

Environmental and developmental controls on specific leaf area are little modified by leaf allometry

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Summary

1. Recent work shows that large leaves tend to require higher biomass investments per unit leaf area than small leaves. As a consequence, specific leaf area (SLA), which is a focus trait for a bulk of physiological and ecological research programs, is dependent on leaf size variation. Here, we address whether size dependency alters the outcome of research dealing with SLA responses to environmental or developmental change.

2. We compiled lamina mass (M) and surface area (A) data for 2158 leaves of 26 species, coming from studies investigating the reaction of SLA to variation in rainfall, growth–season length, light intensity, atmospheric CO₂, fire frequency, type of branch and leaf and plant age. We fitted the function $M = \alpha A^\beta$ to the data of each experimental situation separately, and implemented a method to split SLA response as measured in the original study (SLA_{Δm}) into response due to leaf size dependency (SLA_{Δa}), and response due to treatment effects, after controlling for leaf size dependency (SLA_{Δt}).

3. The sign of the reaction did not differ between SLA_{Δm} and SLA_{Δt}. However, the magnitude of that response changed for most contrasts, though in variable ways.

4. Conclusions of past experiments hold, for the most part, after re-analysis including size dependency. However, given the large heterogeneity found here, we advise that future work investigating SLA be prepared to account for leaf size dependency when the factors under focus are suspected to alter leaf size.

Key-words: environmental change, ontogeny, functional response, LMA, leaf size

Introduction

Specific leaf area (SLA), that is, the light-capturing surface built by the plant per unit investment of dry mass, is an indirect measure of the return on investments in a productive organ (Lambers & Poorter 1992; Niklas *et al.* 2007). If light capture was the sole governing factor of leaf function, SLA would tend to be infinite to maximize return on dry mass investment. However, maximum SLA is constrained by a minimum of dry mass needed to construct support, protection or transport tissues, such as veins or epidermis, which are generally dense. SLA is further particularly sensitive to changes in the external environment and in the internal functioning of the plant, as extensively documented both by experimental and observational studies (Gunn *et al.* 1999; Roumet, Laurent & Roy 1999; Poorter & Nagel 2000; Westoby, Warton & Reich 2000; Niinemets 2001). However,

until recently the dependence of SLA on leaf size had not been comprehensively assessed (Niklas *et al.* 2007; Milla & Reich 2007, but see Shipley 1995 for an earlier assessment).

Shipley (1995) pioneered the study of the effect of leaf allometry on SLA using an ample array of 34 herbaceous species. He showed that, across species, larger leaves show lower SLA, though this pattern was not detected at the intraspecific level (Shipley 1995). However, more recent and more comprehensive compilations show that dry mass costs per unit leaf area do generally increase with leaf size, and hence the return on investment (i.e. light capture) decreases as leaf size increases (Milla & Reich 2007; Niklas *et al.* 2007). This holds both among and within species, and across biomes and growth forms (Milla & Reich 2007; Niklas *et al.* 2007). This probably occurs because of different biomass distribution between productive and support tissues in large compared to small leaves (Niinemets, Portsmouth & Tobias 2006; Niinemets, *et al.* 2007). Nevertheless, prior studies have either examined general trends among species (Shipley 1995; Niklas *et al.* 2007) or examined intraspecific trends at a standard environment (Shipley 1995; Milla & Reich 2007), and it is

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not yet known whether and how the size effects on SLA vary across specific environmental gradients, or across developmental stages or differences in plant structures. To our knowledge, only one previous analysis has quantified the effect of leaf size variation on the response of SLA to a productivity gradient (Poorter & de Jong 1999). Herein we extend this specific question by asking whether variation in leaf size contributes to or compensates for the direct effects of several environmental (light, water, rainfall, growth season length, CO₂, and fire frequency) and developmental (leaf and plant age) factors on SLA.

It has been demonstrated that size-dependency can obscure the detection of the direct experimental response of other ratios frequently used in plant ecology. The root : shoot ratio, for instances, varies in plants of differing sizes, when all other factors are kept constant (McConnaughay & Coleman 1999). This size-dependency varies among treatments and across environmental gradients, which affects the interpretation of studies and, ultimately, ecological theory (Reich 2002). For example, when size-dependency is not controlled for, seedlings under low light regime have lower root : shoot than full-light grown ones, but this trend fades when plants of the same size are compared (Reich 2002, or refs. therein). Similarly, leaf size effects on SLA may either counteract or increase synergistically the response of SLA to environmental or endogenous variation. This has not been explicitly tested so far to our knowledge.

