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Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species

Abstract The relationship between photosynthetic capacity (A_{max}) and leaf nitrogen concentration (N) among all C_3 species can be described roughly with one general equation, yet within that overall pattern species groups or individual species may have markedly different A_{max}-N relationships. To determine whether one or several predictive, fundamental A_{max}-N relationships exist for temperate trees we measured A_{max}, specific leaf area (SLA) and N in 22 broad-leaved deciduous and 9 needle-leaved evergreen tree species in Wisconsin, United States. For broad-leaved deciduous trees, mass-based A_{max} was highly correlated with leaf N ($r^2=0.75$, $P<0.001$). For evergreen conifers, mass-based A_{max} was also correlated with leaf N ($r^2=0.59$, $P<0.001$) and the slope of the regression (rate of increase of A_{max} per unit increase in N) was lower ($P<0.001$) by two-thirds than in the broad-leaved species (1.9 vs. 6.4 µmol CO_2 g^{-1} N s^{-1}), consistent with predictions based on tropical rain forest trees of short vs. long leaf life-span. On an area basis, there was a strong A_{max}-N correlation among deciduous species ($r^2=0.78$, $P<0.001$) and no correlation ($r^2=0.03$, $P>0.25$) in the evergreen conifers. Compared to deciduous trees at a common leaf N (mass or area basis), evergreen trees had lower A_{max} and SLA. For all data pooled, both leaf N and A_{max} on a mass basis were correlated ($r^2\approx0.6$) with SLA; in contrast, area-based leaf N scaled tightly with SLA ($r^2=0.81$), but area-based A_{max} did not ($r^2=0.06$) because of low A_{max} per unit N in the evergreen conifers. Multiple regression analysis of all data pooled showed that both N (mass or area basis) and SLA were significantly ($P<0.001$) related to A_{max} on mass ($r^2=0.80$) and area ($r^2=0.55$) bases, respectively. These results provide further evidence that A_{max}-N relationships are fundamentally different for ecologically distinct species groups with differing suites of foliage characteristics: species with long leaf life-spans and low SLA, whether broad-leaved or needle-leaved, tend to have lower A_{max} per unit leaf N and a lower slope and higher intercept of the A_{max}-N relation than do species with shorter leaf life-span and higher SLA. A single global A_{max}-N equation overestimates and underestimates A_{max} for temperate trees at the upper and lower end of their leaf N range, respectively. Users of A_{max}-N relationships in modeling photosynthesis in different ecosystems should appreciate the strengths and limitations of regression equations based on different species groupings.

Key words Leaf life-span · Evergreen · Deciduous · Photosynthesis · Nitrogen

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Introduction

Across species from diverse ecosystems and of differing life histories, a general relationship between net photosynthetic capacity (A_{max}) and leaf nitrogen (N) has been identified (Field and Mooney 1986). The overall strength and generality of this relationship is impressive – three independent surveys found similar regression relations (Field and Mooney 1986; Reich et al. 1991a, 1992) – but not surprising, as A_{max} is dependent on the concentration of N-containing enzymes, pigments, and electron transport components (Evans 1989). Despite the strength of the general relationship, there may be significant variation within it, as species of contrasting ecological characteristics may differ in the form of, and conformity to, the A_{max}-N relationship (Evans 1989; Reich et al. 1994). Determining how A_{max}-N varies among groups of species may provide a clearer understanding of the central role of N and A_{max} in energy gain by plants and may assist in refining the use of N as a scalar of A_{max} in modeling (Reich et al. 1990; Aber et al. 1995a,b).

