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Energy investment in leaves of red maple and co-occurring oaks within a forested watershed

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Summary Despite its recent expansion in eastern US forests, red maple (*Acer rubrum* L.) generally exhibits a low leaf photosynthetic rate, leaf mass per unit area (LMA) and leaf nitrogen concentration ([N]) relative to co-occurring oaks (*Quercus* spp.). To evaluate these differences from the perspective of leaf energy investment, we compared leaf construction cost (CC) and leaf maintenance cost (MC) with leaf photosynthetic rate at saturating photon flux density and ambient CO_2 partial pressure (A_{max}) in red maple and co-occurring red oak (*Quercus rubra* L.) and chestnut oak (*Quercus prinus* L.). We also examined relationships among leaf physiological, biochemical and structural characteristics of upper-canopy leaves of these three species at lower (wetter) and upper (drier) elevation sites of a watershed in the Black Rock Forest, Cornwall, NY, USA. Although A_{max}, leaf [N], leaf carbon concentration ([C]) and LMA were significantly less in red maple than in either oak species at both sites, CC per unit leaf area of red maple was 28.2 and 35.4% less than that of red oak at the lower and upper site, respectively, and 38.8 and 32% less than that of chestnut oak at the lower and upper site, respectively. Leaf MC per unit leaf area, which was positively associated with leaf CC ($r^2 = 0.95$), was also significantly lower in red maple than in either oak species at both sites. When expressed per unit leaf area, A_{max} was positively correlated with both CC ($r^2 = 0.65$) and MC ($r^2 = 0.59$). The cost/benefit ratio of CC/A_{max} of red maple was significantly less than that of chestnut oak at the lower site, however, CC/A_{max} did not exhibit any significant interspecific differences at the upper site. Expressed per unit leaf area, CC was correlated positively with LMA ($r^2 = 0.90$), leaf [N] ($r^2 = 0.97$), and leaf [C] ($r^2 = 0.89$), and negatively correlated with leaf molar carbon to nitrogen ratio ($r^2 = 0.92$). Combined with red maple's general success in many oak-dominated forests, our findings suggest that reduced leaf-level photosynthetic capacity and related leaf characteristics in red maple are partially balanced by lower energy and resource requirements for leaf biomass construction and maintenance, which could enhance the competitive success of this species.

Keywords: Acer rubrum, competition, construction cost, maintenance cost, photosynthesis, Quercus prinus, Quercus rubra.

Introduction

Forest ecosystems play an important role in global biogeochemical cycles (Schlesinger 1991). Because different tree species have different resource requirements and patterns of resource use (Post and Pastor 1996), species composition can influence the exchange of resources among the terrestrial, atmospheric and soil components of these global cycles. In particular, differences in leaf structure of various species can significantly influence gas exchange and tissue water relations at both community and landscape levels (Abrams et al. 1994). Thus, knowledge of plant community dynamics is important to understanding both forest responses to, and influences on, global biogeochemistry.

In many forests in eastern North America, red maple (*Acer rubrum* L.) has become increasingly dominant during the past century (Lorimer 1984, Abrams and Nowacki 1992, Nowacki and Abrams 1992, Abrams 1998). Yet, the leaf physiology of this species is not considered conducive to its general success across sites with a wide range of environmental conditions (Abrams 1998). In both low- and high-light environments, for example, red maple leaves exhibit relatively low rates of net photosynthesis compared with those of other hardwoods (Reich et al. 1990, Sullivan et al. 1996, Turnbull et al. 2002). Foliar [N], which typically is positively associated with photosynthetic performance (Field and Mooney 1986, Reich et al. 1991, Abrams et al. 1994), and mean leaf mass per unit area (LMA) are also relatively low in red maple (Abrams and Mostoller 1995, Turnbull et al. 2002). These leaf physiological, biochemical and structural traits contradict the widespread expansion of red maple (Abrams 1998). However, the reproductive and growth characteristics of this species, including its prolific seed production, rapid germination, early sexual maturity, ability to hybridize (Abrams and Nowacki 1992) and morphological plasticity (Sipe and Bazzaz 1994), along with land-use changes that include fire suppression, may all contribute to its widespread success (Abrams 1998).

As a consequence of red maple expansion, losses of dominant oak species (*Quercus* spp.) have been predicted in eastern deciduous forest of North America (Abrams 1998). Like red maple, oaks also have been found across a wide range of environmental conditions (Kleiner et al. 1992), though it has been suggested that oaks generally show an affinity for drought-prone sites because they possess a high degree of drought resistance (Abrams 1996). Within the genus, however, different species have exhibited individual environmental preferences. Some studies have concluded that red oak (*Quercus rubra* L.) typically exhibits better growth in mesic areas, whereas chestnut oak (*Quercus prinus* L.) generally exhibits better growth on xeric sites (Hardin et al. 2000); however, other studies have found exceptions to these trends (Keever 1973, Blackman and Ware 1982). Unlike those of red maple, oak leaf characteristics generally include relatively high rates of leaf photosynthesis associated with high leaf [N] (Sullivan et al. 1996) and LMA (Abrams and Kubiske 1990, Turnbull et al. 2002). Yet despite these leaf characteristics and the relatively large seed size of oak species (Kolb and Steiner 1990), oak seedlings often do not compete successfully with red maple seedlings in the understory (Abrams 1996).

Here, we consider the differences in leaf physiological, biochemical and structural properties between red maple and co-occurring oak species from the perspective of leaf energy investment. Because plant growth comes at an energetic expense (Mooney 1972), we have used energy as a basic unit of comparison among plant species. Photosynthesis, which uses solar energy in the formation of carbohydrate molecules, provides a plant's energy supply. Construction cost (CC) is a quantifiable measure of the energy demand of a plant for biomass construction (Griffin 1994). Maintenance cost (MC) is a measure of the energy demand for essential processes that do not result in an increase in biomass, such as the maintenance of ion gradients (Chiariello et al. 1989).

