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Ecophysiological attributes of the native *Acer saccharum* and the exotic *Acer platanoides* in urban oak forests in Pennsylvania, USA

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Summary When the exotic *Acer platanoides* L. (Norway maple) and the native *A. saccharum* Marsh. (sugar maple) grow together in the understories of urban *Quercus* forests in the eastern USA, average annual height growth increments are nearly twice as large in *A. platanoides* as in *A. saccharum*, 19.26 ± 3.22 versus 10.01 ± 1.69 cm. We examined several ecophysiological mechanisms that might be associated with the superior invasive ability and growth of *A. platanoides* in two urban oak forests in Pennsylvania. Leaf longevity was 12 days greater in *A. platanoides* than in *A. saccharum*. In addition, leaf mass/leaf area ratio was greater in *A. platanoides* than in *A. saccharum* (2.67 ± 0.03 versus 2.32 ± 0.02 mg cm^{-2}); however, leaf thickness was significantly lower in *A. platanoides* than in *A. saccharum* suggesting that *A. platanoides* contains more dense palisade and mesophyll cell layers than *A. saccharum*. Field net photosynthesis (mass basis) and photosynthetic light response curves (area basis) indicated significantly greater carbon assimilation, and nitrogen and phosphorus use efficiencies in *A. platanoides* than in *A. saccharum*. *Acer platanoides* also exhibited higher water use efficiency than *A. saccharum* (0.88 ± 0.12 versus 0.32 ± 0.09 mmol CO_2 mol^{-1} H_2O). *Acer platanoides* exhibited significantly lower osmotic potentials than *A. saccharum*, but a similar relative water content at zero turgor. We conclude that *A. platanoides* utilizes light, water and nutrients more efficiently than *A. saccharum*.

Keywords: height growth, leaf structure, Norway maple, photosynthesis, sugar maple, water relations.

Introduction

Historically *Quercus* species have dominated upland forests throughout much of the eastern deciduous biome of the USA (Watts 1980, Webb 1988, Abrams 1992, Nowacki and Abrams 1992). Although several early ecologists concluded that *Quercus* spp. were the true climax species in eastern North America (Clements 1936, Braun 1950), recent studies indicate that *Quercus* spp. are typically early or midsuccessional and that most *Quercus* forest types are transitional (Hix and Lorimer 1991, Abrams and Downs 1990, Abrams 1992). Exceptions to this trend occur on extremely xeric and nutrient-poor sites where *Quercus* spp. may form an edaphic climax (Harshberger 1916, Adams and Anderson 1980, Reich and Hinckley 1980). The transitional nature of *Quercus* spp. on mesic sites may be due to the absence of catastrophic events, particularly fire, during the 20th century (Lorimer 1985, Fralish et al. 1991, Szeicz and MacDonald 1991, Abrams 1992).

The major replacement species of *Quercus* forests in the eastern USA are *Acer saccharum* Marsh. (sugar maple), *A. rubrum* L. (red maple), *Prunus serotina* Ehrh. (black cherry), *Fraxinus americana* L. (white ash) and *Fagus grandifolia* Ehrh. (American beech) (Lorimer 1984, Smith and Vankat 1991, Abrams 1992). However, in many urban woodlots an exotic ornamental species native to Europe, *A. platanoides* L. (Norway maple), is dominating the regeneration layers and young tree classes (Webb and Kaunzinger 1993). In central Pennsylvania, *A. platanoides* is much more aggressive than the native *A. saccharum* and is generating additional competition for *Quercus* regeneration.

The objective of this study was to compare the growth and related ecophysiological variables of *A. platanoides* and *A. saccharum*. We hypothesized that the efficient use of light, water and nutrients, or some combination of these three resources was responsible for the observed difference in growth between *A. platanoides* and *A. saccharum*. We attempted to quantify either the availability of light, water and mineral nutrients, or the efficiency with which the species use each resource in carbon assmimilation, or both.

Materials and methods

Study sites

Two sites, Walnut Springs and Corl Road, both near State College, PA, were selected for observation and measurement. Both sites are typical of mixed *Quercus* forests in central Pennsylvania that are experiencing a shift to more shade-tolerant species as a result of the long-term absence of forest fires. The Walnut Springs site is being subjected to a large influx of exotic seed from nearby suburban ornamental plantings of *A. platanoides*, whereas the Corl Road site is more isolated and is not subject to the influx of exotic seed. As a result, Walnut Springs (40°48′ N, 77°50′ W, altitude 335 m) contains naturally established saplings of both *A. saccharum* and *A. platanoides*, whereas Corl Road (40°47′ N, 77°53′ W, altitude 348 m), which is located approximately 2.4 km from Walnut Springs and about 0.5 km from the nearest cultivated street tree, contains only *A. saccharum* saplings.

