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Photosynthetic characteristics in canopies of *Quercus rubra*, *Quercus prinus* and *Acer rubrum* differ in response to soil water availability

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Abstract Photosynthesis and related leaf characteristics were measured in canopies of co-occurring *Quercus rubra* L. (red oak), *Quercus prinus* L. (chestnut oak) and *Acer rubrum* L. (red maple) trees. Mature (20+ m tall) trees were investigated at sites of differing soil water availability within a catchment (a drier upper site and a wetter lower site). Leaf photosynthetic characteristics differed significantly between species and in response to site and position in the canopy. Photosynthetic capacity (A_{max}) was significantly greater at the wetter site in all canopy strata in *A. rubrum* but not in *Q. rubra* or *Q. prinus*. Our findings for *A. rubrum* are generally consistent with those predicting that species with higher specific leaf area (SLA) will have higher A_{max} per unit leaf nitrogen (N) and that species with leaves with lower SLA (e.g. *Q. rubra* and *Q. prinus*) will have shallower slopes of the A_{max}–N relationship. Importantly, the relationships between A_{max} and N_{area} (and by implication photosynthetic nitrogen-use efficiency, PNUE) differed in *A. rubrum* between the sites, with PNUE significantly lower at the drier site. The lower photosynthetic capacity and PNUE must substantially reduce carbon acquisition capacity in *A. rubrum* under these field conditions. Maximum stomatal conductance (g_{smax}) differed significantly between species, with g_{smax} greatest in *Q. rubra* and *Q. prinus*. In *Q. rubra* and *Q. prinus*, g_{smax} was significantly lower at the upper site than the lower site. There was no significant response of g_{smax} to site in *A. rubrum*. These stomatal responses were consistent with the C_i/C_a ratio, which was significantly lower in leaves of *Q. rubra* and *Q. prinus* at the upper site, but did not differ between sites in *A. rubrum*. Leaf $\delta^{13}C$ was significantly lower in *A. rubrum* than in either *Q. rubra* or *Q. prinus* at both sites. These findings indicate differences in stomatal behaviour in *A. rubrum* which are likely to contribute to lower water use efficiency at both sites. Our results support the hypothesis that the two *Quercus* species, in contrast to *A. rubrum*, maintain photosynthetic capacity at the drier site whilst minimising transpirational water loss. They also suggest, based primarily on physiological evidence, that the ability of *A. rubrum* to compete with other species of these deciduous forests may be limited, particularly in sites of low moisture availability and during low rainfall years.

Keywords Deciduous forest · Photosynthesis · Root-zone water content · Stomatal conductance

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Introduction

Whilst the temperate deciduous forest biome is generally considered to play an important part in global carbon cycling, a detailed understanding of the mechanisms regulating such cycling is limited (Goulden et al. 1996; Bassow and Bazzaz 1998). This is particularly so for interspecific differences in physiology which are likely to influence patterns of forest composition. In addition, the distribution of this biome is likely to be highly sensitive to future environmental change. Under all but the most extreme climate change scenarios, temperate deciduous forests are predicted to both expand and shift to more northern locations, where they are likely to replace

north-eastern mixed forests (Bachelet et al. 2001). Thus, incorporating physiological responses of trees to environmental gradients into models should be an important step in improving predictions of forest carbon budgets and species composition.

Here we examine the potential for species level and environmentally induced differences in (1) photosynthesis and (2) the relationships between photosynthesis and leaf characteristics, in the canopies of three dominant tree species from a temperate deciduous forest in eastern North America [red oak (*Quercus rubra* L.), chestnut oak (*Quercus prinus* L. syn. *Quercus montana* Willd.) and red maple (*Acer rubrum* L.)]. Our study site, at Black Rock Forest in the Highlands Province of New York, is at the northern limit of *Quercus*-dominated temperate deciduous forests. A strong research base exists for forest at the southern limit of this forest type [e.g. Oak Ridge in Tennessee (Gunderson et al. 2000; Wilson et al. 2000) and Coweeta Experimental Forest in North Carolina (Martin et al. 1998; Bolstad et al. 1999; Mitchell et al. 1999)] and for the adjoining northern hardwood forest [e.g. Harvard Forest (Motzkin et al. 1999); Hubbard Brook Experimental Forest (Gill et al. 1998; Likens 1999)]. Black Rock Forest thus represents an important geographic location for the investigation of *Quercus*-dominated deciduous forest responses to environment and future environmental change, as it is located near the leading edge of the hypothesised expansion zone.

Quercus species are adapted to a broad range of soil conditions, particularly with respect to nutrient status and water availability (Abrams 1990; Dickson and Tomlinson 1996). *Quercus* species may be broadly categorised with respect to moisture stress tolerance based on the sites they occupy (Dickson and Tomlinson 1996). On this classification, *Q. prinus* is more drought tolerant than *Q. rubra* (Abrams et al. 1990; Kleiner et al. 1992), although *Q. rubra* is also found on certain xeric sites (Kubiske and Abrams 1992). In comparison to *Quercus* species, those in the genus *Acer* are generally more sensitive to low soil water availability (Bahari et al. 1985), although *A. rubrum* does occur on xeric sites (Kubiske and Abrams 1994).

Both avoidance (e.g. deep rooting, leaf loss) and tolerance (e.g. osmotic adjustment, stomatal control) mechanisms may contribute to drought responses in a given tree species (Ni and Pallardy 1992; Pallardy and Rhoads 1993; Dickson and Tomlinson 1996; Donovan et al. 2000). The extent to which these mechanisms are invoked may change significantly according to the age of the tree (Cavender-Bares and Bazzaz 2000). Although oaks often display high photosynthetic capacity (A_{max}) and maximal stomatal conductance (g_{smax}) in field studies, stomatal control of gas exchange in response to changing water availability is more common in oak species than other co-occurring tree species, including those in the genus *Acer* (Bahari et al. 1985; Ni and Pallardy 1991; Kubiske and Abrams 1993). This may act as an important physiological mechanism influencing the distribution of these species in the field.