Construction cost can be determined from the amount of glucose required by plants to provide carbon skeletons, reductant and energy for the synthesis of organic compounds (Williams et al. 1987). Construction cost can be related to both resource-use efficiency (Williams et al. 1987, Griffin et al. 1996) and growth rates, with high CC typically being associated with slow-growing species (Lambers and Poorter 1992, Poorter and Bergkotte 1992, Griffin et al. 1993, Griffin 1994, Poorter and Villar 1997). Maintenance cost can be estimated from the amount of glucose required by plants to maintain their biomass for a given amount of time (Merino et al. 1984).

We report the findings of our comparison of photosynthesis, leaf CC and MC, and related leaf physiological, biochemical and structural characteristics in red maple, red oak and chestnut oak within a forested watershed in southeastern New York, USA. The high LMA and leaf [N] typically reported for oak species are associated with relatively high carbon assimilation rates that could increase their competitive success. However, these traits are also characteristic of leaves that are relatively expensive to construct (Penning de Vries et al. 1974, Williams et al. 1987, Griffin 1994). In addition, high leaf [N] is associated generally with leaves that are expensive to maintain (Merino et al. 1984). Consequently, although individual oak leaves may exhibit traits indicative of high rates of carbon assimilation, which can be associated with high growth rates (Lambers and Poorter 1992), we hypothesize that such rates are achieved at the expense of high leaf energetic costs. Conversely, we hypothesize that red maple leaves are relatively inexpensive to construct and maintain based on the relatively low LMA and leaf [N] reported for this species.

Materials and methods

Study site

The Black Rock Forest is a 1500-ha preserve established in 1927 (Tryon 1930). The forest is located adjacent to the intersection of the Hudson Highlands and the Hudson River Basin in Cornwall, NY, USA. Mean annual precipitation is 1190 mm, and mean air temperature is strongly seasonal, ranging from –2.7 °C in January to 23.4 °C in July (Black Rock Forest field station database). Forest soils are loams, with bedrock or glacial till parent material at depths ranging from 25 cm to 1 m (Olssen 1981). Along more xeric upper-elevation slopes of the forest, soils are primarily of the Hollis series, whereas soils at more mesic lower elevation sites are primarily of the Charlton series (Olssen 1981). Red oak, the most dominant tree species within the forest as a whole, and chestnut oak account for 66% of the total basal area (Friday and Friday 1985). Red maple has the highest stem density of all tree species in the forest, comprising 31% of stems (Friday and Friday 1985). Along upper slopes of the forest, red and chestnut oaks are among the most dominant species, whereas red maple and red oak are among the most dominant species along lower slopes (Turnbull et al. 2001).

The 135-ha Cascade Brook Watershed is located in the southeastern part of the forest. Within this watershed, elevations range from 210 to 430 m (Turnbull et al. 2001). At both an upper-elevation and a lower-elevation site within the watershed, a permanent 0.1-ha research plot has been established. These sites differed significantly in soil water availability ($P < 0.001$) in June 1999, when the leaf material used in this study was collected. Mean soil water content was 35.1 ± 1.5% at the lower site (59% of field capacity) and 12.6 ± 0.7% at the upper site (36% of field capacity) (Turnbull et al. 2001).

Red maple comprised the largest number of stems at the lower site, followed by yellow birch (*Betula alleghaniensis* Britt.) and red oak, whereas chestnut oak was found only on drier microsites (Turnbull et al. 2001). At the lower site, canopy height ranged from 20 to 30 m and total basal area was 24.9 m^2 ha^{-1}, to which red oak made the largest contribution (Turnbull et al. 2001). At the upper site, chestnut oak comprised the largest number of stems, followed by red oak and red maple (Turnbull et al. 2001). Canopy height at this site ranged from 10 to 16 m and total basal area was 23.7 m^2 ha^{-1}, 78% of which was accounted for by chestnut, red and white (*Quercus alba* L.) oaks (Turnbull et al. 2001).

Three visibly healthy individuals each of red maple, red oak and chestnut oak were chosen at each site. For each individual, three or four fully expanded leaves were selected randomly for measurements. These leaves were fully sunlit upper-canopy leaves for the taller oak species and sub-canopy leaves in canopy gaps that were fully sunlit at the time of measurements for shorter red maple. Turnbull et al. (2002) measured photosynthesis in situ on these leaves in June 1999 (Table 1) and then collected leaf material, which was dried and stored. To examine and compare the leaf energy budgets of red maple, red oak and chestnut oak, we measured construction and maintenance costs on these stored samples and compared these factors to the previously collected photosynthetic measurements. Additional leaf physiological, biochemical and structural measurements made by Turnbull et al. (2002) were also utilized in this study and are presented where appropriate (Table 1).

Leaf costs

Dried leaf material was ground to a fine power with a ball mill (Cianflone Scientific Instruments, Pittsburgh, PA). We measured the mineral content of each selected leaf by burning a small sample of the leaf powder in a 400 °C muffle furnace for 6 h to obtain ash and then dividing the ash weight by the sample dry weight. To measure ash-free heat of combustion (H_C), three 6–20 mg pellets were pressed from the powder from each leaf. Each pellet was weighed and then combusted in a modified Phillipson microbomb calorimeter (Phillipson 1964) (Gentry Instruments, Aiken, SC) calibrated with benzoic acid standards of known calorific value. The H_C values obtained for the triplicate pellets for each leaf were then averaged. Organic [N] data for each selected leaf were obtained from Turnbull et al. (2002) (Table 1), who determined nitrogen content with an elemental analyzer (Carlo Erba, Na 1500, Milan, Italy).

