Photosynthesis and respiration characteristics in canopies of three deciduous tree species vary with site water availability

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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. This is particularly so for interspecific differences in physiology which are likely to influence patterns of forest composition.
- The overall aim of this research was to determine the physiological relationships that regulate the relative contribution of species to carbon uptake in temperate deciduous forests.
- 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.

Methods

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. This enabled us to investigate photosynthetic characteristics of mature (20+ m tall) trees at sites of differing soil water availability within a catchment (a dryer upper site and a wetter lower site).

Based on differences in basal area, 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.

Our study sites were located in The Black Rock Forest, Highlands Province, New York (lat 41° 24' N and long 74° 01' E, 110 to 450 m asl). 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. Average soil water content for the month during which this study was conducted (June) was 35.1 ± 1.5 % (range 48 % to 32 %) at the lower site and 12.6 ± 0.7 % (range 22 % to 10 %) at the upper site.

Parameter	Canopy Position	*Quercus rubra*		*Quercu*
		Upper Catchment	Lower Catchment	Upper Catchm
A_{max} (μmol CO_2 $m^{-2}s^{-1}$)	U	12.7 (0.54) ^{cd}	12.6 (0.49) ^{cd}	11.8 (0.
	M	12.7 (0.60) ^{cd}	11.6 (0.84) ^{c}	12.9 (1.
	L	9.0 (0.62) ^{b}	9.4 (0.46) ^{bc}	10.4 (0.
G_{smax} (mol $m^{-2}s^{-1}$)	U	0.214 (0.02) ^{a}	0.359 (0.06) ^{b}	0.180 (
	M	0.233 (0.02) ^{a}	0.311 (0.06) ^{b}	0.199 (
	L	0.148 (0.01) ^{ab}	0.232 (0.05) ^{b}	0.148 (
C_i / C_a	U	0.65 (0.02) ^{a}	0.74 (0.02) ^{c}	0.63 (0.
	M	0.64 (0.02) ^{a}	0.73 (0.03) ^{b}	0.64 (0.
	L	0.61 (0.02) ^{a}	0.71 (0.03) ^{c}	0.66 (0.

Table 1. Photosynthetic characteristics for leaves in the upper (*U*), middle (*M*) and lower (*L*) strata of canopies of *Quercus rubra*, *Quercus montana* and *Acer rubrum* trees from two sites within a catchment. Values shown are means (± standard error of the mean, SEM) where *n*=9-12. Stomatal responses to above ambient CO_2 partial pressures in Q. montana and upper catchment trees of *A. rubrum* made determination of J_{max} not possible in all leaves. Where this

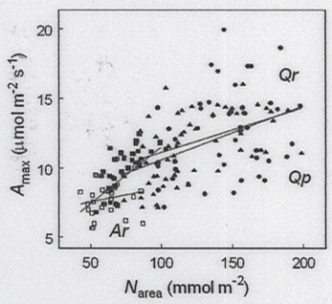

Figure 1. Relationship between photosynthetic capacity (A_{max}) and leaf nitrogen for *Quercus rubra* (*Qr*, triangles), *Quercus prinus* (*Qp*, circles) and *Acer rubrum* (*Ar*, squares). Data pooled for both lower and upper catchment sites for each species unless the relationship for each was found 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.

Parameter	*Quercus rubra*		*Quercus prin*
	Upper Catchment	Lower Catchment	Upper Catchment
R_{15} (μmol CO_2 $m^{-2}s^{-1}$)	0.92 (0.14) ^{bc}	0.71 (0.08) ^{a}	1.02 (0.08) ^{c}
R_{20} (μmol CO_2 $m^{-2}s^{-1}$)	1.20 (0.15) ^{a}	1.00 (0.13) ^{a}	1.27 (0.09) ^{a}
R_{25} (μmol CO_2 $m^{-2}s^{-1}$)	1.56 (0.16) ^{b}	1.39 (0.19) ^{ab}	1.56 (0.09) ^{b}
E_o (J mol^{-1} $°K^{-1}$)	39670 (3880) ^{bc}	46610 (3510) ^{c}	30640 (3260
Q_{10}	1.76 (0.09) ^{bc}	1.93 (0.09) ^{c}	1.56 (0.07) ^{ab}

Table 2. Dark respiration parameters calculated from fitted temperature response curves (see Fig. 1) for leaves of *Quercus rubra*, *Quercus rinus* and *Acer rubrum* trees from two sites of differing root zone water availability within a catchment. R_{15} is respiration rate at the base temperature (15 °C) used to fit equation 1 to actual responses. R_{20} and R_{25} denote respiration rates calculated from the fitted responses at 20 and 25 °C, respectively. E_o is a modelled parameter related to the energy of activation. Q_{10} denotes

Results + Discussion

Photosynthesis

1. Leaf photosynthetic characteristics differed significantly between species and in response to site and position in the canopy (Table 1). A_{max} was significantly greater at the lower site in all canopy strata in *A. rubrum* but not in *Q. rubra* or *Q. prinus*. The greatest rates of photosynthesis (12.6 - 13.6 μmol m^{-2} s^{-1}) were measured in *Q. rubra* and *Q. prinus* at the lower site.