In this study, two sampling locations with contrasting soil water availability were chosen within a defined watershed to examine relationships among water availability, leaf morphological and chemical characteristics, and photosynthesis. We hypothesised that the two *Quercus* species, in contrast to *A. rubrum*, would maintain photosynthetic capacity at the drier site whilst minimising transpirational water loss. The relative performance of *A. rubrum* was of particular interest, as it is hypothesised by others that this species will increase in dominance in forests of the eastern United States over the next century (Abrams 1998). Detailed physiological research to assess the likelihood of this prediction is limited (Gunderson et al. 2000).

Materials and methods

Description of study site

The Black Rock Forest is a 1,500-ha scientific preserve within the Highlands Province of New York and was established in 1927. The forest is located at latitude 41°24′ N and longitude 74°01′ E with elevations ranging from 110 to 450 m above sea level. Average annual precipitation is 1,190 mm. Air temperature is strongly seasonal, with monthly averages ranging from –2.7°C in January to 23.4°C in July. The soils are typically shallow, brown forest soils of medium texture, with granite gneiss bedrock or glacial till parent material at depths ranging from 0.25 m at elevated sites to 1 m at lower sites (Olsson 1981). The forest comprises an average of 734 trees per hectare and an average basal area of 21.0 $m^2\ ha^{-1}$ (Table 1). Red oak (*Q. rubra*) is the dominant species and, along with chestnut oak (*Q. prinus*), comprises 66% of the basal area.

Table 1 Density and basal area of the three dominant tree species from upper and lower catchments of the Cascade Brook watershed. Forest-wide data (for the entire Black Rock Forest Reserve) are taken from K.S. and J.B. Friday (unpublished data)

Species	Forest-wide		Upper catchment		Lower catchment	
	Density (stems ha^{-1})	Basal area ($m^2\ ha^{-1}$)	Density (stems ha^{-1})	Basal area ($m^2\ ha^{-1}$)	Density (stems ha^{-1})	Basal area ($m^2\ ha^{-1}$)
Quercus rubra	168	8.9	170	4.8	100	10.3
Quercus prinus	133	5.0	390	15.7	30	1.5
Acer rubrum	227	1.6	110	0.6	190	7.9
Other (32 spp.)	206	5.5	90	2.5	330	5.2
Total	734	21.0	760	23.6	650	24.9

Red maple (*A. rubrum*) has substantially higher stem numbers than any other tree species, accounting for 31% of the stems across all plots, but only accounts for 8% of the basal area (K. Barringer, unpublished data).

Field plots and species

Field plots were located in the Cascade Brook watershed, which comprises 135 ha in the southeastern portion of the Black Rock Forest. Elevations within the watershed range from 210 to 430 m. A 0.10 ha plot at the top (hereafter referred to as upper site) and bottom (lower site) of the watershed represent the field sites in this study. The lower site was at an elevation of 270 m and had a slope of less than 5%. The upper site was a gently sloping face below the ridgeline with a south/southeast facing aspect at an elevation of 350 m. Both stands are of similar age (approximately 120 years) and shared similar disturbance and establishment regimes (Tryon 1930).

The upper site had 760 trees per hectare and a basal area of 23.7 m^2 ha^{-1} (Table 1). *Q. prinus* was the most common tree, followed by *Q. rubra* and *A. rubrum*. *Q. prinus*, white oak (*Q. alba* L.), and *Q. rubra* together comprised 78% of the basal area. *Q. prinus* was most numerous in the overstorey while *A. rubrum* was most numerous in the understorey. The majority of the basal area was in trees 200–300 mm in diameter and only one tree on the plot was larger than 350 mm. The canopy height ranged from 10 m to 16 m.

Tree numbers at the lower site were 650 trees per hectare, but the site had a slightly higher basal area of 24.9 m^2 ha^{-1} (Table 1). *A. rubrum* was the most common tree, followed by *Betula alleghaniensis* Britt. (yellow birch) and *Q. rubra*, although *Q. rubra* made the greatest contribution to stand basal area. *Q. prinus* occurred only on higher microsites. *Q. rubra* dominated the overstorey along with *A. rubrum*, while *A. rubrum*, sugar maple (*A. saccharum* L.) and *B. alleghaniensis* were most common in the understorey. Much of the basal area was in trees 300–400 mm in diameter and the largest tree was nearly 500 mm. The canopy height ranged from 20 to 30 m.

Root-zone water content

Rainfall for 1999 was 84% of the long-term (1870–1996) average for the nearby West Point, N.Y. weather station. For the months preceding our study, rainfall was 141% (January–March) and 45% (April–June) of long-term monthly average. Continuous measurements of volumetric root-zone water content were made during the study period. At each of the sites, four soil water reflectometers (CS615, Campbell Scientific, Logan, Utah) were placed in the upper horizon (10–15 cm) of the soil profile. At 20-min intervals the probes were automatically activated every 10 s for a total of 5 min. The average values over the 5-min measurement interval were recorded on a datalogger (CR10X, Campbell Scientific, Logan, Utah).

Experimental design

Physiological measurements presented here were undertaken in early summer (June 1999). Measurements of photosynthetic and related characteristics were made on fully expanded leaves from three positions in the canopy of each experimental tree (upper fully sunlit leaves for *Q. rubra* and *Q. prinus* but partially shaded sub-canopy leaves in canopy gaps for *A. rubrum*; mid-leaves in the middle third of the canopy; lower leaves on the lowest branches in the canopy). Access to leaves was achieved using a cherry-picker with a 20 m boom. Three to four leaves from at least two separate branches on three individual trees were measured for each species per site (thus n=12–14 leaves per stratum). Leaf carbohydrate, protein, chorophyll, $\delta^{13}C$ and specific leaf area (SLA) analyses were performed on the same leaves used for gas exchange measurements, or on the next fully expanded leaf along the branch.