The following equation developed by Williams et al. (1987) was used to calculate leaf CC in terms of the amount of glucose required to supply the energy necessary to synthesize plant biomass (eq. g glucose g^{-1} leaf dry mass):

$$\mathrm{CC} = [(0.06968\ \Delta H_C - 0.065)(1 - \mathrm{Ash}) + 7.5(k[\mathrm{N}]/14.0067)](1/E_G),$$

where k is oxidation state of the nitrogen substrate and E_G is growth efficiency (Williams et al. 1987). In terms of its deviation from 100%, E_G represents the fraction of cost required to provide reductant that is not incorporated into biomass and is estimated to be 0.87 (Penning de Vries et al. 1974). Because k is 5 for nitrate and –3 for ammonium, and the form of nitrogen substrate was unknown in our samples, leaf CC for each individual was calculated twice, once with $k = 5$ and once with $k = -3$, and then estimated as the mean of these two values.

To measure the lipid content of our dried samples, we used the extraction technique described by Bligh and Dyer (1956). Minimum and maximum leaf MC (eq. g glucose g^{-1} leaf dry mass day^{-1}) were calculated according to the methods of Merino et al. (1984) and averaged for each sample. The maintenance coefficients used were 0.0425 for lipid, 0.028 (minimum) and 0.053 (maximum) for protein, and 0.006 (minimum) and 0.01 (maximum) for ash.

Leaf photosynthesis

Turnbull et al. (2002) determined A_{max} at saturating photon flux density and ambient CO$_2$ partial pressure on all selected

Table 1. Leaf characteristics of red maple (*Acer rubrum*), red oak (*Quercus rubra*) and chestnut oak (*Quercus prinus*) from the lower (wetter) and upper (drier) catchment sites within a watershed in the Black Rock Forest, Cornwall, NY, USA. Values are means ± 1 SE. Values followed by the same letter are not significantly different at the $P \le 0.05$ level of significance. Abbreviations: leaf mass per unit area (LMA), photosynthetic rate at saturating photon flux density and ambient CO$_2$ partial pressure (A_{max}), [N] and [C] on a mass basis (N_{mass} and C_{mass}, respectively), [N] and [C] on a leaf area basis (N_{area} and C_{area}, respectively) and molar ratio of carbon to nitrogen (C/N).

	Lower site			Upper site			ANOVA statistics		
	A. rubrum	*Q. rubra*	*Q. prinus*	*A. rubrum*	*Q. rubra*	*Q. prinus*	Species	Site	Sp. × Site
LMA[1] g m^{-2}	71.9 b ± 1.5	90 c ± 2.8	101 d ± 3.5	60.7 a ± 2.3	109.5 d ± 3.1	104.1 d ± 6.5	< 0.001	0.208	0.001
A_{max}[1] µmol kg^{-1} s^{-1}	154.6 c ± 4.4	140.2 bc ± 6.3	136 abc ± 10.2	137.7 abc ± 10.7	115.1 a ± 4.1	118.3 ab ± 13.6	0.046	0.006	0.860
A_{max}[2] µmol m^{-2} s^{-1}	11.1 b ± 0.3	12.6 cd ± 0.5	13.5 d ± 0.9	8.2 a ± 0.5	12.7 cd ± 0.5	11.5 bc ± 0.6	< 0.001	0.001	0.029
N_{mass}[1] mg g^{-1}	22.7 a ± 0.7	26.7 b ± 0.5	32.4 d ± 0.4	24.2 a ± 0.4	29.3 c ± 0.8	30.1 c ± 0.6	< 0.001	0.204	< 0.001
N_{area}[1] g m^{-2}	1.6 a ± 0.1	2.4 b ± 0.1	3.3 c ± 0.1	1.5 a ± 0.1	3.2 c ± 0.1	3.1 c ± 0.2	< 0.001	0.086	< 0.001
C_{mass} mg g^{-1}	580.0 ab ± 1.6	584.1 bcd ± 1.6	578.1 a ± 1.3	582.4 abc ± 2.4	588.3 d ± 2.6	587.6 cd ± 1.7	0.047	0.002	0.126
C_{area} g m^{-2}	41.8 b ± 0.9	52.6 c ± 1.8	58.4 cd ± 2	35.3 a ± 1.4	64.3 d ± 1.6	61.2 d ± 3.8	< 0.001	0.128	< 0.001
C/N	30.1 e ± 0.9	25.6 c ± 0.4	20.8 a ± 0.3	28.1 d ± 0.4	23.6 b ± 0.6	22.8 b ± 0.4	< 0.001	0.129	0.001

[1] Recalculated from Turnbull et al. 2002.

[2] From Turnbull et al. 2002.

leaves in the late morning or early afternoon on clear, warm days with portable gas exchange systems (LI-6400, Li-Cor, Lincoln, NE) equipped with CO_2 control modules (Table 1). Leaf temperatures were maintained at 25 °C with thermoelectric coolers and the water vapor pressure deficit was regulated generally between 1.0 and 1.5 kPa. A constant photon flux density of 2000 μmol m^{-2} s^{-1} was provided by blue-red light-emitting diodes mounted above the leaf cuvette.

Additional biochemical and structural traits

Leaf organic [C] and the molar ratio of carbon to nitrogen (C/N) were measured with an elemental analyzer (Carlo Erba Na 1500) (Table 1). Leaf mass per area (LMA) was calculated from measurements made by Turnbull et al. (2002) with a portable area meter (Li-Cor Model LI-3000A) (Table 1).

Statistical analysis

Two-way analysis of variance (ANOVA) was performed to test for the main effects and interactions of species and site for all measured variables (SPSS for Windows, Rel. 7.5.1, 1996, SPSS, Chicago, IL). Mean differences were considered significant if $P \leq 0.05$. A nested model was used to account for species versus individual tree variation in parameters, and in all cases, between tree variation was not significant. Treatment means were compared to determine if means of the dependent variable were significant at the 0.05 probability level with least significant difference (LSD) post-hoc analysis (Sokal and Rohlf 1981). Linear regression analysis was used to determine the degree of correlation between selected measured variables.