To date, much of the work on A_{max}-N relations in field grown plants has explored tropical or mediterranean shrubs and trees, or desert and old-field annuals (Field and Mooney 1986; Chazdon and Field 1987; Walters and Field 1987; Reich et al. 1991a, 1994). Data for the important and widespread temperate forest biome are less abundant (but see Reich et al. 1991b; Ellsworth and Reich 1993). Hence, it may be useful to determine how A_{max}-N relationships in temperate trees compare with those developed elsewhere and to examine whether the two main tree groups found in this region, broad-leaved deciduous and needle-leaved evergreen species, have different A_{max}-N relationships. In particular, we ask whether differences in A_{max}-N relations observed between tropical broad-leaved evergreen species with short or long leaf life-spans (Reich et al. 1994) are paralleled by similar differences between temperate hardwood and coniferous tree species, given the additional contrasts of leaf type and habit (broad-leaved vs. needle-leaved, deciduous vs. evergreen) in the two temperate species groups.

Species adapted to environments rich in resources tend to have a form and physiology that maximize assimilation and growth rate (Chapin 1980; Reich et al. 1992). At the leaf level, this often includes short leaf life-span, and high N concentrations, specific leaf area (SLA), and A_{max}. We therefore hypothesize that deciduous hardwood species, which are generally adapted to higher resource levels than evergreen conifers in temperate biomes, will have a higher A_{max} per unit leaf N and a steeper slope of the A_{max}-N relationship than the conifers, indicating a higher short-term or potential photosynthetic return per unit N invested in foliage.

Materials and methods

We studied a total of 22 deciduous hardwood and 9 evergreen coniferous species growing in the field in southern Wisconsin (Table 1). Three of the hardwoods and two of the conifers were exotics (see Table 1). Most (25) of the species were studied at the University of Wisconsin (UW) Arboretum in Madison, Wisconsin. Nine of these species were also studied at one of five additional sites, and six species were studied only at one of these latter sites. These measures at the additional sites enabled us to broaden the species pool and to examine if relationships hold across sites. The region has a cold temperate, continental climate. Mean January and July temperatures at all six sites are approximately $-10°C$ and $23°C$ and mean annual precipitation ranges between 700 and 800 mm (data not shown).

At the UW Arboretum, open-grown individuals (usually 4–10 m tall, except for shrub species) of 25 species were studied, and "sun" leaves in high light microenvironments were sampled. At the Coulee Experimental Forest, near Bangor, in LaCrosse County, Wisconsin, upper crown foliage of plantation grown trees of four species (three in 28-year-old stands and one, red pine, in 28- and 9-year-old stands) were studied. Upper crown foliage of red pine was also studied in 34-year-old plantations (1987) in Big Flats, Adams County, Wisconsin. Young individuals of four species were studied in intermediate-sized gaps (250–500 m²) in a 30-year old oak-maple-birch forest at the Schmeeckle Reserve of the University of Wisconsin-Stevens Point, in Stevens Point, Wisconsin. Three tree species were also studied in a cedar-tamarack swamp along the periphery of Cedarburg Bog, at the University of Wisconsin-Milwaukee Field Station, in Saukville, Ozaukee County, Wisconsin. Three

species were studied in clearings and/or at the top of a sugar maple-oak forest canopy on the Jordan Timberland, near Dodgeville, in Iowa County, Wisconsin. The six sites were located on alfisols or entisols and span a range of distance of ≈250 km east-west and ≈160 km north-south in the southern half of Wisconsin. For convenience we describe all conifers as "needle-leaved", thereby lumping needle-like and scale-like foliage together.

