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## PHOTOSYNTHETIC RATES AND NUTRIENT-USE EFFICIENCY AMONG EVERGREEN AND DECIDUOUS SHRUBS IN OKEFENOKEE SWAMP

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We compared photosynthetic rates and indices of nutrient-use efficiency for evergreen and deciduous shrubs growing in the Okefenokee swamp. Despite statistically significant differences between evergreen and deciduous species, photosynthetic variables and leaf-level nutrient-use efficiencies did not sort cleanly into two groups representing differences in leaf longevity—instead, traits varied continuously with specific leaf mass (SLM). *Lyonia lucida*, an evergreen (SLM: 161.1 g/m<sup>2</sup>), and *Itea virginica*, a deciduous shrub (SLM: 75.1 g/m<sup>2</sup>), represent the extremes of the gradient. Net photosynthesis on a leaf area basis ( $A_{area}$ ) was higher for evergreen than deciduous shrubs but was lower for evergreens when calculated on a leaf mass basis ( $A_{mass}$ ). There was, however, considerable overlap among species with different leaf longevities. Discriminant analysis indicated that SLM was the most important variable differentiating species. Thus, SLM rather than leaf longevity per se is a better predictor of leaf function. Instantaneous photosynthetic nitrogen-use efficiency (PNUE) or phosphorus-use efficiency (PPUE) did not predict whole plant nutrient-use efficiency, measured as percent nutrient retranslocation from leaves prior to abscission. Evergreen species had significantly higher P and N retranslocation efficiency than deciduous species, yet slightly lower PNUE and PPUE. The evergreen *Cyrilla racemiflora* retranslocated >90% of leaf P. High retranslocation efficiency for P indicates that this resource may be an important limiting nutrient in this swamp, and high retranslocation efficiency and a longer growing season may explain the higher productivity of evergreen than deciduous shrubs in the nutrient-limited swamp habitat. Midday stomatal closure for *L. lucida* (evergreen) and *I. virginica* (deciduous) corresponded with decreasing xylem pressure potential in conjunction with high evaporative demand. The development of large differences between root, stem, and leaf water potential indicates that high resistance to water flux may limit leaf conductance. Phosphorus limitations increase hydraulic resistance in some herbaceous plants and may contribute to water stress in the swamp habitat. Thus, in addition to the direct effects of nutrient limitations, reduced water uptake and transport may be an important stress for swamp shrubs.

### Introduction

Assessments of the relative advantages of the evergreen compared with the deciduous leaf habit are important for interpreting the ecological significance of differences in leaf longevity (Chabot and Hicks 1982; Reich et al. 1992). As a result of high specific leaf mass (leaf mass/leaf area) and low nitrogen content per unit leaf mass, evergreen leaves typically have lower maximum rates of net photosynthesis (dry-mass basis) than deciduous leaves (Reich et al. 1992). Differences in resource-use efficiency are also evident among leaves of varying life span. In a comparison of trees and shrubs of a desert ecosystem, DeLucia and Schlesinger (1991) found higher water-use efficiency for evergreen trees than for deciduous shrubs but lower photosynthetic nitrogen-use efficiency in the evergreen trees. This study and many others comparing the function of evergreen and deciduous leaves confound differences in growth form, root distribution, leaf morphology, and other variables with leaf longevity per se (Reich et al. 1992).

The evergreen habit is thought to be an ad-

aptation to nutrient-poor environments, and many evergreen species are found in nutrient-limited bogs and swamps (Monk 1966). In the Okefenokee Swamp of south Georgia in the United States, a variety of shrubs compose a dense understory in cypress (*Taxodium disticum*) forests (Schlesinger 1978). The shrub layer includes both deciduous and evergreen species that have relatively similar aboveground structure and gross leaf morphology. Many of the species are members of the Ericaceae. One objective of this study was to use this suite of species to compare the photosynthetic performance of evergreen and deciduous leaf types in the same environment.

We focused on measurements of nutrient-use efficiency (NUE), which should be adaptive in nutrient-limited environments, such as the Okefenokee Swamp. NUE has been defined in a variety of ways. Working with single leaves, Field et al. (1983) defined photosynthetic NUE as an index of the efficiency of nitrogen use during the biochemical reactions of photosynthesis. Typically, photosynthetic NUE is estimated with gas-exchange measurements over short intervals, providing an instantaneous index of NUE. Whole-plant NUE has been examined using indices of growth per unit of nutrient uptake (Cole and Rapp 1981) and nutrient retranslocation before abscission (Vitousek 1982). Both of these measurements extend the assessment of NUE to the life span of the plant. High NUE in growth is often

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attributed to evergreen species, but Sobrado (1991) found that photosynthetic NUE was lower in evergreen than in coexisting deciduous tropical trees. The second objective of this study was to compare various indices of photosynthetic performance and NUE among the deciduous and evergreen species of Okefenokee Swamp.

Standing water in the cypress forest of Okefenokee swamp restricts the establishment of shrubs to the swollen bases of the cypress trees and dead stumps. Using cypress trees as a substrate, shrub roots extend through about 1 m of water to the underlying peat, which is anaerobic and methanogenic (King et al. 1981). In addition to nutrient limitations, Schimper (1898) proposed that anaerobic conditions in bogs reduce water uptake by roots, leading to "physiological drought." His hypothesis helps to explain why species with evergreen sclerophyllous leaves, normally associated with arid climates, are abundant in many swamps and bogs. Phosphorus deficiency may also contribute to drought in plants inundated with water by reducing root hydraulic conductivity (Radin and Boyer 1982). However, studies of plant water relations in bogs have offered little empirical support for the physiological drought hypothesis (Small 1972; Marchand 1975; Schlesinger and Chabot 1977). Our third objective was to examine temporal changes in the water potential and stomatal conductance of a representative deciduous and evergreen shrub as an indication of water stress.

