Eco-physiology of *Acer saccharum* Trees on Glade-like Sites in Central Missouri

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Abstract: Although sugar maple (*Acer saccharum* Marsh.) is not considered drought tolerant, it is common on xeric limestone glade-like sites in central Missouri. *Acer saccharum* on such sites may be a drought-tolerant ecotype or may have access to deep water supply through bedrock cracks. We investigated these possibilities during the 1990 growing season by comparing water relations and photosynthetic rates of *A. saccharum* trees growing on glade-like and typical upland sites.

Late-summer drought caused reductions in pre-dawn leaf water potential, but there were no significant differences in this parameter between trees growing on the two sites, nor were there differences in patterns of diurnal Ψ_l. Net photosynthetic rate (P_{net}) did not differ between sites either under dry or moist soil conditions. Regression analysis of responses of P_{net} and several environmental factors revealed no differences that would indicate differential physiological adaptation of trees between sites. It is most likely that *A. saccharum* trees growing on glade-like sites have access to deep water and are not a drought-tolerant ecotype.

Sugar maple (*Acer saccharum* Marsh.) is becoming an increasingly important species in the oak-hickory forests of Missouri (Nigh et al. 1985, Pallardy et al. 1988). Studies over the last 20 years have shown that oak species are regenerating poorly and that *A. saccharum* is now entering large sapling and small tree strata in many stands (Rochow 1972, Nigh et al. 1985, Pallardy et al. 1988).

The success of *A. saccharum* over *Quercus* spp. is due in large degree to the former's superior shade tolerance, i.e., its ability to survive better than species such as black oak (*Quercus velutina* Lam.), northern red oak (*Q. rubra* L.) and white oak (*Q. alba* L.) under low light conditions until an opening in the canopy occurs (Hinckley et al. 1978, Weber et al. 1985). Hett and Loucks (1971) reported that *A. saccharum* seedlings could survive, at a low rate of growth, for 10 or more years in the forest understory where light intensity generally was low. The ability of understory *A. saccharum* to utilize low light levels was further demonstrated by Weber et al. (1985). In this study, it was reported that up to 65 percent of the net carbon gain in this species occurred when photosynthetic photon flux density (PPFD) was between 50 and 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

Success of *A. saccharum* may be hampered by its relatively low drought tolerance, particularly in cases where trees achieve canopy status on drier sites, a situation in which transpirational demand would be substantially greater. *Acer saccharum* is considered less drought tolerant than the four oak species previously mentioned (Hinckley et al. 1978, Hinckley et al. 1979, Bahari et al. 1985). However, paradoxically, *Acer saccharum* is common on xeric glade-like sites in central Missouri (Rochow 1972, Nigh et al. 1985, Pallardy et al. 1988). These sites are characterized by shallow soil with high pH and low water holding capacity, which developed in limestone residuum (Nigh et al. 1985). Two hypotheses concerning the development of *A. saccharum* on these sites have been advanced. Rochow (1972) suggested that *A. saccharum* trees on these sites were in fact

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a drought tolerant genotype that were able to colonize these poor sites. Nigh et al. (1985) suggested that either *A. saccharum* is more drought tolerant than previously thought or that on these sites it is able to develop a root system that penetrates cracks in the limestone bedrock, thereby acquiring access to water that accumulates in cavities between beds (Gates 1983).

The objective of this study was to examine the water relations and photosynthetic characteristics of two groups of *A. saccharum* trees—one group growing on a typical upland site, the other on a glade-like site—to determine whether *A. saccharum* on glade-like sites might be a drought-tolerant genotype or whether these trees have access to more abundant soil moisture than suggested by the xeric nature of the site.

