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Photosynthetic Competence of an Endangered Shrub, Lindera melissifolia

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PHOTOSYNTHETIC COMPETENCE OF AN ENDANGERED SHRUB, *LINDERA MELISSIFOLIA*

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ABSTRACT

Net photosynthesis and water relations were investigated *in situ* for a population of *Lindera melissifolia* in northeast Arkansas. Photosynthetic light use efficiency was found to be characteristic of a shade plant. Response of photosynthesis to temperature and CO_2 was insensitive over ranges found during the growing season. High water use efficiency was demonstrated, but under typical conditions of low light this was marginally beneficial. In comparison with competing understory plants, the species proved to be photosynthetically competent. The data are evaluated in terms of the survival potential of the species.

INTRODUCTION

Lindera melissifolia (pondberry) is an understory species of seasonally flooded bottomland hardwood forest in the southeastern United States (Klomps, 1980). It is listed as endangered by both the US Fish and Wildlife Service and the Arkansas Department of Natural Heritage. In Arkansas the habitat is exclusively the bottoms and edges of small shallow seasonal ponds in old dune fields in the northeastern part of the state. Dunes were formed from glacial outwash, and have eroded to land of low relief which is in row crops, except for depressed features such as the ponds (Saucier, 1978). Ponds fill during winter rains, usually to depths of 50 cm or less, and tend to retain water until after expansion of forest leaves. Water depth over pondberries has not been observed to exceed 40 cm in Arkansas. Pond size ranges up to several hectares, but pondberry typically exists in stands no more than 50 m across. Populations are well isolated from each other, either by cropland or by ponds having no pondberries (Wright, 1989a).

There is no indication that *Lindera melissifolia* has recently spread to new sites in Arkansas. It is therefore of prime concern that it survive in sites it now occupies, if it is to remain extant. The species reproduces by vigorous sprouting from underground rhizomes, and from seed (Wright, 1989b). Seed production has been low and erratic in 1986 through 1989, and very few seedlings have been found. Existence of some single-sex stands suggests that seed reproduction has been ineffective in this dioecious species, and that present stands represent the vegetative descendents of relatively few ancestors (Wright, 1989a).

In most locations pondberry makes closed shrub canopies with little competition from other shrubs and vines, but there are several potential competitors including *Brunnichia ovata, Smilax glauca, Sassafras albidum* and *Callicarpa americana*. This study evaluated the photosynthetic competence of pondberry during periods of spring flooding, summer drought, and low light intensity common to its habitat, including some comparisons with competing species.

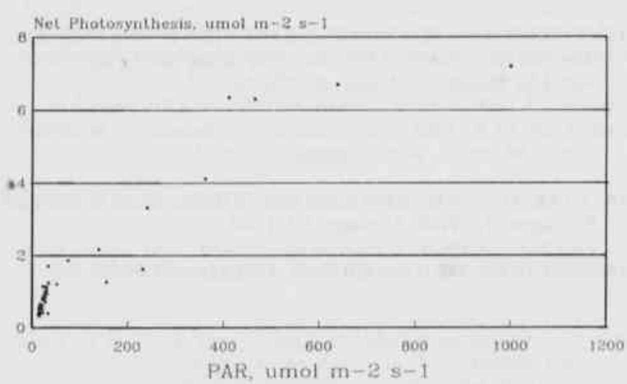
METHODS

A population in Woodruff County, AR was visited 6 times between first leaf expansion (May 12) and shortly before the onset of leaf senescence (Sept. 29). One visit was also made to a site near Swifton in Jackson County on July 14. Net photosynthesis and stomatal conductance were determined on randomly selected leaves during the course of the day, using a closed system LI-6200 Portable Photosynthesis System (LI-COR, Inc., Lincoln, NE). A 1 1 LI-COR chamber was suported by tripod so that the leaf could be enclosed in its natural orientation. UP to 5 readings were obtained from a single leaf, with the chamber open for a minimum of 60 s between readings. CO_2 span was 1 or 2 ppm for shaded leaves, and up to 5 ppm for leaves in full light. Leaf temperature was measured by a thermocouple in contact with the abaxial surface, and rose less than 1 C during runs. For each of approximately 600 rate measurements during the season, the system recorded photosynthetically active radiation (PAR), CO_2, leaf temperature and other critical variables.

Shoot water potential (WP) was determined at the start and end of each day's field work, using a PMS pressure bomb (PMS Instruments, Corvallis, OR). Leaf WP and osmotic potential were determined at the end of each day's field work, using screen cage thermocouple psychrometers (J.R.D. Merrill Specialty Equipment, Logan, UT) according to the method of Walker and Oosterhuis (1982).