## Material and methods

### LEAF GAS EXCHANGE

Gas-exchange measurements were made on the youngest fully expanded leaves on five to eight shrubs of each of two evergreen (*Cyrilla racemiflora* and *Lyonia lucida*) and three deciduous (*Clethra alnifolia*, *Itea virginica*, and *Leucothoe racemosa*) species. Often two to four shrubs of different species grew on a single cypress stump, and measurements were made from the front of a flatboat during May 1990. Leaves that were experiencing or had just experienced a change in incident irradiance and leaves with herbivore damage were avoided. Following the gas-exchange measurements, each leaf was harvested for area determination and measurement of nutrient (N and P) contents as described below.

Exchanges of CO<sub>2</sub> and water vapor were measured with a closed infrared gas analysis system (model LI-6200, LICOR, Inc., Lincoln, Nebr.), by enclosing individual leaves or portions of leaves in a well-mixed 4.0-dm<sup>3</sup> cuvette. Measurements were made during a 5–10 mm<sup>3</sup> dm<sup>-3</sup> depletion of CO<sub>2</sub>, which typically took 20–60 s. Net photosynthesis, transpiration, and stomatal conductance to water vapor were calculated as in

von Caemmerer and Farquhar (1981). For the calculations, we assumed that leaves were predominantly hypostomatal and that cuticular transpiration was negligible. Boundary layer conductance to water vapor in the cuvette, calculated with a filter paper leaf replicate, was 1.56 mol m<sup>-2</sup> s<sup>-1</sup>.

Measurements of leaves in their natural orientation were made between 700 and 1200 hours (EDT). The mean atmospheric CO<sub>2</sub> concentration and leaf-to-air vapor pressure deficit for all measurements were 349 (±10; SD) μL/L and 3.2 (±1.1) kPa, respectively. Mean leaf and air temperatures were 33.0°C (±3.5) and 32.2°C (±3.3), respectively, and most measurements were made at irradiances >1,000 μmol m<sup>-2</sup> s<sup>-1</sup> (PPFD).

The variance in gas-exchange rates within a species was high. This may have been caused, in part, by changing environmental conditions and large variation in leaf N and P. Thus, we made interspecific comparisons on the entire data set as well as on a selected subset of the data. The photosynthetic data were selected to reflect the photosynthetic capacity (net photosynthesis at optimal temperature and leaf-to-air water vapor pressure difference (LAVPD) and saturating irradiance) of each species. This was accomplished by constructing scatter plots of photosynthesis (area basis) versus three environmental variables (leaf temperature, incident PPFD, and leaf-air vapor pressure deficit). Values below light saturation or, if a clear temperature optimum or LAVPD response was evident from the scatter plots, values less than 50% of the maximum rates were discarded. The 50% level provided a conservative selection of the data, and mean values for the entire data set and the selected values are presented. Photosynthetic data and leaf N and P were used to calculate the potential photosynthetic nitrogen-use efficiency (PNUE) and the potential photosynthetic phosphorus-use efficiency (PPUE) as defined by Field et al. (1983).

The response of stomatal conductance ( $g$ ) to the combined influence of assimilation rate and the partial pressures of CO<sub>2</sub> and water vapor at the leaf surface was examined following Ball et al. (1987). The partial pressures of gases at the leaf surface were calculated by applying the Ohm's law analogy to the flux from inside the leaf to the leaf surface and from the leaf surface through the boundary layer. The equation was then solved for the surface condition. The slope of the response of  $g$  to an index, defined as the assimilation rate ( $A$ ) times the ratio of surface humidity ( $H_s$ ) to surface CO<sub>2</sub> ( $C_s$ ), was calculated by least squares regression. This slope provided a measure of "stomatal responsiveness" to the combined influence of intrinsic (photosynthesis) and extrinsic (humidity and CO<sub>2</sub> at leaf surface) factors.

### WATER RELATIONS

An experiment was conducted to determine if hydraulic resistance to water flux from free water to the leaves may have been sufficiently great to cause a decrease in  $g$  during periods of high evaporative demand. Several pairs of branches were selected on four shrubs each of *I. virginica* (deciduous) and *L. lucida* (evergreen). One branch of each pair was wrapped with aluminum foil to minimize transpiration and to bring that branch into equilibrium with stem water potential. On two consecutive days, the water potentials of wrapped and exposed branches were measured at periodic intervals from ca. 0700 to 1200 hours. Intermittent clouds in the afternoon made measuring gas exchange problematic. Following excision of the branch (ca. 10-cm long), bulk shoot water potential was measured in a pressure chamber (SoilMoisture Equipment, Santa Barbara, Calif.). Prior to excision, gas-exchange measurements were made on leaves of the exposed shoot as described previously.

### NUTRIENT CONTENT AND RETRANSLOCATION

Supplemental collections of fully expanded first-year leaves were made from three to nine shrubs of the species used for gas-exchange measurements and other species representing deciduous and evergreen leaf types. The leaves from a single shrub were combined, dried, and ground to pass through a 40-mesh screen. Concentrations of N and P were analyzed with a Traacs 800 Autoanalyzer (Bran and Luebbe Analyzing Technologies 1986), following digestion of the ground tissue in  $H_2SO_4$  and  $H_2O_2$  (Lowther 1980). The carbon isotopic ratio,  $^{13}C/^{12}C$ , was analyzed on the VG Isogap Mass Spectrometer at Duke University and expressed relative to the Pee Dee belemnite standard as  $\delta^{13}C$ .