Leaf photosynthetic rates of young mature leaves were measured in the field in 1986–1990 using an open gas-exchange system (Analytical Development Corporation, Hoddesdon, UK). Measurements were made during periods of minimal water stress. The CO_2 and water vapor sensors were calibrated against known gas standards. For purposes of this study, the following protocol was followed to ensure that near-maximum field photosynthetic rates were measured (see Reich et al. 1991a for more detail). Leaves were measured in early to late morning under ambient CO_2 concentrations, air temperatures, relative humidities and natural saturating irradiances. Under such conditions, temperatures were moderate and relative humidities high, and thus were near optimal. For each species, fully-expanded young mature leaves were measured during July and August since A_{max}-N relationships are relatively stable once leaves are fully expanded (see Reich et al. 1991a,b). Leaves sampled for deciduous species were ≈2-4 months old and for conifers were ≈2-4 months old and/or approximately 1 year old (after full needle development current-year conifer needles have similar gas exchange rates to previous-year needles), and both needle age classes were lumped in all analyses presented here. Among all 31 species, the range of sample sizes for photosynthetic rates was wide (5–179 leaves per species per site). In most species, between 2 and 5 individuals were sampled on a site. Differences among individuals within species were small and all leaves were pooled per species per site. On nine broad-leaved and seven coniferous species, leaf sample sizes were relatively large (n ranged from 40 to 179). Despite the low sample size for some species, we could not discern any differences in A_{max}-N relations between groups partitioned into low- and high-sampling regimes, and thus even low sample sizes appear to be representative for the species on that site at that time. To avoid undue influence of heavily sampled species on a site, the data set used in this analysis uses the average A_{max} and N values per species per site. All data were pooled over time. Results were similar when analyzed using a data set where each species was included on only one site. There were no apparent differences in A_{max}-N relationships for planted or natural vegetation. Use of the six sites enabled us to broaden the species pool and to test whether A_{max}-N relations are common among diverse species and sites.

Immediately after photosynthesis measurements, each leaf was harvested and its projected leaf area determined by optical planimetry (Li-3000 leaf area meter, LiCor Inc., Lincoln, Neb.), and leaves were then oven-dried and weighed. Errors in leaf area determination, and hence in SLA and A_{max} per unit area, are larger for coniferous species since needles are not flat. All area-based measures are for single-sided projected leaf area and thus will not be directly comparable to values for conifers expressed per total leaf surface area. Leaves were analyzed for total organic N by the University of Wisconsin Soil and Plant Analysis Laboratory using a micro-Kjehldahl assay. Data were analyzed using regression analyses and separate slopes analyses of covariance (SAS 1994).

Results

There was a significant linear correlation of mass-based A_{max} and N for all data pooled, but two statistically distinct ($P<0.001$) relationships were observed for deciduous broad-leaved and evergreen needle-leaved species groups (Fig. 1, $r^2=0.75$ and 0.59, respectively). The slope of the mass-based A_{max}-N relationship (rate of increase of A_{max} per unit increase in N) was significantly lower ($P<0.001$) in the evergreen than deciduous species
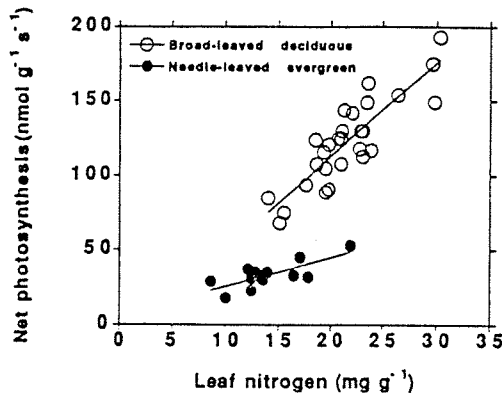
Fig. 1 Relationship between maximum mass-based net photosynthesis (nmol g^{-1} s^{-1}) and leaf nitrogen (mg g^{-1}) for broad-leaved deciduous tree species (*open circles*) and needle-leaved evergreen conifers (*closed circles*) in Wisconsin. The regression relationships are: for deciduous trees, $y = -14.1 + 6.35 \times N$ ($r^2 = 0.75$, $P < 0.001$); for evergreen conifers, $y = 6.5 + 1.92 \times N$ ($r^2 = 0.59$, $P < 0.001$)

Fig. 2 Relationship between maximum area-based net photosynthesis (μmol m^{-2} s^{-1}) and leaf nitrogen (g m^{-2}) for broad-leaved deciduous tree species (*open circles*) and needle-leaved evergreen conifers (*closed circles*) in Wisconsin. The regression relationships are: for deciduous trees, $y = 0.31 + 5.45 \times N$ ($r^2 = 0.78$, $P < 0.001$); for evergreen conifers, $y = 7.59 + 0.19 \times N$ ($r^2 = 0.03$, $P < 0.75$)

(1.9 μmol CO_2 g^{-1} N s^{-1} vs. 6.4 μmol CO_2 g^{-1} N s^{-1}, respectively).

