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Photosynthetic differences between saplings and adult trees: an integration of field results by meta-analysis

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Summary Ontogenetic changes in gas exchange parameters provide both insight into mechanisms underlying tree growth patterns, and data necessary to scale environmental impacts on young trees to predict responses of older trees. We present a quantitative review and meta-analysis of field measurements of gas exchange parameters in saplings and mature trees of 35 tree species (seven conifers, seven temperate deciduous trees, and 21 tropical evergreen trees). Data for saplings were obtained in both understory environments and open areas or large gaps. We also present data on ontogenetic changes in photosynthesis for *Pseudotsuga menziesii* (Mirb.) Franco and *Tsuga heterophylla* (Raf.) Sarg., species of particular interest because of their large maximal heights and long life-spans.

Among tree species, there is evidence for both ontogenetic increases and ontogenetic decreases in photosynthetic capacity on a leaf area basis (A_{area}). Overall, A_{area} is generally higher for upper-canopy leaves of adult trees than for saplings, especially in temperate deciduous trees. However, the pattern for photosynthetic capacity on a leaf mass basis (A_{mass}) is the reverse of that observed for A_{area}. Saplings of both conifers and broad-leaved trees, even when acclimated to low-light conditions, characteristically have a higher A_{mass} than adult trees. This pattern is driven largely by an ontogenetic increase in leaf mass per unit area (LMA), as found in 100% of studies reviewed. Data for Pacific Northwest conifers, although including measurements on some of the tallest trees studied, did not differ greatly from patterns found in other tree species. We conclude that ontogenetic changes in LMA are the single most consistent difference between saplings and adult trees, and that changes in LMA and related aspects of leaf morphology may be critical to understanding both variation in gas exchange during tree growth, and stage-dependent responses of trees to environmental change.

Keywords: allometry, leaf mass per area, ontogeny, phase-change, photosynthesis, photosynthetic capacity, Pseudotsuga menziesii, size-dependence, stomatal conductance, Tsuga heterophylla.

Introduction

Many biological processes change in rate as organisms grow and age. Size-dependence of basal metabolic rate has been a central concept in comparative zoology for more than 70 years (e.g., Haldane 1928, Kleiber 1932, Schmidt-Nielsen 1975, Calder 1983). By comparison, size-dependence of physiological traits in plants has received much less attention, and research on size-dependent physiological patterns in trees is a relatively recent development (e.g., Cregg et al. 1989, Ryan et al. 1997, Thomas and Bazzaz 1999, Bond 2000, Cavender-Bares and Bazzaz 2000). Canopy access has been a major limitation to such studies. However, the recent worldwide proliferation of canopy towers, cranes and other means of access is providing new opportunities for detailed studies of canopy physiology. Recent studies have also emphasized the importance of ontogenetic changes in physiology to understanding tree responses to atmospheric pollutants, rising CO_2, and other anthropogenic environmental changes (e.g., Bazzaz et al. 1996, Kolb et al. 1998). We are thus only now in a position to begin to assemble an integrated picture of patterns of size-related change in tree physiological parameters.

As trees develop, they increase in both size and structural complexity. Size-related physiological changes include increases in the volume and depth of soil explored by root systems, and increased distances over which photosynthate and hormone molecules must be transported (e.g., Maggs 1964, Clark 1983). Recent emphasis has been placed on the importance of increased path length for water transport on stomatal function and photosynthetic performance in tall trees (Ryan and Yoder 1997, Hubbard et al. 1999; but see Becker et al. 2000, Niinemets 2002). Increased size also results in increased biomechanical loading of stem tissues (Holbrook and Putz 1989), and carbon costs of mechanical support have figured centrally in some efforts to predict maximal tree height from physiological first principles (Givnish 1988). Trees develop through the proliferation of meristematic tissue, and this aspect of structural complexity has important physiological consequences as trees grow. For example, branch proliferation results in an increased number of junctions between xylem bundles, which represent points of high hydraulic resistance

(Ewers and Zimmermann 1984, Rust and Huttl 1999). Internal shading also increases with increasing size (e.g., Niinemets 1995). Large trees produce leaves acclimated to a variety of light conditions, whereas all leaves on seedlings and small saplings experience essentially the same light environment. In an analogous fashion, increases in the magnitude of root systems will generally result in an increase in overlap of nutrient depletion zones around roots (Berntson 1994).

Older trees are exposed to pathogens, pests and symbionts over a longer time period than younger trees. Because of the large potential effects of, for example, mycorrhizal or pathogenic fungal infection on physiological performance, some size-related changes may result from time-dependent biotic interactions. Similarly, older trees are known to accumulate somatic mutations over time (Gill et al. 1995), and the occurrence of genetic mosaics in trees may contribute to variability in physiology as well. Older trees will also be exposed to disturbance events over time. One notable consequence is the production of epicormic shoots in older trees (e.g., Ishii and Ford 2001).

In addition to changes resulting from proximate effects of increased size, complexity and age, old trees may differ from young trees as a result of genetically determined developmental patterns. Natural selection is likely to produce such patterns as a result of systematic differences in environments experienced by younger and older trees in prior generations. For example, among primary rain forest trees, species reaching larger maximal sizes among adult trees are necessarily exposed to higher irradiances late in ontogeny than species that remain in the shaded understory. Tall primary forest species show higher photosynthetic capacities and other "sun-plant" characteristics than small species, even when compared at similar irradiances and sizes (Thomas and Bazzaz 1999), suggesting that the light environment experienced by adult trees is an important selective force on photosynthetic parameters expressed at all ontogenetic states (Reich 2000).