Results

Leaf energy investment

There was a significant species effect ($P = 0.000$) on mean CC per unit leaf area (CC_{area}) and a significant species % site interaction effect ($P = 0.003$) on mean CC per unit leaf dry mass (CC_{mass}). Leaf CC_{area} was significantly less in red maple than in either red oak or chestnut oak at the lower site (28.2 and 38.8%, respectively) and the upper site (35.4 and 32%, respectively) (Figure 1A). Leaf CC_{mass} was significantly greater in red maple than in either red oak or chestnut oak at the upper site (14.7 and 16.4%, respectively) and significantly less than chestnut oak only at the lower site (12.5%) (Figure 1B). In intraspecific comparisons, CC_{mass} was 14.7% less in red maple at the lower site than at the upper site and 11.8% less in chestnut oak at the upper site than at the lower site (Figure 1B), whereas CC_{area} was not significantly different between sites for any of the sampled species.

Leaf maintenance costs expressed both per unit leaf area (MC_{area}) and per unit leaf mass (MC_{mass}) exhibited a significant species effect ($P \leq 0.001$), and MC_{area} also exhibited a significant species × site interaction effect ($P = 0.003$). Leaf MC_{area} was significantly less in red maple than in either red oak or chestnut oak at the lower site (25.8 and 46.9%, respectively) and the upper site (49.7 and 48.6%, respectively) (Figure 2A). Likewise, leaf MC_{mass} was significantly less in red maple than in either red oak or chestnut oak at the upper site (12.7 and 17.5%, respectively), whereas red maple had significantly lower MC_{mass} than chestnut oak only at the lower site (22.6%) (Figure 2B). Neither red maple nor chestnut oak exhibited any intraspecific differences in MC_{area} or MC_{mass} between sites, whereas red oak had a 25.8% lower MC_{area} at the lower site compared with the upper site. Considering the mean values for all species at both sites, there was a strong positive correlation between MC_{area} and CC_{area} (Figure 3), although these variables were not significantly correlated when expressed on a leaf mass basis.

Photosynthetic comparisons

As calculated from Turnbull et al. (2002), area-based leaf A_{max} ($A_{max,area}$) was significantly less in red maple than in either red oak or chestnut oak at both the lower (11.9 and 17.8%, respectively) and the upper site (35.4 and 28.7%, respectively), whereas mass-based A_{max} ($A_{max,mass}$) was not significantly different between species at either site (Table 1). In intraspecific comparisons, $A_{max,area}$ was 35.4% greater in red maple at the lower site than at the upper site and 17.4% greater in chestnut oak at the lower site than at the upper site, whereas $A_{max,mass}$ was 21.8% greater in red oak at the lower site than at the upper site (Table 1).

Considering all species at both sites, a moderate positive correlation was exhibited between mean leaf CC and A_{max}

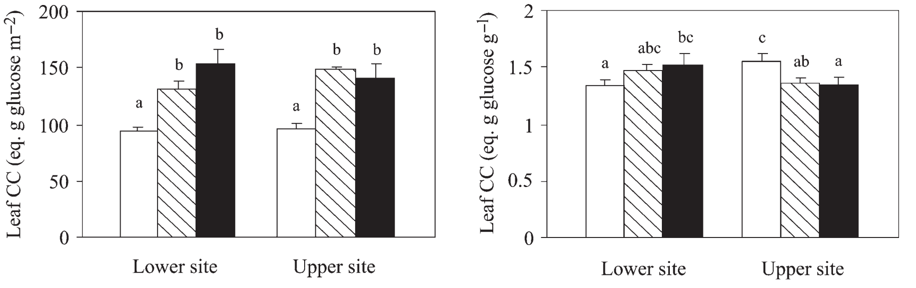

Figure 1. Mean leaf construction cost (CC) of red maple (*Acer rubrum*; open bars); red oak (*Quercus rubra*; hatched bars); and chestnut oak (*Quercus prinus*; solid bars) at the lower (wetter) and upper (drier) catchment sites within the Cascade Brook watershed (A) expressed per unit leaf area and (B) expressed per unit leaf dry mass. Error bars represent 1 SE of the mean. Means shown below the same letter are not statistically different at $P \leq 0.05$.

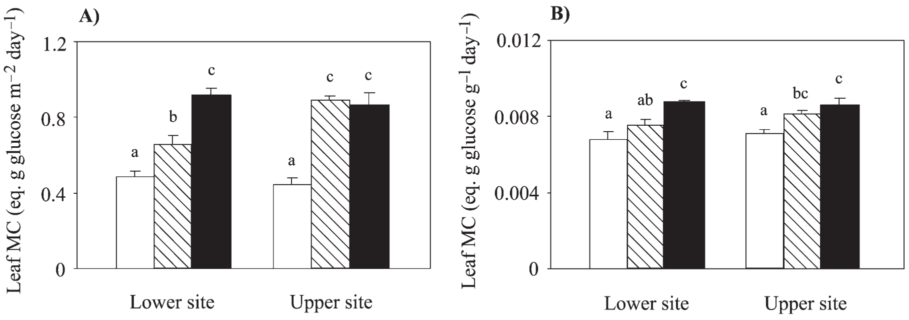

Figure 2. Mean leaf maintenance cost (MC) of red maple (*Acer rubrum*; open bars), red oak (*Quercus rubra*; hatched bars) and chestnut oak (*Quercus prinus*; solid bars) at the lower and upper catchment sites within the Cascade Brook watershed (A) expressed per unit leaf area and (B) expressed per unit leaf dry mass. Error bars represent 1 SE of the mean. Means shown below the same letter are not statistically different at $P \leq 0.05$.

when these factors were expressed on a leaf area basis (Figure 4A), whereas only a weak correlation was exhibited between these factors when expressed per unit leaf mass. Leaf MC and A_{max} expressed per unit leaf area also exhibited a moderate positive correlation (Figure 4B), although these variables were less strongly associated when expressed per unit leaf mass. At the lower site, the ratio of CC to A_{max} (CC/A_{max}), expressed per unit leaf area, was significantly less in red maple than in chestnut oak (~26.5%), but not significantly different from the ratio for red oak (Figure 5). At the upper site, there were no significant differences in CC/A_{max} between species (Figure 5). In intraspecific comparisons, CC/A_{max} of red maple was significantly less in red maple at the lower site than at the upper site (~30.5%), whereas there were no significant differences in this ratio between sites for either oak species.