In this paper, we aim (i) to assess whether and to what extent variation in leaf size accompanies and/or accounts for variation in SLA in experimental-gradient studies; and (ii) to quantitatively separate the effect of leaf size from that of the environmental–developmental change (see Fig. 1). By doing so, we seek to answer the following question: do studies investigating SLA response to a changing environment or

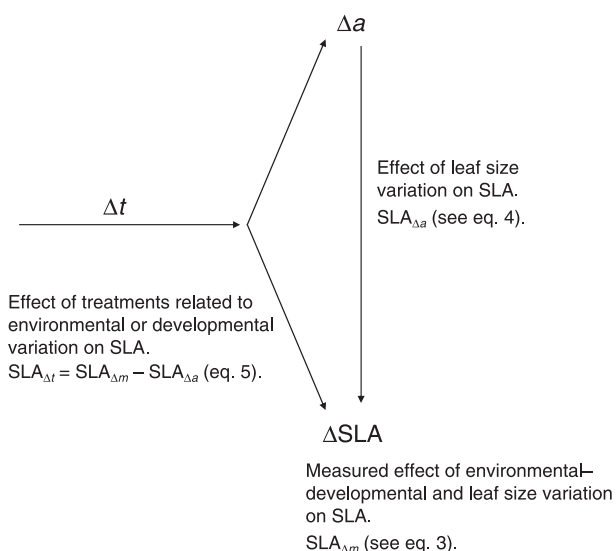


Fig. 1. Path diagram showing how an environmental or developmental variation (Δt , variation in treatment, see text) can affect specific leaf area (ΔSLA , variation in SLA), but also leaf size (Δa , variation in leaf area).

developmental feature have to correct for leaf size dependency? We compile and re-examine data on previous, or unpublished, investigations on SLA response to experimental or gradient contrasts, and propose a new way to incorporate size-dependency in the analysis of data.

Materials and methods

COMPILATION OF DATA

We searched the literature for papers that evaluated the response of SLA to a given change in the leaf environment or developmental situation. We also used our own unpublished data bases. Although apparently numerous, the amount of suitable sources of data were significantly reduced because of the following constraints: first, we incorporated only the studies that had measured leaf area (i.e. individual leaf area, cm², A hereafter) and leaf dry mass (g, M hereafter) separately in at least 10 leaves per experimental or sampling unit (i.e. species and treatment level, or location along a given gradient). Second, data were not used when the range of leaf size variation within each treatment was less than twofold. If leaf size variation was too low, this would constrain the possibilities to detect leaf size effects, if present, or make the detection of such effects highly unpredictable. Third, data were discarded if the goodness-of-fit (r^2) of the regression between ($\log A$ and ($\log M$ was lower than 0.80. The ability to compare slopes under different environmental conditions requires reasonable relationships to be compared. Relationships with poorer fits add experimental error in a disproportionate fashion, which makes the detection of effects rather arbitrary, regardless of estimated parameters of the models.

We initially gathered data from 12 sources comprising 32 species with leaf-per-leaf measurements of at least 10 leaves per experimental unit. Raw data were obtained from corresponding authors upon request, or from our own data bases. Because of the second constraint mentioned above we discarded two species. Four other species yielded low ($\log A$ vs. ($\log M$ goodness-of-fit and were also discarded (third constraint mentioned above). The final data set was thus composed of 2158 leaves from 26 species coming from nine independent studies. This compilation includes data from widely different contrasts of experimental or gradient factors: atmospheric CO₂ concentration, growing season length, light environment, rainfall, soil salinity, fire frequency, leaf and plant age, and type of shoot (Table 1). If a study measured each species in more than two treatments or two locations, we only used the data from the two most contrasting environments (e.g. very low vs. very high fire frequency). This was aimed to obtain higher response ratios of SLA, and thus facilitate the appreciation of how much variation in SLA was due to treatment vs. leaf size effects. Only when the goodness-of-fit of ($\log M$ vs. ($\log A$ regressions was lower than 0.80 we selected treatments or locations other than the two most contrasting ones. Our final set of species was diverse in growth form and leaf habit types (Table 2).

APPROACH AND ESTIMATION OF THE VARIATION OF SLA WITH LEAF SIZE

We used a bivariate line-fitting approach to calculate leaf size effects on SLA, and to assess the relative extent of environment vs. leaf size effects on SLA (Warton & Weber 2002). We made use of the approach by Shipley (1995) and Milla & Reich (2007) to evaluate the relationship of leaf size to SLA as follows.

Table 1. Sources of data used in this compilation

Data source	Reference	Type of contrast	Number of species	Sample size per species and treatment	Growth form	Ecosystem	Region
Castro-Diez	Trees 11:127–134, and PhD thesis	rainfall	2	50	S(e)	Mediterranean	Europe
Kudo	Ecoscience 6:439–450	growth season length	6	20	S(e), H(d), S(d)	Tundra	Europe
Roumet	New Phytol. 143:73–81.	CO ₂	2	150	G(d)	Mediterranean	Europe
Prior	Aust.J.Bot 53: 323–335.	rainfall	2	18	T(sd), T(e)	Seasonally-dry Tropical forest	Australia
Milla1	Unpublished	type of branch	2	40	S(e), S(d)	Mediterranean	Europe
Milla2	unpublished	leaf age	6	15–25	S(e), T(e), T(d)	Mediterranean	Europe
Reich	unpublished	fire frequency	3	10–20	G(d), H(d)	Temperate prairie	N America
Niinemets1	unpublished	light	2	30–100	T(d)	Temperate forest	Europe
Niinemets2	New Phytol. 162:683–696.	plant age	1	17	H(d)	Temperate forest	Europe

Growth form categories: T: tree; S: shrub; V: vine; H: herb; G: grass. Leaf habit in parentheses: (d): deciduous; (e): evergreen; (sd): semi-deciduous.