Other differences in the data (comparisons of exotic and native species or site contrasts) had no significant effect on A_{max}, N and SLA relationships, which were consistent across sites and species origin. For species where data were collected at two or more sites, higher mass-based A_{max} corresponded with higher leaf N in all nine cases. Moreover, A_{max}-N regressions for both species groups (broad-leaved and needle-leaved) made separately for the Madison data versus data from the other five sites were not statistically different, and the data points for all sites appear to fit the combined regression line for each group equally well. Thus, species groups matter to a great degree for A_{max}-N relationships, whereas site differences did not in this case (but see Reich and Schoettle 1988; Reich et al. 1994).

For area-based A_{max} and N, there was a strong correlation among all broad-leaved species ($r^2 = 0.78$) and no correlation ($r^2 = 0.03$) in the conifers or for all data pooled ($r^2 = 0.02$) (Fig. 2). The relationships for the conifers or for the pooled data did not improve significantly if estimated total leaf surface area was used instead of projected leaf area. Use of total leaf surface area expressions for both broad and needle leaves did bring the evergreen conifer data "nearer" to the broad-leaved deciduous cluster, but at a given leaf N per area they were still at a lower area-based A_{max}.

Evergreen needle-leaved species had substantially lower A_{max} per N than deciduous broad-leaved species even at a common range of leaf N (Table 1, Figs. 1 and 2). For all data pooled (evergreen and deciduous species), both A_{max} and leaf N expressed on a mass basis were positively related to SLA (Fig. 3 A, B). At common leaf N (≈ 15–22 mg g^{-1}), evergreen conifers always had lower SLA than deciduous hardwoods. For all data pooled, leaf N on an area basis was highly correlated with SLA ($r^2 = 0.81$, Fig. 4A); the scaling of area-based N
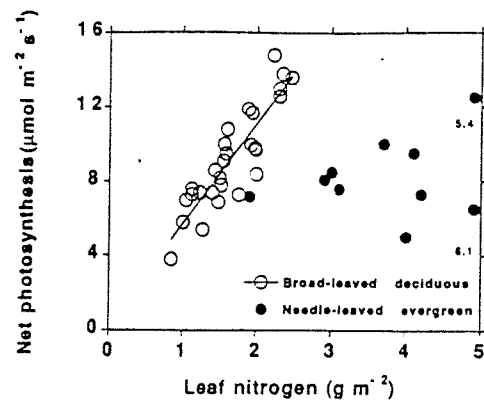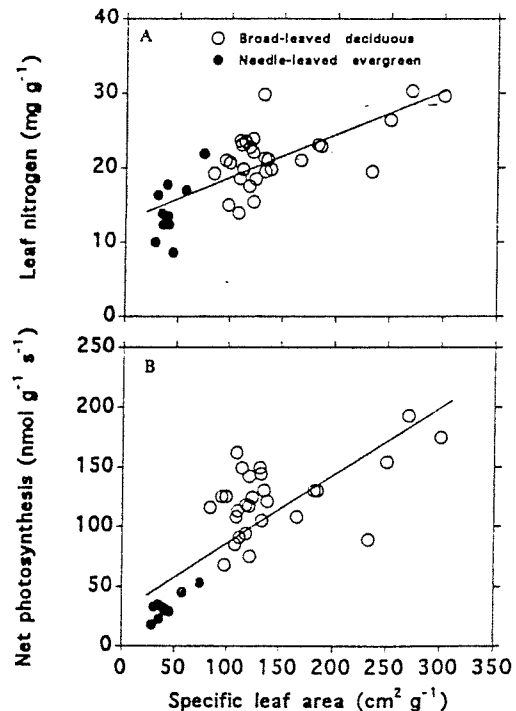