Related physiological, biochemical and structural traits

As calculated from data of Turnbull et al. (2002), mean LMA of the upper-canopy in red maple was 20.1% less than in red oak and 28.8% less than in chestnut oak at the lower site, and 44.6% less than in red oak and 41.7% less than in chestnut oak at the upper site (Table 1). Likewise, leaf [N] expressed per unit leaf dry mass (N_{mass}) and both leaf [N] and [C] expressed on a leaf area basis (N_{area} and C_{area}) were all significantly less in red maple than in either oak species at both sites. In contrast, leaf C/N was significantly greater in red maple than in either of the oak species at both sites (Table 1). Chestnut oak had sig-

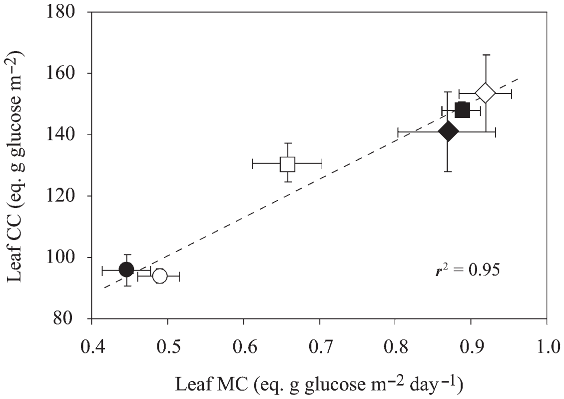

Figure 3. The association of mean leaf maintenance cost (MC) with leaf construction cost (CC) expressed per unit leaf area of red maple (*Acer rubrum*) (●, ○), red oak (*Quercus rubra*) (■, □) and chestnut oak (*Quercus prinus*) (◆, ◇) at the lower (open symbols) and upper (solid symbols) catchment sites within the Cascade Brook watershed. Error bars represent 1 SE of the mean. Regression line and r^2 value illustrate the degree of positive correlation between mean leaf MC and CC when all species at both sites are considered.

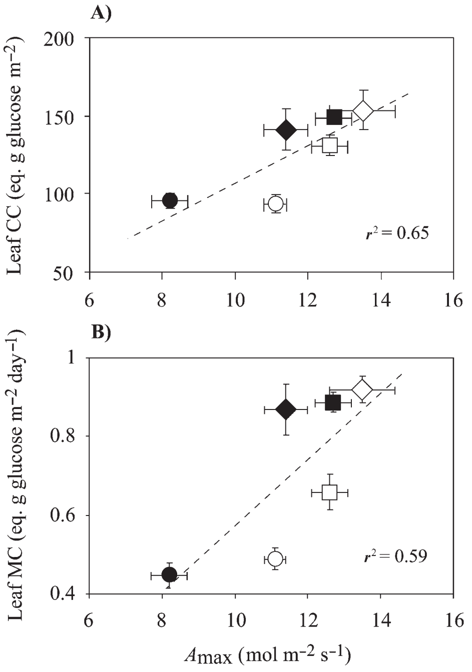

Figure 4. The relationships of mean leaf photosynthetic rate at saturating photon flux density and ambient CO_2 partial pressure (A_{max}) with (A) leaf construction cost (CC) and (B) leaf maintenance cost of red maple (*Acer rubrum*) (●, ○), red oak (*Quercus rubra*) (■, □) and chestnut oak (*Quercus prinus*) (◆, ◇) at the lower (open symbols) and upper (solid symbols) catchment sites within the Cascade Brook watershed. All factors are expressed per unit leaf area. Error bars represent 1 SE of the mean. Regression lines and r^2 values illustrate the degree of positive correlation between these factors when all species at both sites are considered.

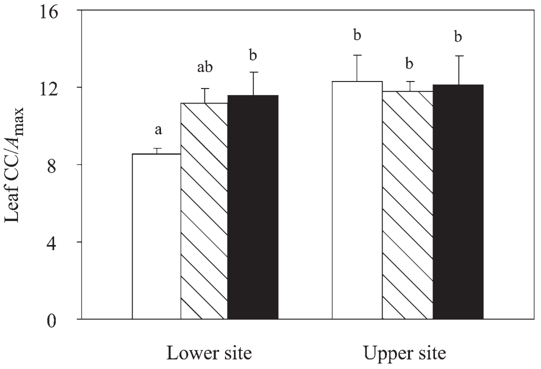

Figure 5. The energetic cost/benefit ratio of mean leaf construction cost (CC) to mean leaf photosynthetic rate at saturating photon flux density and ambient CO_2 partial pressure (A_{max}) expressed per unit leaf area of red maple (*Acer rubrum*) (open bars), red oak (*Quercus rubra*) (hatched bars), and chestnut oak (*Quercus prinus*) (solid bars) at the lower and upper catchment sites within the Cascade Brook watershed. Error bars represent 1 SE of the mean. Means shown below the same letter are not statistically different at $P \leq 0.05$.

nificantly greater LMA, N_{area} and N_{mass} and lower leaf C_{mass} and C/N than red oak at the lower site, but there were no significant differences in these factors between the oak species at the upper site (Table 1).

