angles, and chlorophyll amounts of cypress seedlings grown in 5 levels of light.

Parameter	Taxon	Percent Light[1]				
		100	75	50	25	5
Height Growth (cm)	Bald	64.8 ± 2.4 (c)[2]	65.5 ± 2.2 (c)	73.0 ± 2.7 (b)	81.4 ± 2.0 (a)	56.6 ± 2.4 (d)
	Pond	61.5 ± 2.0 (ab)	52.6 ± 2.0 (c)	57.8 ± 2.3 (bc)	66.6 ± 2.1 (a)	37.6 ± 3.6 (d)
		NS	**	**	**	***
Diameter Growth (mm)	Bald	8.2 ± 0.4 (ab)	8.8 ± 0.3 (a)	7.9 ± 0.2 (b)	7.5 ± 0.2 (b)	3.8 ± 0.2 (c)
	Pond	7.1 ± 0.2 (ab)	7.0 ± 0.4 (a)	6.4 ± 0.1 (bc)	6.0 ± 0.3 (c)	2.0 ± 0.2 (d)
		**	***	***	***	***
Branchlet Angle[3]	Bald	54 ± 7 (bc)	53 ± 13 (c)	66 ± 10 (b)	91 ± 13 (a)	97 ± 12 (a)
	Pond	39 ± 6 (c)	45 ± 6 (c)	46 ± 10 (c)	65 ± 9 (b)	99 ± 15 (a)
		**	**	**	**	NS
mg chlorophyll/cm^{2}	Bald	4.44 ± 0.66 (bc)[4]	2.79 ± 0.43 (a)	3.48 ± 0.29 (c)	4.18 ± 0.19 (bc)	5.15 ± 0.28 (b)
	Pond	5.83 ± 0.34 (ab)	4.38 ± 0.48 (c)	4.58 ± 0.30 (bc)	5.31 ± 0.54 (ab)	6.68 ± 0.57 (a)
		*	**	NS	NS	NS
mg chlorophyll/gdw	Bald	6.29 ± 0.78 (b)	4.24 ± 0.70 (a)	6.46 ± 0.54 (b)	11.43 ± 0.68 (c)	26.61 ± 1.47 (d)
	Pond	7.09 ± 0.52 (ab)	5.57 ± 0.69 (b)	7.42 ± 0.16 (a)	11.43 ± 0.90 (c)	24.35 ± 2.11 (d)
		NS	*	NS	NS	NS

[1] Expressed as percent of full sunlight.
[2] Data are $\bar{x}$ ± standard error. For height and diameter growth N = 10 except for pond in 50% and 5% light where N = 9. Letters in ( ) refer to treatment differences within a taxon. Treatments followed by the same letter are not statistically different at p = .05 according to Duncan's New Multiple Range Test. NS = not significant. Asterisks indicate differences between taxa.
[3] The angle between the branchlet adaxial side and the main stem (N = 11).
[4] Values for chlorophyll are means of 5 determinations. NS p > .05, * p < .05, ** p < .01, *** p < .001.

proximately 2X that of pondcypress in all treatments.

Both taxa allocated between 35–43% of their total biomass to stem tissue, and no significant differences were apparent among treatments. Percent leaf weight increased with lower light levels though no differences between the taxa were observed. Relative root weight decreased for the two lower light levels, and there were no significant differences between the taxa except in the 5% light treatment, where the percentage allocation by baldcypress was greater than that by pondcypress. As a result, root/shoot ratios decreased at the two lower light levels.

Baldcypress seedlings produced much greater leaf areas than did pondcypress seedlings (Fig. 2), and these differences were significant for all treatments. Leaf areas of both taxa were significantly greater in 25% light than in the other treatments. No significant differences within the taxa were noted among the other treatments. Specific leaf weights were generally higher in pondcypress than baldcypress (Fig. 2), and declined in the two lower light treatments for both taxa.