2. 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 (Fig. 1).

3. Importantly, the relationships between A_{max} and N_{area} (and by implication photosynthetic nitrogen-use efficiency, PNUE) differed in *A. rubrum* at the lower and upper sites (Fig. 1). At the upper site, no relationship was displayed between A_{max} and either N_{area} or SLA, indicating that PNUE was extremely low in *A. rubrum* at the drier site. The lower photosynthetic capacity and PNUE must substantially reduce carbon acquisition capacity in *A. rubrum* under these field conditions.

4. Maximum stomatal conductance (g_{smax}) differed significantly between species, with g_{smax} greatest in *Q. rubra* and *Q. prinus* (Table 1). 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*.

5. Leaf $\delta^{13}C$ was significantly lower in *A. rubrum* than in either *Q. rubra* or *Q. prinus* at both sites (Fig. 2). These findings indicate differences in stomatal behaviour in *A. rubrum* which are likely to contribute to lower water use efficiency in this species (cf. *Quercus* species) at both sites.

Respiration

1. The response of respiration to temperature differed significantly between the three species, with *A. rubrum* displaying a much smaller increase in respiration with increasing temperature than the other two species (Table 2 + Fig. 3).

2. Corresponding Q_{10} values (the relative change in respiration for a 10 degree change in temperature) ranged from 1.5 in *A. rubrum* to 2.1 in *Q. prinus* (Table 2).

3. In addition to interspecific differences, trees also differed significantly in their response to temperature at low and high water availability (i.e. a significant site effect at 15 °C but a significant species effect at 25 °C - Table 2).

4. Dark respiration at ambient air temperatures, expressed on a leaf area basis (R_{area}), was not significantly affected by species but was significantly greater ($P<0.01$) in trees at the upper site than at the lower site (*Q. rubra* 0.8 - 1.1 μmol m^{-2} s^{-1} and *Q. prinus* 0.95 - 1.2 μmol m^{-2} s^{-1} only). In contrast, when expressed on a leaf mass basis (R_{mass}), respiration rate was significantly different between species ($P<0.01$), with rates in *A. rubrum* (12.5 - 14.6 μmol CO_2 kg^{-1} s^{-1}) greater than those for *Q. rubra* (8.6 - 9.9 μmol CO_2 kg^{-1} s^{-1}) and *Q. prinus* (9.2 - 10.6 μmol CO_2 kg^{-1} s^{-1}) at the lower and upper sites, respectively.

5. Respiration on a nitrogen basis (R_N) displayed a similar response to R_{mass}. The consistency in R_{mass} and R_N between sites indicates a strong coupling between factors influencing respiration and those affecting leaf characteristics.

6. The relationships between dark respiration and A_{max} differed between the drier and wetter site (Fig. 4). Importantly, trees at the upper site had higher rates of leaf respiration and lower A_{max} than those at the lower site. This shift in the balance of carbon gain and loss clearly limits the carbon acquisition capacity of trees at sites of low water availability, particularly for *A. rubrum*.

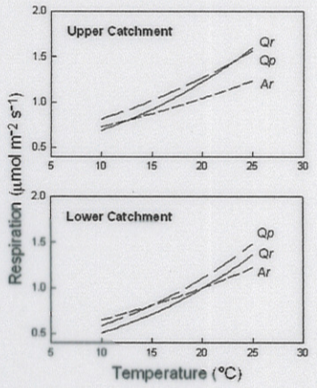

Figure 3. Response of respiration rate, R_d, to temperature for leaves of *Quercus rubrum* (*Qr*), *Quercus prinus* (*Qp*) and *Acer rubrum* (*Ar*) from two sites of differing root zone water availability within a single watershed. Data shown are modelled responses derived using the mean parameters from 6-7 replicate response curves at each site (individual curves fitted using a modification of the Arrhenius equation described by Lloyd & Taylor (1994)). For statistical comparison of respiration parameters see Table 2.

Conclusions

- Differences in leaf-level photosynthetic characteristics play an important role in the relative contribution our study species make to carbon uptake in forests occupying sites along this environmental gradient (relatively dry upper site to moister lower site). The two *Quercus* species, in contrast to *A. rubrum*, maintain photosynthetic capacity at the drier site whilst minimising transpirational water loss.
- The species differences in response to root-zone water content we have observed should have important implications for accurate modeling of the distribution and carbon fluxes from the temperate deciduous forest biome, particularly in response to environmental change. If the warmest climate change scenarios were borne out, the potential for temperature-induced droughts could severely limit the ability of *A. rubrum* to extend its dominance in temperate deciduous forests.
- The response of respiration to temperature and related leaf characteristics (e.g. A_{max} and N_{area}), may differ significantly in trees growing at sites with contrasting water availability.
- Clearly, environmental variables (temperature, soil characteristics), leaf characteristics (N content, SLA, carbohydrate content) and respiration co-vary across landscapes and between species. This has important implications for accurate modelling of respiratory carbon fluxes from forests, particularly for forest-gap models that assume single temperature optima for

Acknowledgements