Intraspecific comparisons calculated from data of Turnbull et al. (2002), showed that LMA was 18.5% greater in red maple at the lower site than at the upper site, whereas red oak LMA was 17.8% less at the lower site than at the upper site (Table 1). Both N_{area} and N_{mass} were significantly greater (25 and 9.6%, respectively) in red oak at the upper site than at the lower site, whereas N_{mass} was 7.5% greater in chestnut oak at the lower site than at the upper site (Table 1). Leaf C_{area} was 18.4% greater in red maple and 18.2% less in red oak at the lower site than at the upper site, whereas leaf C_{mass} was 1.6% greater in chestnut oak at the upper site than at the lower site (Table 1). Leaf C/N was significantly greater in both red maple and red oak (7 and 8.3%, respectively) and significantly less in chestnut oak (8.8%) at the lower site than at the upper site (Table 1). Considering the mean values for all species at both sites, mean CC_{area} was strongly correlated positively with LMA (Figure 6A), N_{area} (Figure 6B) and C_{area} (Figure 6C) and negatively with C/N (Figure 6D).

Discussion

Leaf energetic characteristics may have important implications for the relative competitive success of red maple, red oak and chestnut oak at our study sites. Despite the comparatively low A_{max} of red maple, which suggests that its competitive success may be limited by low carbon assimilation capacity, this species is both prolific and common in deciduous forests of the northeastern USA (Abrams 1998). Therefore, we examined leaf CC, MC and A_{max} in the context of their supply and demand functions in plant energy budgets to obtain a more complete understanding of the relative competitive success of plant species than is possible by examining these factors alone.

Significant differences in CC_{mass} and MC_{mass} between red maple and co-occurring oaks at both the lower and upper sites suggest there may be fundamental interspecific differences in the biochemical composition of leaf biomass (Chapin 1989, Griffin 1994). In particular, our leaf CC_{mass} results indicate that both red oak and chestnut oak leaf biomass contain com-

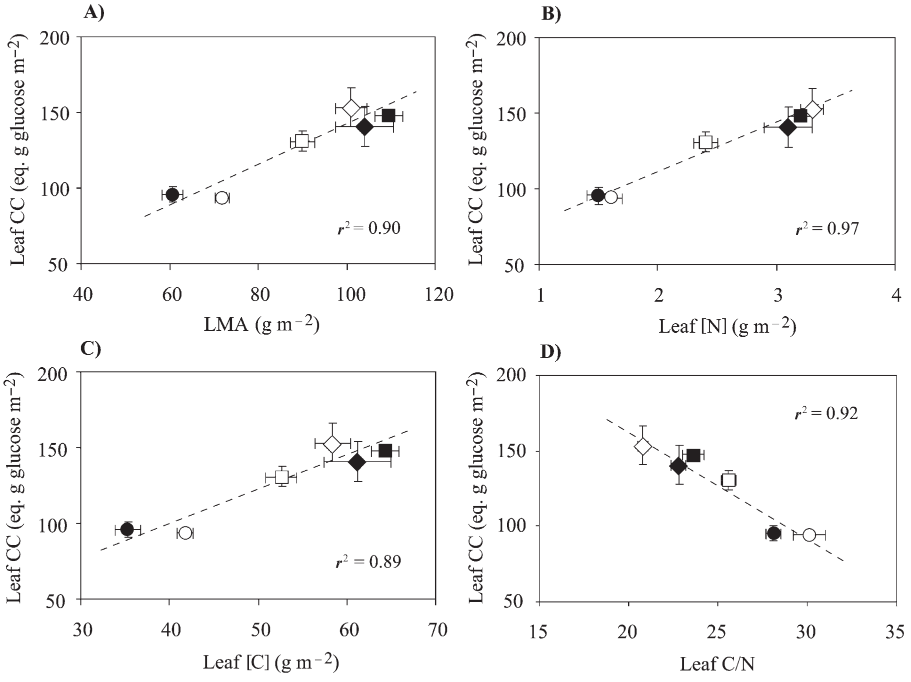

Figure 6. The relationships of mean construction cost (CC) per unit leaf area and (A) leaf dry mass per unit area (LMA), (B) leaf nitrogen concentration ([N]) per unit area, (C) leaf carbon concentration ([C]) per unit area, and (D) the molar ratio of leaf C to N (C/N) of red maple (*Acer rubrum*) (●, ○), red oak (*Quercus rubra*) (■, □) and chestnut oak (*Quercus prinus*) (◆, ◇) at the lower (open symbols) and upper (solid symbols) catchment sites within the Cascade Brook watershed. Error bars represent 1 SE of the mean. Regression lines and r^2 values illustrate the degree of positive correlation between these leaf variables when all species at both sites are considered.

pounds that are energetically less expensive to construct than those of red maple at the upper site, whereas red maple leaf biomass contains energetically less expensive compounds than chestnut oak only at the lower site. Interspecific differences in MC_{mass} suggest that red maple leaf biomass contains compounds that are energetically less expensive to maintain than those in either oak species at the upper site and those in chestnut oak only at the lower site. However, the lack of any interspecific differences in leaf $A_{max,mass}$ at either the upper or lower site suggests that differences in leaf biochemical composition between species do not significantly affect leaf photosynthetic capacity. Instead, the marked differences in CC_{area}, MC_{area} and $A_{max,area}$ between red maple and co-occurring oak species at both the lower and upper sites suggest differences in LMA between species may significantly influence leaf energetic properties. The relatively low CC_{area} and MC_{area} of red maple compared with the oak species at both sites indicates that, at our study sites, red maple requires less energy and resources to increase and maintain its leaf surface area than either red oak or chestnut oak.

Values of CC and MC reflect the energy that a plant must invest in the construction and maintenance of leaf biomass, whereas A_{max} is a measure of the potential energy supply of a leaf. As such, the relationship between these factors reflects a trade-off between leaf energetic gains and costs (Givnish 1983), which can have important ecological implications for species distribution and diversity, as well as net primary productivity and biogeochemical processes in ecosystems. The positive correlation between leaf CC_{mass} and MC_{mass} suggests that these factors had a compound, rather than contrasting, influence on leaf energy investment in our samples. Although the red maple leaves had a lower photosynthetic capacity than the leaves of co-occurring oak species per unit leaf area, this reduced capacity to capture energy was partially compensated by lower energy requirements for leaf biomass construction and maintenance, as indicated by the positive correlation of $A_{max,area}$ with both CC_{area} and MC_{area} and the interspecific comparisons of CC/A_{max}.