As a result of large shrub-to-shrub variation in nutrient concentrations observed in the May 1990 collections and seasonal changes in nutrient concentration observed during previous work, we labeled individual shrubs for sequential leaf collections during 1991. On July 29, fully expanded first-year leaves were collected from seven to nine individuals of each of five species. Individual leaf areas were measured on a LiCor Model 3100 leaf area meter, and each leaf was dried, weighed, and analyzed for N and P. Abscising leaves from the same shrubs were collected in November 1991. We used the same methods to measure the area, mass, and N and P content of the abscising leaves. For the evergreen species, the abscising leaves were produced in years earlier than 1991, although most were probably produced in 1990.

Leaf nutrient content at abscission (November 1991) was calculated and compared to the July 1991 collections. Changes in concentration per

unit mass (%ODM) or per unit leaf area ( $mg/cm^2$ ) were used to calculate percent retranslocation, using the following approaches:

#### Retranslocation

$$= (\text{July \%ODM or } mg/cm^2 \\ - \text{November \%ODM or } mg/cm^2) \\ \div (\text{July \%ODM or } mg/cm^2)$$

The first expression (%ODM) focuses on differences in the nutrient concentration per unit mass (or volume) of leaf tissue in which biochemical reactions take place, whereas the second method ( $mg/cm^2$ ) focuses on changes in concentration per unit of leaf area that captures solar radiation for photosynthesis. These expressions will differ to the extent that the accumulation of photosynthetic products and leaf thickening during the growing season result in apparent decreases in concentration per unit mass but no change in concentration per unit of leaf area.

### STATISTICAL ANALYSIS

One-way ANOVA (SAS 1985) was used to determine significant differences ( $P < .05$ ) among species for the dependent variables, including photosynthetic variables, specific leaf mass, tissue N, P, and carbon isotope ratio, and nutrient retranslocation. Prior to running the ANOVAs, data were subjected to Bartlett's test of homogeneity of variances. If there was significant heteroscedasticity, the appropriate data transformations were applied prior to running the ANOVA. Significant differences predicted by the ANOVA were also confirmed with the Kruskal-Wallis one-way ANOVA for nonparametric data. Tukey's multiple range test was used to determine, for each dependent variable, which means were significantly different at  $P < .05$ . A  $t$ -test was used to compare variables combined into an "evergreen" and a "deciduous" group, and discriminant analysis was used to identify which variables (photosynthesis on an area or mass basis, specific leaf mass [SLM], N, P, PNUE, or PPUE) were most important in differentiating among species.

## Results

### LEAF NUTRIENTS, RETRANSLOCATION, AND GAS EXCHANGE

In the initial analysis, leaf N and P contents were determined for the 368 leaves used for gas-exchange measurements. Despite a careful selection for uniformity of sample leaves (similar age, position, condition, etc.), the variation in N and P content was high (table 1). For P, the coefficient of variation ranged from ca. 20 to greater than 60% among species. Within a species leaf N and P content were poorly correlated. The slopes of

Table 1  
THE COEFFICIENT OF DETERMINATION ( $r^2$ ) FOR LINEAR REGRESSIONS  
OF P (mmol/g) AS A FUNCTION OF LEAF N (mmol/g)

Species	$r^2$	N mmol/g	P mmol/g	$n$
Evergreen:				
<i>Cyrilla racemiflora</i> . . . . .	.38	.85a (35.7)	.017e (27.1)	50
<i>Lyonia lucida</i> . . . . .	.35	.49b (21.0)	.023ac (67.8)	101
Deciduous:				
<i>Clethra alnifolia</i> . . . . .	.65	.85a (29.9)	.021bd (37.5)	66
<i>Itea virginica</i> . . . . .	.07	.83a (36.6)	.021bc (31.1)	98
<i>Leucothoë racemosa</i> . . . . .	.11	.75a (24.5)	.015ad (20.7)	53

Note. The mean leaf nitrogen and phosphorus content are designated by "N" and "P," respectively, followed by the coefficient of variation in parentheses. The sample size ( $n$ ) is provided for each species in the last column. Means within a column designated by a different letter are significantly different at  $P < .01$ , and the mean N and P contents for evergreen species as a group were significantly different from deciduous species ( $t$ -test;  $P < .01$ ).

leaf P regressed on N were significant ( $P < .01$ ); however, with the exception of *Clethra alnifolia*, the regression models accounted for 38% of the variation or less. Thus, further statistical comparisons of gas exchange and leaf structural and chemical characteristics were made on the entire data set and on data selected to reflect the photosynthetic capacity of each species. The selection criteria were, however, rather conservative and resulted in relatively small changes in mean values (table 2).

As a group, evergreen species had significantly

higher SLM than the deciduous species (table 2); the mean SLM for evergreen species was 124.4 g/m<sup>2</sup> compared with 81.2 g/m<sup>2</sup> for deciduous species). However, *Cyrilla racemiflora*, an evergreen species, had similar SLM to the deciduous species indicating continuous variation in sclerophylly among evergreen and deciduous species (table 2). Most of the difference in SLM between evergreen and deciduous shrubs was caused by the high value for *Lyonia lucida*, an evergreen species. Despite significant differences between combined data for evergreen and deciduous shrubs, there