The soils at Walnut Springs and Corl Road are characterized as a Hagerstown series with a silt loam texture and moderate drainage (Braker 1981). Because no major topographic features are located between the Walnut Springs and Corl Road sites, the meteorological data from the Pennsylvania State University Meteorological Station, located between Walnut Springs and Corl Road, is applicable for both sites. Average (30-year) daily minimum winter temperatures (December–February) range from –5 to –7 °C, whereas average (30-year) daily maximum summer temperatures (June–August) range from 26 to 28 °C. Average total annual precipitation is 979 mm with little monthly variation in rainfall throughout the year.

The 10-ha Walnut Springs woodlot is composed of 73-year-old even-aged mixed *Quercus* hardwoods. The dominant overstory species are *Q. velutina* Lam. (black oak), *Carya glabra* (Mill.) Sweet (pignut hickory), *P. serotina, Q. rubra* L. (northern red oak), *Q. alba* L. (white oak) and *A. saccharum*. The sapling and seedling size classes are primarily *A. rubrum*, *A. platanoides*, *P. avium* L. (mazzard cherry), *P. serotina* and *A. saccharum*. The 7-ha Corl Road site is composed of predominantly 70-year-old mixed hardwoods with several 140-year-old *Quercus* trees left after extensive logging in 1920 and 1950 (Abrams and Nowacki 1992). Dominant overstory species include *A. saccharum*, *Q. alba*, *P. serotina* and *Juglans nigra* L. (black walnut), whereas the sapling and seedling understory is almost exclusively *A. saccharum*. Average canopy coverage is 90% at Walnut Springs and 93% at Corl Road. Stand basal area is also similar at the sites, indicating similar competition for light and water.

Leaf longevity

In spring 1991, 15 *A. saccharum* saplings at Corl Road were tagged within a circular plot of approximately 75 m^2. Similarly, 15 saplings each of *A. platanoides* and *A. saccharum* were located and tagged on separate plots at Walnut Springs. Approximately every 2 days during bud break (April 15 to May 10), the size of the expanding terminal bud and subsequent leaf were measured on each tagged sapling, and the date when the immature leaf reached a width of 1 cm was recorded. Observations continued until all terminal buds produced leaves. Subsequently in the fall, leaf senescence was monitored (October 15 to November 10) and the date when > 90% of the surface of the terminal leaf was chlorotic was recorded on all tagged saplings. Frequently, leaf abscission occurred within 5 days of discoloration. These two end points were used to calculate leaf longevity.

Soil water

Ecophysiological parameters were measured five times during the 1991 growing season: June 7, June 25, July 11, August 7 and August 23. Predawn (0600 h solar time) xylem water potential and soil water were measured at each site on each sampling date. Xylem water potential (Ψ) was measured on one leaf of each sapling ($n = 15$) at each site with a pressure chamber (PMS Instrument Co., Corvallis, OR). Gravimetric soil water (0–25 cm) was measured on five replicate samples from each site.

Gas exchange

A calibrated open-flow system (Model LCA-2, Analytical Development Co., Herts, U.K.) was used to measure foliar gas exchange. One representative leaf from each of the 15 saplings of each species × site combination was measured four times at 2-h intervals. Bulk leaf water potential was measured on each leaf used for gas exchange measurements on June 25 and August 7, but not on the other sampling dates to minimize damage. Calculations of gas exchange parameters were made according to von Caemmerer and Farquhar (1981) and included: foliar net photosynthesis (A), stomatal conductance to water vapor (g_s), transpiration (J), instantaneous water use efficiency (WUE), leaf temperature, and leaf-to-air vapor pressure deficit (VPD). The leaf measured on each sapling during the second diurnal round was placed in a plastic bag and stored in a cooler for later determination of leaf mass to area ratio (LMA). Leaf area was measured without petioles with an LI-3100 leaf area meter (Li-Cor Inc., Lincoln, NE). Afterward, leaf samples were dried to a constant mass at 70 °C and weighed.