Gas exchange measurements

Leaf photosynthetic characteristics were determined using portable photosynthesis systems (Li-Cor model 6400, Lincoln, Neb.) equipped with CO_2 control modules. A/C_i response curves were generated following measurements of steady-state responses of photosynthesis (A) to internal leaf CO_2 partial pressures (C_i). External CO_2 partial pressures (C_a) were supplied in 13 steps from 150 to 0 Pa. Measurements were made at each C_a setpoint when photosynthetic gas exchange had equilibrated [taken to be when the coefficient of variation (CV) for the CO_2 partial pressure differential between the sample and reference analysers was below 1%]. This condition was typically achieved in 1–2 min after a stable setpoint had been reached. Measurements were made on clear, warm days between 0930 and 1600 hours. Leaf temperatures were maintained at 25°C using thermoelectric coolers and water vapour pressure deficit was generally held between 1.0 and 1.5 kPa. A constant photon flux density (PFD) of 2,000 µmol m^{-2} s^{-1} was provided by blue-red light emitting diodes mounted above the leaf cuvette.

Analysis of A/C_i response curves involved calculation of parameters potentially limiting to photosynthesis: V_{cmax} (maximum carboxylation rate of rubisco) and J_{max} (RuBP regeneration capacity mediated by maximum electron transport rate). This was achieved using Photosynthesis Assistant (Dundee Scientific, UK) which uses the biochemical model describing A by Farquhar et al. (1980). Comparison of photosynthetic characteristics between sites and canopy positions was assisted by calculation of A_{max} (net photosynthetic rate at a CO_2 concentration of 36 Pa and saturating PFD, 2,000 µmol m^{-2} s^{-1}), g_{smax} (stomatal conductance at A_{max}) and C_i / C_a (the ratio of internal to external CO_2 partial pressure under saturating PFD at ambient C_a).

Leaf carbohydrate and nitrogen and stable isotope analysis

All analyses were determined on leaf material harvested directly following gas exchange measurements. Soluble sugar content and starch content of leaves were determined colorimetrically using a phenol-sulphuric acid technique (Tissue and Wright 1995). Total non-structural carbohydrate (TNC) content was calculated as the sum of soluble sugar and starch. Leaf nitrogen content was determined on dried and ground material using a CNS autoanalyser (Carlo Erba Na 1500, Milan, Italy). Analysis of leaf carbon isotope composition ($\delta^{13}C$) was performed on dried material from the upper canopy level of each tree using only a PDZ Europa 20–20 mass spectrometer with an ANCA-SL combustion system (Crewe, UK). Samples were analysed against a sucrose standard and had a routine precision (±1 SD) of ±0.13‰ for $\delta^{13}C$. Leaf protein content was determined on frozen material using the Bradford technique (Sigma Chemical, St. Louis, USA).

Statistical analysis

Analysis of variance (ANOVA) was used to test for the main effects and interactions of species, site and canopy stratum on photosynthetic and leaf characteristics (S-Plus v3.3, MathSoft, Seattle, USA). A nested model (individual leaves nested within trees) was used to account for pseudoreplication (Underwood 1981). Differences were considered significant if probabilities (P) were less than 0.05. Treatment means were compared by least significant difference to determine whether they were significantly different at the 0.05 probability level (Sokal and Rohlf 1981). Analysis of the relationships between gas exchange characteristics and leaf characteristics was performed using linear regression.

Results

Root-zone water content

Root-zone water content decreased steadily over the month during which this study was conducted (June), but did not change significantly during the actual days of study (Fig. 1). The upper and lower sites differed significantly with respect to water availability (P<0.001). Average root-zone water content was 35.1±1.5% (59% of field capacity) at the lower site and 12.6±0.7% (36% of field capacity) at the upper site during the study period.

Photosynthetic characteristics

Leaf photosynthetic characteristics differed significantly between species and in response to site and position in the canopy (Table 2). Overall, V_{cmax} (maximum carboxylation rate of rubisco) was greater in *Q. rubra* and *Q. prinus* than in *A. rubrum*. Although there was no significant effect of site, there was a significant species × site interaction (P=0.05), with V_{cmax} being significantly greater in *Q. rubra* at the upper site than at the lower site in all three canopy strata. Canopy position had a significant effect on V_{cmax} (P<0.001), with the decrease in the lower strata most pronounced in *A. rubrum*. Determination of J_{max} (RuBP regeneration capacity mediated by maximum electron transport rate) was made difficult by stomatal closure at above ambient CO_2 partial pressures in *Q. prinus* and upper catchment trees of *A. rubrum*. This had the effect of reducing the range of C_i over

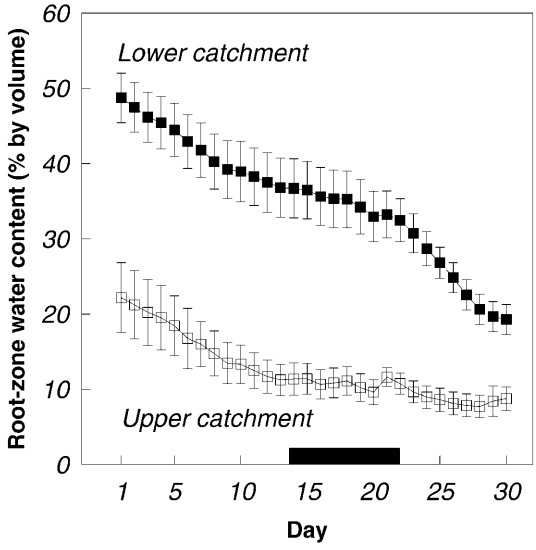


Fig. 1 Root-zone water content from the lower and upper catchment sites used in the present study (June 1999). The *horizontal bar* indicates the period over which the physiological measurements in this study were made

Table 2 Photosynthetic characteristics for leaves in the upper (*U*), middle (*M*) and lower (*L*) strata of canopies of *Quercus rubra*, *Q. prinus* and *Acer rubrum* trees from two sites within a catchment. Values shown are means (± SEM) where n=9–12. Stomatal responses to above ambient CO_2 partial pressures in *Q. prinus* and upper catchment trees of *A. rubrum* made determination of J_{max} not possible in all leaves. Where this is the case, the actual n has been indicated as a superscript. Significance of treatment effect for species (*Sp*), site (*Site*), canopy position (*Pos*) and the interaction between species and site (Sp×S) are indicated as the value of P or as non-significant (*n.s.*). Different letters within rows indicate statistically different values at P<0.05 using least significant difference test of treatment means