Table 2  
PHYSIOLOGICAL, CHEMICAL, AND STRUCTURAL ATTRIBUTES FOR  
LEAVES OF EVERGREEN AND DECIDUOUS SHRUBS

	Evergreen		Evergreen vs. deciduous	Deciduous		
	<i>Lyonia lucida</i>	<i>Cyrilla racemiflora</i>		<i>Leucothoë racemosa</i>	<i>Itea virginica</i>	<i>Clethra alnifolia</i>
SLM (g/m <sup>2</sup> ) . . . . .	165.1a (172.2)a	96.0b (103.0)b	**	92.4c (88.8)c	75.1c (71.2)c	81.3c (85.5)c
N (mmol/g) . . . . .	(.5)f	(.9)bd	**	(.7)ab	(.8)ac	(.9)ce
P (μmol/g) . . . . .	(11.1)c	(17.8)ab	**	(15.5)a	(21.5)b	(21.8)b
$A_{area}$ (μmol/m <sup>2</sup> /s) . . . . .	6.4a (7.8)ab	8.8b (11.0)d	*	5.9a (7.0)ac	6.2a (6.3)c	7.6b (8.3)b
$A_{mass}$ (nmol/g/s) . . . . .	40.3d (48.2)d	91.4ab (108.3)bc	**	65.3e (80.1)a	88.4ac (90.5)ab	116.8b (128.1)c
PNUE (μmol/mol/s) . . . . .	83.2a (97.3)a	116.0b (129.3)bc	**	91.2ac (110.0)ab	118.3b (108.1)a	133.4b (138.2)c
PPUE (μmol/mol/s) . . . . .	3.9a (5.0)ab	5.4cd (6.3)fg	*	4.6ab (5.5)ad	4.7bd (4.7)bd	5.5e (5.9)ce

Note. Values represent the means for the entire data set, and the values in parentheses are for leaves that were selected (Methods) to represent the maximum photosynthetic rates (dry-mass basis) for each species. Net photosynthetic rates expressed on an area or dry-mass basis are designated as  $A_{area}$  or  $A_{mass}$ , respectively; and the instantaneous nitrogen-use efficiency and instantaneous phosphorus-use efficiency are designated as PNUE and PPUE, respectively. Specific leaf mass is SLM. Means designated by different letters were significantly different at  $P < .01$ , and statistical differences between combined data for evergreen compared with deciduous species are shown in the column marked Evergreen vs. deciduous.

\*  $P < .01$ .  
\*\*  $P < .05$ .

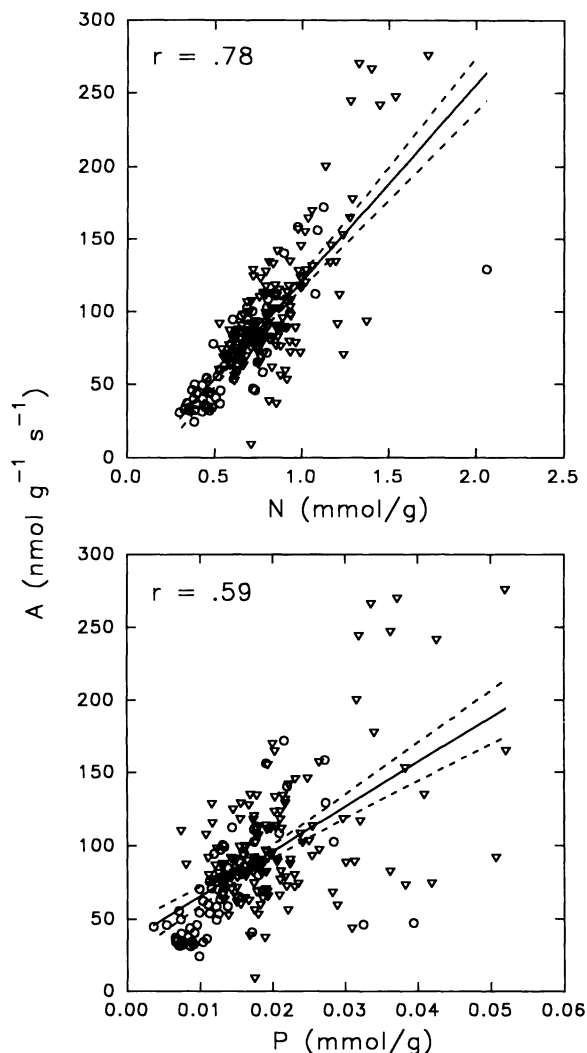


Fig. 1 Net photosynthesis (dry-mass basis) as a function of leaf N or P concentration for several evergreen (circles) and deciduous (inverted triangles) swamp shrubs. The species are: *Lyonia lucida*, *Cyrilla racemiflora*, *Clethra alnifolia*, *Itea virginica*, and *Leucothoë racemosa*. The regression lines and the 95% confidence intervals are shown.

was considerable overlap among species for all leaf characteristics (table 2). For example, net photosynthesis expressed per unit leaf mass was significantly lower for *L. lucida*, an evergreen, compared with any of the deciduous species. But *C. racemiflora*, also an evergreen, had a rate similar to the deciduous shrubs (table 2). Across species, net photosynthesis reported on a dry-mass basis ( $A_{mass}$ ) was inversely related to SLM (linear regression model;  $r = -0.53$ ,  $P < .001$ ,  $n = 214$ ). Leaf N and P contents were also significantly lower for evergreen than deciduous shrubs, but most of this difference was related to the very low concentrations for the evergreen shrub *L. lucida* (tables 1, 2). For selected data, SLM was negatively correlated with instantaneous PNUE ( $r = -0.44$ ,  $P < .001$ ,  $n = 213$ ) and weakly correlated