MATERIALS AND METHODS

Study Area

The experiments were conducted at the Thomas H. Baskett Wildlife Area (BWA), formerly referred to as the Ashland Wildlife Area, located in southern Boone County, Missouri (38°N, 92°W). BWA is a 890-ha reserve owned and managed by the University of Missouri. The area is diverse in its cover types with old fields, plantations and second-growth hardwood forest (dominant canopy trees ranging from age 65 to 150 years) located in patches throughout the area. The area is underlain by limestone with the dominant soil types being: 1) Steep Stony Land, which is a broad classification for rocky slopes covered with a thin layer of soil and 2) Weller silt loam, which is an upland soil derived from loess parent material overlying glacial till (Pallardy et al., 1988).

The area selected for the experiments was chosen based on the presence of glade-like and upland sites in close proximity (< 200 meters) to one another. The second-growth forest occupying both sites has previously been described (Rochow 1972, Pallardy et al. 1988). The northern (Upland) site was a gentle East-facing slope in which the soil was relatively deep (> 1 m) with no bedrock outcroppings present. Dominant species on this site included *Q. alba* and *Q. velutina* and an understory dominated by *A. saccharum*. The Glade-like site was on a steep Southeast-facing slope possessing a shallow (≤ 15 cm estimated depth) poorly-developed soil, and abundant limestone outcroppings. Dominant species on the Glade-like site included *A. saccharum*, chinkapin oak (*Quercus muehlenbergii* Engelm.) and eastern redcedar (*Juniperus virginiana* L.) with an understory that included species characteristic of prairies and xeric glades (e.g., sensitive brier [*Schrankia uncinata* Willd.], rose verbena [*Verbena canadensis* (L.) Britt.], puccoon [*Lithospermum canescens* (Michx.) Lehm., long-bracted wild indigo [*Baptisia leucophaea* Nutt.]).

Plant Material

Five *A. saccharum* trees were selected at each site. All were in the understory and less than 15 cm dbh. Trees were selected based on the following criteria:

1) availability of a large number of leaves and twigs within reaching distance,
2) healthy and vigorous appearance,
3) similarity in exposure (which was not more than 50 percent coverage by the canopy),

The same five upland and four of five glade-like site trees were sampled throughout the study. One glade-like site tree suffered severe insect damage in August and a different tree was selected for the final two sampling days.

Sampling Procedures

Pre-dawn leaf water potential (Ψ_{pd}), diurnal leaf water potential (Ψ_l) and diurnal net photosynthetic rate (P_{net}) were measured on five dates in 1990: June 11 and 12 (days 162 and 163); August 30 and September 4 (days 242 and 247) and September 20 (day 263). Days 162 and 163 followed a week in which 11.7 cm of rain fell at nearby Columbia Regional Airport (11 km distant). Days 242 and 247 were associated with a period of summer drought during which only 1.5 cm of rain fell in an 18 day period and day 263 was selected following two days in which about 1.5 cm of rain fell, partially recharging the surface soil.

Pre-dawn and Diurnal Physiological Measurements

One twig from each of five Upland and five Glade-like site trees was collected prior to sunrise. Twigs were sealed in a plastic bag with a moist paper towel. After all ten samples were collected, Ψ_{pd} was measured with a pressure chamber, using a pressurization rate of 0.005 MPa·s^{-1} (Ritchie and Hinckley 1975). Water potential was measured on twigs because *A. saccharum* leaves bubble profusely from the petiole, preventing accurate endpoint determination (Bahari et al. 1985).

Net photosynthesis was measured on two leaves per tree for each of the five control and each of the five exposed trees for a total of 20 measurements for each time period. Measurements were taken at four times: 0700-0800, 1000-1200, 1400-1500 and 1700-1800 hours. Net photosynthesis was measured with a LI-6200 Portable Photosynthesis System fitted with a 1 L leaf chamber (Li-Cor Inc., Lincoln, NE, USA). Photosynthetic Photon Flux Density (PPFD in μmol·m^{-2}·s^{-1}) was measured during measurement of P_{net} by a quantum sensor attached to the leaf chamber. Leaf temperature (T_l) was measured by a thermistor appressed to the lower leaf surface during P_{net} measurement and vapor pressure difference between leaf and air (VPD) was calculated from this variable and relative humidity of the air as measured in the cuvette. The analyzer was calibrated twice daily using bottled gas of a known CO_2 concentration.