Light response curves

Light response curves were generated by compiling the diurnal observations from each species × site combination over the growing season. Because the saplings were measured *in situ* under natural understory conditions, photosynthetically active radiation (PAR) values were typically not greater than 1500 $\mu mol\ m^{-2}\ s^{-1}$. A Michaelis-Menten model was used in conjunction with an iterative nonlinear curve fitting procedure (PROC NLIN, SAS Institute Inc., Cary, NC) to estimate area-based net photosynthesis from observed PAR and A values (Sheve 1984, Givnish 1988, Kloeppel et al. 1993). This model can be solved for $A = 0$ to estimate the light compensation point:

$$A = \frac{A_{max} \times \mathrm{PAR}}{(\mathrm{PAR} + K) - R_s},$$

where A is net photosynthesis ($\mu mol\ m^{-2}\ s^{-1}$), A_{max} is maximum asymptotic photosynthesis ($\mu mol\ m^{-2}\ s^{-1}$), PAR is photosynthetically active radiation ($\mu mol\ m^{-2}\ s^{-1}$), K is the light saturation constant at one half of predicted A_{max} ($\mu mol\ m^{-2}\ s^{-1}$), and R_s is dark respiration equal to negative A when PAR = 0 ($\mu mol\ m^{-2}\ s^{-1}$).

Tissue water relations

Pressure-volume (P-V) data were obtained within 4 days of each of the June 25, July 11 and August 23 measurement days by sampling one midcrown leaf from 10 of the 15 tagged saplings at each species × site combination before dawn (0600 h solar time). Each leaf was sealed in a dark plastic bag with a damp paper towel and transported back to the laboratory. Samples were not rehydrated to avoid potential shifts in P-V relationships (Parker and Pallardy 1987, Kubiske and Abrams 1991). A $1/\Psi$ versus relative water content (RWC) curve was generated for each leaf by periodically measuring bulk leaf water potential and leaf mass as the leaf dried by free transpiration on the laboratory bench (cf. Robichaux 1984, Turner 1988). Tissue mass at saturated Ψ was estimated by linear regression of P-V data above and including the turgor loss point for each sample (Ladiges 1975, Kubiske and Abrams 1991). Estimated saturated sample mass was then used to calculate RWC. Least squares regression was employed to calculate the P-V parameters (SAS Institute Inc.): osmotic potential at full turgor (Ψ_π^{100}) and zero turgor (Ψ_π^0), and RWC at zero turgor (RWC_0). Bulk modulus of elasticity (ε) between full and zero turgor was calculated according to Robichaux and Canfield (1985).

Leaf structure

Because Kloeppel et al. (1993) found stomatal density, guard cell length and leaf thickness were constant during the growing season, we only measured these parameters on July 19, 1991. Leaf thickness was measured on one fresh leaf from each tagged sapling at each site with an ocular micrometer. Impressions were then made of each leaf abaxial surface with an acetate-acetone technique (Payne 1968, Payne 1970). The direct impressions were then measured with an ocular micrometer and a Whipple density grid to estimate guard cell length and stomatal density, respectively.

Foliar and soil nutrients

Foliar and soil nutrient samples were collected for analysis on August 7 and 23, 1991. One midcanopy leaf was collected from each sapling and randomly allocated to five pooled samples per site. Leaf mass to area ratio was measured as described above. Foliar nitrogen and phosphorus contents were determined and used to calculate nitrogen and phosphorus use efficiency (NUE and PUE, respectively, defined as mass-based *A* divided by foliar N or P concentration, respectively) for each species × site combination. Five random soil samples (0–25 cm) were also collected from each plot and air dried in the laboratory. Foliar and soil samples were digested and analyzed at the Pennsylvania State University Soil and Tissue Analysis Laboratory.

Statistical analyses

Statistical analyses for leaf longevity, gravitational and potential soil water, nutrient content, gas exchange, tissue water relations, and leaf structural parameters were conducted with the SAS software package (SAS Institute Inc.) using one- and two-way general linear models for a completely randomized design, linear and nonlinear regression, and the least squares difference (LSD) mean separation test at $\alpha = 0.05$.

Results

Height growth and leaf longevity

From 1987 to 1991, average annual height growth increment of the *A. platanoides* saplings at Walnut Springs was 19.26 ± 3.22 cm compared with the significantly lower values of 10.01 ± 1.69 and 8.31 ± 1.27 cm for the *A. saccharum* saplings at Walnut Springs and Corl Road, respectively. In 1991, leaf longevity averaged 191 days for *A. platanoides*, and 179 and 180 days for *A. saccharum* at Walnut Springs and Corl Road, respectively.

Site conditions and microenvironment

Monthly average maximum and minimum air temperatures were within 1 °C of 30-year averages (Figure 1). Although precipitation in June 1991 was only 45% of the 30-year average, it recovered to 97 and 80% of the 30-year average in July and August, respectively. Gravimetric soil water was stable during the growing season except for significantly lower values ($P < 0.05$) on August 7 caused by low precipitation during the previous 20 days (Figure 1). On all measurement dates, the *A. saccharum* plot at Walnut Springs had significantly lower gravimetric soil water than the *A. saccharum* plot at Corl Road. Values at the *A. platanoides* plot at Walnut Springs were intermediate between the other two plots.