In this paper we provide a quantitative summary of studies comparing photosynthetic processes of saplings and large, mature trees. We focused on these two ontogenetic states for several reasons. First, we wished to exclude from consideration physiological changes occurring in seedlings (i.e., physiological differences associated with reliance on stored seed reserves). Likewise, at least some tree species show physiological senescence (e.g., Foster 1977), which we also consider a phenomenon different from more typical size-related physiological changes. We recognize that leaf characteristics may show continuous, and potentially nonlinear, patterns during tree ontogeny (e.g., Thomas and Ickes 1995). However, sapling and mature tree phases are commonly well represented in natural forests, and the majority of published studies have focused on comparisons of these stages.

Most studies that have examined ontogenetic differences in physiological traits of canopy trees have been compromised to some extent in terms of replication. Frequently, comparisons have been made based on a relatively small number of individual mature trees, and often a single canopy site has been compared to a single site with experimental or natural populations of saplings, raising the specter of pseudo-replication (Hurlbert 1984). The limitations associated with restricted sampling may be significant because there is often substantial tree-to-tree variation in physiological properties (e.g., Bassow and Bazzaz 1997, S.C. Thomas and W.E. Winner, unpublished data) as well as site-to-site variation in edaphic conditions. Quantitative analyses that make use of data compiled across studies are thus necessary to better differentiate signal from noise in any patterns that may exist.

To this end, we assembled data from published studies comparing gas exchange characteristics of saplings and mature trees. We then examined these data using both formal meta-analysis techniques (cf. Gurevitch et al. 1992, Curtis 1996) and conventional statistical analyses that pool data across studies. We also present a comparison of saplings and adult old-growth trees of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), the dominant conifers at the Wind River Canopy Crane site in southwestern Washington. These species attain heights of 55 m or more, and we predicted that they would show large ontogenetic changes if tree height affects gas-exchange processes. We used our data from the Canopy Crane site together with published data to answer four questions. (1) Does photosynthetic capacity differ between saplings and adult trees? (2) Do such ontogenetic comparisons depend on the units in which photosynthesis is expressed (i.e., photosynthetic capacity on a leaf area or mass basis)? (3) How do other related gas-exchange and morphometric characteristics (i.e., stomatal conductance, leaf mass/area) differ between saplings and adult trees? (4) Do comparisons between saplings and adults show any systematic differences between tree phenological types or biogeographic regions?

Materials and methods

Field studies

Measurements of photosynthetic capacity, stomatal conductance and branch morphometrics were made on large, canopy trees of *P. menziesii* and *T. heterophylla* at the Wind River Canopy Crane site as part of a long-term study of temporal variation in canopy gas exchange. We compared a subset of these canopy data with measurements on saplings of these species in open areas near the Canopy Crane site. All measurements were made during the annual peak in photosynthetic performance (July–September) in 1996 and 1998. The saplings were 5–10 years old, of healthy appearance, and ranged in height from 0.5 to 2 m; measurements were made on fully expanded current-year foliage on the upper third of the crown. Mature trees ranged in height from 46 to 61 m, with maximum ages estimated at ~500 years. Canopy openness for both saplings and tops of mature trees, estimated from hemispherical photographs, ranged from 56 to 100%. Further details on vegetation, soils and canopy structure of the Wind River site (located in the T.T. Munger Research Natural Area of the Gifford Pinchot National Forest) are given elsewhere (Franklin et al. 1972, Parker 1997, Thomas and Winner 2000).

We used an LI-6400 portable photosynthesis system (Li-Cor, Lincoln, NE) with a 6-cm^2 cuvette for all gas exchange measurements. Temperature was controlled to approximate ambient conditions and ambient CO_2 concentration was set at 350 $\mu\text{mol mol}^{-1}$. Measurements were made before afternoon decreases in photosynthesis were apparent, and carbon exchange rates were monitored before each measurement to ensure full induction. Each measurement consisted of triplicate instantaneous readings made at 20-s intervals. Measurements were made on the most recent fully expanded leaves of intact shoots, which were collected immediately following each triplicate reading. Digital images were collected of each shoot in the cuvette, of the entire clipped shoot, and of the excised needles and stem of each shoot. No adjustment was made for the three-dimensional structure of leaves in computing leaf area. *Pseudotsuga menziesii* and *T. heterophylla* possess relatively flat needles, with conversion factors relating "projected" leaf area to "half-total" leaf area of ~1.18 and ~1.07, respectively (Gholz et al. 1976); however, we did not correct for differences in needle shape. Needles of each shoot were dried (> 24 h at 60 °C) and weighed. These measurements were used to determine silhouette to total leaf area (i.e., total projected leaf area) (STAR) for each measured shoot (see Stenberg et al. 1995) and leaf mass to leaf area ratio (LMA). They also allowed us to express photosynthetic capacity on the basis of projected shoot area, total leaf area and leaf mass.

Literature survey

The literature review included all studies meeting the following requirements: (1) the study examined tree species, defined operationally as woody plants attaining a height of 5 m or more; (2) the study presented data on maximum photosynthetic rates under saturating light conditions for both saplings and adult trees growing in field conditions. We defined saplings as trees < 3 m in height or < 3 cm in diameter. Where possible, we made a distinction between seedlings (i.e., plants dependent in whole or in part on stored seed reserves for growth and development), and saplings, corresponding to the growth stage immediately following the seedling stage; (3) the study presented variance and sample size statistics, or sufficient information to enable their calculation; and (4) the study included only field-grown trees with no greenhouse or nursery specimens (but including field-grown saplings grown in pots > 1 dm^3 in volume). For many studies, data were obtained by digitizing and measuring figures from publications. In cases where sample sizes were specified as a range, we used the lowest end of the reported range. In studies presenting seasonal or diurnal time courses, the seasonal or diurnal maximum values were used. The species included in the meta-analyses are listed in Table 1.