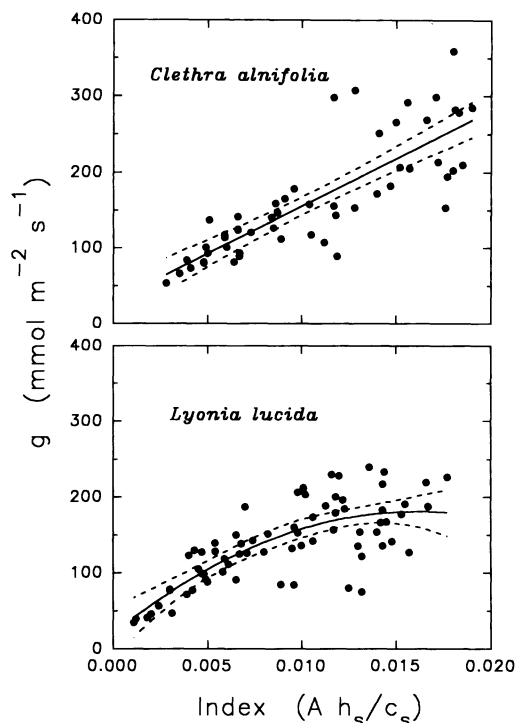


Fig. 2 Empirical models of stomatal conductance for *Clethra alnifolia* (deciduous) and *Lyonia lucida* (evergreen). The model, derived by Ball et al. (1987), predicts stomatal conductance ( $g$ ) as a function of net photosynthesis and the partial pressures of  $CO_2$  ( $C_s$ ) and water vapor ( $h_s$ ) at the leaf surface. The slope of the regression lines represents stomatal responsiveness to the combined influence of these variables. The regression lines include the 95% confidence intervals. A second order polynomial is shown for *L. lucida*. The slopes for the regression equations are shown in table 3.

to PPUE ( $r = -0.18$ ,  $P = .01$ ,  $n = 213$ ). These correlations were also statistically significant ( $P < .01$ ) when run with the entire data set ( $n = 368$ ); however, the correlation coefficients were very low.

The discriminant analysis provided highly significant differentiation among species based on the physiological and leaf structural attributes from table 2. The multivariate test statistics (Wilk's Lambda, Pillai Trace, and Hotelling Lawley Trace  $F$ -statistic) were all highly significant ( $P < .001$ ). The first discriminant axis was positively correlated with SLM,  $A_{area}$ , and stomatal conductance ( $g$ ), and negatively correlated with N and P concentration and  $A_{mass}$ . The second axis was negatively correlated with SLM and positively with all other variables. SLM provided the strongest differentiation among species. Overall, the discriminant analysis was able to place 66% of the cases (measured leaves) within the correct species. But, the analysis placed 92% of the deciduous leaves with deciduous species and 81% of the evergreen leaves with evergreen species.

Across species,  $A_{mass}$  was significantly correlated with tissue N and P ( $P < .001$ ,  $n = 213$ ; fig.

Table 3

STOMATAL CONDUCTANCE ( $g$ ) AND STOMATAL RESPONSIVENESS (slope) TO THE COMBINED INFLUENCE OF PHOTOSYNTHESIS, LEAF-SURFACE HUMIDITY, AND SURFACE  $CO_2$  CONCENTRATION

Species	Slope	$r^2$	$g_{max}$ (mmol/m <sup>2</sup> /s)
Evergreen:			
<i>Cyrilla racemiflora</i> . . . . .	8.7	.54	198c
<i>Lyonia lucida</i> . . . . .	7.6	.61	158a
Deciduous:			
<i>Clethra alnifolia</i> . . . . .	12.5	.67	176ac
<i>Itea virginica</i> . . . . .	7.1	.51	109b
<i>Leucothoë racemosa</i> . . . . .	8.5	.54	124b

Note. Data were selected to reflect maximum photosynthetic rates (Material and methods). Responsiveness is defined as the slope of the regression of stomatal conductance on the index illustrated in figure 2. All of the slopes and  $y$ -intercepts were significantly different from 0 ( $P < .05$ ), and the  $y$ -intercepts varied among species from .03 to .07. Values followed by different letters are statistically different at  $P < .05$ . The group mean conductance for evergreen species (171 mmol m<sup>-2</sup> s<sup>-1</sup>) was significantly different from the group mean conductance for deciduous species (134 mmol m<sup>-2</sup> s<sup>-1</sup>).

1). The correlations between  $A_{area}$  and N or P per unit area were, however, not significant ( $P > .1$ ).

Leaf longevity may influence the responsiveness of stomata to environmental conditions and thus influence water-use efficiency. The response of stomata to combined variation in net photosynthesis and humidity and  $CO_2$  concentrations at the leaf surface was examined with an empirical model (see Material and methods; fig. 2). We treated the slope of conductance as a function of the index derived from the model as a measure of the responsiveness or sensitivity of the stomata. With the exception of *L. lucida*, this model yielded a linear relationship between stomatal conductance and the composite index. For ease of comparisons among species, we also assumed a linear model for *L. lucida*. The deciduous species *C. alnifolia* had the highest stomatal responsiveness, measured as the slope of conductance versus index, and the highest maximum stomatal conductance,  $g_{max}$  (table 3). However, there was no clear gradient between stomatal responsiveness and SLM; *I. virginica* and *L. lucida* had similar stomatal responsiveness, yet these species represent the extremes of SLM.

Based on the supplemental leaf collections from May 1990, evergreen species had slightly higher (less negative)  $\delta^{13}C$  values than the deciduous species (table 4;  $-27.79$  compared with  $-28.39\%$  for evergreen and deciduous species, respectively), indicating a lower intercellular  $CO_2$  concentration and higher water-use efficiency for the evergreens. For species for which SLM was measured (table 2),  $\delta^{13}C$  was positively correlated with SLM ( $r = .92$ ;  $P = .026$ ) and inversely correlated with PNUE ( $r = -.96$ ;  $P = .011$ ). There was no re-

lationship between  $\delta^{13}C$  and leaf N, P, or PPUE in these collections.