Fig. 3 A Relationship between mass-based leaf nitrogen (N)(mg g^{-1}) and specific leaf area, SLA (cm^2 g^{-1}), and **B** relationship between maximum mass-based net photosynthesis (nmol g^{-1} s^{-1}) and SLA, both for broad-leaved deciduous tree species (*open circles*) and needle-leaved evergreen conifers (*closed circles*) in Wisconsin. The regression relationships are: for all species pooled, $N = 12.6 + 0.062 \times SLA$ ($r^2 = 0.59$, $P < 0.001$); for broad-leaved deciduous trees, $N = 14.9 + 0.047 \times SLA$ ($r^2 = 0.41$, $P < 0.001$); for evergreen conifers, $N = 6.8 + 0.18 \times SLA$, ($r^2 = 0.40$, $P < 0.001$); for all species pooled, $A_{max} = 30.2 + 0.61 \times SLA$ ($r^2 = 0.66$, $P < 0.001$); for deciduous trees, $A_{max} = 82.8 + 0.29 \times SLA$ ($r^2 = 0.35$, $P < 0.01$); for evergreen conifers, $A_{max} = 6.0 + 0.63 \times SLA$ ($r^2 = 0.75$, $P < 0.001$)

with SLA appeared to be continuous and smooth across both species types. Despite this, area-based A_{max} was not significantly correlated ($r^2 = 0.06$) to SLA, because of low A_{max} per N in the evergreen conifers (Fig. 4B).

Table 1 Listing of species, sites and leaf data in Wisconsin (sites: _1_ Madison, Dane County, _2_ Coulee Experimental Forest, LaCrosse County, _3_ Stevens Point, Portage County, _4_ Big Flats, Adams County, _5_ Saukville, Ozaukee County, _6_ Dodgeville, Iowa County, _NA_ data not available)

	Sites	N (mg g^{-1})	A_{max} (nmol g^{-1} s^{-1})	N (g m^{-2})	A_{max} (µmol m^{-2} s^{-1})	A_{max}/N (µmol mol^{-1} N s^{-1})	SLA (cm^2 g^{-1})
Broad-leaved deciduous hardwoods							
Acer rubrum	1	21.0	108	1.50	8.2	72.0	166
A. rubrum	3	19.5	89	0.84	3.8	63.9	233
A. saccharum	1	19.5	105	1.40	7.4	75.4	133
A. saccharum	6	17.6	94	1.52	7.8	74.8	118
Betula nigra	1	22.8	118	1.92	10.0	72.5	113
B. pumila	5	15.1	68	1.48	6.9	63.0	98
Carya ovata	1	19.8	91	1.99	8.4	64.3	112
Catalpa speciosa[a]	1	18.5	124	1.56	10.0	93.8	124
Celtis occidentalis	1	23.9	117	1.98	9.7	68.5	121
Cornus florida	1	14.0	85	1.12	7.3	85.0	108
Fraxinus americana	6	21.3	144	1.60	10.8	94.6	132
F. americana	1	19.8	121	1.43	8.6	85.6	138
Ilex verticillata	5	15.5	75	1.27	5.4	67.7	122
Juglans nigra	1	29.6	175	1.01	5.8	82.8	305
Lonicera×bella[a]	1	18.6	108	1.55	9.1	81.3	109
Morus rubra	1	23.1	130	1.56	7.3	78.8	182
Populus deltoides	1	23.6	162	2.22	14.8	96.1	109
P. tremuloides	1	22.1	142	1.88	11.9	90.0	121
Prunus serotina	1	20.7	125	1.93	11.7	84.5	99
P. serotina	3	26.4	154	1.04	7.0	81.7	250
Quercus ellipsoidalis	1	21.0	125	2.30	13.0	83.3	95
Q. ellipsoidalis	3	22.9	130	1.23	7.4	79.5	185
Q. macrocarpa	1	23.5	149	2.46	13.6	88.8	114
Q. rubra	2	29.8	149	2.30	12.6	70.1	131
Q. rubra	6	21.1	130	1.58	9.5	86.3	135
Rhamnus cathartica[a]	1	23.1	113	1.97	9.8	68.5	110
Rubus alleghaniensis	3	30.3	193	1.12	7.6	89.2	270
Ulmus americana	1	19.3	116	2.34	13.8	84.1	84
Needle-leaved evergreen conifers							
Juniperus virginia	1	16.4	33	6.1	6.5	28.2	30
Picea abies[a]	2	17.8	32	3.7	10.0	25.2	39
P. glauca	1	12.4	23	4.2	7.3	26.0	35
P. mariana	1	12.1	37	NA	NA	42.8	NA
Pinus banksiana	1	12.4	31	4.1	9.5	35.0	41
P. resinosa	2	13.5	30	3.1	7.6	31.1	40
P. resinosa	4	10.0	18	4.0	5.0	25.2	28
P. strobus	1	17.0	45	2.9	8.1	37.1	57
P. strobus	2	21.9	53	2.7	8.5	33.9	74
P. sylvestris[a]	1	13.9	35	5.4	12.5	35.3	34
Thuja occidentalis	1	8.6	29	1.9	7.2	47.2	45
T. occidentalis	5	12.8	35	NA	NA	38.3	NA