Table 2. List of study species, together with taxonomical and growth form affiliation, data source provenance, and type of experimental–developmental contrast involved for each species. Also, scores of several estimated parameters of interest to the study

Species	Type of contrast	Treatment level or placement along gradient	α	β	r^2	P	Growth form	Family	Data source
<i>Amelanchier ovalis</i>	Type of shoot: long (dolichoblast) vs. short (brachyblast)	Long	–1.980	0.906	0.944	0.001	S(d)	<i>Rosaceae</i>	Milla1
		Short	–2.075	1.039	0.954		S(d)	<i>Rosaceae</i>	Milla1
<i>Bupleurum fruticosum</i>	Type of shoot: Vegetative vs. reproductive	Reproductive	–1.883	1.020	0.903	0.282	S(e)	<i>Apiaceae</i>	Milla1
		Vegetative	–1.926	1.090	0.947		S(e)	<i>Apiaceae</i>	Milla1
<i>Bromus erectus</i>	Atmospheric CO ₂ level: Elevated vs. ambient	Elevated	–2.380	1.011	0.957	0.006	G(d)	<i>Poaceae</i>	Roumet
		Ambient	–2.288	0.940	0.946		G(d)	<i>Poaceae</i>	Roumet
<i>Dactylis glomerata</i>	Atmospheric CO ₂ level: Elevated vs. ambient	Elevated	–2.486	1.050	0.973	0.005	G(d)	<i>Poaceae</i>	Roumet
		Ambient	–2.433	1.000	0.973		G(d)	<i>Poaceae</i>	Roumet
<i>Andropogon gerardi</i>	Fire frequency: High vs. low	High	–2.158	0.959	0.836	0.299	G(d)	<i>Poaceae</i>	Reich
		Low	–2.353	1.133	0.946		G(d)	<i>Poaceae</i>	Reich
<i>Aster azureus</i>	Fire frequency: High vs. low	High	–2.354	1.171	0.868	0.015	H(d)	<i>Asteraceae</i>	Reich
		Low	–2.206	0.817	0.920		H(d)	<i>Asteraceae</i>	Reich
<i>Panicum praecociosus</i>	Fire frequency: High vs. low	High	–2.392	1.050	0.871	0.893	G(d)	<i>Poaceae</i>	Reich
		Low	–2.511	1.060	0.988		G(d)	<i>Poaceae</i>	Reich
<i>Betula nana</i>	Growing season length:	Long	–2.085	0.981	0.800	0.541	S(d)	<i>Betulaceae</i>	Kudo