In leaf tissues collected in May 1990 and July 1991, mean concentrations of N (%ODM) were higher in deciduous species compared to evergreens (ANOVA  $P < .006$ ; table 4). However, as a result of their greater SLM, evergreen species had greater N per unit leaf area (mg/cm<sup>2</sup>) in the July 1991 collections ( $P < .0001$ ). For P there was no difference in concentration (%ODM) between leaf type in May. Deciduous species had significantly higher P concentrations (%ODM) than evergreen species in July 1991 ( $P < .0001$ ), but this difference was not significant when the data were expressed per unit of leaf area.

At leaf abscission, evergreen leaves had lower concentrations (%ODM) of N and P than deciduous leaves ( $P < .0001$ ), but this difference was significant only for P when the data are expressed per unit leaf area ( $P < .0006$ ). Retranslocation of P was greater among evergreen species than among deciduous species ( $P < .0001$ ), with *C. racemiflora* showing more than 90% retranslocation of P. Evergreen and deciduous species showed no difference in the retranslocation of N per unit of leaf area. Mean specific leaf mass in *L. lucida* was 234 g/m<sup>2</sup> in abscising leaves (vs. 165 g/m<sup>2</sup>; table 2), indicating the potential for significant dilution of leaf nutrient content by the accumulation of photosynthetic products and leaf thickening before abscission. For *L. lucida*, nitrogen retranslocation was 57.7% when expressed per unit of leaf mass but was only 36.6% when expressed per unit of leaf area. In other species there was little difference in the calculated percent retranslocation using concentration per unit mass or per unit leaf area.

#### WATER RELATIONS

Changes in shoot and stem water potential during the morning indicated inherent resistance to water flow in the soil-plant-atmosphere continuum for *L. lucida* and *I. virginica* (fig. 3). During the day, the nontranspiring covered shoots were presumably in equilibrium with stem water potential. The water potentials of aluminum-wrapped shoots were ca.  $-.1$  MPa in the early morning. These high values represent the equilibrium water potential between the plant and water/substrate. By midday, water potentials of transpiring shoots decreased to below  $-0.8$  MPa. Given that the root systems were inundated, this decrease may indicate a significant resistance to water flow from the substrate/water to the transpiring surfaces in the leaves. The difference in water potential between freely transpiring shoots and the stem, as measured with the covered shoots, further indicates that resistance from the stems through the leaves may be an important limitation to water flux in these species. As the

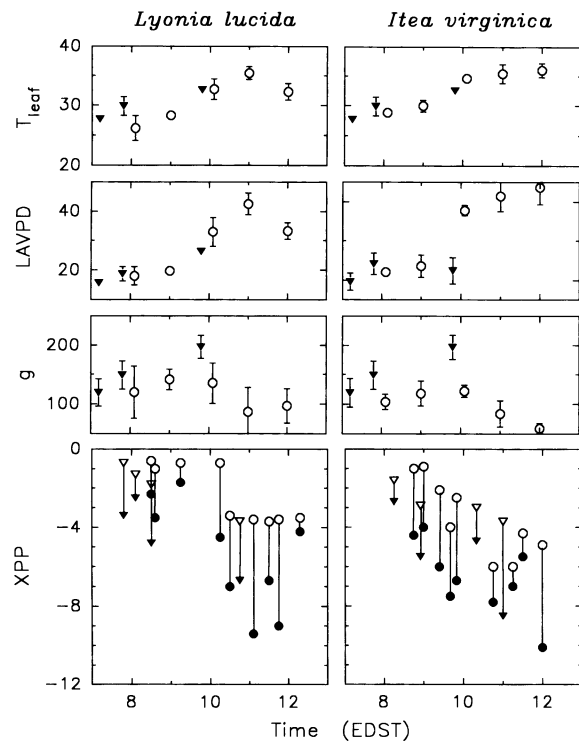
Table 4

## NITROGEN AND PHOSPHORUS CONTENT, CARBON ISOTOPE RATION, AND RETRANSLLOCATION EFFICIENCY FOR EVERGREEN AND DECIDUOUS SHRUBS

Attribute	Evergreen			Ever-green vs. deciduous	Deciduous			
	<i>Pieris phillyrifolia</i>	<i>Ilex cassine</i>	<i>Cyrilla racemiflora</i>		<i>Lyonia lucida</i>	<i>Decodon verticillatus</i>	<i>Itea virginica</i>	<i>Leucothoë racemosa</i>
$\delta^{13}C$	-27.33a	-28.14ab	-28.1ab	-27.32a	-27.16a	-28.73ab	-28.34ab	-29.36b
Fresh leaves:								
Nitrogen:								
May 1990 %	.71a	1.17ab	1.03ab	.69a	1.89c	1.31b	1.03ab	1.08ab
July 1991 %	...	...	1.21a	.82b	...	1.13a	1.12a	1.25a
July 1991 (mg/cm <sup>2</sup> )	...	...	.149a	.128ab	...	.099b	.114b	.126ab
Phosphorus:								
May 1990 %	.054ab	.078ab	.05b	.054ab	.139c	.083a	.048b	.058ab
July 1991 %	...	...	.032ac	.029a	...	.043bc	.037ab	.046b
July 1991 ( $\mu g/cm^2$ )	...	...	3.96a	4.53a	...	3.74	3.76a	4.59a
Abscised leaves:								
Nitrogen:								
November 1991 %	...	...	.38a	.32a	...	.57b	.55b	.61b
November 1991 (mg/cm <sup>2</sup> )	...	...	.039a	.074a	...	.047ad	.05ad	.06bcd
Phosphorus:								
November 1991 %	...	...	.003a	.006ab	...	.022c	.011b	.018c
November 1991 ( $\mu g/cm^2$ )	...	...	.31a	1.35b	...	1.84b	1.01ab	1.78b
Retranslocation %:								
Nitrogen:								
Per unit mass	...	...	68.4a	57.7bc	...	47.1b	47.9abcd	51.5bd
Per unit area	...	...	76.1a	36.6bc	...	49.7b	57.1abcd	50.5bd
Phosphorus:								
Per unit mass	...	...	89.8ab	77.9ad	...	53.1c	73.8bde	58.7ce
Per unit area	...	...	93.7a	67.3bd	...	55.1b	78.3acd	59.7bd