RESULTS

Light intensity. Light reaching the pondberry leaves was typically at 1 to 2% of full sun PAR, or 15 to 30 umol $m^{-2}\ s^{-1}$. Leaves reached about 20% of their light-saturated rate of net photosynthesis at these low intensities (Fig. 1). Net photosynthesis was attained at PAR as low as 5 umol $m^{-2}\ s^{-1}$, and was highly correlated with light intensity ($r^2 = .86$, $P < .00001$).



PHOTOSYNTHESIS vs. LIGHT
Figure 1. Net photosynthesis of *Lindera melissifolia* related to light intensity.

In sun flecks light intensity exceeded 1000 umol $m^{-2}\ s^{-1}$. Comparable intensities wer reached in large canopy gaps. Where pondberries occurred in these large gaps they produced a thicker sun leaf capable of over twice the rate of net photosynthesis as shade leaves in sun flecks of comparable intensity. At light levels greater than 970 umol $m^{-2}\ s^{-1}$, ambiant CO_2 of 350 ± 10 ppm and leaf temperature of 37 ± 1 C, net photosynthesis of sun leaves was 9.9 umol m^{-2} s^{-1}, while net photosynthesis of shade leaves was 4.4 umol m^{-2} s^{-1} (t-test $P<0.0001$).

Temperature. Daytime leaf temperatures under the closed tree canopy were generally between 25 and 35 C during the growing season. In low light characteristic of this habitat (20-35 umol m^{-2} s^{-1}) net photosynthesis was not correlated with temperature over the range 24.15 - 33.4 C ($r^2=.09$, $P>.05$). In the large canopy gap containing plants with sun leaves, leaf temperatures on July 14 ranged from 34.28 to 41.29 C. Net photosynthesis of these well-lit leaves was also not correlated with temperature ($r^2=.004$, $P>.9$).

Carbon dioxide. Ambient CO_2 levels ranged from around 400ppm early in the day to 350 ppm from late morning on through the end of the light period. During the morning transition net photosynthesis was weakly correlated with CO_2 (366-408ppm, leaf temp 28 ± 2 C, PAR 15-20 umol m^{-2} s^{-1}, $r^2=.25$, $P<.05$). At slightly higher light intensities, PAR 30-36, there was no significant correlation between net photosynthesis and CO_2 over a range of 351-398ppm.

Water relations. Leaf and shoot WP ranged between -0.5 MPa and -1.0 MPa throughout the season whenever soil moisture was high (above $-.01$ MPa in the root zone). On 18 August after a period with little rain, leaf and shoot WP were between -1.0 and -2.0 MPa, with soil WP from -0.1 MPa to -1.0 MPa. Analysis of Variance (ANOVA) revealed no significant differences in plant moisture stress among dates, beginning and end of days, or method of determination ($F=0.67$, $P>.8$).

Under midday levels of CO_2 (350 ± 15 ppm) and low light (PAR 15-30 umol m^{-2} s^{-1}), net photosynthesis was correlated with stomatal conductivity ($r^2=.2$, $P<0.01$) but not with leaf WP ($r^2=.04$, $P>0.10$ for PMS bomb, $r^2=.01$, $P>0.5$ for psychrometer). At PAR above 200 umol m^{-2} s^{-1} in the same CO_2 range, net photosynthesis was correlated with both stomatal conductivity ($r^2=.36$, $P<.001$) and leaf WP (PMS bomb $r^2=.74$, $P<.0001$; psychrometer $r^2=.60$, $P<.0001$).

The above water relations results were obtained on data gathered throughout the growing season. Data from one day, June 14, were used in addition to calculate water use efficiency (WUE), net photosynthesis/stomatal conductivity. Regression analysis revealed correlation of photosynthesis with stomatal conductivity ($r^2=.60$, $P<0.0001$) and with WUE ($r^2=.65$, $P<.0001$).

Competition. Net photosynthesis and stomatal conductance were determined for competing species in the shrub layer and compared with performance of pondberry under the same conditions. Environmental parameters were: temperature, 30 ± 2 C; PAR 25-30 umol m^{-2} s^{-1}; CO_2 360 ± 15 ppm. Results are shown in Table 1.

Table 1. Net photosynthesis and stomatal conductance, umol CO_2 m^{-2} s^{-1}.

	photosynthesis	conductivity
Brunnichia ovata	1.05 ns	0.21 *
Callicarpa americana	0.97 ns	0.13 ns
Lindera melissifolia	1.04	0.10
Smilax glauca	1.02 ns	0.14 ns
Sassafras albidum	0.80 ***	0.05 ***

T-test comparisons with Lindera melissifolia, ns=P>.05; *=P<.05; ***=P<.001

DISCUSSION

With rare species found in a few isolated locations scattered over a considerable range, it seems likely that distribution was once more continuous. An important question is whether loss of stands has been due to stochastic events, either natural or man-caused, or to natural selection. If survival has been due to chance, extant populations would not necessarily be well adapted to their sites, whereas forces of natural selection would tend to have weeded out poorly adapted populations. Although limited largely to one population, this study indicates that pondberry possesses several physiological adaptations appropriate to its habitat, and may therefore have been selected for the sites where it grows.