Soils from all plots had a similar total Kjeldahl nitrogen concentration and pH (Table 1). Soil samples from the *A. pla-*

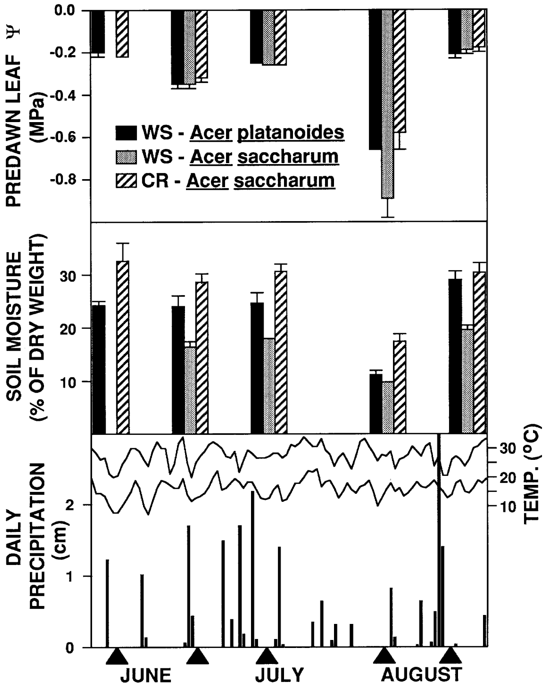

Figure 1. Daily precipitation and temperature profiles for the mid-1991 growing season in central Pennsylvania. Mean (± SE) gravimetric soil water and predawn leaf water potential (Y) are presented for five sampling dates at two sampling sites. The Walnut Springs (WS) site contains one *A. platanoides* and one *A. saccharum* plot, whereas the Corl Road (CR) site contains one *A. saccharum* plot.

Table 1. Soil nutrient concentrations (0–25 cm) and chemical properties (mean ± SE) of two central Pennsylvania sites supporting *A. platanoides* or *A. saccharum*. Nitrogen values are based on total Kjeldahl nitrogen; soil pH was determined from aqueous extractions, and cation exchange capacity (CEC) was obtained from potassium chloride extractions. Means within the same row followed by the same letter are not significantly different using the LSD mean separation test at the $\alpha = 0.05$ level.

Soil parameter	*A. platanoides* Walnut Springs	*A. saccharum* Walnut Springs	*A. saccharum* Corl Road
Nitrogen (% mass)	0.15 ± 0.01 a	0.12 ± 0.01 a	0.15 ± 0.02 a
Phosphorus (ppm)	10.17 ± 1.59 a	10.50 ± 1.15 a	3.17 ± 0.60 b
Potassium (ppm)	59.8 ± 3.4 a	23.4 ± 0.1 b	52.0 ± 13.0 a
Calcium (ppm)	1240 ± 303 b	373 ± 104 c	2007 ± 101 a
Magnesium (ppm)	496.0 ± 117.2 a	124.0 ± 34.2 b	140.0 ± 14.4 b
Soil pH	6.40 ± 0.49 a	5.40 ± 0.26 a	6.23 ± 0.14 a
CEC (meq per 100 g soil)	13.77 ± 1.06 a	6.93 ± 0.12 b	14.30 ± 0.46 a

tanoides plot at Walnut Springs had significantly greater ($P < 0.05$) magnesium concentrations than soil samples from the other plots. Soil samples from the *A. saccharum* plot at Walnut Springs contained significantly lower potassium and calcium concentrations and cation exchange capacity (CEC) than soil samples from the other plots, whereas soil samples from the *A. saccharum* plot at Corl Road contained significantly lower phosphorus concentrations than soil samples from the other plots. Foliar nitrogen concentrations were similar among plots, but foliar magnesium concentrations were significantly lower in *A. saccharum* saplings than in *A. platanoides* saplings (Table 2). Foliar phosphorus and potassium concentrations were similar in *A. saccharum* saplings at both plots regardless of soil concentrations, and foliar calcium concentrations were similar in saplings at all sites. *Acer platanoides* saplings at Walnut Springs had higher concentrations of all foliar nutrients except calcium than the other saplings. The foliar calcium concentrations of *A. platanoides* saplings at Walnut Springs were intermediate between the concentrations found in *A. saccharum* saplings at Walnut Springs and Corl Road. Foliar nutrient contents paralleled foliar nutrient concentrations

The mean seasonal vapor pressure deficit (VPD) was significantly greater ($P < 0.05$) at the *A. saccharum* plot at Corl Road than at the other plots (Table 3). Predawn and mean leaf water potentials were similar in saplings at all plots on all measurement dates except August 7 when saplings in all plots reached their lowest seasonal values. On August 7, *A. saccharum* saplings at Walnut Springs had significantly lower predawn water potentials than *A. platanoides* saplings at Walnut Springs and *A. saccharum* saplings at Corl Road (Figure 1).