Note. Within a row, mean values followed by different letters are significantly different ( $P < .05$ ). The asterisk indicates that the group mean for evergreen species is significantly different than the group mean for evergreen species ( $P < .05$ , or as indicated in the Results).





**Fig. 3** The pattern of stomatal conductance ( $g$ ) and xylem pressure potential ( $XPP$ ) for *Lyonia lucida* (evergreen) and *Itea virginica* (deciduous) during two consecutive mornings. The observations were terminated at midday when intermittent cloud cover rendered irradiance highly erratic. Data taken on May 19 and 20, 1990, are indicated with open circles and inverted triangles, respectively. The units for the dependent variables are: stomatal conductance ( $g$ ;  $\text{mmol m}^{-2} \text{s}^{-1}$ ); leaf-to-air water vapor pressure difference ( $LAVPD$ ;  $10 \times \text{kPa}$  or  $\text{mbar}$ ); xylem pressure potential ( $XPP$ ;  $\text{MPa} \times 10$ , or bars). For the water potential data, open symbols are for branches that were wrapped in aluminum foil and the connected closed symbols are for adjacent freely transpiring branches. Values are means of five independent measurements  $\pm$  SD, except for water potential data, where each value is a single measurement.

differences in water potential between the substrate, shoots, and leaves increased after 1000 hours, stomatal conductance ( $g$ ) decreased. Thus, moderate water deficits caused by high resistance to water flow during times of high evaporative demand may have caused a reduction in stomatal conductance for these species (fig. 3).

### Discussion

The leaf life span of the evergreen species *Lyonia lucida* and *Cyrtilla racemiflora* is approximately 18 mo, whereas the leaves of the deciduous species *Clethra alnifolia*, *Itea virginica*, and *Leucothoe racemosa* live for 6–7 mo (W. H. Schlesinger, personal observation). Despite this clear difference in leaf longevity, physiological traits did not sort cleanly into two groups representing evergreen or deciduous species. There was considerable overlap in physiological traits among species. These five species formed a gradient of

sclerophylly, and leaf photosynthetic characteristics varied continuously among species with variation in SLM. *Lyonia lucida*, an evergreen, and *C. alnifolia* and *I. virginica*, two deciduous species, formed the extremes of this gradient and clear distinctions in their mass-based photosynthetic characteristics were evident ( $A_{\text{mass}}$ , PNUE, and PPUE; table 2). Similarly, Reich et al. (1992) found that leaf physiological characteristics were more similar between deciduous and evergreen species with leaves lasting 9–10 mo and 2–3 yr, respectively, than between deciduous species with leaf longevity of 2–3 mo and 9–10 mo. Thus, evergreenness per se is not meaningful in comparisons of physiological function without consideration of leaf structure, as measured by SLM.

The suite of photosynthetic traits associated with variations in SLM among swamp shrubs supports previous conclusions derived from comparisons of plants with disparate physiognomy (DeLucia and Schlesinger 1991).  $A_{\text{mass}}$  was lower for the evergreen than deciduous species (table 2), but the photosynthetic rate on a leaf area basis ( $A_{\text{area}}$ ) was not consistently different between leaf types. Reich et al. (1992) found a better relation for  $A_{\text{mass}}$  than for  $A_{\text{area}}$  against leaf longevity in a literature survey of a large number of species. For  $A_{\text{area}}$ , the evergreen *C. racemiflora* had the highest rates, and the species representing the extremes of SLM, *L. lucida* and *I. virginica*, had similar rates. These results are consistent with the observation that area-based photosynthetic rates of deciduous plants were only about 15% higher than those of evergreen plants in a bog in southern Canada (Small 1972).

We were surprised to find such large variation in the N and P content for leaves of the same species, age, and position among the shrubs of the Okefenokee swamp. At Hubbard Brook, the coefficient of variation was 7.2%–9.6% for N and 0%–25% for P for several deciduous and evergreen trees (Likens and Bormann 1970). The maximum coefficient of variation for N and P for Douglas fir measured over 2 yr and on two soil types was 10.5% and 18.2%, respectively (van den Driessche 1974). In the swamp, the coefficient of variation was as high as 36% and 67% for N and P, respectively. These swamp shrubs must have differential access to nutrient-rich microsites in the underlying peat, since one would expect that the nutrient content of the well-mixed swamp water that bathes their roots is relatively uniform. The poor correlation between N and P within species (table 1) indicates that the uptake of these limiting nutrients may be uncoupled in the swamp environment.