Low light strongly affected both leaf arrangement patterns and branchlet orientation (Table 1 and Fig. 3). Pondcypress leaves were radially arranged about the branchlet in the three higher light treatments while in 25% light they began to appear more distichous, and in 5% light were totally distichous. Baldcypress leaves remained distichous in all treatments and differences between the taxa were significant for all treatments except 5% light. Branchlets in both taxa which formed in the two lower light treatments were significantly more horizontally oriented with respect to the main stem than those formed in the higher light treatments. In 100%, 50% and 25% light pondcypress branchlets were significantly more vertically oriented than those of baldcypress while in 5% light this difference disappeared. The lack of a difference in 75% light seems anomalous. In the 5% light treatment, due to the distichous leaf arrangement and horizontal branchlet orientation, pondcypress seedlings closely resembled baldcypress seedlings in casual appearance.

For both taxa, total chlorophyll amounts dropped from the 100% to the 75% light treatments and then increased as light levels decreased (Table 1). On a leaf area
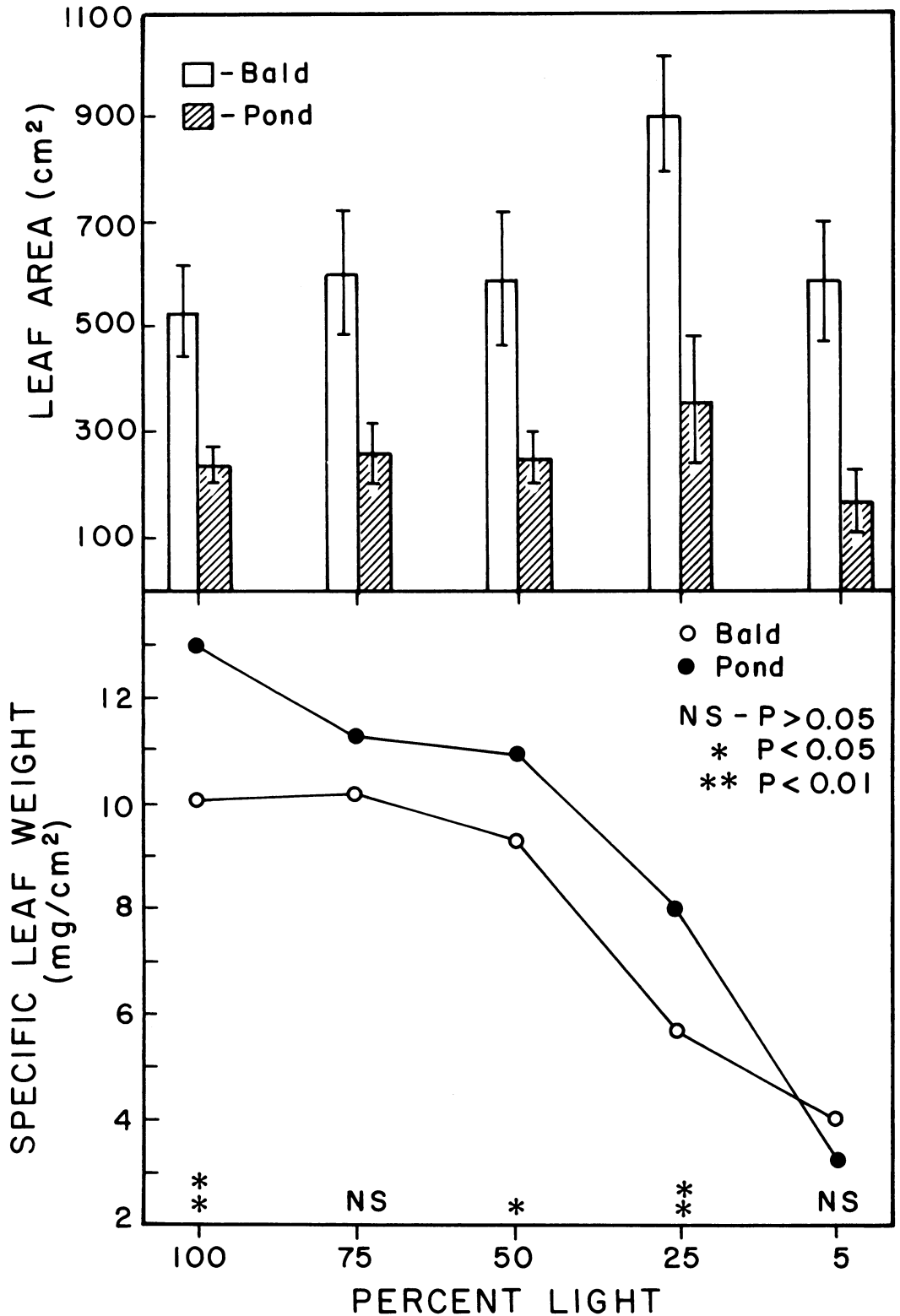
Fig. 2. Leaf areas (upper graph) and specific leaf weights (lower graph) of cypress seedlings grown in 5 levels of light for 117 days. Error bars indicate mean ± 95% confidence interval. N = 10 except for pondcypress in 50% and 5% light where n = 9. Light levels expressed as percent of full sunlight.
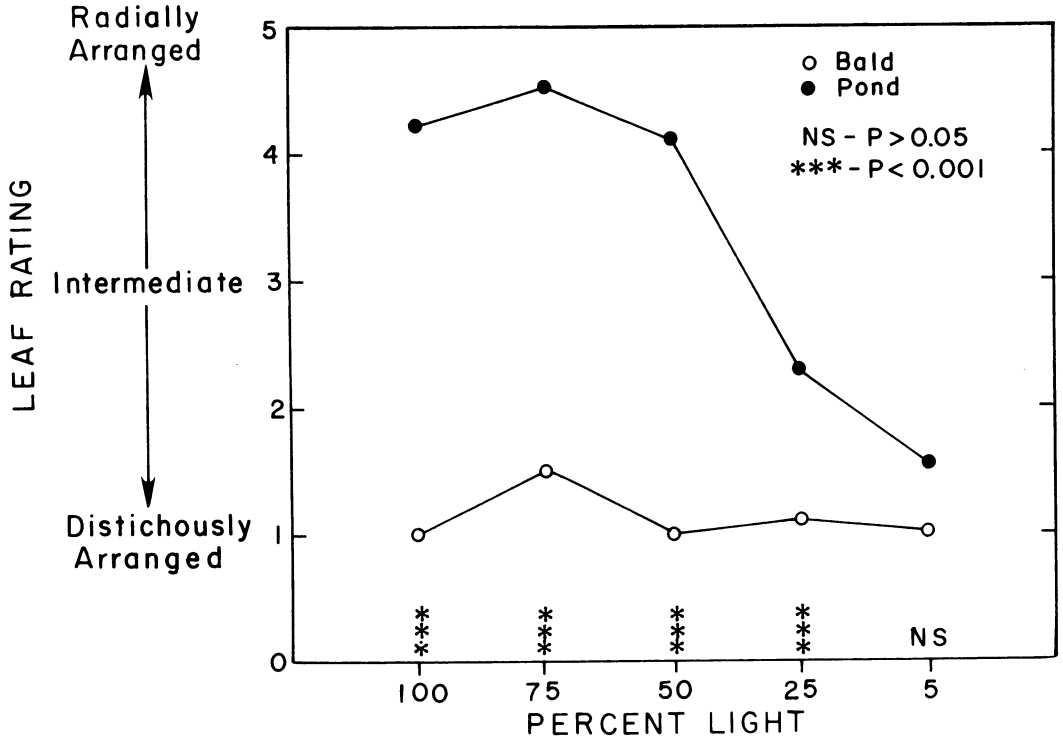
Fig. 3. Effects of light on leaf arrangement in cypress seedlings. Values are means of 10 evaluations except for pondcypress in 50% and 5% light where only 9 were done. Light levels expressed as percent of full sunlight.