Parameter	Canopy position	*Q. rubra*		*Q. prinus*		*A. rubrum*		ANOVA statistics
		Upper catchment	Lower catchment	Upper catchment	Lower catchment	Upper catchment	Lower catchment	
V_{cmax} (µmol CO_2 $m^{-2}s^{-1}$)	U	55.5 (2.7)^{a}	50.3 (2.7)^{a}	49.3 (2.8)^{a}	51.1 (3.2)^{a}	53.0 (3.9)^{a}	50.1 (2.5)^{a}	Sp<0.001
	M	57.6 (3.9)^{c}	49.4 (2.1)^{ab}	57.3 (4.3)^{c}	51.6 (3.0)^{bc}	43.0 (2.4)^{a}	46.7 (2.3)^{ab}	Site n.s.
	L	48.9 (2.8)^{d}	41.2 (3.3)^{bc}	44.4 (3.3)^{cd}	47.8 (3.3)^{d}	32.4 (1.8)^{a}	37.4 (1.7)^{ab}	Pos<0.001
								Sp×S <0.05
J_{max} (µmol CO_2 $m^{-2}s^{-1}$)	U	145 (14.1)^{c}	116 (8.3)^{ab}	112 (11.6)^{3ab}	103 (14.7)^{3a}	136 (20.0)^{3c}	126 (11.2)^{bc}	Sp 0.010
	M	144 (16.3)^{d}	120 (9.3)^{c}	96.3 (23.8)^{2a}	101 (14.6)^{3ab}	94.9 (6.8)^{4a}	115 (3.8)^{bc}	Site 0.028
	L	111 (13.0)^{b}	90.6 (6.1)^{a}	85.6 (–)^{1a}	83.3 (22.9)^{3a}	86.7 (5.7)^{2a}	95.4 (6.1)^{ab}	Pos<0.001
								Sp×S <0.05
A_{max} (µmol CO_2 $m^{-2}s^{-1}$)	U	12.7 (0.54)^{cd}	12.6 (0.49)^{cd}	11.5 (0.60)^{bc}	13.5 (0.90)^{d}	8.21 (0.51)^{a}	11.1 (0.28)^{b}	Sp<0.001
	M	12.7 (0.60)^{cd}	11.6 (0.84)^{c}	12.9 (1.1)^{cd}	13.4 (0.99)^{d}	8.25 (0.30)^{a}	9.8 (0.47)^{b}	Site <0.01
	L	9.0 (0.62)^{b}	9.4 (0.46)^{bc}	10.4 (0.81)^{cd}	11.0 (1.80)^{d}	6.76 (0.34)^{a}	8.5 (0.32)^{b}	Pos <0.001
								Sp×S <0.05
g_{smax} (mol $m^{-2}s^{-1}$)	U	0.214 (0.02)^{a}	0.359 (0.06)^{b}	0.180 (0.01)^{a}	0.385 (0.05)^{b}	0.199 (0.02)^{a}	0.192 (0.07)^{a}	Sp<0.001
	M	0.233 (0.02)^{a}	0.311 (0.06)^{b}	0.199 (0.03)^{a}	0.379 (0.04)^{b}	0.185 (0.02)^{a}	0.143 (0.01)^{a}	Site<0.001
	L	0.148 (0.01)^{ab}	0.232 (0.05)^{b}	0.148 (0.01)^{ab}	0.361 (0.04)^{c}	0.170 (0.02)^{ab}	0.122 (0.01)^{a}	Pos n.s.
								Sp×S <0.01
C_i/C_a	U	0.65 (0.02)^{a}	0.74 (0.02)^{c}	0.63 (0.01)^{a}	0.70 (0.02)^{bc}	0.64 (0.02)^{a}	0.68 (0.02)^{ab}	Sp n.s.
	M	0.64 (0.02)^{a}	0.73 (0.03)^{b}	0.64 (0.01)^{a}	0.72 (0.02)^{b}	0.68 (0.01)^{ab}	0.69 (0.02)^{ab}	Site<0.001
	L	0.61 (0.02)^{a}	0.71 (0.03)^{c}	0.66 (0.01)^{b}	0.71 (0.03)^{c}	0.72 (0.01)^{c}	0.71 (0.02)^{c}	Pos n.s.
								Sp×S <0.01

Table 3 Leaf characteristics in the upper (*U*), middle (*M*) and lower (*L*) strata of canopies of *Q. rubra*, *Q. prinus* and *A. rubrum* trees from two sites within a catchment. Values shown are means (± SEM) where *n*=9–12. Significance of treatment effect for species (*Sp*), site (*Site*), canopy position (*Pos*) and the interaction between species and site (Sp×S) are indicated as the value of *P* or as non-significant (*ns*). Different letters within rows indicate statistically different values at $P<0.05$ using least significant difference test of treatment means