In the literature review, we included comparisons of understory saplings and canopy trees (common for shade-tolerant species) as well as comparisons between canopy trees and saplings acclimated to high-light conditions. In many shade-tolerant tree species, saplings rarely occur in full-sun conditions. Also, many sub-canopy tree species rarely occur in full-sun conditions as adults, and some species cannot successfully grow and establish if experimentally placed in open conditions. Differences between shade-grown saplings and canopy leaves of mature trees grown under high light conditions may be a result of light acclimation responses, size-related developmental changes, or a combination of both. Separate analyses are presented for comparisons between leaves of sapling and canopy foliage of adult trees (understory-canopy comparisons) and between leaves of saplings and canopy trees both grown and sampled under high light conditions (open-canopy comparisons). In addition, results are presented for analyses in which both types of comparisons are pooled. For studies that included saplings sampled under both low- and high-light conditions (e.g., Pearcy 1987, Cavender-Bares and Bazzaz 2000, Rijkers et al. 2000), we used data only for the saplings grown under high-light conditions in the pooled analyses.

Statistical analysis

To compare field data of canopy trees at the Canopy Crane site with open-grown saplings, we used one-way analysis of variance for a given species, in which measured branches were considered the level of replication (at least three trees/species/ontogenetic class were measured). Because we were concerned with comparisons between saplings and mature trees, no results are presented for differences in vertical patterns within trees. Tests for differences between upper-canopy measurements for saplings and upper-, mid- and lower-canopy measurements for old-growth trees were treated as a priori statistical comparisons.

We conducted a formal meta-analysis comparing gas exchange characteristics of saplings and adult trees following methods presented by Hedges and Olkin (1985) (see also Gurevitch et al. 1992, Curtis 1996). Effect size (d) was calculated as:

$$d = \frac{X_a - X_s}{s} J, \tag{1}$$

where X_a is the mean value for adult trees, X_s is the mean value for saplings and s is the pooled variance, calculated as:

$$s = \sqrt{\frac{(n_s - 1)(s_s)^2 + (n_a - 1)(s_a)^2}{n_s + n_a - 2}}, \tag{1a}$$

where s_s and s_a are the variances for sapling and adult samples, respectively, and n_s and n_a are the sample sizes for sapling and adult samples, respectively. The effect size (d) is adjusted by a weighting factor (J), calculated as:

$$J = 1 - \frac{3}{4(n_s + n_a - 2) - 1}. \tag{1b}$$

The variance of d ($\hat{s}^2(d)$) is approximated by:

$$\hat{s}^2(d) = \frac{n_s + n_a}{n_s n_a} + \frac{d^2}{2(n_s + n_a)}. \tag{2}$$

Table 1. Species, study locations, light environment of saplings and variables measured in the studies used in comparative analyses. Cases in which presentation of data (for at least one variable) permitted formal meta-analysis are indicated under "Meta-". Sapling environment (env.) codes are as follows: O = open (full sun); G = gap; and U = understory. Variables include photosynthetic capacity on an area basis (A_{area}), leaf mass per area (LMA), photosynthetic capacity on a leaf mass basis (A_{mass}), foliar dark respiration (R) and stomatal conductance under saturating light conditions (g_s). An asterisk indicates data on variables directly presented in a study; an asterisk in parentheses indicates variables that could be estimated based on mean values for other data presented.