[a] Exotic species

Multiple regression analyses for all data pooled showed that A_{max} on a mass basis was significantly related to both mass-based N and SLA ($r^2=0.80$) and A_{max} on an area basis was significantly related to both area-based N and SLA ($r^2=0.57$). In essence, high SLA and high N combine to yield higher A_{max} than either high N or high SLA alone.

Discussion

The form of the A_{max}-N relation varied substantially between broad-leaved deciduous and needle-leaved evergreen groups of tree species, yet within these groups strong relationships were observed. In general, results were consistent with differential A_{max}-N relationships observed among contrasting tropical rain forest trees (Reich et al. 1994), all of which were broad-leaved evergreen, but which varied in leaf lifespan. In Wisconsin, SLA, mass-based A_{max}, A_{max}/N, and the slope of A_{max}-N were all roughly 3 times greater in deciduous hardwoods with leaf life-spans of about 6 months than in evergreen conifers with needle life-spans of 2.5–6.5 years. In the Amazon rain forest, secondary successional trees with leaf life-spans of 3–8 months had 2–5 times greater SLA, mass-based A_{max}, A_{max}/N, and slope of A_{max}-N than species groups from three late successional rain forest communities with leaf life-spans of 1–4 years (Reich et al. 1994). Thus, in general, differences in A_{max}-N relations among different "functional" groups of tree species (in
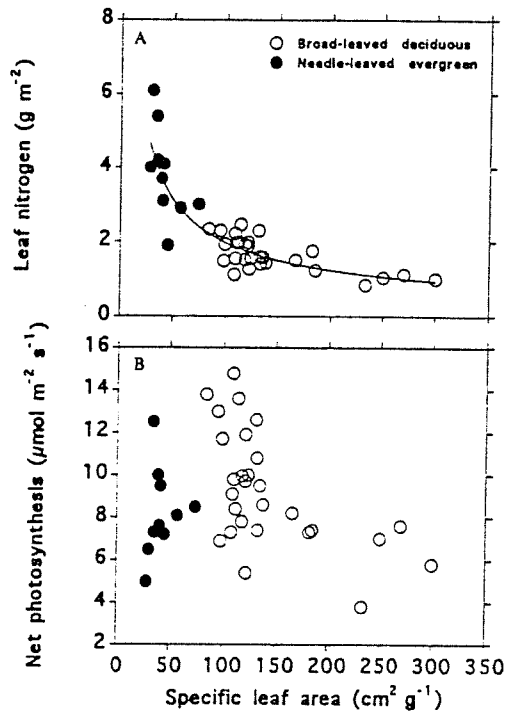
Fig. 4 **A** Relationship between area-based leaf nitrogen (N)(g m^{-2}) and specific leaf area, SLA (cm^2 g^{-1}), and **B** relationship between maximum area-based net photosynthesis (μmol m^{-2} s^{-1}) and SLA, for broad-leaved deciduous tree species (*open circles*) and needle-leaved evergreen conifers (*closed circles*) in Wisconsin. The regression relationships for all species pooled are: area-based $N=44.8\times$(SLA$^{-0.679}$) ($r^2=0.81$, $P<0.001$); area-based A_{max} was not significantly related to SLA ($r^2=0.06$, $P>0.20$)