Immediately following measurement of P_{net}, a twig was clipped from the sample tree and sealed in a plastic bag with a damp paper towel. Leaf Ψ was measured with a pressure chamber as described previously.

Data Analysis

The experiment was analyzed by repeated measures analysis of variance (PROC GLM, SAS Institute, Inc. 1982) with plants and times considered as repeated measures. Unless otherwise noted, least square means were calculated and mean comparisons performed if the treatment F-test was significant ($p \leq 0.05$). Multiple regression analysis of environmental variables and site on P_{net} also was conducted to examine the possibility of genetic differences in responses of trees on the two sites to environmental factors.

RESULTS

Pre-dawn Leaf Water Potential

Seasonal changes in Ψ_{pd} were evident in *A. saccharum* trees from both sites (Table 1). Analysis of variance of Ψ_{pd} indicated that there was a significant influence of sample day (i.e., representing variation in soil moisture), but no effect of treatment (Upland versus Glade-like site) nor was there an interaction effect of soil moisture and site (Table 1). Pre-dawn Ψ was significantly greater for trees sampled during periods when soil was moistened by recent rains.

Table 1.—Mean values of predawn and diurnal leaf water potential (Ψ_{pd}, Ψ_l) and diurnal net photosynthetic rate (P_{net}) of *Acer saccharum* trees growing on Upland (U) and Glade-like (G) sites. Within a column mean values not superscripted with the same letter are significantly different ($p \leq 0.05$). There were no significant differences between sites for either Ψ_{pd} or diurnal Ψ_l on any sample day.

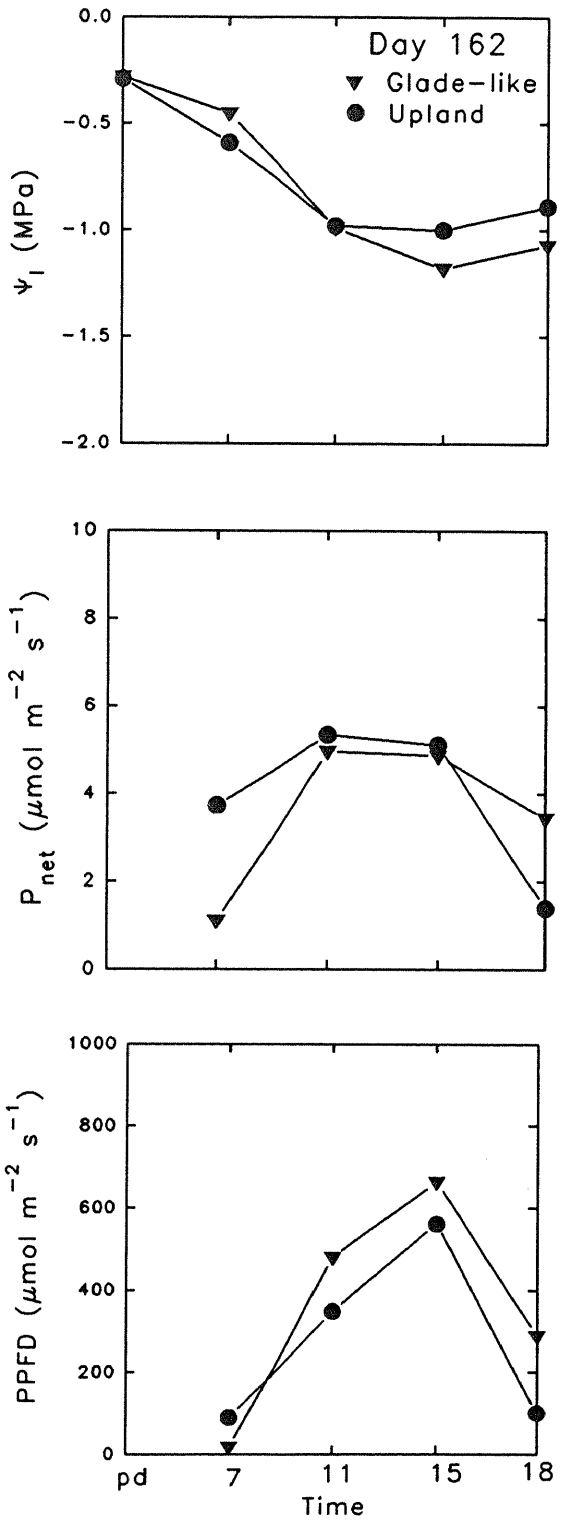
	Ψ_{pd} (MPa)		Ψ_l (MPa)		P_{net} (μmol m^{-2} s^{-1})	
Day	U	G	U	G	U	G
162	-0.29^a	-0.28^a	-0.86^a	-0.93^{ab}	3.89^a	3.60^a
163	-0.21^a	-0.27^a	-0.95^{ab}	-0.81^a	3.88^a	3.08^a
242	-0.72^b	-0.60^b	-1.34^{cd}	-1.27^c	3.54^a	3.48^a
247	-1.13^c	-1.16^c	-1.47^d	-1.35^{cd}	1.86^b	3.22^a
263	-0.41^b	-0.50^b	-0.83^a	-1.07^b	1.97^b	1.28^b