Table 2. Continued

Species	Type of contrast	Treatment level or placement along gradient	α	β	r^2	P	Growth form	Family	Data source
<i>Diapensia lapponica</i>	Sites of long vs. short GSL	Short	-2.093	1.053	0.917		S(d)	<i>Betulaceae</i>	Kudo
	Growing season length:	Long	-1.783	1.001	0.932	0.332	S(e)	<i>Diapensiaceae</i>	Kudo
<i>Empetrum hermaphroditum</i>	Sites of long vs. short GSL	Short	-1.965	0.834	0.823		S(e)	<i>Diapensiaceae</i>	Kudo
	Growing season length:	Long	-1.726	1.038	0.843	0.586	S(e)	<i>Empetraceae</i>	Kudo
<i>Pedicularis lapponica</i>	Sites of long vs. short GSL	Short	-1.905	0.974	0.933		S(e)	<i>Empetraceae</i>	Kudo
	Growing season length:	Long	-2.002	1.230	0.909	0.167	H(d)	<i>Scrophulariaceae</i>	Kudo
<i>Salix herbacea</i>	Sites of long vs. short GSL	Short	-2.038	1.060	0.896		H(d)	<i>Scrophulariaceae</i>	Kudo
	Growing season length:	Long	-2.031	1.130	0.949	0.185	S(d)	<i>Salicaceae</i>	Kudo
<i>Vaccinium vitis-idaea</i>	Sites of long vs. short GSL	Short	-2.046	1.270	0.925		S(d)	<i>Salicaceae</i>	Kudo
	Growing season length:	Long	-1.733	0.970	0.851	0.541	S(e)	<i>Ericaceae</i>	Kudo
<i>Betula pendula</i>	Sites of long vs. short GSL	Short	-1.671	1.051	0.850		S(e)	<i>Ericaceae</i>	Kudo
	Light environment:	Long	-2.313	1.250	0.819	0.543	T(d)	<i>Betulaceae</i>	Niinemets1
<i>Populus tremula</i>	High vs. low incoming light	Short	-2.498	1.300	0.962		T(d)	<i>Betulaceae</i>	Niinemets1
	Light environment:	High	-2.321	1.170	0.904	0.194	T(d)	<i>Salicaceae</i>	Niinemets1
<i>Erythrophleum chlorostachys</i>	High vs. low incoming light	Low	-2.382	1.110	0.908		T(d)	<i>Salicaceae</i>	Niinemets1
	Rainfall:	High	-2.258	1.180	0.849	0.771	T(sd)	<i>Caesalpiniaceae</i>	Prior
<i>Eucalyptus tetrodonta</i>	Sites of high vs. low precipitation	Low	-2.108	1.150	0.889		T(sd)	<i>Caesalpiniaceae</i>	Prior
	Rainfall:	High	-1.852	1.040	0.855	0.306	T(e)	<i>Myrtaceae</i>	Prior
<i>Viburnum tinus</i>	Sites of high vs. low precipitation	Low	-1.974	1.150	0.817		T(e)	<i>Myrtaceae</i>	Prior
	Rainfall:	High	-2.217	1.170	0.957	0.230	S(e)	<i>Caprifoliaceae</i>	Castro-Diez
<i>Rhamnus alaternus</i>	Sites of high vs. low precipitation	Low	-1.999	1.100	0.973		S(e)	<i>Caprifoliaceae</i>	Castro-Diez
	Rainfall:	High	-2.093	1.200	0.871	0.106	S(e)	<i>Rhamnaceae</i>	Castro-Diez
<i>Arbutus unedo</i>	Sites of high vs. low precipitation	Low	-1.799	1.070	0.886		S(e)	<i>Rhamnaceae</i>	Castro-Diez
	Leaf age:	Young	-2.012	0.930	0.928	0.001	S(e)	<i>Ericaceae</i>	Milla2
<i>Buxus sempervirens</i>	Young vs. old leaves	Old	-2.028	1.439	0.814		S(e)	<i>Ericaceae</i>	Milla2
	Leaf age:	Young	-1.830	1.030	0.934	0.004	S(e)	<i>Buxaceae</i>	Milla2
<i>Quercus ilex</i>	Young vs. old leaves	Old	-1.723	1.330	0.894		S(e)	<i>Buxaceae</i>	Milla2
	Leaf age:	Young	-1.843	1.110	0.901	0.409	T(e)	<i>Fagaceae</i>	Milla2
<i>Cistus laurifolius</i>	Young vs. old leaves	Old	-1.733	1.200	0.897		T(e)	<i>Fagaceae</i>	Milla2
	Leaf age:	Young	-1.718	0.912	0.958	0.054	S(e)	<i>Cistaceae</i>	Milla2
<i>Quercus coccifera</i>	Young vs. old leaves	Old	-1.876	1.151	0.883		S(e)	<i>Cistaceae</i>	Milla2
	Leaf age:	Young	-1.742	0.981	0.855	0.049	S(e)	<i>Fagaceae</i>	Milla2
<i>Quercus faginea</i>	Young vs. old leaves	Old	-1.667	1.171	0.974		S(e)	<i>Fagaceae</i>	Milla2
	Leaf age:	Young	-2.261	1.080	0.968	0.065	T(d)	<i>Fagaceae</i>	Milla2
<i>Leontodon hispidus</i>	Young vs. old leaves	Old	-2.115	1.230	0.923		T(d)	<i>Fagaceae</i>	Milla2
	Plant age:	Juvenile	-2.493	1.180	0.987	0.161	H(d)	<i>Asteraceae</i>	Niinemets2
	Juvenile vs. post-reproductive plants	Post-reproductive	-2.345	1.040	0.900		H(d)	<i>Asteraceae</i>	Niinemets2

α and β are parameters of the power relation of leaf mass and leaf area ($M = \alpha A^\beta$), computed for each experimental situation separately. r^2 is the goodness-of-fit of the RMA regression between $(\log) A$ and $(\log) M$ used to estimate β . P is the P -value of the common-slopes test between treatments (see Methods). Sample size is the number of leaves where A and M were measured separately. Growth form categories as in Table 1.