Table 2. Foliar nutrient concentrations and contents (mean ± SE) of *A. platanoides* and *A. saccharum* at two central Pennsylvania sites in 1991. Means within the same row followed by the same upper case letter (comparing weight-based nutrient concentration) and means within the same row followed by the same lower case letter (comparing area-based nutrient content) are not significantly different using the LSD mean separation test at the $\alpha = 0.05$ level.

Element	*A. platanoides*—Walnut Springs		*A. saccharum*—Walnut Springs		*A. saccharum*—Corl Road	
	Concentration (% mass)	Content (mg cm^{-2})	Concentration (% mass)	Content (mg cm^{-2})	Concentration (% mass)	Content (mg cm^{-2})
Nitrogen[1]	2.01 ± 0.04 A	6.14 ± 0.13 a	1.99 ± 0.06 A	5.18 ± 0.17 b	2.07 ± 0.04 A	5.82 ± 0.08 a
Phosphorus	0.20 ± 0.01 A	0.62 ± 0.01 a	0.12 ± 0.01 B	0.31 ± 0.01 b	0.12 ± 0.01 B	0.32 ± 0.01 b
Potassium	1.44 ± 0.04 A	4.41 ± 0.15 a	1.22 ± 0.06 B	3.18 ± 0.15 b	1.05 ± 0.04 C	2.96 ± 0.12 b
Calcium	1.79 ± 0.04 AB	5.47 ± 0.17 a	1.70 ± 0.07 B	4.40 ± 0.16 b	1.88 ± 0.02 A	5.28 ± 0.01 a
Magnesium	0.51 ± 0.02 A	1.56 ± 0.01 a	0.32 ± 0.01 B	0.82 ± 0.01 b	0.21 ± 0.01 C	0.59 ± 0.01 c

[1] Total Kjeldahl nitrogen.

Table 3. Seasonal mean vapor pressure deficit (VPD), leaf temperature and leaf xylem water potential (Ψ) (mean ± SE) of natural understory *A. platanoides* and *A. saccharum* saplings at two sites in central Pennsylvania. All parameters were measured four times on each of five sampling dates (except Ψ, which was measured on June 25 and August 7 only) during the 1991 growing season. Means within a row followed by the same letter are not significantly different using the LSD mean separation test at the $\alpha = 0.05$ level.

Variable	*A. platanoides* Walnut Springs	*A. saccharum* Walnut Springs	*A. saccharum* Corl Road
Vapor pressure deficit	1.19 ± 0.04 b	1.24 ± 0.04 b	1.60 ± 0.04 a
Leaf temperature	24.03 ± 0.24 c	24.75 ± 0.24 b	25.65 ± 0.18 a
Leaf xylem water potential	−0.87 ± 0.04 a	−0.83 ± 0.04 a	−0.91 ± 0.04 a

Tissue water relations

Osmotic potentials at full (Ψ_π^{100}) and zero turgor (Ψ_π^0) exhibited a significant ($P < 0.05$) seasonal decline in all saplings (Figure 2). The decline occurred primarily between July 15 and August 25, which coincides with the driest portion of the growing season. On all measurement dates, *A. platanoides* saplings at Walnut Springs had significantly lower (more negative) osmotic potentials than *A. saccharum* saplings at the same site, whereas *A. saccharum* saplings at Corl Road had osmotic potentials that were intermediate in value. Elastic modulus (ε) peaked in both species on July 15 with *A. platanoides* exhibiting greater values than *A. saccharum.* All saplings at Walnut Springs exhibited a seasonal peak in RWC_0 on July 15 with lower values earlier and later in the growing season, whereas *A. saccharum* saplings at Corl Road displayed a significant decline in RWC_0 from June 26 to August 25.

Leaf structure

Stomatal density, guard cell length and leaf thickness were similar among *A. saccharum* saplings at both sites (Table 4); however, the *A. platanoides* saplings at Walnut Springs had significantly lower ($P < 0.05$) stomatal density and leaf thickness than *A. saccharum*, but similar guard cell length. *Acer platanoides* saplings at Walnut Springs had significantly higher LMA values than *A. saccharum* saplings at the same site, whereas *A. saccharum* saplings at Corl Road had intermediate LMA values.