Diurnal Leaf Water Potential

The diurnal pattern of leaf water potential was similar for both control and exposed trees for all five sampling days (Figures 1, 2). Leaf Ψ for both Upland and Glade-like site trees was generally lowest in mid-afternoon, and in all but one case (Glade-like site trees on day 247) Ψ_l had recovered at least partially by late afternoon. Analysis of variance indicated that mean diurnal Ψ_l responded to soil moisture ($p \leq 0.05$), but there was no effect of site. Diurnal Ψ_l tended to decline and rise in concert with Ψ_{pd}.

Net Photosynthetic Rate

Net photosynthetic rate followed light intensity for both Upland and Glade-like site trees under both moist and dry soil conditions (Figures 1, 2). Net photosynthetic rate increased with PPFD except in cases where mean light intensity exceeded 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$, in which case P_{net} declined (e.g., Figure 1). Diurnal patterns of PPFD and P_{net} were generally consistent for all five sampling days and for trees on both sites. Peak P_{net} generally occurred in the early or mid-afternoon; subsequent declines in P_{net} preceded the recovery of Ψ_l. There was no significant effect of site on P_{net} and no systematic relationship between soil moisture (represented by Ψ_{pd} and, indirectly, Ψ_l) and P_{net} over the course of the study (Tables 1, 2). Although late-season declines in P_{net} were observed, they had no discernible relationship to soil moisture patterns; rather, they were more closely related to diurnal PPFD ($p \leq 0.05$). While results of multiple regression analysis of P_{net} versus site and PPFD, Ψ_l, T_l and VPD (Table 2) revealed relationships between environmental variables and P_{net}, there were no differences in response of P_{net} to environmental variables between sites. The apparent site difference in response of P_{net} to PPFD was actually related to variation in mean PPFD levels between Upland and Glade-like sites (mean PPFD on these sites was 296 and 149 $\mu mol\ m^{-2}\ s^{-1}$, respectively).