Species	Site	Meta-	Sapling env.	A_{area}	LMA	A_{mass}	R	g_s	Reference
Tropical rain forest trees									
Anacardium excelsum (Bert. & Balb.) Skeels	Panama	*	U	*	*	(*)	*		Zotz and Winter 1996
Aporosa bracteosa Pax & K. Hoffm.	Malaysia	*	U	*	*	*			Thomas and Bazzaz 1999
Aporosa lunata (Miq.) Kurz	Malaysia	*	G and U	*	*	*			Thomas and Bazzaz 1999
Aporosa microstachya (Tul.) Muell. Arg.	Malaysia	*	U	*	*	*			Thomas and Bazzaz 1999
Argyrodendron perlatum (Bailey) Edlin ex J. H. Boas	Australia	*	U	*	*	(*)	*	*	Pearcy 1987
Baccaurea parviflora (Muell. Arg.) Muell. Arg.	Malaysia	*	U	*	*	*			Thomas and Bazzaz 1999
Baccaurea racemosa (Reinw.) Muell. Arg.	Malaysia	*	U	*	*	*			Thomas and Bazzaz 1999
Baccaurea reticulata Hook. f.	Malaysia	*	U	*	*	*			Thomas and Bazzaz 1999
Castanospermum australe (Cunn.) Frazer & Cook	Australia		U	*					Pearcy 1987
Dicorynia guianensis Amsh.	Fr. Guiana	*	G and U	*	*	(*)			Rijkers et al. 2000
Diospyros cauliflora Blume	Malaysia	*	U	*	*	*			Thomas and Bazzaz 1999
Diospyros maingayi (Hiern) Bakh.	Malaysia	*	U	*	*	*			Thomas and Bazzaz 1999
Diospyros nutans King & Gamble	Malaysia	*	U	*	*	*			Thomas and Bazzaz 1999
Dipterocarpus sublamellatus Foxw.	Malaysia	*	U	*	*	*	*	*	Manokaran et al. 1998
Duguetia surinamensis R. E. Fr.	Fr. Guiana	*	G and U	*	*	(*)			Rijkers et al. 2000
Garcinia bancana Miq.	Malaysia	*	U	*	*	*			Thomas and Bazzaz 1999
Garcinia malaccensis Hook. f. ex T. Anders.	Malaysia	*	U	*	*	*			Thomas and Bazzaz 1999
Garcinia sp.	Malaysia	*	U	*	*	*			Thomas and Bazzaz 1999
Goupia glabra Aubl.	Fr. Guiana	*	G and U	*	*	(*)			Rijkers et al. 2000
Toona australis (F. Muell.) Harms	Australia		U	*					Pearcy 1987
Vouacapoua americana Aubl.	Fr. Guiana	*	G and U	*	*	(*)			Rijkers et al. 2000
Temperate deciduous trees									
Acer negundo L. (female)	Utah	*	O	*				*	Dawson and Ehleringer 1993
Acer negundo (male)	Utah	*	O	*				*	Dawson and Ehleringer 1993
Acer pensylvanicum L.	Michigan	*	U	*	*	(*)		*	Jurik 1986, Jurik et al. 1988
Acer rubrum L.	Michigan	*	U	*	*	(*)		*	Jurik 1986, Jurik et al. 1988
Acer rubrum (2 sites)	Tennessee	*	U	*				*	Samuelson and Kelly 1997
Fagus grandifolia Ehrh.	Michigan	*	U	*	*	(*)		*	Jurik 1986, Jurik et al. 1988
Fagus sylvatica L.	Germany		U	*			*		Stickan and Zhang 1992
Prunus serotina Ehrh.	Pennsylvania	*	G	*	*	(*)	*		Fredericksen et al. 1996
Prunus serotina (2 sites)	Tennessee	*	U	*				*	Samuelson and Kelly 1997
Quercus rubra L.	Massachusetts	*	O and U	*				*	Cavender-Bares and Bazzaz 2000
Quercus rubra	Michigan	*	U	*	*	(*)		*	Jurik 1986, Jurik et al. 1988
Quercus rubra	Tennessee	*	O	*	*	(*)		*	Hanson et al. 1994
Quercus rubra	Tennessee	*	U	*				*	Samuelson and Kelly 1997
Boreal coniferous trees									
Picea abies L. Karst.	Estonia		O	*	*	(*)			Kull and Koppel 1987
Pinus banksiana Lamb.	Saskatchewan	*	O	*			*	*	Sullivan et al. 1997
Temperate coniferous trees									
Pinus ponderosa Dougl. ex Laws	Arizona		O	*					Kolb and Stone 2000
Pinus aristata Engelm.	Colorado	*	O	*	*	*			Schoettle 1994
Pseudotsuga menziesii	Washington	*	O	*	*	*		*	Thomas and Winner (this study)
Sequoiadendron giganteum (Lindl.) Buchh.	California	*	O	*			*	*	Grulke and Miller 1994
Tsuga heterophylla	Washington	*	O and U	*	*	*		*	Thomas and Winner (this study)

The mean effect size across k studies (d_+) was calculated as:

$$d_+ = \sum_{i=1}^{k} \frac{d_i}{\hat{s}^2(d_i)} \Bigg/ \sum_{i=1}^{k} \frac{1}{\hat{s}^2(d_i)}, \tag{3}$$

with variance:

$$\hat{s}^2(d_+) = 1 \Bigg/ \sum_{i=1}^{k} \frac{1}{\hat{s}^2(d_i)}. \tag{4}$$

Confidence limits for d_+ were estimated by a normal approximation (see Hedges and Olkin 1985).

The appropriate level of replication for the meta-analytic statistics listed above is individual trees or stands. Because none of the studies treated interspersed trees or stands as sampling units, sample sizes were those reported in the individual studies and generally corresponded to physiological measurements with > 1 measurement per individual tree. This approach, although not ideal, is consistent with previous meta-analyses of studies that lack appropriate replication, such as studies of plant responses to increased atmospheric CO_2 concentration (Curtis 1996, Curtis and Wang 1998), where ~80% of published comparisons are pseudo-replicated (Jasienski et al. 1998).

In addition to formal meta-analyses, we made comparative analyses using standard general linear models. In these analyses, sapling gas-exchange and morphometric parameters of individual species were treated as independent variables, the corresponding adult parameters as dependent variables, and species characteristics (i.e., tree phenological group) as covariates (i.e., an analysis of covariance (ANCOVA) with tests for heterogeneity of slopes). Although these analyses do not incorporate error variance for individual species, the approach has the advantage of not requiring assumptions about sampling and experimental design in generating results for individual species. Additional published studies that did not report sample sizes or variances were included in these analyses, as indicated in Table 1.

Results

Field study at the Wind River site

Photosynthetic capacity and stomatal conductance differed between saplings and old-growth trees (Table 2). Among canopy levels, differences were most pronounced between saplings and canopy tops of mature trees. However, the direction and magnitude of these differences was highly dependent on the units in which gas-exchange rates were expressed.

For *P. menziesii*, A_{area} on either a projected leaf area or a total leaf area basis was higher in the upper canopies of mature trees than in saplings, whereas A_{mass} was marginally higher for saplings than for mature trees. Lower-canopy foliage of mature *P. menziesii* trees also showed a higher A_{area} on a total leaf area basis than that of saplings. Similarly, saplings of *T. heterophylla* had significantly lower A_{area} on either a projected or total leaf area basis than the upper canopies of mature trees, and A_{mass} was slightly higher for saplings than for upper- and mid-canopy foliage of adult trees.