Parameter	Canopy Position	*Q. rubra*		*Q. prinus*		*A. rubrum*		ANOVA Statistics
		Upper catchment	Lower catchment	Upper catchment	Lower catchment	Upper catchment	Lower catchment	
SLA (m^2 kg^{-1})	U	9.2 (0.26)^{a}	11.2 (0.33)^{b}	10.2 (1.0)^{ab}	10.0 (0.39)^{ab}	16.7 (0.65)^{d}	14.0 (0.30)^{c}	Sp<0.001
	M	11.1 (0.91)^{a}	12.8 (0.53)^{b}	11.0 (0.34)^{a}	12.2 (1.05)^{ab}	19.8 (0.58)^{d}	16.7 (0.64)^{c}	Site<0.01
	L	14.3 (0.45)^{a}	15.2 (0.52)^{ab}	16.1 (0.61)^{bc}	14.4 (0.86)^{a}	22.8 (0.61)^{d}	17.2 (0.39)^{c}	Pos<0.001
								Sp×S <0.001
N_{mass} (mmol N g^{-1})	U	1.49 (0.04)^{d}	1.36 (0.03)^{c}	1.54 (0.03)^{d}	1.65 (0.03)^{e}	1.24 (0.02)^{b}	1.16 (0.04)^{a}	Sp<0.001
	M	1.49 (0.03)^{c}	1.42 (0.03)^{b}	1.65 (0.04)^{d}	1.64 (0.03)^{d}	1.18 (0.03)^{a}	1.17 (0.03)^{a}	Site<0.01
	L	1.39 (0.02)^{d}	1.31 (0.05)^{c}	1.70 (0.03)^{f}	1.62 (0.04)^{e}	1.14 (0.04)^{b}	1.07 (0.04)^{a}	Pos 0.019
								Sp×S <0.01
N_{area} (mmol N m^{-2})	U	163 (4.9)^{c}	123 (5.5)^{b}	159 (9.5)^{c}	166 (5.2)^{c}	75 (3.1)^{a}	82.6 (2.9)^{a}	Sp<0.001
	M	144 (13.5)^{c}	114 (6.1)^{b}	151 (3.4)^{c}	144 (11.8)^{c}	59.9 (2.0)^{a}	71.1 (1.8)^{a}	Site ns
	L	98.6 (3.9)^{bc}	86.4 (3.9)^{b}	106 (3.2)^{cd}	116 (6.5)^{d}	50.4 (1.1)^{a}	62.2 (1.4)^{a}	Pos<0.001
								Sp×S <0.001
Soluble sugar (g m^{-2})	U	4.96 (0.83)^{c}	3.66 (0.36)^{b}	7.71 (1.01)^{d}	5.93 (0.59)^{c}	1.63 (0.21)^{a}	2.64 (0.31)^{b}	Sp<0.001
	M	4.91 (0.46)^{c}	3.23 (0.26)^{b}	5.85 (0.19)^{c}	3.57 (0.38)^{b}	1.45 (0.18)^{a}	1.51 (0.20)^{a}	Site<0.001
	L	3.07 (0.31)^{b}	2.51 (0.22)^{b}	4.07 (0.46)^{c}	3.23 (0.24)^{bc}	1.32 (0.21)^{a}	2.29 (0.12)^{ab}	Pos<0.001
								Sp×S <0.001
Starch (g m^{-2})	U	5.56 (0.88)^{b}	5.16 (0.61)^{b}	5.31(0.51)^{b}	6.24 (0.67)^{b}	3.17 (0.72)^{a}	3.86 (0.47)^{a}	Sp<0.001
	M	5.56 (0.68)^{c}	4.13 (0.33)^{b}	5.05 (0.52)^{bc}	4.27 (0.59)^{b}	2.40 (0.39)^{a}	4.05 (0.50)^{b}	Site ns
	L	4.33 (0.36)^{b}	3.76 (0.17)^{b}	3.36 (0.19)^{b}	4.01 (0.50)^{b}	1.62 (0.07)^{a}	3.98 (0.43)^{b}	Pos<0.001
								Sp×S <0.001

which the A/C_i response could be calculated. For this reason, replication in J_{max} in these trees was limited (Table 2). Nevertheless, J_{max} displayed a response similar to V_{cmax}, with the highest values found in *Q. rubra* at the upper site. A weak effect of site was noted, but only in *Q. rubra*. Unlike V_{cmax} and J_{max}, which showed virtually no response to site, A_{max} (photosynthetic rate at saturating PFD and ambient CO_2 partial pressure) was strongly influenced by site in *A. rubrum* but not in *Q. rubra* or *Q. prinus*. In *A. rubrum*, A_{max} was significantly greater at the lower site in all canopy strata (Table 2). The greatest rates of photosynthesis (12.6–13.5 µmol m^{-2} s^{-1}) were measured in *Q. rubra* and *Q. prinus* at the lower site. Maximum stomatal conductance (g_{smax}) differed significantly between species, with g_{smax} greatest in *Q. rubra* and *Q. prinus* (Table 2). In *Q. rubra* and *Q. prinus*, g_{smax} was significantly lower at the upper site than the lower site. There was no significant response to site in *A. rubrum*. C_i / C_a ratio was significantly lower in leaves of *Q. rubra* and *Q. prinus* at the upper site than the lower site, but did not vary in response to site in *A. rubrum*.

Leaf structural and chemical characteristics

Leaf characteristics were also significantly influenced by species, site and canopy position (Table 3). SLA was highest in *A. rubrum* and in this species displayed a significant increase at the upper site. *Q. rubra* and *Q. prinus* displayed no significant response to site. In all species, SLA displayed a consistent increase in the middle and lower canopy strata. Leaf nitrogen concentration, both on a mass (N_{mass}) and area (N_{area}) basis, was highest in the upper canopy stratum, although there was very little decrease in N_{mass} through the canopy (Table 3). There was a trend toward higher N_{mass} at the upper site in *Q. rubra* and *A. rubrum*, but N_{area} did not differ between sites. Nitrogen concentrations were lowest in *A. rubrum*, particularly when calculated on an area basis. Soluble protein concentration in leaves ranged from 4.2 to 9.3 g m^{-2} in *Q. prinus*, 6.9 to 13.2 g m^{-2} in *A. rubrum* and 12.6 to 15.4 g m^{-2} in *Q. rubra*. There was no overall effect of site or canopy position.

Carbohydrate concentrations in leaves were most responsive to within-canopy and within-catchment environmental gradients in *Q. rubra* and *Q. prinus*, but less so in *A. rubrum* (Table 3). Soluble sugar concentrations were more sensitive to site and canopy position than starch concentrations. In both *Q. rubra* and *Q. prinus*, soluble sugar concentration in leaves was greater at the upper site than at the lower site. In *A. rubrum*, soluble sugar concentrations were lower (1.3–2.6 g m^{-2}) and did not differ between site. In contrast to soluble sugars, starch concentrations did not differ significantly between sites, although they were greater at the lower site in *A. rubrum*. Patterns in TNC concentration were not clear, although they were generally greater at the upper site in

Table 4 Summary of regression statistics ($P<0.05$) for the relationships between photosynthetic and leaf characteristics (as shown in Fig. 3) for trees of *Q. rubra* (*Qr*), *Q. prinus* (*Qp*) and *A. rubrum* (*Ar*) from two sites within a catchment. Data pooled for both lower and upper catchment sites for each species unless the relationship for each was found to be significantly different ($P<0.05$)