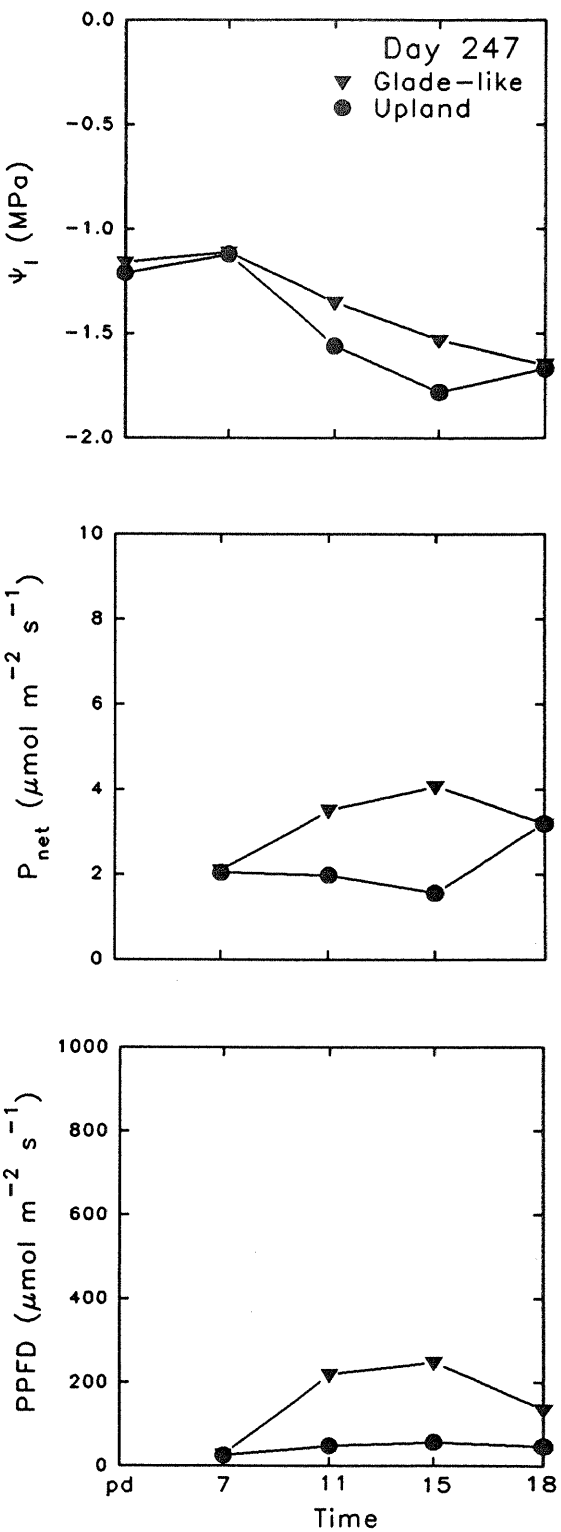


Figure 1. (Left).—Diurnal cycle of mean light intensity (PPFD), net photosynthetic rate (P_{net}) and leaf water potential (Ψ_l) of Upland (•) and Glade-like (▽) site trees for a sample day representing moist soil conditions (Day 162).

Figure 2. (Right).—Diurnal cycle of light intensity (PPFD), net photosynthetic rate (P_{net}) and leaf water potential (Ψ_l) of Upland (•) and Glade-like (▽) site trees for a sample day representing dry soil conditions (Day 247).

Table 2.—Results of multiple regression analysis of net photosynthetic rate as a function of site and environmental variables (diurnal leaf water potential [Ψ_l], photosynthetic photon flux density [PPFD] leaf temperature, [T_l]) and vapor pressure difference between leaf and air [VPD]).

Independent variable	Source		
	Variable	Site	Variable x Site
Ψ_l	ns[a]	ns	ns
PPFD	**	ns	**
T_l	**	ns	ns
VPD	**	ns	ns

[a] ns = not significant ($p > 0.05$); ** = significant ($p \leq 0.01$)

DISCUSSION

Analysis of Ψ_{pd} showed that trees on both sites experienced a period of drought late in the summer, despite precipitation that was above normal for the entire growing season. Pre-dawn leaf water potential approximates the equilibrium water potential reached between the plant and the soil as transpiration is negligible at this time (Ritchie and Hinckley 1975). No differences in Ψ_{pd} were observed between Upland and Glade-like site trees under moist or dry soil moisture conditions. It can be inferred, then, that *A. saccharum* on both sites had approximately equal access to a water supply, both during drought and in moist soil.