this case with respect to leaf life-span and SLA) seem to be consistent regardless of the taxonomy, morphology or biome of the groups involved.

How well would the general mass-based A_{max}-N regression relationship that holds roughly for all C$_3$ species pooled (average of similar relationships in Field and Mooney 1986; Reich et al. 1991a, 1992) predict mass-based A_{max} of temperate deciduous and evergreen trees in Wisconsin? Because of the low *y*-intercept and high slope of this general relationship ($A_{max}= -88+11.2\times$leaf N) it would overestimate A_{max} at high N (especially for conifers) and underestimate A_{max} at low N. For instance, at leaf N of 8, 18 and 28 mg g^{-1} the general A_{max}-N regression predicts A_{max} of 2, 114 and 226 nmol g^{-1} s^{-1}, the first value being lower and the third higher than the values seen in Fig. 1. Moreover, even the overall mass-based A_{max}-N regression for all tree species pooled in this study ($A_{max}= -62+8.2\times$leaf N, $r^2=0.78$) would substantially underestimate evergreen conifer A_{max} at low N. In contrast, a relationship (slope of 7.2 μmol CO$_2$ g^{-1} N s^{-1}) developed in a detailed study of seasonal and annual changes in leaf physiology for three hardwood species (*Acer rubrum, A. saccharum* and *Quercus ellipsoidalis*) (Reich et al. 1991b and unpublished work) better predicts mass-based A_{max} for the 19 other deciduous species in this study. Thus, predicting A_{max} based on leaf N is

probably best approached from a functional-group perspective.

A strong area-based A_{max}-N relation in the deciduous broad-leaved group is consistent with similar patterns for broad-leaved species with short leaf life-span (Field and Mooney 1986; Reich et al. 1991a, 1992). The slope of the area-based A_{max}-N relation for 22 temperate broad-leaved species is similar to that found for secondary successional Amazon trees with leaf life-span of 3–8 months (5.5 vs. 6.8 μmol CO$_2$ g^{-1} N s^{-1}, respectively) (Reich et al. 1994) and is also similar to detailed species-specific relationships (slopes from 5.6 to 6.7 μmol CO$_2$ g^{-1} N s^{-1}) observed in *A. rubrum, A. saccharum* and *Q. ellipsoidalis* (Reich et al. 1991b). The lack of an area-based A_{max}-N relation for evergreen species is similar to weak or non-significant relationships for evergreen broad-leaved species in the Amazon (Reich et al. 1991a, 1994) and for sclerophyllous evergreen species in general (Reich et al. 1992). Moreover, the lack of general area-based A_{max}-N or A_{max}-SLA relationships among all temperate trees suggests that, despite the tight scaling of area-based N and SLA, this latter relationship may be of limited use in modeling photosynthesis across broad species groups. It is important to note, however, that strong correlations of area-based A_{max}, N and SLA have been observed vertically within a forest canopy (Ellsworth and Reich 1993) and relationships of this type may thus be useful in canopy scale modeling (Aber et al. 1995b).