Studies of both deciduous and evergreen species in warm climates indicate that increases in CC/A_{max} are generally associated with increased leaf life-spans (Sobrado 1991, Eamus and Pritchard 1998, Eamus et al. 1999). Although we did not measure leaf longevity, these findings suggest red maple may have shorter leaf longevity than the co-occurring oak species at the lower site. However, for competing deciduous species growing within a northeastern U.S. forest ecosystem, it does not seem particularly advantageous to invest increased energy in leaves to increase leaf longevity for greater carbon return because the growing season typically is about 6 months long. In the Black Rock Forest, in particular, red maple trees tend to leaf out earlier in the growing season than co-occurring oak species, with no noticeable differences in leaf loss during the growing season. Thus, it seems more likely that increased energy would be invested in structural and chemical herbivory defense compounds. Such relatively expensive carbon-based phenolic defense compounds are typical of many oak species (Abrams 1996).

Intraspecific comparisons between sites revealed different leaf energetic requirements in red maple, red oak and chestnut oak that could provide information about their relative competitive success. In red maple, a lower energy requirement for leaf biomass construction (CC_{mass}) at the lower site compared with the upper site corresponds with an increase in the capacity to assimilate energy and resources (A_{max}), possibly influenced by greater soil water availability at the lower site. This mass-based cost reduction at the lower site could be the result of dilution by an accumulation of relatively inexpensive storage carbohydrates made available by increased photosynthetic activity without a corresponding increase in leaf [N] as may be inferred from the significantly greater C_{area}, C/N and LMA in red maple leaves at the lower site compared with the upper site. The relatively low CC_{area} of red maple may not be as sensitive to such environmental changes as CC_{mass}, which was significantly greater than that of the oaks at the upper site where soil water and photosynthesis were more limited. When considered on a leaf area basis, however, these mass-based differences in CC were offset by large interspecific differences in LMA.

Unlike red maple, the influence of site differences in energy and resource capture and leaf energetic costs appeared more limited in red oak, for which no significant differences in leaf CC were exhibited between sites. However, increased $A_{max,mass}$ in this species at the lower site compared with the upper site was associated with a significant decrease in MC_{area}. In contrast to red maple, significantly greater $A_{max,area}$ in chestnut oak at the lower site than at the upper site was associated with a corresponding increase in CC_{mass}. In this species, increased photosynthetic activity at the lower site may be the result of significantly greater leaf N_{mass}, which is typically found in more expensive plant compounds including photosynthetic machinery (Penning de Vries et al. 1974).

Although all measurements reported here were from upper-canopy leaves of emergent trees, these findings could have significant implications for forest regeneration and seedling dynamics. In the understory, where red maple is particularly abundant in many deciduous forest ecosystems (Abrams 1998), light can be a limiting resource. Sipe and Bazazz (1994) found that red maple tended to respond to the increased light availability afforded by forest gaps in the understory by developing large numbers of leaves, and it has previously been suggested that the architectural plasticity of this species influences its success in understory or gap environments (Wallace and Dunn 1980). Although leaf-level A_{max} may be relatively low in red maple, its low CC_{area}, MC_{area} and MC_{mass} indicates that it can construct and maintain leaves at a lower energetic cost than can the co-occurring oak species. This allows red maple to produce many low-cost leaves at the same energetic cost as fewer, more expensive leaves with higher individual photosynthetic capacity in co-occurring oak species.

We suggest that lower leaf CC, combined with lower leaf MC, may provide a leaf-level physiological explanation for the recently observed expansion of red maple in eastern deciduous forests, despite its relatively low leaf-level photosynthetic capacity and related physiological, biochemical and structural characteristics. Combined with other physiological and ecological considerations, such as its genetic diversity and response to land-use changes (Abrams 1998), we suggest that low leaf CC and MC may enhance the competitive success of red maple over co-occurring oak species. Additional research examining leaf CC, MC and $A_{\max}$ of red maple and co-occurring species in various environments and the influence of global change on these factors could provide insight into the potential competitive success of these species in the future. Furthermore, it needs to be determined if patterns of resource and energy allocation in red maple and co-occurring oaks to structures other than leaves, such as stems and roots, also influence the relative competitive success of these species.

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References

Abrams, M.D. 1996. Distribution, historical development and ecophysiological attributes of oak species in the eastern United States. Ann. Sci. For. 53:487–512.

Abrams, M.D. 1998. The red maple paradox. BioScience 48: 355–364.

Abrams, M.D. and M.E. Kubiske. 1990. Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: influence of light regime and shade tolerance rank. For. Ecol. Manage. 31:245–253.

Abrams, M.D. and G.J. Nowacki. 1992. Historical variation in fire, oak recruitment and post-logging accelerated succession in central Pennsylvania. Bull. Torrey Bot. Club 119:19–25.

Abrams, M.D., M.E. Kubiske and S.A. Mostoller. 1994. Relating wet and dry year ecophysiology to leaf structure in contrasting temperate tree species. Ecology 75:123–133.

Blackman, D. and S. Ware. 1982. Soil moisture and the distribution of *Quercus prinus* and *Quercus rubra*. Castanea 47:360–367.

Bligh, E.G. and W.J. Dyer. 1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37:913–917.

Chapin, F.S. III. 1989. The cost of tundra plant structures: evaluation of concepts and currencies. Am. Nat. 133:1–19.

Chiariello, N.R., H.A. Mooney and K. Williams. 1989. Growth, carbon allocation and cost of plant tissues. *In* Plant Physiological Ecology. Field Methods and Instrumentation. Eds. R.W. Pearcy, J.R. Ehleringer, H.A. Mooney and P.W. Rundell. Chapman Hall, London, pp 327–365.