Stomatal conductance was ~60–70% higher for upper-canopy foliage of adult trees than for saplings of both *P. menziesii* and *T. heterophylla* (Table 2), but there were no significant differences in g_s between saplings and mid- or lower-canopy foliage of mature trees of either species. The ratio of assimilation to transpiration (A/E), often used as an index of photosynthetic water-use efficiency, was also significantly higher for upper-canopy foliage of mature trees than for saplings in both species. For both *P. menziesii* and *T. heterophylla*, branchlet silhouette to total leaf area ratios (STAR) of saplings were higher than that of upper-canopies of mature trees but similar to mid-canopy values. Leaf mass per area (LMA) was consistently higher for mid- and upper-canopy branches of mature trees than for saplings in both species. Values of LMA were also lower for saplings than for lower-canopy branchlets in *P. menziesii*, though the difference was not significant in *T. heterophylla*.

Meta-analyses

Patterns of differences in photosynthetic parameters between saplings and canopy tops of mature trees observed at Wind River are similar to the patterns included in the formal meta-analysis (Table 3). Across all studies, A_{area}, g_s and LMA were higher for mature trees than for saplings, while A_{mass} showed the opposite pattern.

Considering all species and comparisons combined, the upper foliage of mature trees had higher A_{area} than sapling foliage; however, mature trees had significantly lower A_{mass} and higher LMA than saplings (Figure 1; Table 3). The comparison for LMA also exhibited a large effect size (~2), compared with relatively low effect sizes for ontogenetic comparisons of the other variables considered (between 1 and –1). In every species reviewed, LMA was higher in mature trees than in saplings.

Our meta-analyses included studies examining differences between understory saplings and canopy foliage of adult trees as well as studies comparing saplings and mature trees under similar light conditions. In the case of comparisons betweeen understory saplings and canopy foliage of mature trees, we found significant ontogenetic differences for all variables examined (Table 3). In contrast, comparisons between open-grown saplings and canopy foliage of adult trees showed significant differences only for comparisons of A_{mass}, g_s and LMA, providing strong evidence that the ontogenetic changes in these parameters are independent of acclimation responses to light.

Ontogenetic differences between gas-exchange characteristics varied considerably among phenological or biogeographic groups. Increases in A_{area} in mature trees were greatest for temperate deciduous species, whereas both conifers and tropical evergreen species showed weak nonsignificant trends (Table 3). All three groups of trees showed strong LMA trends. In general, A_{mass} has not generally been reported in previous stud-

Table 2. Comparison of gas exchange and morphometric parameters of saplings versus upper-, mid- and lower-canopy foliage of old-growth trees at the Wind River Canopy Crane facility, Washington. Parameters measured include photosynthetic capacity on a projected leaf area basis ($A_{proj,area}$), on a total leaf area basis ($A_{tot,area}$), and on a mass basis (A_{mass}), stomatal conductance at light saturation (g_s), the ratio of assimilation to water loss (A/E), the ratio of branchlet silhouette to total leaf area (STAR) and leaf mass per area (LMA). Sample sizes list number of branches sampled, with 3–10 individual trees measured per category. Measurements were made during the annual peak of photosynthetic activity during July–September 1996 and 1998. Means are listed ± SE. Significance levels are given for a priori comparisons between saplings versus each canopy tree stratum: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Parameters	Saplings	Old-growth tress		
		Upper-canopy	Mid-canopy	Lower-canopy
Pseudotsuga menziesii	$n = 9$	$n = 21$	$n = 8$	$n = 16$
$A_{proj,area}$ (μmol m^{-2} s^{-1})	8.51 ± 0.46	13.12 ± 0.57***	9.87 ± 0.74	8.75 ± 0.62
$A_{tot,area}$ (μmol m^{-2} s^{-1})	4.04 ± 0.31	5.15 ± 0.29*	4.78 ± 0.35	5.25 ± 0.39*
A_{mass} (nmol g^{-1} s^{-1})	33.0 ± 4.0	27.5 ± 1.5	28.9 ± 2.0	33.6 ± 2.0
g_s (mol m^{-2} s^{-1})	0.141 ± 0.015	0.243 ± 0.016***	0.125 ± 0.009	0.135 ± 0.016
A/E (mmol mol^{-1})	3.83 ± 0.43	6.18 ± 0.36***	6.00 ± 0.28**	3.50 ± 0.25
STAR (m^2 m^{-2})	0.479 ± 0.033	0.393 ± 0.013*	0.500 ± 0.049	0.616 ± 0.033**
LMA (g m^{-3})	132 ± 10	189 ± 7***	166 ± 10*	157 ± 6***
Tsuga heterophylla	$n = 12$	$n = 16$	$n = 4$	$n = 9$
$A_{proj,area}$ (μmol m^{-2} s^{-1})	3.50 ± 0.38	8.97 ± 0.69***	4.74 ± 0.93	3.24 ± 0.20
$A_{tot,area}$ (μmol m^{-2} s^{-1})	4.06 ± 0.43	6.99 ± 0.51***	5.59 ± 1.76	2.38 ± 0.16*
A_{mass} (nmol g^{-1} s^{-1})	38.5 ± 4.4	36.1 ± 2.5	27.2 ± 6.0	25.0 ± 1.8*
g_s (mol m^{-2} s^{-1})	0.078 ± 0.012	0.126 ± 0.012**	0.060 ± 0.009	0.045 ± 0.010
A/E (mmol mol^{-1})	2.71 ± 0.20	4.94 ± 0.38***	3.68 ± 0.47	4.77 ± 0.41***
STAR (m^2 m^{-2})	1.192 ± 0.069	0.799 ± 0.058***	1.159 ± 0.196	0.739 ± 0.028***
LMA (g m^{-2})	107 ± 3	193 ± 8***	196 ± 17***	97 ± 6

ies of temperate tree species, and the overall pattern of decreased A_{mass} in mature trees was significant only for the tropical species. Both temperate deciduous and tropical species showed strong trends toward increased dark respiration rates in mature tree foliage.