basis, the increases at lower light levels were not significant, whereas on a dry weight basis they were highly significant. Comparisons between the taxa of total chlorophyll on a dry weight basis revealed essentially no significant differences in any treatments except 75% light, in which case the difference was due primarily to data from one leaf. Total chlorophyll on a leaf area basis was consistently higher for pondcypress in all treatments and significant differences occurred between the taxa in the 100% and 75% light treatments and at $p < .0519$ in the 50% light treatment. Chlorophyll a and b amounts paralleled total chlorophyll amounts and were not significantly different between the taxa in any treatment. In addition, chlorophyll a to b ratios averaged 3.11 for all taxon-treatment combinations.

Leaf width and thickness differed between the taxa in both the 100% and 5% light treatments. Baldcypress leaves were significantly wider and thinner than those of pondcypress in both treatments. For

baldcypress, leaf width changed nonsignificantly from 1.02 ± 0.05 mm to 1.19 ± 0.08 mm (NS, $p > .05$) while thickness decreased from 0.23 ± 0.01 mm to 0.17 ± 0.01 mm (Sig., $p < .05$) in 5% light. Pondcypress leaves also showed no change in width (0.80 ± 0.03 mm in 100% light versus 0.79 ± 0.03 mm in 5% light) although they did decrease significantly in thickness from 0.27 ± 0.01 mm in 100% light to 0.19 ± 0.01 mm in 5% light. All cited values are mean $\pm$ standard error with $N = 4$.

The mean maximum rates of photosynthesis per unit leaf area (rates at 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$) for baldcypress seedlings grown in the four higher light treatments were not significantly different (Table 2). Rates for seedlings grown in 5% light were significantly lower than those for seedlings from the three higher light treatments. For pondcypress, the highest average rate occurred for seedlings from 75% light, although this was not significantly different from the rates for seedlings grown in 100%

Table 2. Average photosynthetic rates at 2000 μmol·m^{-2}·s^{-1} and light compensation points of cypress seedlings grown in 5 levels of light.

Parameter	Taxon	Percent Light[1]				
		100	75	50	25	5
(1) On a leaf area basis:						
Net Photosynthesis	Bald	13.27 ± 1.27 (a)[2]	13.94 ± 1.18 (a)	14.58 ± 0.98 (a)	10.86 ± 1.00 (ab)	8.36 ± 0.53 (b)
(mgCO$_2$·dm^{-2}·hr^{-1})	Pond	18.94 ± 1.72 (ab)	19.63 ± 1.01 (a)	15.85 ± 1.05 (bc)	16.71 ± 0.80 (ab)	11.19 ± 1.64 (c)
		*	*	NS	*	NS
(2) On a leaf dry weight basis:						
Net Photosynthesis	Bald	11.48 ± 1.05 (a)	13.21 ± 1.25 (a)	16.92 ± 1.60 (ab)	16.34 ± 1.35 (ab)	20.89 ± 0.59 (b)
(mgCO$_2$·gdw^{-1}·hr^{-1})	Pond	13.72 ± 0.51 (a)	16.39 ± 1.85 (a)	16.06 ± 1.33 (a)	17.22 ± 1.28 (a)	20.14 ± 2.46 (a)
		NS	NS	NS	NS	NS
Light Compensation Point[3]	Bald	41 ± 3 (a)	28 ± 1 (b)	19 ± 1 (c)	22 ± 3 (c)	11 ± 1 (d)
(μmol·m^{-2}·s^{-1})	Pond	46 ± 2 (a)	34 ± 5 (b)	35 ± 9 (b)	21 ± 5 (c)	22 ± 4 (c)
		*	*	**	NS	**

[1] Expressed as a percent of full sunlight.

[2] Data are $\bar{x}$ ± standard error (N = 3). Letters in ( ) refer to treatment differences within a taxon. Means followed by the same letter are not statistically different at p = .05 according to the Student-Newman-Keuls Test. NS = not significant. Asterisks indicate differences between taxa.

[3] Compensation points estimated by eye and rounded to nearest integer. NS p > .05, * p < .05, ** p < .001.

and 25% light. Rates for seedlings from 5% light were significantly lower than those for seedlings from 100%, 75%, and 25% light. Pondcypress seedlings had significantly higher rates than baldcypress seedlings in the 100%, 75%, and 25% light treatments. The lack of a difference in the 50% light treatment seems anomalous, and no explanation for this can be offered. Rates per seedling (not shown) were generally higher for pondcypress than baldcypress, except in 50% light, but that difference though was small.

On a leaf dry weight basis (Table 2) no significant differences among treatments occurred for either taxon except for baldcypress seedlings grown in 5% light, which had higher photosynthetic rates than seedlings from 75% and 100% light. There was a general trend, although not significant, for rates to increase as treatment light levels declined. There were no significant differences between taxa in any treatment. Dark respiration rates, ranging from 0.39 to 1.99 mg CO$_2$·dm^{-2}·hr^{-1}, showed no trend with treatment, either on a leaf area or dry weight basis and no significant differences were observed between taxa within treatments or among treatments within each taxon.

Light compensation points, as estimated by eye, generally decreased as the level of light in which the seedlings had grown decreased. Compensation points were significantly higher for pondcypress than baldcypress in all treatments except the 25% light treatment.