Dependent variable	Independent variable	Species	Site	Regression relationship	r^2
V_{cmax} (μmol CO_2 $m^{-2}s^{-1}$)	N_{area}	*Qr*	Pooled	$36.9+(0.11\times N_{area})$	0.16
		Qp	Pooled	$33.4+(0.12\times N_{area})$	0.13
		Ar	Pooled	$14.2+(0.44\times N_{area})$	0.31
A_{max} (μmol CO_2 $m^{-2}s^{-1}$)	N_{area}	*Qr*	Pooled	$6.64+(0.039\times N_{area})$	0.33
		Qp	Pooled	$6.15+(0.043\times N_{area})$	0.16
		Ar	Lower	$2.32+(0.103\times N_{area})$	0.51
			Upper	ns	ns
V_{cmax} (μmol CO_2 $m^{-2}s^{-1}$)	SLA	*Qr*	Pooled	$69.5-(1.56\times SLA)$	0.15
		Qp	Pooled	$64.9-(1.20\times SLA)$	0.15
		Ar	Pooled	$71.5-(1.55\times SLA)$	0.26
A_{max} (μmol CO_2 $m^{-2}s^{-1}$)	SLA	*Qr*	Pooled	$17.3-(0.48\times SLA)$	0.25
		Qp	Pooled	$16.4-(0.33\times SLA)$	0.13
		Ar	Lower	$17.5-(0.48\times SLA)$	0.38
			Upper	ns	ns
Soluble protein (g m^{-2})	N_{area}	*Qr*	Pooled	ns	ns
		Qp	Pooled	$-2.97+(0.067\times N_{area})$	0.35
		Ar	Pooled	$0.01+(0.145\times N_{area})$	0.23
N_{area} (mmol N m^{-2})	SLA	*Qr*	Pooled	$268-(12.2\times SLA)$	0.78
		Qp	Pooled	$254-(9.2\times SLA)$	0.91
		Ar	Pooled	$125-(3.3\times SLA)$	0.72

Q. rubra and *Q. prinus* but greater at the lower site in *A. rubrum* (data not shown). In all species, soluble sugar, starch and TNC concentrations decreased in the lower canopy strata.

$\delta^{13}C$ values in fully exposed upper canopy leaves differed significantly between species and in response to site (Fig. 2). Leaf $\delta^{13}C$ was significantly lower in *A. rubrum* than in either *Q. rubra* or *Q. prinus* at both sites. *A. rubrum* also displayed a significantly lower leaf $\delta^{13}C$ at the lower site compared to the upper site. In contrast, $\delta^{13}C$ did not differ between sites for either *Q. rubra* or *Q. prinus*.

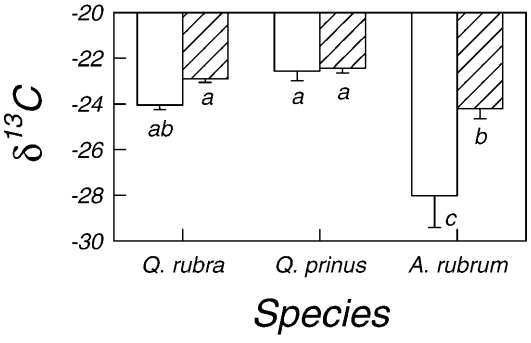


Fig. 2 Leaf carbon isotope composition ($\delta^{13}C$) at the upper canopy of *Quercus rubra* (red oak), *Quercus prinus* (chestnut oak) and *Acer rubrum* (red maple) from lower (*open bars*) and upper (*hatched bars*) catchment sites. Values shown are means (±SEM) where n=7–8. Significance of treatment effects: species ($P<0.001$), site ($P<0.01$) and species×site ($P=0.025$). Different *letters below bars* indicate statistically different values at $P<0.05$ using least significant difference test of treatment means

Relationships between photosynthetic parameters and leaf characteristics

Relationships between photosynthetic parameters and leaf characteristics did not differ amongst the two *Quercus* species, but were different in *A. rubrum* (Fig. 3). The relationship between V_{cmax} and N_{area} (Fig. 3a), although significant for all species, was stronger in *A. rubrum* (r^2=0.31) than in either *Q. rubra* (r^2=0.17) or *Q. prinus* (r^2=0.13) (Table 4). The slope in the relationship was significantly steeper in *A. rubrum* than the other species. In no species did the relationship differ between the lower and upper sites. The relationship between A_{max} and N_{area} did not differ between *Q. rubra* and *Q. prinus*, but was significantly steeper in trees of *A. rubrum* at the lower site (Fig. 3b). In *A. rubrum* the relationship also differed between the lower (significant slope and r^2=0.51) and upper (slope ns) sites (Table 4). No differences between species were displayed in the relationship between V_{cmax} and SLA (Fig. 3c and Table 4). The relationship between A_{max} and SLA did not differ between *Q. rubra*, *Q. prinus* and *A. rubrum* at the lower site (Fig. 3d). In *A. rubrum* the relationship between A_{max} and SLA was significant at the lower site but not at the upper site (Table 4).

Significant species differences were also noted in relationships amongst leaf characteristics. Soluble protein concentration in leaves was related to N_{area} in *Q. prinus* (r^2=0.35) and *A. rubrum* (r^2=0.24), but not in *Q. rubra* (Fig. 3e, Table 4). A very strong linear relationship between N_{area} and SLA was noted in all species (Fig. 3f), with r^2 values ranging from 0.73 in *A. rubrum* to 0.93 in *Q. prinus* (Table 4).