Maximum photosynthetic rate measured on a dry-mass basis ( $A_{\text{mass}}$ ) was correlated with leaf N and P (fig. 1). A high proportion of leaf N is invested in ribulose biphosphate carboxylase

(Evans 1989), and the correlation between leaf N and  $A_{\text{mass}}$  is likely to represent a functional relationship (Field and Mooney 1986). Reich et al. (1992, p. 370) suggest that “the photosynthesis-leaf N relationship among species should be considered universal when expressed on a mass, but not on a leaf area, basis.” The weak, albeit statistically significant correlation between  $A_{\text{mass}}$  and leaf P indicates that P may also limit photosynthesis in this swamp habitat. Dilution of P concentrations in leaf tissues during the growing season (May vs. July; table 4) and the higher retranslocation efficiencies for P also indicate that P may be in especially short supply for plant growth in Okefenokee Swamp.

For the swamp shrubs, high  $A_{\text{mass}}$  was also associated with high PNUE and low SLM. In an extensive survey of  $C_3$  plants, Field and Mooney (1986) observed a similar relationship for PNUE. They propose that low PNUE may be functionally related to the high SLM of evergreens; the leaves of these species may invest proportionally more N in nonphotosynthetic functions such as defensive compounds, and these leaves may also have relatively high cell wall resistance to gas diffusion. The slightly lower integrated intercellular  $\text{CO}_2$  concentration for the evergreen species as a group, indicated by less negative  $\delta^{13}\text{C}$  (table 4), supports the idea that internal resistance to gas diffusion is greater in the leaves of evergreen than deciduous swamp shrubs (Lloyd et al. 1992).

PNUE and PPUE provide measures of the efficiency of nutrient use on an instantaneous leaf basis. They do not necessarily indicate lifetime NUE or the efficiency of nutrient use on a whole-plant basis. For the swamp shrubs, the instantaneous measures of NUE in photosynthesis (PNUE and PPUE) were inversely related to NUE in retranslocation; evergreen shrubs had higher retranslocation efficiency yet low PNUE compared with deciduous shrubs. There was no consistent difference in PPUE among shrubs with different leaf longevity. Similar observations for PNUE are reported for a variety of species by DeLucia and Schlesinger (1991) and Reich et al. (1992). Instantaneous measures of photosynthetic NUE, while providing information about leaf-level partitioning and efficiency of nutrient use, do not provide meaningful ecological information regarding patterns of whole-plant nutrient use. Given the greater longevity of evergreen leaves, lifetime carbon gain per unit leaf N or P may be considerably higher for this leaf-type (Escudero et al. 1992). Moreover, a more integrated measure of whole-plant nutrient use, such as nutrient reabsorption prior to leaf abscission, indicates that evergreen species may have substantially higher NUE than deciduous species, especially for phosphorus among the shrubs of Okefenokee swamp (table 4).

Evergreen swamp shrubs showed higher rates of retranslocation of P per unit of leaf mass, and they dropped leaves of extremely low nutrient content compared with the deciduous shrubs. These characteristics provided the most clear distinction between evergreen and deciduous shrubs. Retranslocation of P in excess of 90% has also been observed for *C. racemiflora* in pocosin bogs of North Carolina (Walbridge 1991). Regardless of the method of calculation, retranslocation of P was greater than retranslocation of N in every species. This contrasts with the findings of Chapin and Kedrowski (1983), who report 52% retranslocation of N and 43% retranslocation of P among a wide range of species in the boreal forest. Walbridge (1991) also found higher retranslocation of P than N among five species in pocosin bogs, and he observed relatively low retranslocation of N (36.1%) in *L. lucida*, similar to our results. High rates of P retranslocation may be an adaptation to low P availability in ombrotrophic habitats, such as Okefenokee.

The preponderance of evergreen species and sclerophyllous leaves, apparent adaptations to xeric conditions, in bog and swamp habitats has led to the speculation that anaerobic conditions in these habitats cause “physiological drought” (Schimper 1898). Low  $\text{O}_2$  concentration causes reduced root growth and water uptake, but a comparison of the water potential of bog plants with adjacent upland plants provided no evidence for unusually low water potentials in the bog plants (Small 1972). Bog plants may, however, have closed their stomata at relatively high water potentials to avoid drought. Our observation that *L. lucida* and *I. virginica* had potentially significant internal resistances to water uptake resulting in late-morning to midday stomatal closure, supports the concept that water acquisition or transport is hindered in the swamp habitat. Similarly, Schlesinger and Chabot (1977) observed that decreased stomatal conductances at midday were associated with an increase in shoot water potentials of *L. lucida* and *C. alnifolia*, well before the waning of afternoon irradiance. Shoot water potentials never declined below  $-1.01$  and  $-1.25$  MPa in these species, respectively, compared with a midday water potential of  $-1.72$  for *Lyonia ferruginea* in upland habitats (Schlesinger and Chabot 1977). This apparent manifestation of water stress in the swamp habitat (midday stomatal closure related to high soil plant atmosphere continuum resistance) may be linked to low P availability. In addition to anaerobic conditions, low P has been shown to decrease root hydraulic conductivity and water uptake in terrestrial plants (Radin and Boyer 1982; Radin and Eidenbock 1984). Thus, water stress should not be dismissed as an evolutionary force on swamp shrubs.

Our results indicate that, for shrubs with similar physiognomy, the evergreen habit does not pose a limitation to instantaneous net photosynthetic rates expressed on a leaf area basis. The construction cost of producing evergreen leaves may be higher, based on higher SLM, than it is for deciduous leaves, and evergreen leaves had lower photosynthesis on a dry-mass basis and lower PNUE and PPUE. These costs are largely offset by the ability to acquire carbon throughout the year in the moderate climate of the Okefenokee swamp; the ability to maximize carbon gain per unit nutrient by extended leaf longevity

and efficient recycling of nutrients may be highly adaptive in this P-limited habitat.

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