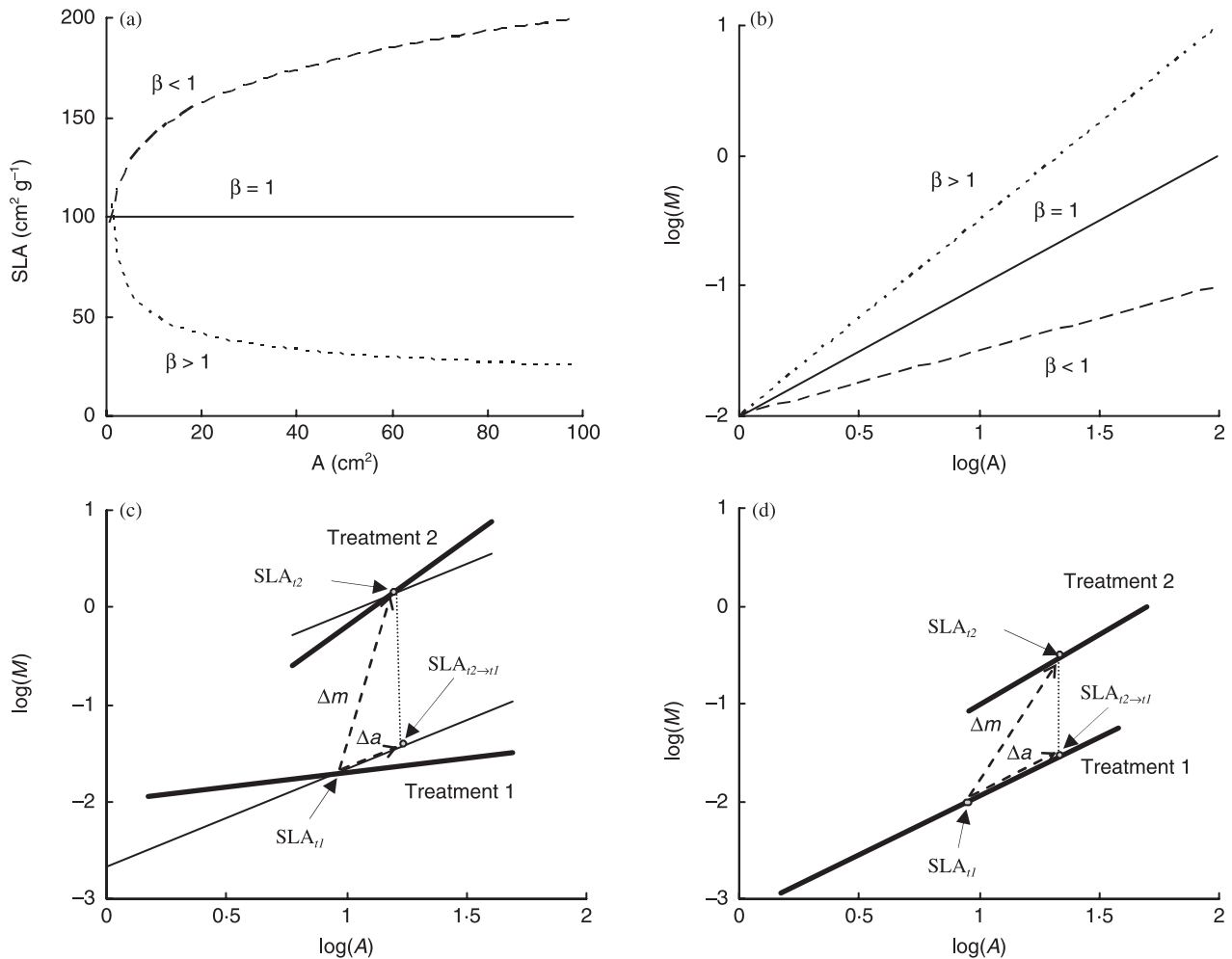


Fig. 2. Approach for the computation of the effects of leaf allometry on the reaction of SLA to environmental–developmental change. Upper graphs: (a) Theoretical relationships between leaf area (A , cm^2) and specific leaf area (SLA, $\text{cm}^2 \text{g}^{-1}$) assuming three scenarios: (1) SLA is unaffected by A ; (2) SLA increases as A increases; (3) SLA decreases as A increases. (b) Reflection of the scenarios depicted in (a) to the scaling of A to leaf mass (M , g). β = exponent of the power function $M = \alpha A^\beta$. See text for further explanations. Lower graphs: graphical expression of the way of calculating the effect of leaf size variation on SLA (Δa in the graphs). Δm is the effect of treatment variation as computed in original studies. (c) Computation when β differs between treatments; and (d): Computation when β is statistically equal.

We *a priori* defined SLA as the target, and A as the explanatory variable. This can alternatively be viewed as A and M being the target traits under physiological control, and SLA as an outcome, by definition. However, there is abundant literature available about the importance of SLA in itself, from a plant's resource economy viewpoint (see e.g. Dijkstra 1989). So, even if the effect of the environment on SLA is by definition a statistically indirect effect on mass, controlling for area, our view is predicated on the notion that SLA is in fact what is being modulated by environment both phenotypically and evolutionarily (not area or mass).