Additional comparative analyses

Among-species correlations between sapling and adult-tree characteristics were generally high, ranging from 0.66 to 0.84 for A_{area}, A_{mass}, LMA and dark respiration (R) ($P < 0.01$ in each case). The exception was the sapling–adult correlation for stomatal conductance ($r = 0.07$), a result mainly driven by a single outlying value for *Sequoiadendron giganteum* (Grulke and Miller 1994).

Analyses of covariance for sapling–adult relationships were conducted treating phenological type as a covariate. For A_{area}, there was a significant main effect term for phenological type ($P < 0.001$), chiefly because mature trees of temperate deciduous species tended to have higher photosynthetic rates than saplings, whereas the reverse was found for conifers (Figure 2). The apparent heterogeneity of slopes among phenological types was not significant. The ANCOVA for A_{mass} showed a similar result, but with a significant interaction term indicating heterogeneity of slopes ($P = 0.003$); however, only two values were available for deciduous broad-leaved trees. The analysis for R showed a significant main effect of phenological group ($P = 0.011$), with results for conifers deviating strongly from those for other species groups. There were insufficient observations across phenological groups for the other variables (LMA and g_s) to permit meaningful analysis.

Discussion

Several recent studies have emphasized the generality and importance of age-related declines in photosynthetic performance in arborescent plants (Ryan et al. 1997, Bond 2000, Niinemets 2002). We found that, although some species show decreases in A_{area} through ontogeny, many species show increases. Moreover, the pattern depended strongly on the measure of photosynthetic performance considered. Because nearly all species-specific comparisons are compromised in terms of replication, we suggest that any quantitative assessment of patterns of changes in photosynthetic parameters with tree size or age should be based on some quantitative analysis that pools existing data. Pooling data is important not only to insure that generalizations are robust, but also to provide strong inference that such a pattern is actually related to ontogenetic stage.

Our quantitative assessment supports the following generalizations. (1) Photosynthetic capacity, expressed on a leaf area basis (A_{area}), tends to be greater in adult trees than in saplings; however, the statistical significance of this result is driven mainly by comparisons between understory saplings and canopy trees. The meta-analysis for studies comparing open-grown saplings with mature trees shows no significant difference in A_{area}. (2) Photosynthetic capacity, expressed on a leaf mass basis (A_{mass}), shows a consistent trend of higher values in

Table 3. Meta-analyses for leaf-level gas-exchange characteristics. Results for each variable are listed both by tree phenological type (conifers, temperate deciduous and tropical evergreen species), and by light environment of saplings (understory canopy comparisons versus comparisons where both saplings and adult trees foliage were in high-light conditions). The mean effect size (d_+) is defined by Equation 3 (see methods): positive values indicate that mature trees show higher values than saplings. Values are listed ± the 95% confidence interval. Sample sizes are listed for both the number of species (n), and total number of studies (k) in each category, followed by the percent of comparisons in each category showing the predominant effect. Data sources and abbreviations for gas exchange parameters are listed in Table 1. Significance levels are given for d_+ for each variable listed: ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Parameter	n	k	%	d_+
A_{area}				
All species	29	34	74%	0.524 ± 0.203 ***
Conifers	5	5	40%	0.011 ± 0.358 ns
Temperate deciduous	5	10	100%	1.867 ± 0.424 ***
Tropical	19	19	68%	0.204 ± 0.304 ns
Open-canopy comparisons	12	12	67%	0.179 ± 0.302 ns
Understory-canopy comparisons	25	28	79%	0.872 ± 0.252 ***
A_{mass}				
All species	16	16	94%	–0.568 ± 0.286 ***
Conifers	3	3	100%	–0.501 ± 0.469*
Temperate deciduous	0	0		
Tropical	13	13	92%	–0.608 ± 0.361 ***
Open-canopy comparisons	5	5	80%	–0.569 ± 0.427 **
Understory-canopy comparisons	13	13	69%	–0.608 ± 0.360 ***
LMA				
All species	20	20	100%	2.101 ± 0.350 ***
Conifers	3	3	100%	2.438 ± 0.673 ***
Temperate deciduous	2	2	100%	1.793 ± 1.254 **
Tropical	15	15	100%	1.999 ± 0.433 ***
Open-canopy comparisons	7	7	100%	2.522 ± 0.566 ***
Understory-canopy comparisons	15	15	100%	1.999 ± 0.433 ***
g_s				
All species	9	12	83%	0.820 ± 0.273 ***
Conifers	4	4	50%	0.333 ± 0.392 ns
Temperate deciduous	3	6	100%	1.300 ± 0.404 ***
Tropical	2	2	100%	1.138 ± 1.153 ns
Open-canopy comparisons	6	6	67%	0.486 ± 0.381 *
Understory-canopy comparisons	5	7	100%	1.207 ± 0.385 ***
R				
All species	9	9	67%	0.269 ± 0.429 ns
Conifers	2	2	0%	–0.346 ± 0.510 ns
Temperate deciduous	4	4	75%	1.293 ± 1.002 *
Tropical	3	3	100%	2.500 ± 1.292 ***
Open-canopy comparisons	3	3	33%	–0.192 ± 0.497 ns
Understory-canopy comparisons	7	7	86%	1.747 ± 0.792 *

saplings than in adult trees (in 94% of the species reviewed). This trend is present even when comparisons are made between understory saplings growing under low-light conditions and leaves of canopy trees (cf. Thomas and Bazzaz 1999). Reduced A_{mass} for adult trees is largely driven by changing leaf mass per area (LMA), which is higher in adult trees than in saplings for every tree species examined. (3) Stomatal conductance is higher for adult trees than for saplings, though this pattern is driven mainly by results for temperate deciduous trees. (4) Finally, there is strong evidence for differences in ontogenetic trends in relation to tree phenology and growth form: namely, ontogenetic decreases in A_{area} are found most commonly among conifers, whereas increases in A_{area} are generally found among broad-leaved deciduous trees. Evergreen tropical trees appear to be intermediate, showing relatively small differences in A_{mass} between saplings and adult trees (Figure 2).