There were no indications, at least at the level of the phenotype, that the *A. saccharum* population growing on the Glade-like site were more drought tolerant. Bunce et al. (1977) suggested that species which were more dehydration tolerant would be better able to sustain gas exchange under drought than species which were less dehydration-tolerant. This line of reasoning would suggest that a dehydration-tolerant genotype of *A. saccharum* should show greater P_{net} during drought conditions. Analysis of the responses of P_{net} to environmental variables indicated no phenotypic differences between trees growing on the two sites in physiological responses to leaf water stress, nor to light intensity or leaf temperature. It must be noted that the drought developed during 1990 was not as severe as in certain other years (e.g., Hinckley et al. 1979, Bahari et al. 1985). This was reflected in the lack of a relationship between leaf water status and gas exchange (Table 2). It is possible that during an extreme drought year site differences might have been evident, but the evidence presented here offers no support for such a possibility.

These facts, coupled with the lack of significant differences between Upland and Glade-like site trees in Ψ_{pd} and Ψ_l as outlined previously, argues against the existence of a dehydration-tolerant genotype of *A. saccharum*, as was suggested by Rochow (1972). Nigh et al. (1985) further reported that there were no obvious morphological distinctions between *A. saccharum* inhabiting the glade-like limestone outcroppings and those growing on more mesic sites. These authors suggested that *A. saccharum* might have access to deep sources of water through root growth into the cracks between limestone beds. Excavation of dolomitic limestone beds by Gates (1983) revealed large cavities between the beds which could serve as reservoirs of water. The evidence presented here is consistent with this proposed mechanism.

LITERATURE CITED

Bahari, Z.A., S.G. Pallardy and W.C. Parker. 1985. Photosynthesis, water relations, and drought adaptation in six woody species of oak-hickory forests in central Missouri. For. Sci. 31: 557-569.

Bunce, J.A., L.N. Miller and B.F. Chabot. 1977. Competitive exploitation of soil water by five eastern North American tree species. Bot. Gaz. 138: 168-173.

Gates, J. 1983. The hydrology of a glade in southwest Missouri. M.S. Thesis, University of Missouri, Columbia. 164 p.

Hett, J.M. and O.L. Loucks. 1971. Sugar maple (*Acer saccharum* Marsh.) seedling mortality. J. Ecol. 59: 507-520.

Hinckley, T.M., et al. 1978. Leaf conductance and photosynthesis in four species of the oak-hickory forest type. For. Sci. 24: 73-84.

Hinckley, T.M., et al. 1979. A severe drought: impact on tree growth, phenology, net photosynthetic rate and water relations. Am. Midl. Nat. 102: 307-316.

Nigh, T.A., S.G. Pallardy and H.E. Garrett. 1985. Sugar maple-environment relationships in the River Hills and central Ozark Mountains of Missouri. Am. Midl. Nat. 114: 235-251.

Pallardy, S.G., T.A. Nigh and H.E. Garrett. 1988. Changes in forest composition in central Missouri: 1968-1982. Am. Midl. Nat. 120: 380-389.

Ritchie, G.A. and T.M. Hinckley. 1975. The pressure chamber as an instrument for ecological research. pp. 165-254. In Advances in Ecological Research, (A. Macfayden, ed.), Vol. 9. Academic Press, New York.

Rochow, J.J. 1972. A vegetational description of a mid-Missouri forest using gradient analysis techniques. Am. Midl. Nat. 87: 377-396.

SAS Institute, INc. 1982. User's guide to the Statistical Analysis System: Statistics. SAS Institute, Cary, North Carolina.

Weber, J.A., et al. 1985. Analysis of gas exchange in seedlings of *Acer saccharum*: integration of field and laboratory studies. Oecologia 65: 338-347.