SLA and leaf size (measured as A) are functionally linked by definition ($\text{SLA} = A/M$). Thus, to quantify how a given change in leaf size affects SLA we examined the scaling relationship of M to A . If we express that relationship in a log–log form as:

$$\log(M) = \log(\alpha) + \beta \log(A) \quad \text{eqn 1}$$

and given that $\text{SLA} = A/M$, and after re-arrangement:

$$\text{SLA} = \frac{A^{1-\beta}}{\alpha} \quad \text{eqn 2}$$

β higher than 1 means that M scales 'faster' than A , and larger leaves show lower SLA than smaller ones. The opposite would be the case for β lower than 1, while $\beta = 1$ would mean that SLA is independent of leaf size variations (Fig. 2a, and Milla & Reich 2007).

We used Type II linear regression procedures to fit regressions (Sokal & Rohlf 1995). Type I regression calculates parameters so that the sum of the residuals to the regression line is minimum at the y -axis. Type II, or standardized major axis (SMA), regression minimizes both the error associated to variation in dependent and independent variables. Type II regression is often considered more appropriate when knowledge on scaling exponents, instead of prediction of y values, are the focus of the study (Warton *et al.* 2006).

The above procedure assumes linearity of the relationship between $(\log) A$ and $(\log) M$. This is a common assumption rarely checked explicitly (Poorter & Nagel 2000). Therefore, we fitted polynomial, exponential and power equations to the raw data. None of the nonlinear alternatives yielded significant improvement on goodness-of-fit or on significance of the estimation of regression parameters (data not shown), thus linear relationships between $(\log) A$ and $(\log) M$ are used throughout the paper in the seek of simplicity and comparability with previous literature.

CALCULATION OF THE EFFECTS OF LEAF SIZE AND ENVIRONMENTAL–DEVELOPMENTAL EFFECTS ON SLA

We extended the above calculations to quantify the differential effect of changes in leaf size vs. changes in the environment–development on the SLA response. ANCOVA approaches to correct for the effect of leaf size are not suitable, again because the response variable (SLA) depends on the co-variable (leaf size) (see, e.g. ANCOVA vs. allometry in shoot : root relations in Reich 2002). Allometric analysis provides a more appropriate alternative. In this paper, we proceed as follows to split up the effect of the environment to that of leaf size variation.

Line fitting

First, we fitted a regression line to the (log) A vs. (log) M data separately for each species and for each treatment level or location. We arbitrarily labelled as ‘treatment 1’ the ‘high’ treatment level or location in a gradient (e.g. high atmospheric CO_2 , long growing season length, etc), and as ‘treatment 2’ the opposite. To simplify, hereafter we refer to any level of any type of contrast compiled here as ‘treatment’, even if no experimental manipulation was involved in the original study, or if development instead of environmental is the type of contrast.

Calculation of leaf size effects

Second, we proceeded to calculate the relative strength of A and treatment effects on triggering variation on SLA. In order to split the effects of A and treatment on SLA, we first estimated the average SLA change induced by a change in treatment as measured in the original source without leaf size corrections (measured effect, $\text{SLA}_{\Delta m}$), and the SLA change induced solely by shifts in A between treatment levels (A effect, $\text{SLA}_{\Delta t}$). The calculation procedure differed between species which shared and did not share a common (log) A vs. (log) M slope (β) among treatment levels, which was established by means of a slope heterogeneity test (Warton & Weber 2002).

Calculation for treatments with common slopes. For the 18 species that shared a common slope among treatment levels, we computed SLA for three points in the (log) A – (log) M space: (i) SLA of the mean A of treatment 1 (SLA_{t1}); (ii) SLA of the mean A of treatment 2 (SLA_{t2}); and (iii) SLA of a hypothetical leaf that is the size of the SLA_{t2} leaf, but M of which is calculated from its projection into the treatment 1 regression line ($\text{SLA}_{t2 \rightarrow t1}$). See Fig. 2d for a graphical explanation of the above procedures. Then, the measured response ratio of SLA to the treatment change ($\text{SLA}_{\Delta m}$) was computed as:

$$\text{SLA}_{\Delta m} = ((\text{SLA}_{t1} - \text{SLA}_{t2}) / \text{SLA}_{t1}) \times 100 \quad \text{eqn 3}$$

The effect of changing A among treatments (leaf size effect) was calculated as:

$$\text{SLA}_{\Delta t} = ((\text{SLA}_{t1} - \text{SLA}_{t2 \rightarrow t1}) / \text{SLA}_{t1}) \times 100 \quad \text{eqn 4}$$

And the effect of the environmental–developmental change, after the effect of changing leaf size had been removed, was calculated as:

$$\text{SLA}_{\Delta t} = \text{SLA}_{\Delta m} - \text{SLA}_{\Delta t} \quad \text{eqn 5}$$

Note that, for the effect of leaf size to exist, two events have to co-occur: first, there should be a change in mean leaf size among

treatments (if not, the numerator of eqn 4 is 0); and, second, A and M should be related allometrically (i.e. $\beta \neq 1$, as if $\beta = 1$, again, leaves of any size along the treatment 1 regression line would share exactly the same SLA, yielding a 0 in the numerator of eqn 4). Note also that the effect of the treatment ($\text{SLA}_{\Delta t}$) is the higher the more different are the regression lines in elevation.