Photosynthesis data on single branchlets (data not presented) obtained after completion of the photosynthesis measurements described above eliminated self-shading as a complicating factor in the latter experiment.

Discussion. The results of this study have shown that when pond and baldcypress are grown together in a common garden they maintain differences in certain morphological and physiological traits. In particular, differences were observed for (1) leaf arrangement and branchlet angle, (2) height and diameter growth, (3) leaf area and specific leaf weight, and, (4) chlorophyll amounts and photosynthetic rates per unit leaf area. Some of these differences persisted over the range of light levels in which the seedlings were grown and it thus seems that they are genetically rather than environmentally controlled.

Branchlets of pondcypress were generally more vertically oriented in high light than those of baldcypress, while this difference disappeared in low light. Leaves of pondcypress responded to low levels of

light by altering their placement from radial to distichous, such that they resembled baldcypress leaves in 5% light. Baldcypress leaves remained distichous regardless of the level of light. These results corroborate work by Gunderson (1977) who found that field grown pondcypress in uncleared plots had more distichously arranged leaves and horizontally oriented branchlets than those grown in cleared plots, a response possibly to differing light levels between the plots. An analogous phenomenon has been reported by Withers (1979) for leaves of *Acacia pycnantha*. Under low levels of light *A. pycnantha* produces bipinnate foliage which is horizontally held, whereas in high light phyllodes are produced which are more vertically oriented. Withers (1979) has suggested that the bipinnate foliage increases the shade tolerance of this species by maximizing light interception and such may be the case for pondcypress seedlings when grown in low light environments. Reorientation of leaves and branches in response to low light has been noted for a variety of tree species (McMillen and McClendon 1979).

The more vertical branchlet angles and radially placed leaves of pondcypress might be mechanisms by which this taxon avoids high radiation fluxes, since these adaptations would reduce the incident flux density upon the leaves around solar noon. As a result, leaf temperatures might be reduced (Medina *et al.* 1978), lowering the vapor pressure gradient from leaf to air, and thereby reducing the driving force for transpirational water loss. These leaf and branch arrangements then may result in lower water loss rates from pondcypress seedlings than baldcypress seedlings. Both Mohr (1901) and Brown (1981) have speculated that the foliage of pondcypress trees might confer greater tolerance to or avoidance of water stress effects than baldcypress trees. This is currently under investigation by the author.

In general, baldcypress seedlings grew more rapidly than pondcypress seedlings. For all light treatments, diameter growth of baldcypress seedlings exceeded that of pondcypress seedlings and—with the exception of the 100% light treatment—so did

height growth. Biomass accumulation and leaf area in all treatments were almost twice as large for baldcypress seedlings. This corresponds with higher growth rates in the field reported for baldcypress (Harper 1902; Mattoon 1915; Langdon 1965). However, the results here differ from those of Murphy (1974) where, in a comparative study, pondcypress seedlings grew 50% taller than baldcypress seedlings, and in addition did not differ in diameter growth. Since he used the same seed sources as used here, and grew the seedlings for similar lengths of time at the same period during the year, no explanation for this difference can be offered.

The growth data reported here suggest that some of the variation observed in productivity between, for example, strand forests (dominated by baldcypress) and cypress domes (dominated by pondcypress) may be partially due to inherent differences in the maximum potential growth rates of these two taxa, and not due solely to different hydrologic or edaphic factors (Brown 1981; Conner and Day 1976; Schlesinger 1978). Why pondcypress always grows more slowly than baldcypress is unclear, but it may reflect an adaptation to anaerobic and/or nutrient deficient soils (Brown 1981; Grime 1979).

There are several reports of shading effects on the growth of baldcypress seedlings. Browder *et al.* (1974) grew baldcypress seedlings under five levels of light and reported trends for height, diameter, and biomass accumulation similar to those obtained here. Blanck (1980) also grew baldcypress seedlings under several light regimes, and reported the greatest height and diameter growth at a light irradiance of 641 $\mu mol \cdot m^{-2} \cdot s^{-1}$, comparable to the 25% light treatment used here.