Gas exchange

Daily mean net photosynthesis on a mass basis (*A*) exhibited high variation as a result of the variable understory light regime (Figure 3). Values of *A* were consistently higher in *A. platanoides* saplings at Walnut Springs than in *A. saccharum* saplings at either site. Significant plot differences ($P < 0.05$) were not present on the first sampling date, but were evident later in the season. The *A. platanoides* saplings at Walnut Springs showed a significant seasonal increase in *A*, whereas the *A. saccharum* saplings at Corl Road displayed a significant drop in *A* after July 11 with no subsequent recovery. The *A. saccharum* saplings at Walnut Springs exhibited low values of *A* throughout the season. Stomatal conductance to water

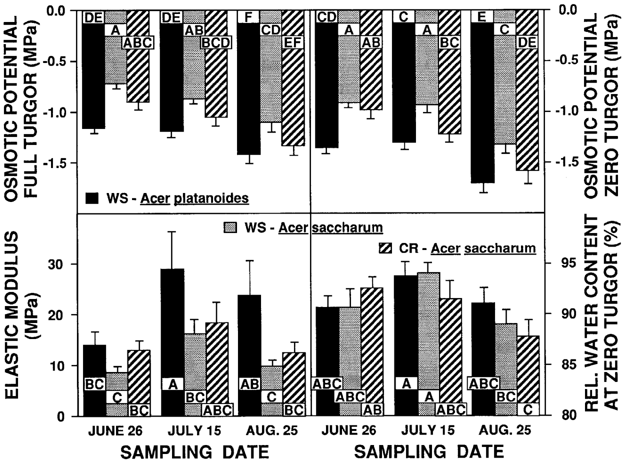

Figure 2. Tissue water relations estimates on three 1991 sampling dates for *A. platanoides* and *A. saccharum* saplings. Both species are located on individual plots at Walnut Springs (WS), but only *A. saccharum* is located at Corl Road (CR). Means (± SE) within a variable labeled with the same letter are not significantly different when compared with the LSD mean separation test at the $\alpha = 0.05$ level.

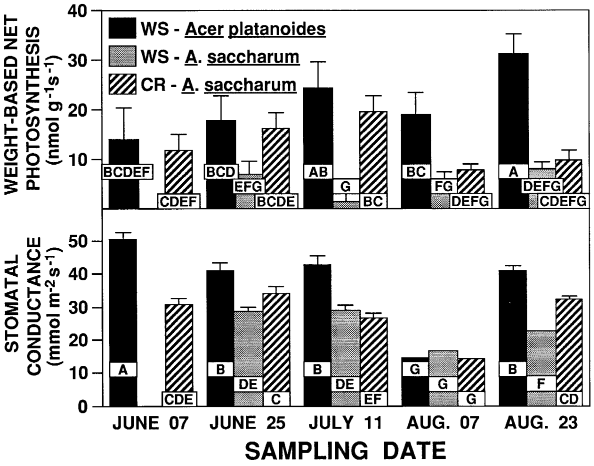

Figure 3. Daily mean net photosynthesis (mass basis) and stomatal conductance to water vapor of understory saplings of *A. platanoides* and *A. saccharum* in central Pennsylvania. Measurements were conducted on two sites, Walnut Springs (WS) and Corl Road (CR), during the 1991 growing season. Means (± SE) within a variable labeled with the same letter are not significantly different when compared with the LSD mean separation test at the $\alpha = 0.05$ level.

Table 4. Stomatal density, guard cell length, leaf thickness and leaf mass to area ratio (LMA) (mean ± SE) of saplings of *A. platanoides* and *A. saccharum* at two sites in central Pennsylvania. The parameters were measured during midgrowing season on July 19, 1991, except for the LMA ratio which was determined on five dates from June 7 to August 23, 1991. Means within a row followed by the same lower case letter are not significantly different using the LSD mean separation test at the $\alpha = 0.05$ level.

Parameter	*A. platanoides* Walnut Springs	*A. saccharum* Walnut Springs	*A. saccharum* Corl Road
Stomatal density (no. mm^{-2})	198.89 ± 8.85 b	232.75 ± 7.98 a	231.77 ± 12.09 a
Guard cell length (μm)	9.16 ± 0.15 a	9.64 ± 0.25 a	9.52 ± 0.27 a
Leaf thickness (μm)	154.95 ± 8.56 b	180.15 ± 8.56 a	174.00 ± 4.58 ab
LMA (mg cm^{-2})	2.67 ± 0.03 a	2.32 ± 0.02 c	2.52 ± 0.02 b
Seasonal range	2.53 to 2.76	2.26 to 2.38	2.45 to 2.59

vapor (g_s) was significantly higher in *A. platanoides* saplings at Walnut Springs than in *A. saccharum* saplings at either site (Figure 3). On August 7, saplings at all sites displayed low g_s values probably as a result of reduced soil water content. *Acer saccharum* saplings at Walnut Springs exhibited significantly lower ($P < 0.05$) mean instantaneous water use efficiency (WUE), defined as A divided by transpiration, than *A. saccharum* saplings at Corl Road or *A. platanoides* saplings at Walnut Springs (0.32 ± 0.09 versus 0.74 ± 0.07 and 0.88 ± 0.12, respectively). Saplings at all sites exhibited a seasonal increase in WUE (data not shown).