Calculation for treatments with different slopes. For the seven species that differed in slope among treatments, we first calculated the average slope between both treatments, and then calculated new regression lines that crossed the mean A of each treatment. In that way, the effect of leaf size variation ($\text{SLA}_{\Delta t}$) was computed from a balance between the effect of leaf size in each treatment. After that, we proceeded as explained in ‘Calculation for treatments with common slopes’ section (See Fig. 2c).

In Milla & Reich (2007) we evaluated whether β scores depended on the phylogenetic position of different taxa, in a set of 157 species. We found no phylogenetic structure. Thus, in the current study, more restricted in number of species, and evaluating the same suite of response variables, we did not evaluate putative phylogenetic signals on the effect of treatment–leaf size interaction on SLA.

STATISTICS

Differences between treatment effects, as measured in the original study ($\text{SLA}_{\Delta m}$), and treatment effects after removing leaf size dependency ($\text{SLA}_{\Delta t}$) were considered to be significantly different at $P = 0.05$ if the 95% confidence intervals of both variables do not overlap. To compute these confidence intervals we proceeded as explained in the Appendix. Note that confidence intervals of calculated variables, taken from sample statistics, instead of raw data, are notably wider, because calculations assume maximum outcrossing possibilities among raw data. Type II regression procedures were carried out using (SMATR (Version I, Falster DS, Warton DI & Wright IJ, <<http://www.bio.mq.edu.au/ecology/SMATR>>). All other statistics were performed with spss 14.0.

Results

The target traits examined here showed an ample range of variation. SLA varied 15-fold, from a high of $481 \text{ cm}^2 \text{ g}^{-1}$ in *Bromus erectus* under ambient CO_2 , to low of $32.5 \text{ cm}^2 \text{ g}^{-1}$ in *Eucalyptus tetradonta* from low rainfall sites. Leaf area ranged from the smallest leaf of *Empetrum hermaphroditum* (0.02 cm^2), to the largest leaf of *E. tetradonta* (183 cm^2), thus spanning four orders of magnitude.

In the original studies compiled here, SLA responded to the various environmental and endogenous changes in distinct ways (Table 3). For example, three out of four species showed a marked decrease in SLA as a response to diminishing water availability. A decrease in light incidence triggered a sharp increase in SLA. Also, probably linked to the decrease in light irradiance in sites burnt infrequently, SLA was higher in those sites that were burnt less frequently. All species but *Vaccinium vitis-idaea* showed an increase in SLA in sites where growing season length was shorter. The response to CO_2 was species-dependent: *B. erectus* showed an increase in SLA under elevated CO_2 , while *Dactylis glomerata* reached higher values of SLA under ambient than under elevated CO_2 . Ontogenetic factors also affected SLA. Leaves from long and