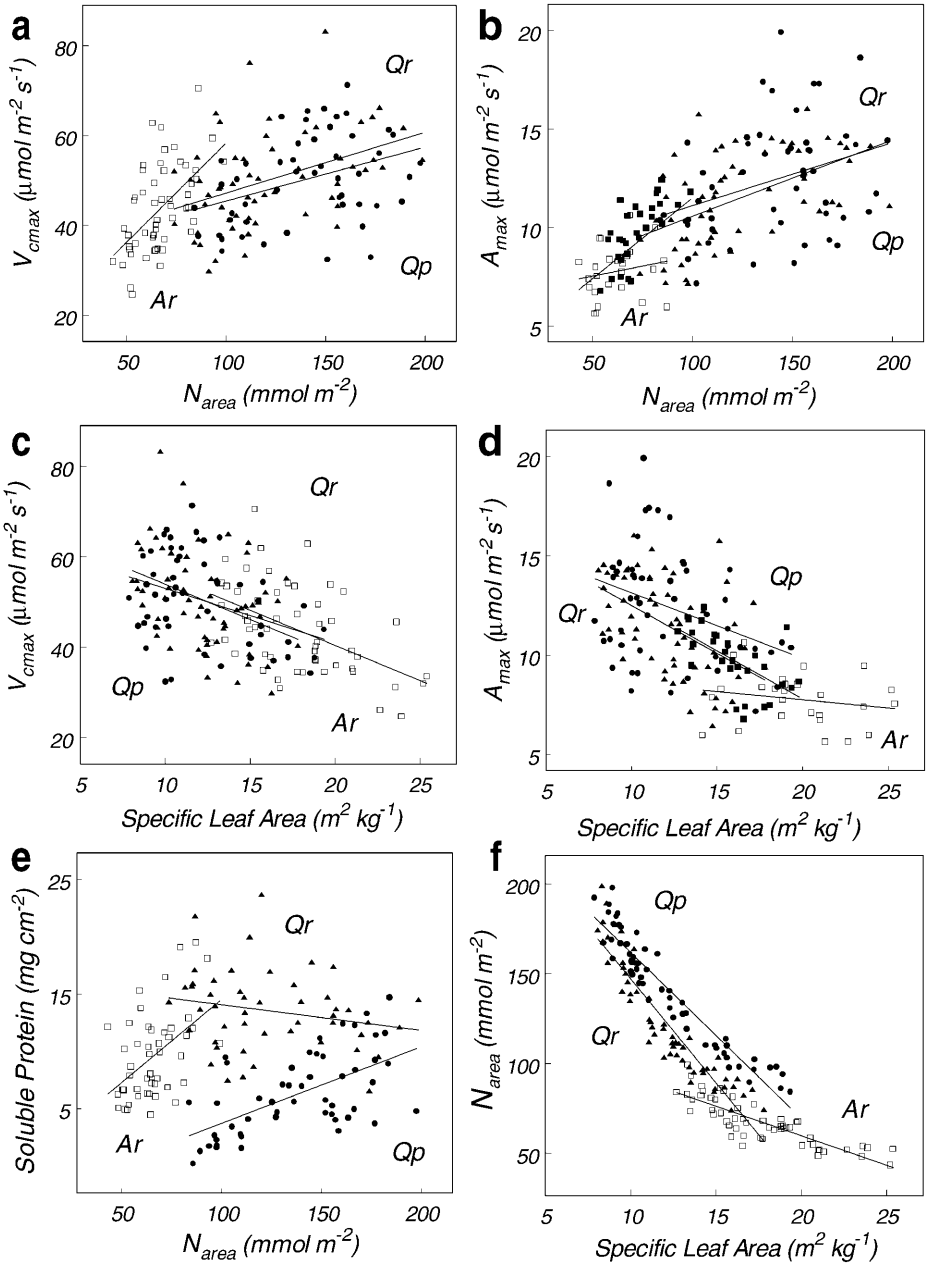


Fig. 3 Relationships amongst photosynthetic and leaf characteristics for *Q. rubra* (*Qr, triangles*), *Q. prinus* (*Qp, circles*) and *A. rubrum* (*Ar, squares*). Data pooled for both lower and upper catchment sites for each species unless the relationship for each was found to be significantly different (P <0.05) – in these cases separate symbols indicate data for trees from the lower (*closed symbols*) and upper (*open symbols*) catchment sites. Regression statistics are given in Table 4. Differences in slopes between species are indicated in the text

Discussion

In this temperate deciduous forest patterns of photosynthesis differed significantly amongst the three dominant tree species, particularly in response to root-zone water availability. The fact that leaf N contents in our study species did not differ significantly between the upper and lower sites indicates that nutrient supply is unlikely to be more limiting at the drier site. We suggest that these differences in leaf-level photosynthetic characteristics may play an important role in species responses along this environmental gradient (relatively dry upper site to moister lower site). In particular, the sensitivity of gas exchange characteristics in *A. rubrum* to site differences may be an important potential limitation to this species at sites with limited water availability.

Photosynthesis – leaf characteristic relationships

Patterns of distribution of photosynthetic capacity through the canopy were much less well defined than patterns of distribution of leaf traits (N_{area} and SLA). Upper canopy leaves had the highest N_{area} because of their relatively low SLA. This demonstrates that N allocation patterns within the canopy change with decreasing light level so as to maximise the rate of photosynthesis per unit N allocated (Field 1983; Hirose and Werger 1987; Ellsworth and Reich 1993) through an increase in the allocation of N to the photosynthetic apparatus (Evans 1989). We found that N_{area} and SLA were much more strongly related to each other than to any measure of photosynthetic capacity (Fig. 3). This may, in part, be explained by interspecific differences in the allocation of nitrogen to soluble protein.

The low N_{area}, A_{max} and high SLA in *A. rubrum* is typical of shaded leaves. However, although *A. rubrum* trees in this forest do not reach the upper canopy, our study trees were in canopy gaps, and A_{max} and g_{smax} values are consistent with previous values obtained for *A. rubrum* under open field conditions (Abrams and Mostoller 1995). Our findings for *A. rubrum* demonstrate that species with higher SLA will have higher A_{max} per unit leaf *N* and that species with leaves with lower SLA (e.g. *Q. rubra* and *Q. prinus*) will have shallower slopes of the $A_{max} - N$ relationship (Reich et al. 1998a). The steeper slope of the relationship between A_{max} and N_{area} in *A. rubrum* at the lower site indicates a greater photosynthetic nitrogen-use efficiency (PNUE) in this species. But importantly, the relationships between A_{max} and both N_{area} and SLA differed in *A. rubrum* at the lower and upper sites (Fig. 3b, d). At the upper site, no relationship was displayed between A_{max} and either N_{area} or SLA. Clearly, PNUE is extremely low in *A. rubrum* in the more open canopy and drier conditions at the upper site (see also Abrams and Mostoller (1995) and Kubiske and Pregitzer (1996)). In addition, while previous studies have shown that photosynthesis-tissue *N* relationships are valid across a number of species and functional groups (Ryan 1995; Reich et al. 1998a, 1998b), our finding that this relationship differed between sites for *A. rubrum* should act as a caution against assuming such relationships hold across all site conditions.