Our findings of higher photosynthetic capacity and stomatal conductance for mature trees than for saplings contrast with previous conclusions based on qualitative assessments of published data (cf. Kolb et al. 1998, Bond 2000). The differing conclusions are partly a consequence of differences in the data considered. Previous reviews have included many studies on small shrubs from arid environments (e.g., Donovan and

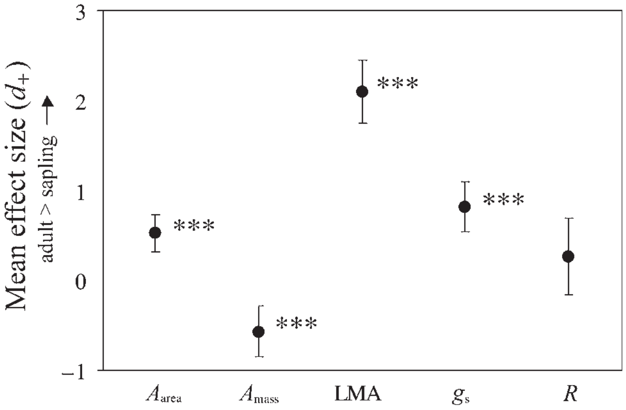

Figure 1. Mean effect size (d_+) for differences between adult and sapling photosynthetic and morphometric characteristics. We calculated d_+ as the difference between mean values for the specified character divided by a pooled variance estimate and adjusted for sample sizes within and among studies, as in Equation 3. Error bars represent 95% confidence limits calculated with Equation 4. The zero line corresponds to no difference between adult and sapling characteristics. All studies reviewed, including comparisons in which saplings were measured in open conditions and in forest understories, are included. Variables include photosynthetic capacity on a leaf area basis (A_{area}) (computed on a total leaf area basis rather than projected leaf area basis for conifers), photosynthetic capacity on a leaf mass basis (A_{mass}), leaf mass per area (LMA), stomatal conductance (g_s) and foliar dark respiration (R). Significance levels are given testing deviations of d_+ from zero: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Ehleringer 1991), and experiments with grafted scions (e.g., Momen et al. 1997). In contrast, our analyses were restricted to field data on trees, operationally defined as woody plants attaining a height > 5 m. We also excluded comparisons between intermediate-sized and older trees (e.g., Yoder et al. 1994), because few data are available and differing processes (e.g., maturation) may be important in this case. With this in mind, one possible reconciliation of our results with previous reviews is that A_{area} and g_s may reach a peak at some intermediate tree size, with a subsequent decrease late in tree ontogeny. Such a pattern has been found for leaf size in certain tropical species, with peak leaf size corresponding closely to size at reproductive onset (Thomas and Ickes 1995). Surveys of gas exchange parameters in trees spanning a range of sizes are necessary to test this idea. A recent compilation of physiological measurements on *Picea abies* and *Pinus sylvestris* L. suggests that the pattern of change in A_{area} and g_s with tree size is monotonic, and approximately linear on a log-log scale (Niinemets 2002).

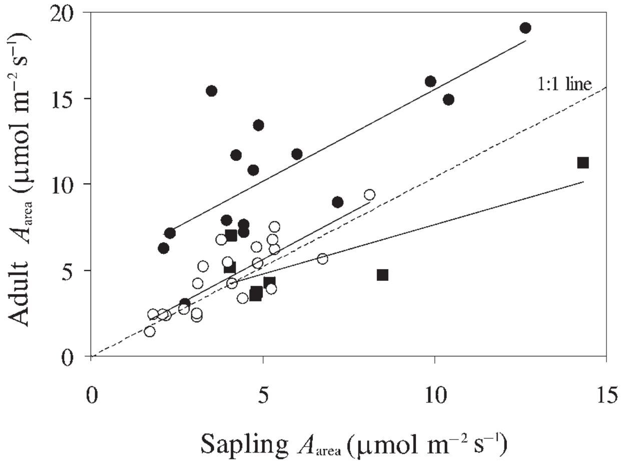

Figure 2. Relationship of adult photosynthetic capacity (leaf area basis) to sapling photosynthetic capacity, pooling data from all studies reviewed. Model 1 regression lines are shown for conifers (■), tropical evergreen species (○), and temperate deciduous trees (●). Regression equations are: $y = 1.92 + 0.57x$; $r^2 = 0.63$ (conifers); $y = 0.27 + 1.07x$; $r^2 = 0.70$ (tropical evergreen trees); $y = 4.81 + 1.07x$; $r^2 = 0.58$ (temperate deciduous trees).

Our analyses also suggest that ontogenetic patterns in gas-exchange parameters may differ among trees across biogeographic regions or among phenological types. We note that our analyses included many tropical studies and other data not considered in previous analyses (e.g., Pearcy 1987, Sullivan et al. 1997, Manokaran et al. 1998, Thomas and Bazzaz 1999, Rijkers et al. 2000), as well as original data on *P. menziesii* and *T. heterophylla*. Based on our analyses and previous work, it appears that tree species characterized by a tall stature generally show increases in maximum stomatal conductance with tree size, whereas species of small stature, especially arid-land shrubs, commonly show the reverse pattern. These results are thus inconsistent with simple proximate effects of increased hydraulic path length on stomatal conductance.