Eamus, D. and H. Prichard. 1998. A cost–benefit analysis of leaves of four Australian savanna species. Tree Physiol. 18:537–545.

Eamus, D., B. Myers, G. Duff and R. Williams. 1999. A cost-benefit analysis of leaves of eight Australian savanna tree species of differing leaf life-span. Photosynthetica 36:575–586.

Friday, K.S. and J.B. Friday. 1985. Black Rock Forest Inventory. Harvard Black Rock Forest Internal Report, 125 p.

Givnish, T.J. 1983. Economics of gas exchange. *In* On the Economy of Form and Function. Ed. T.J. Givnish. Cambridge University Press, Cambridge, pp 11–24.

Griffin, K.L. 1994. Calorimetric estimates of construction cost and their use in ecological studies. Funct. Ecol. 8:551–562.

Griffin, K.L., R.B. Thomas and B.R. Strain. 1993. Effects of nitrogen supply and elevated carbon dioxide on construction cost in leaves of *Pinus taeda* (L.) seedlings. Oecologia 95:575–580.

Griffin, K.L., W.E. Winner and B.R. Strain. 1996. Construction cost of loblolly and ponderosa pine leaves grown with varying carbon and nitrogen availability. Plant Cell Environ. 19:729–738.

Hardin, J.W., D.J. Leopold and F.M. White. 2000. Harlow and Harrar's textbook of dendrology. 9th Edn. McGraw-Hill, New York, 544 p.

Keever, C. 1973. Distribution of major forest species in southeastern Pennsylvania. Ecol. Monogr. 43:303–332.

Kleiner, K.W., M.D. Abrams and J.C. Schultz. 1992. The impact of water and nutrient deficiencies on the growth, gas exchange and water relations of red oak and chestnut oak. Tree Physiol. 11: 271–287.

Kolb, T.E. and K.C. Steiner. 1990. Growth and biomass partitioning of northern red oak and yellow-poplar seedlings: Effects of shading and grass root competition. For. Sci. 36:34–44.

Lambers, H. and H. Poorter. 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Adv. Ecol. Res. 23:188–261.

Lorimer, C.G. 1984. Development of the red maple understorey in northeastern oak forests. For. Sci. 30:3–22.

Merino, J., C. Field and H.A. Mooney. 1984. Construction and maintenance costs of Mediterranean-climate evergreen and deciduous leaves. II. Biochemical pathway analysis. Acta Oecol. Oecol. Plant. 5:211–229.

Mooney, H.A. 1972. The carbon balance of plants. Annu. Rev. Ecol. Syst. 3:315–346.

Nowacki, G.J. and M.D. Abrams. 1992. Community, edaphic and historical analysis of mixed oak forests of the Ridge and Valley Province in central Pennsylvania. Can. J. For. Res. 22:790–800.

Olssen, K.S. 1981. Soil survey of Orange County, New York. USDA Soil Conservation Service, U.S. Government Printing Office, Washington, DC, 192 p.

Penning de Vries, F.W.T., A.H.M. Brunsting and H.H. van Laar. 1974. Products, requirements and efficiency of biosynthesis: A quantitative approach. J. Theor. Biol. 45:339–377.

Phillipson, J. 1964. A miniature bomb calorimeter for small biological samples. Oikos 15:130–139.

Poorter, H. and M. Bergkotte. 1992. Chemical composition of 24 wild species differing in relative growth rate. Plant Cell Environ. 15: 221–229.

Poorter, H. and R. Villar. 1997. The fate of acquired carbon in plants: chemical composition and construction costs. *In* Plant Resource Allocation. Eds. F. Bazzaz and J. Grace. Academic Press, San Diego, pp 39–72.

Post, W.M. and J. Pastor. 1996. Linkages—An individual-based forest ecosystem model. Clim. Change 34:253–261.

Reich, P.B., M.D. Abrams, D.S. Ellsworth, E.L. Kruger and T.J. Tabone. 1990. Fire affects ecophysiology and community dynamics of central Wisconsin oak forest regeneration. Ecology 71: 2179–2190.

Schlesinger, W.H. 1991. Biogeochemistry: An analysis of global change. Academic Press, New York, 443 p.

Sipe, T.W. and F.A. Bazzaz. 1994. Gap partitioning among maples (*Acer*) in central New England—survival and growth. Ecology 75: 2318–2332.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. Freeman, San Francisco, 859 p.

Sobrado, M.A. 1991. Cost–benefit relationships in deciduous and evergreen leaves of tropical dry forest species. Funct. Ecol. 5: 608–616.

Sullivan, N.H., P.V. Bolstad and J.M. Vose. 1996. Estimates of net photosynthetic parameters for twelve tree species in mature forests of the southern Appalachians. Tree Physiol. 16:397–406.

Tryon, H.H. 1930. The Black Rock Forest. Black Rock Forest Bulletin No. 1, Cornwall Press, Cornwall, NY, 42 p.

Turnbull, M.H., D. Whitehead, D.T. Tissue, W. Schuster, K.J. Brown and K.L. Griffin. 2001. Responses of leaf respiration to temperature and leaf characteristics in three deciduous tree species vary with site water availability. Tree Physiol. 21:571–578.

Turnbull, M.H., D. Whitehead, D.T. Tissue, W. Schuster, K.J. Brown, V.C. Engel and K.L. Griffin. 2002. Photosynthetic characteristics in canopies of *Quercus rubra*, *Quercus prinus* and *Acer rubrum* differ in response to soil water availability. Oecologia 130: 515–524.

Wallace, L.L. and E.L. Dunn. 1980. Comparative photosynthesis of three gap phase successional tree species. Oecologica 45:331–340.

Williams, K., F. Percival, J. Merino and H.A. Mooney. 1987. Estimation of tissue construction cost from heat of combustion and organic nitrogen content. Plant Cell Environ.10:725–734.