In its dune ponds under hardwood forest canopies, pondberry clearly escapes some stresses. Light levels are low, daytime leaf tempratures are moderated, and transpiration stress is thereby reduced. Net photosynthesis was competent at light levels typical of shaded conditions, and indicated that the species possess properties of shade plants (Boardman, 1977). Net photosynthesis did not respond significantly to leaf temperature over ranges found throughout the day and season. Since temperature is typically correlated with net photosynthesis (Pearcy *et al.*, 1987), it must be that other limiting factors are more critical here. Light is a likely critical factor at the low irradiances normally found in pondberry habitat.

CO_2 was weakly correlated with photosynthesis at very low (15-20 umol m^{-2} s^{-1}) light but not in slightly brighter conditions (30-36 umol m^{-2} s^{-1}) typical of the shaded habitat. Thus response to CO_2, widely demonstrated at higher light levels in many studies (Strain and Bazzaz, 1983) is apparently suppressed under these conditions of light limitation, as found by Zangerl and Bazzaz (1984) for 6 co-occurring disturbed site annuals.

A review by Strain (1985) suggested that stomatal conductance and CO_2 may cancel each other in their combined effect on net photosynthesis. As pointed out by Farquhar and Sharkey (1982), stomata impose less limitation on photosynthesis at low irradiances. Leaf water potential did not correlate with net photosynthesis under typical shaded conditions (15-30 umol m^{-2} s^{-1}), but only under high light (above 200 umol m^{-2} s^{-1}). Gauhl (1979) demonstrated a similar response of shade ecotypes of *Solanum dulcamara*.

The above findings indicate that in the benign environment where it grows, pondberry is buffered against some potential stresses. Other woody competitors may of course enjoy the same buffered conditions, and could conceivably respond more favorably to them. Of the 4 principal competitors, none showed more efficient rates of net photosynthesis, and one, *Sassafras albidum*, was less efficient. At the same time its stomatal conductivity was lower, making it potentially more drought-tolerant. Another competing species, *Brunnichia ovata*, had stomatal conductivity higher than pondberry, increasing its susceptibility to drought, but gained no advantage in net photosynthesis. I have found that under drought more severe than occurred during 1988, the competing species became deciduous more rapidly than pondberry (Wright, 1989a). Thus *Lindera melissifolia* in general displayed photosynthetic competence comparable to that of its competitors under undisturbed conditions.

Although an efficient photosynthesizer in low light, pondberry can respond to large canopy gaps with the production of sun leaves (Wright, 1989a). These had more than twice the photosynthetic capacity of shade-grown leaves, well within the fivefold potential range suggested by Bjorkman (1981). Net photosynthesis of competing woody understory species was not measured under large gap conditions, but they were observed to grow vigorously. The vines *Brunnichia ovata* and *Smilax glauca* easily overtopped pondberries. Along with vigorous growth of herbaceous old-field species in large gaps (Wright, 1989a), this suggests that pondberries could be suppressed in large canopy gaps.

Percent of total daily photosynthesis occurring in light flecks under the closed canopy was not evaluated. While this may be appreciable (Chazdon, 1986), it does not appear to work to the detriment of pondberry.

While the pond sites have saturated soils into the growing season, soil water potential will drop in summer droughts. Even though 1988 was considered a dry year, precipitation was fairly timely at the study site, with soil WP observed dropping to -1 MPa on only one date. Across the range of leaf WP on June 14, when soil WP was high, pondberry demonstrated good stomatal control. Net photosynthesis was well correlated with both stomatal conductivity and WUE on this date, when irradiance ranged from 15 to 1000 umol m^{-2} s^{-1}.

Lindera melissifolia thus proves to be photosynthetically competent in a dune pond site in Arkansas. If the forest canopy were opened to permit large light gaps this picture could change, but in undisturbed dune ponds the species appears fairly secure. Clearing for farming may be constrained by the "Swamp Buster" provisions of the 1985 Farm Act, but permitted agricultural interference with dune hydrology still has the potential for altering pond depth or duration, thus affecting growth of competing species. It is also not known whether the species, which is dioecious, is sexually dimorphic in ways that affect physiological competence. The questions of hydrology and sexual dimorphism are currently under investigation.

It appears that under the newly unified Federal methodology for identifying and delineating wetlands (Anthony V. Nida, Corps of Engineers, pers. comm.), all the ponds and possibly their surrounding dunes will quality for protection. This will enhance survival of pondberry in Arkansas.

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