Comparisons of integrated leaf-level carbon gain between age classes provide a measure of realized rather than potential carbon uptake (Yoder et al. 1994). Few studies have presented diurnal photosynthesis data collected in situ for saplings and mature trees of the same species under similar environmental conditions. However, a recent study of adult trees and saplings of *Quercus rubra* suggests that age-related patterns for diurnal integrated carbon gain mirror age-related differences in photosynthetic capacity (Cavander-Bares and Bazzaz 2000). In a year of high rainfall, the adult/sapling ratio for photosynthetic capacity was ~3.8, whereas the adult/sapling ratio for integrated carbon gain was ~3.1; in a drought year the corresponding values were ~8.6 and ~7.8, respectively (data from Figures 2 and 5 in Cavander-Bares and Bazzaz 2000). Similarly, diurnal photosynthesis data for *Prunus serotina* indicate that the sapling/adult ratio for maximum photosynthesis is almost exactly the same as that for diurnal integrated carbon gain (~1.03 and ~1.04 respectively, from Figure 1 in Fredericksen et al. 1996). These results suggest that age-related patterns for diurnal photosynthetic carbon gain are similar to those for photosynthetic capacity.

To the extent that there is a general trend of declining photosynthetic performance with tree size, our analyses indicate that such a trend is driven by ontogenetic changes in LMA, and not by increased stomatal limitation. Consistent increases in LMA with tree size have also been found in studies of the variation in leaf traits in forest canopies, where both tree height and incident light were treated as statistical covariates (Niinemets and Kull 1995, Poorter et al. 1995, Niinemets 1997, Rijkers et al. 2000). The relationship between LMA and tree size raises several questions. What proximate mechanisms cause ontogenetic changes in LMA? What selection pressures lead to the apparent universality of increases in LMA through ontogeny among arborescent plants? And what are the underlying morphological changes and functional consequences of increased LMA in mature trees?

One possible proximate mechanism involves the effects of water transport limitation on leaf expansion. Leaves must maintain positive turgor in order to expand. One common response of plants to drought stress is reduced leaf size and increased LMA (Hsiao 1973, Smith and Nobel 1978). Thus, although mid- or late-day stomatal closure in canopy trees has recently been emphasized, we suggest that another aspect of hydraulic limitation may be equally or more important; namely, restriction of water transport as a result of increased hydraulic resistance in tall trees driven by a vertical gradient in leaf turgor during expansion. Reductions in leaf expansion by this mechanism should result not only in increased LMA in adult tree leaves, but also in reduced leaf size, reduced cell size, and increased cell wall thickness. A similar hypothesis has been suggested by Niinemets (2002), who additionally argues that decreases in the maximum carboxylation capacity of Rubisco with tree size may be driven by increased diffusive resistances in the intercellular airspace related to increasing LMA. Direct tests of each of these predictions are needed.

Although the direct effects of hydraulic limitation on leaf morphology are worth exploring, we note that there is evidence suggesting that increases in LMA are a result of altered gene expression. In general, genetically determined changes should be species-specific, reflecting differences in the environment characteristically experienced by adult and juvenile trees in prior generations. Also, it is likely that both adult and juvenile traits are affected by genetic correlations between ontogenetic stages (Thomas and Bazzaz 1999, Reich 2000). We speculate that three kinds of selection pressures commonly differ between saplings and adult trees. First, selection may result from differences in ambient light conditions. Irradiance is likely to be higher for adult trees than for saplings of shade-tolerant species that reach the canopy, but may be similar across ontogenetic states in shade-intolerant species that do not recruit in the understory. Second, wind exposure and physical abrasion are likely to be higher in canopy environments than in the understory, potentially favoring greater leaf lignification in adult-phase leaves. Finally, compared with saplings, exposure to herbivores and pathogens is likely to be higher in canopy trees that remain exposed to biotic agents over long periods of time. Each of these general classes of selective pressures is expected to favor increased lignification of leaves in older trees. A dramatic case of apparently genetically determined ontogenetic changes in leaf structure is the formation of lignified astrosclerid cells in mature *P. menziesii*, a cell type scarce or absent in young trees (Apple et al. 2002).

Pseudotsuga menziesii is among the world's tallest tree species, and individual trees commonly live 500 years or more. We predicted that *P. menziesii* and other tall Pacific Northwest conifers would show pronounced ontogenetic changes. However, we found little evidence that either *P. menziesii* or *T. heterophylla* showed substantially different patterns of ontogenetic change in photosynthesis than other tree species. For both species, A_{area} on either a projected or total leaf area basis was higher for upper-canopy foliage than for saplings. Nevertheless, both species showed a trend toward reduced A_{mass}, which is consistent with the pattern found in other species, suggesting the existence of compensatory mechanisms that counteract reductions in photosynthesis per unit leaf area caused by hydraulic limitation. Increased LMA and reduced A_{mass} in foliage of mature trees may themselves reflect such a compensatory mechanism, in that these changes correspond to increased packing of photosynthetic structures per unit of transpiring leaf area.

We conclude that analysis of changes in photosynthetic performance during tree development need to account for ontogenetic changes in LMA and related aspects of leaf morphology. In general, increased LMA in mature trees leads to a decrease in photosynthetic capacity expressed on a leaf mass basis (i.e., to a decrease in mol C fixed per mol C invested). Although we caution against linking physiological patterns directly to growth processes at the stand or whole-tree level (Weiner and Thomas 2001), we speculate that increasing LMA during tree ontogeny may be an important determinant of both tree growth patterns and differences in ecosystem processes between young and old stands.

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