In this study baldcypress accumulated essentially the same amount of dry weight in light levels ranging from 100% to 25% light, which confirms reports by Mattoon (1915) and Putnam (1951) that it can tolerate a wide range of light. Pondcypress showed a consistent trend for biomass reduction as light levels decreased, although it survived all the treatments. As seen by the ratio of biomass production in 5% light

to that in 100% light pondcypress was more adversely affected by the low light, producing only 19% as much biomass as compared to 30% for baldcypress. This supports the hypothesis of Mattoon (1915) that it may not tolerate low light as well as baldcypress. The higher photosynthetic light compensation points exhibited by pondcypress also support this hypothesis. Data on light levels beneath undisturbed cypress canopies are scarce, but PPFD in closed baldcypress stands may be as low as 25 μmol $\cdot$ m^{-2} $\cdot$ s^{-1} (Blanck 1980) and in closed pondcypress stands 34 μmol $\cdot$ m^{-2} $\cdot$ s^{-1} (unpublished data of author), levels which, as shown by this study, are probably below those needed for survival. Seedling establishment for both taxa may ultimately depend on openings in the canopy where light levels are higher.

The photosynthetic data suggest that there is an inherent difference in the potential for CO_2 uptake between the taxa. Many studies now suggest that differences in internal leaf surface area caused by environmental factors such as light intensity or salinity may account for some of the differences in photosynthetic rates between individuals of a taxon (Patterson et al. 1978; Longstreth and Nobel 1979; Nobel and Hartsock 1981). For pondcypress grown in 100%, 50%, and 25% light, specific leaf weights were higher than those for baldcypress as determined from the biomass data and photosynthetic rates were higher in the 100%, 75%, and 25% light treatments. Also, cross-sections of pondcypress leaves were thicker than baldcypress leaves, both in 100% and 5% light. If thickness is correlated with increased internal surface area, which is probable (Nobel and Hartsock 1981), then differences in internal surface area available for CO_2 assimilation may account for some of the differences in the observed photosynthetic rates. For both taxa there is a significant correlation between mean maximum photosynthetic rate based on leaf area and specific leaf weight ($r^2 = .78$, $p < .05$ for baldcypress, $r^2 = .82$, $p < .05$ for pondcypress). The fact that differences in photosynthetic rates and chlorophyll amounts are eliminated when calculated on the basis of leaf dry weight strongly supports the interpretation that differences in internal leaf area available for CO_2 assimilation are responsible for the differences in the photosynthetic rates per unit leaf area between the taxa.

A paradox of this study was that areal photosynthetic rates, even when adjusted for proportion of total biomass as leaves, were significantly greater for pondcypress than baldcypress, while biomass accumulation was significantly greater for baldcypress than pondcypress. Similar results have been reported for other tree species (Logan and Krotkov 1969; Ledig 1974) and serve to illustrate the difficulty of predicting long-term growth trends from short-term measurements of net photosynthesis. The inability of these short-term photosynthetic measurements to be accurate predictors of growth may arise from a failure to account for seasonal and/or ontogenetic changes in net photosynthesis, and differences in patterns of shoot and root growth (Ledig 1974). In this particular study, differences in respiration rates could not be invoked as the cause of the paradox, since rates were essentially identical between the taxa. Differences in growth activity do not seem to have been a factor either, since both taxa were still growing at the time photosynthesis was measured. There is the possibility of experimental error, but considering the randomized manner in which plants were selected for measurement, it is difficult to imagine how this could have resulted in consistently higher rates for only pondcypress seedlings. Baldcypress seedlings may have produced greater leaf areas at an earlier stage than pondcypress seedlings, resulting in a higher capacity for CO_2 uptake. This difference could then have been compounded over time, with subsequently greater growth for baldcypress than pondcypress seedlings (Ledig 1974), although no data are available to substantiate this speculation. Further studies of biomass allocation patterns in younger seedlings are needed to clarify the relationships between photosynthesis and growth for these taxa.

In conclusion, the results of this study demonstrate that there are differences between the taxa in growth, morphology,

and physiology when grown in a common garden. However, the mechanisms by which baldcypress seedlings outgrow pondcypress seedlings remain unexplained. More work is needed on the carbon allocation dynamics of cypress seedlings in order to reconcile the patterns of photosynthesis observed here with those of biomass production. Finally, it is important to distinguish the taxa, where possible, when investigating cypress growth, since some differences between sites may be due to genetic rather than environmental factors.

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