Light response curves were similar for *A. saccharum* saplings at both sites (Figure 4); however, *A. saccharum* saplings at both sites had significantly lower A_{max} and K than *A. platanoides* saplings at Walnut Springs (Table 5). Saplings at all three plots had similar respiration rates (R_s) and light compensation points, but nitrogen and phosphorus use efficiencies (NUE and PUE) were significantly higher in *A. platanoides* than in *A. saccharum* on two sampling dates (Figure 5).

Discussion

The greater height growth of *A. platanoides* saplings may be partly explained by their consistently greater rates of A compared with *A. saccharum* saplings. In *A. platanoides* saplings, the values of A_{max} and K were twice those of *A. saccharum* saplings although both species had similar R_s rates and light compensation points. These characteristics may enable *A. platanoides* saplings to maintain maximum carbon assimilation rates throughout the wide range of irradiances and water deficits typical of eastern forest understories (cf. Malkina 1976). Several studies have reported that *A. platanoides* saplings exhibit low rates of carbon assimilation unless their foliage develops in a high light environment (Logan and Krotkov 1968, Lei and Lechowicz 1990, Ellsworth and Reich 1992*a*). The thin, but dense leaves of *A. platanoides*, indicated by low leaf thickness and high LMA, may also facilitate high rates of net photosynthesis as a result of a denser mass of chloroplasts in the palisade and mesophyll cell layers (Wylie 1949, Abrams et al. 1994). However, the denser mass of chloroplasts did not result in enhanced R_s rates and light compensation points.

Although the low soil water content on August 7 resulted in a large decrease in g_s in saplings on all plots, the *A. platanoides* saplings maintained a higher rate of net photosynthesis than the *A. saccharum* saplings thereby further contributing to a more positive carbon balance. In response to the drought, *A. platanoides* saplings exhibited lower osmotic potentials and higher ε (lower tissue elasticity) than *A. saccharum* saplings resulting in a similar RWC_0 in the two species (Abrams 1990, Kloeppel et al. 1994). Seasonal tissue water relations similar to those observed in *A. platanoides* at Walnut Springs have also been observed in drought treated sycamore maple (*A. pseudoplatanus* L.) seedlings, a European relative of *A. platanoides*; that is, decreasing osmotic potentials and increasing ε with no net effect on RWC_0 (Khalil and Grace 1992). The seasonal bell-shaped curve of ε in *A. saccharum* on both sites is similar to that reported by Tyree et al. (1978). Ellsworth and Reich (1992*b*) observed seasonally decreasing osmotic poten-

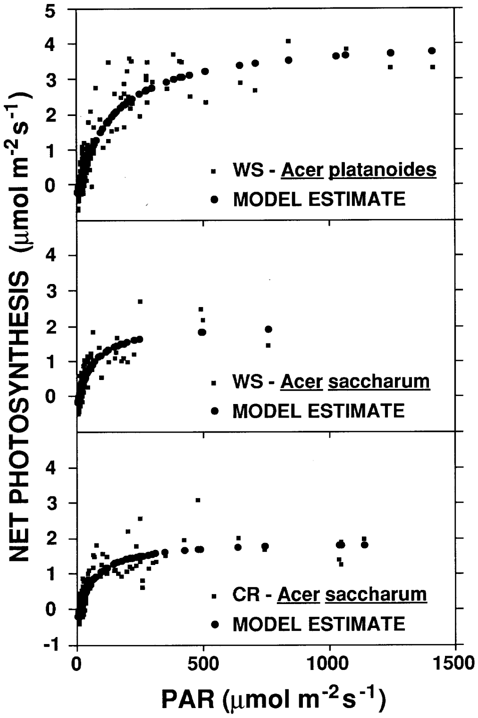

Figure 4. Light response data and Michaelis-Menten model estimates of net photosynthesis on three site × species combinations in central Pennsylvania. *Acer platanoides* was located at Walnut Springs (WS), whereas *A. saccharum* was located at both Corl Road (CR) and WS. Photosynthetically active radiation (PAR) and net photosynthesis measured during the 1991 growing season are both presented on an area basis. The Michaelis-Menten model variable estimates are located in Table 5.