The slopes of both mass and area-based A_{max}-N relations were greater in the deciduous hardwood species that as a group had higher A_{max}, leaf N and SLA and shorter leaf life-span than in the evergreen conifers. Differences in A_{max} per unit N in the two species groups appear to be related to their differences in leaf structure, since it has been shown that for a common N, plants with higher SLA will tend to have higher rates of A_{max} (Reich et al. 1994). Moreover, even at a similar leaf N, the deciduous broad-leaved group had a greater A_{max}-N slope than evergreen coniferous species. These results suggest that species traits that confer high instantaneous photosynthetic N use efficiency, other than leaf N concentration per se, play an important role in the response of A_{max} to variation in leaf N. It is probable that features associated with sclerophylly, such as variation in investment of N among different photosynthetic and non-photosynthetic compounds (Evans 1989), greater diffusional limitations (Field and Mooney 1986; Vitousek et al. 1990; Lloyd et al. 1992), and greater irradiance limitations (due to greater reflectance and/or internal shading) (DeLucia et al. 1992) are responsible for the lower A_{max} at a common N in long-lived conifer foliage than in deciduous broad-leaved foliage.

Why should evergreen conifers as a group have long-lived foliage, low A_{max} and "flatter" A_{max}-N relations? Although it is evolutionary speculation to assess why conifers are adapted to lower-resource sites, it has been repeatedly shown to be a real pattern, albeit with exceptions. Evergreen conifers as a group are found on more

nutrient-poor sites than deciduous trees (Chapin 1980; Reich et al. 1992) and evergreen conifers also generally reduce site N availability more than hardwoods (except perhaps oak) due to differences in litter quality, soil acidity and understory microenvironment (Pastor et al. 1984; Gower and Son 1992; Ferrari 1993). Given that evergreen conifers are found on, adapted to, and "drive" sites towards resource-poor conditions, both theory (Kikuzawa 1991) and data (Reich et al. 1991a, 1992; Gower et al. 1993; Reich 1993) suggest that they will have longer-lived foliage with lower SLA and mass-based N and A_{max} than foliage of deciduous broad-leaved species with whom they share the region. Based on this study and our previous work with tropical rain forest trees (Reich et al. 1994), we suggest adding a low slope of the A_{max}-N relationship and low A_{max} per unit N (even at common N) to this suite of co-occurring, mutually supporting leaf traits.

Potential photosynthetic N-use efficiency (PPNUE), defined either as the ratio of A_{max} per unit N or the potential increment in A_{max} per unit increase in leaf N, is lower in needle-leaved or broad-leaved species with long leaf lifespans than in those with short leaf lifespans (this paper, and see Reich et al. 1994). High instantaneous PPNUE may have obvious advantages (along with other traits) for carbon gain in high light and in a vertical race for canopy dominance, but does low PPNUE ever provide an advantage? It probably does not do so in a direct way, but may be advantageous indirectly (via impact on other traits that confer low PPNUE) in determining achieved (rather than potential maximum) photosynthetic N use efficiency either instantaneously or over the leaf life-span. Lower PPNUE may be linked with lower respiratory costs, extended leaf durability and carbohydrate and N storage functions in such a way that positive net carbon gain under low resource conditions, amortization of leaf construction costs over an extended period (Williams et al. 1989; Kikuzawa 1991), enhanced whole canopy light interception (Sprugel 1989), and lower overall N costs to produce foliage (Chapin 1980) may enhance competitiveness of evergreen species with long leaf lifespans and low SLA on nutrient-poor and/or heavily shaded microsites over the long time frames relevant to survival and population dynamics. Alternatively, use of N for photosynthesis may not be as predominant a priority for long-lived as for short-lived leaves, with other potential N-based functions for evergreen needles outside the context of carbon gain.

In summary, these results support the idea that the relationship between A_{max} and leaf N is variable among species (Evans 1989), and varies in ecologically patterned ways (Reich et al. 1994; Reich and Walters 1994) with respect to species habitat affinities and leaf structure. The data also suggest that leaf N and SLA together may be more useful in understanding variation in and predicting A_{max} among disparate species groups than either variable alone. To the extent that the A_{max}-N or A_{max}-N-SLA relationships offer predictive capability (e.g., among all species for global analyses, in species groups for regional analyses) they should be useful as scalars of

leaf chemistry and structure to leaf metabolic activity to productivity of stands, ecosystems, and biomes (Reich et al. 1990; Aber et al. 1995a,b).

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