Species differences in gas exchange characteristics

Photosynthetic values reported here are consistent with previous in situ measurements made in mature trees of these or related species (e.g. Jurik et al. 1988; Kleiner et al. 1992; Kubiske and Abrams 1993; Abrams and Mostoller 1995; Bassow and Bazzaz 1998; Cavender-Bares and Bazzaz 2000; Donovan et al. 2000; Kazda et al. 2000; Wilson et al. 2000). Given that photosynthetic rates in *Quercus* species have been found to be sensitive to severe water stress (Abrams et al. 1990; Weber and Gates 1990; Epron et al. 1993), the rates obtained here indicate that, while rainfall was significantly lower than average, the effect of the drought was not severe during the period of our study. This is also supported by rates of photosynthesis and g_{smax} in *A. rubrum* at the lower site, which were similar to those found under open canopy and well-watered conditions (Abrams and Mostoller 1995). The maintenance of relatively high A_{max} in the *Quercus* species at the upper site was likely to have been partly facilitated by deep rooting (Parker et al. 1982; Bahari et al. 1985; Abrams 1990).

Although V_{cmax} did not differ greatly between species, maximum photosynthesis at saturating PFD (A_{max}) was significantly lower in *A. rubrum* than either of the *Quercus* species. This reduced photosynthetic capacity, particularly at the upper site, must limit carbon acquisition in *A. rubrum* under these field conditions. In addition, lower photosynthetic capacity at the upper site in *A. rubrum* is associated with an increase in leaf respiration, and thus a lower A_{max} / R_d ratio (8.2 at the upper site compared to 11.9 at the lower site; Turnbull et al. 2001). Although there was no difference in A_{max} between sites for *Q. rubra* and *Q. prinus*, higher rates of net carbon uptake in *Q. rubra* than *Q. prinus* at the lower site are indicated by the greater A_{max}/R_d ratio displayed in leaves (Turnbull et al. 2001).

Values of g_{smax} obtained from A/C_i responses were within the range of previous findings for *Q. rubra* (Abrams et al. 1990; Weber and Gates 1990; Kleiner et al. 1992), *Q. prinus* (Abrams et al. 1990; Kleiner et al. 1992) and *A. rubrum* (Kubiske and Abrams 1993; Abrams and Mostoller 1995). Unlike *Q. rubra* and *Q. prinus*, which displayed significant reductions in g_{smax} (approximately 40% in *Q. rubra* and 54% in *Q. prinus*) at the drier upper site compared to values at the wetter lower site, there was no response of g_{smax} to site in *A. rubrum*. This is despite a significant reduction in A_{max} at all canopy levels in *A. rubrum* at the drier site. Thus, both *Quercus* species maintained high levels of photosynthetic capacity at both sites, but were able to restrict potential transpirational water loss at the drier site. This was particularly so for *Q. prinus*. The lack of stomatal response in the face of lower water availability and lower photosynthesis in *A. rubrum* offers little support to the notion that *A. rubrum* conserves moisture through effective stomatal control (Abrams 1998).

Differences in stomatal responses to soil water availability may, in part, explain differences in $\delta^{13}C$ in response to site. Given that trees at each site in the present study are growing under common conditions, it is appropriate to use $\delta^{13}C$ as an indicator of water use efficiency (WUE) (Farquhar et al. 1989; Stewart et al. 1995). Lower $\delta^{13}C$ values clearly indicate differences in stomatal behaviour in *A. rubrum* which are likely to contribute to lower WUE in this species (cf. *Quercus* species) at both sites. The ability of the *Quercus* species to restrict potential water loss by reducing g_{smax} at the upper site would have the effect of maintaining low levels of discrimination against ^{13}C (Farquhar et al. 1989). $\delta^{13}C$ values in *Q. rubra* and *Q. prinus* were high even at the lower site, indicating a more conservative water-use strategy even under relatively high soil water availability (Cavender-Bares and Bazzaz 2000).

Although differences in $\delta^{13}C$ between *A. rubrum* and *Q. rubra*/*Q. prinus* were less pronounced at the upper site, the difference that was displayed is likely to be significant given the low root-zone water content at this site. In this context we conclude that *Q. rubra* and *Q. prinus* are more water use efficient than *A. rubrum* under the range of conditions displayed at our two study sites. Previous findings indicate that $\delta^{13}C$ values in *Quercus* species may be biased towards photosynthesis at the time of leaf production, and thus indicative of WUE during the early part of the season only (Damesin et al. 1997; Cavender-Bares and Bazzaz 2000). However, the substantial reductions in both instantaneous g_{smax} and C_i/C_a we measured in *Q. rubra* and *Q. prinus* at the drier

site give us confidence that these species retain significantly greater WUE than *A. rubrum* throughout the growing season. These findings are consistent with long-term measurements of significantly higher rates of tree mortality in *A. rubrum* in drier sites in this forest (W. Schuster, unpublished data).

Although we cannot rule out the potential impacts of characteristics such as seed dispersal, establishment and biomass allocation on tree distributions (Abrams 1998), the apparent adaptation of *Q. rubra* and *Q. prinus* for higher WUE in comparison to *A. rubrum* is likely to be an important factor regulating species performance in this forest. Simulation models based on the responses of vegetation to atmospheric and soil conditions (e.g. MAPPS, see Neilson 1995; Bachelet et al. 2001) predict significant changes in both the distribution and extent of temperate deciduous forest. If the warmest climate change scenarios were borne out, the potential for temperature-induced droughts (Neilson and Drapek 1998) could severely limit the ability of *A. rubrum* to extend its dominance in temperate deciduous forests (cf. Abrams 1998).

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