Table 5. Light response curve estimates (mean ± asymptotic standard error) for saplings of *A. platanoides* and *A. saccharum* at two sites in central Pennsylvania during the 1991 growing season. Maximum photosynthesis (A_{max}), dark respiration (R_s), saturation constant (K), residual degrees of freedom (df), and residual mean squares (RMS) were estimated with PROC NLIN in SAS; the light compensation point (LCP) was determined by solving the Michaelis-Menten model for $A = 0$. Means in a column followed by the same letter are not significantly different using the LSD mean separation test at the $\alpha = 0.05$ level. The units for A_{max}, R_s, K and LCP are µmol m^{-2} s^{-1}.

Species	Site	A_{max}	R_s	K	LCP	Residual df	RMS
A. platanoides	Walnut Springs	4.54 ± 0.20 a	0.39 ± 0.07 a	135.25 ± 19.90 a	13	279	0.24
A. saccharum	Walnut Springs	2.42 ± 0.10 b	0.34 ± 0.05 a	58.50 ± 9.58 b	10	236	0.05
A. saccharum	Corl Road	2.30 ± 0.07 b	0.37 ± 0.07 a	57.20 ± 8.98 b	11	275	0.06

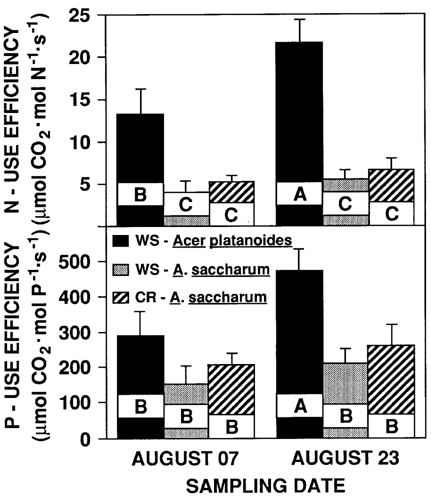

Figure 5. Foliar nitrogen and phosphorus use efficiencies in *A. platanoides* and *A. saccharum* in central Pennsylvania. The daily mean (± SE) of each species at Walnut Springs (WS) and Corl Road (CR) is presented for the two 1991 gas exchange sampling dates nearest to foliar nutrient determination. Within each variable, means labeled with the same letter are not significantly different using the LSD separation test at the $\alpha = 0.05$ level.

tials in *A. saccharum* despite increasing values of predawn Ψ, which is similar to the seasonal dynamics that we observed in *A. saccharum* saplings at both sites. The lack of recovery of net photosynthesis in *A. saccharum* after the dry period suggests that the saplings may have experienced some lasting effect of the drought, such as xylem cavitation (Tyree and Yang 1992, Yang and Tyree 1993).

Leaf phenology and life span may play a role in the carbon balance of exotic species. *Lonicera* spp. (honeysuckle), *Rhamnus* spp. (buckthorn) and *Berberis* spp. (barberry) all exhibit earlier bud break and longer leaf life spans than native understory shrubs thereby extending the photosynthetic season and contributing to a more positive carbon balance (Harrington et al. 1989). *Acer platanoides* is native to higher latitudes in Europe than that of central Pennsylvania (Ambler 1965, Murray 1970, Nowak and Rowntree 1990) which may account for its having a longer leaf life span than *A. saccharum* when growing at a lower latitude. Typically, *A. saccharum* is intermediate in bud break and leaf life span compared with other native tree species in eastern forests (McGee 1986).

The high shade tolerance of *A. saccharum* enables the species to survive for decades in forest understories (Burns and Honkala 1990, Hix and Lorimer 1991). *Acer saccharum* displays an increased growth response whenever canopy gaps are formed (Amthor et al. 1990, Hix and Lorimer 1991, Tryon et al. 1992), and young saplings display plastic allometric patterns when light is limiting (Bonser and Aarssen 1994). Therefore, its ecological and physiological response patterns are well suited for its role as a late successional species in eastern *Quercus* forests.

The biological invasion of the exotic *A. platanoides* into areas currently supporting native understory *A. saccharum* is widespread across the eastern USA (Webb and Kaunzinger 1993). There is concern that *A. platanoides* could become a problematic invader such as *Lonicera* spp. and *Rhamnus* spp. shrubs and the native tree *A. negundo* L. (box elder). *Acer platanoides* is also expanding its range in Europe where it is expected to become a major component of forest communities near Berlin, Germany (Sachse 1988, Sachse et al. 1989). In its natural European range, *A. platanoides* forms large continuous stands over a range of soil types suggesting that the same community dynamics may occur in the USA if its spread continues (Ambler 1965, Ellenberg 1988). Therefore, the ecophysiological attributes as well as the biological and community dynamics of *A. platanoides* forest may play a role in the continued invasion of this exotic species versus the native *A. saccharum* into the understory of *Quercus* forests in the eastern USA.

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