Table 3. Effects of leaf size and treatment on SLA variation

Species	Type of contrast	Treatment level or placement along gradient	<i>A</i> (cm ²)	SLA (cm ² g ⁻¹)	Arbitrarily considered direction of change	SLA _{Δm} (measured effect, % change)	SLA _{Δt} (treatment effect, % change)	SLA _{Δa} (leaf size effect, % change)	(SLA _{Δt} /SLA _{Δt})* 100																																																																																																																																																																																																																																																																				
<i>Amelanchier ovalis</i>	Type of shoot:	Long	2.11	102.46	Long → short	+14.43 (± 3.7)a	+15.53 (± 47.7)a	-1.09	7.05																																																																																																																																																																																																																																																																				
	Long vs. short	Short	1.42	117.25						<i>Bupleurum fruticosum</i>	Type of shoot:	Reproductive	3.71	71.07	Rep → veg	+13.90 (± 2.59)a	+10.73 (± 29.3)a	+3.16	29.47	Vegetative vs. reproductive	Vegetative	2.10	80.95	<i>Bromus erectus</i>	Atmospheric CO ₂ level:	Elevated	18.11	232.36	Elevated → ambient	-1.71 (± 6.69)a	-1.25 (± 17.3)a	-0.45	35.80	Elevated vs. ambient	Ambient	15.07	228.39	<i>Dactylis glomerata</i>	Atmospheric CO ₂ level:	Elevated	32.14	257.42	Elevated → ambient	+5.28 (± 6.65)a	+4.85 (± 12.2)a	+0.43	35.80	Elevated vs. ambient	Ambient	27.10	271.02	<i>Andropogon gerardi</i>	Fire frequency:	High	16.83	126.36	High → low	+59.70 (± 15.7)a	+57.77(± 829)a	+1.93	3.35	High vs. low	Low	11.09	201.80	<i>Aster azureus</i>	Fire frequency:	High	10.35	151.51	High → low	+64.11 (± 32.6)a	+64.08 (± 64.7)a	+0.0	0.04	High vs. low	Low	10.86	248.65	<i>Panicum praecociosum</i>	Fire frequency:	High	2.77	233.18	High → low	+33.13 (± 21.5)a	+31.90 (± 46.9)a	+1.22	3.83	High vs. low	Low	2.22	310.43	<i>Betula nana</i>	Growing season length:	Long	0.55	122.86	Long → short	+1.69 (± 7.13)a	+1.86 (± 9.49)a	-0.16	8.85	Sites of long vs. short GSL	Short	0.61	124.94	<i>Diapensia lapponica</i>	Growing season length:	Long	0.07	48.79	Long → short	+52.34 (± 4.31)a	+52.15 (± 93.1)a	+0.19	0.36	Sites of long vs. short GSL	Short	0.07	74.34	<i>Empetrum hermaphroditum</i>	Growing season length:	Long	0.04	54.25	Long → short	+51.28 (± 3.33)a	+51.10 (± 13.4)a	+0.18	0.36	Sites of long vs. short GSL	Short	0.03	82.07	<i>Pedicularis lapponica</i>	Growing season length:	Long	0.69	105.94	Long → short	+10.54 (± 8.78)a	+8.79 (± 64.2)a	+1.75	19.91	Sites of long vs. short GSL	Short	0.62	117.11	<i>Salix herbacea</i>	Growing season length:	Long	0.88	110.26	Long → short	+5.05 (± 6.42)a	+3.57 (± 10.2)a	+1.48	41.62	Sites of long vs. short GSL	Short	0.81	115.82	<i>Vaccinium vitis-idaea</i>	Growing season length:	Long	0.20	54.99	Long → short	-13.2 (± 4.14)a	-13.31 (± 86.2)a	+0.11	41.62	Sites of long vs. short GSL	Short	0.18	47.72	<i>Betula pendula</i>	Light environment:	Long	7.38	118.66	High → low	+43.35 (± 8.15)a	+49.72 (± 19.9)a	-6.37	12.81	High vs. low incoming light	Short	9.38	170.10	<i>Populus tremula</i>	Light environment:	High	32.14	128.83	High → low	+12.43 (± 4.12)a	+14.73 (± 5.77)a	-2.29	15.57	High vs. low incoming light	Low	37.93	144.86	<i>Erythrophleum chlorostachys</i>	Rainfall:	High	22.34	108.50	High → low	-30.6 (± 5.91)a	-28.6 (± 14.4)a	-1.99	6.96	Sites of high vs. low precipitation	Low	22.34	75.28	<i>Eucalyptus tetradonta</i>	Rainfall:	High	94.84	46.15	High → low	+38.20 (± 3.97)a	+33.84 (± 12.2)a	+4.36	12.87	Sites of high vs. low precipitation	Low	60.53	63.78	<i>Viburnum tinus</i>	Rainfall:	High	16.75	112.66	High → low	-32.12 (± 4.16)a	-44.24 (± 16.1)a	+12.11	27.38	Sites of high vs. low precipitation	Low	7.18	76.46	<i>Rhamnus alaternus</i>	Rainfall:	High	4.14	102.26	High → low	-33.27 (± 4.59)a	-64.57 (± 45.8)a	+31.29	48.46	Sites of high vs. low precipitation	Low	0.55	68.23	<i>Arbutus unedo</i>	Leaf age:	Young	4.33	113.90	Young → old	-56.78 (± 4.83)a	-51.45 (± 12.4)a
<i>Bupleurum fruticosum</i>	Type of shoot:	Reproductive	3.71	71.07	Rep → veg	+13.90 (± 2.59)a	+10.73 (± 29.3)a	+3.16	29.47																																																																																																																																																																																																																																																																				
	Vegetative vs. reproductive	Vegetative	2.10	80.95						<i>Bromus erectus</i>	Atmospheric CO ₂ level:	Elevated	18.11	232.36	Elevated → ambient	-1.71 (± 6.69)a	-1.25 (± 17.3)a	-0.45	35.80	Elevated vs. ambient	Ambient	15.07	228.39	<i>Dactylis glomerata</i>	Atmospheric CO ₂ level:	Elevated	32.14	257.42	Elevated → ambient	+5.28 (± 6.65)a	+4.85 (± 12.2)a	+0.43	35.80	Elevated vs. ambient	Ambient	27.10	271.02	<i>Andropogon gerardi</i>	Fire frequency:	High	16.83	126.36	High → low	+59.70 (± 15.7)a	+57.77(± 829)a	+1.93	3.35	High vs. low	Low	11.09	201.80	<i>Aster azureus</i>	Fire frequency:	High	10.35	151.51	High → low	+64.11 (± 32.6)a	+64.08 (± 64.7)a	+0.0	0.04	High vs. low	Low	10.86	248.65	<i>Panicum praecociosum</i>	Fire frequency:	High	2.77	233.18	High → low	+33.13 (± 21.5)a	+31.90 (± 46.9)a	+1.22	3.83	High vs. low	Low	2.22	310.43	<i>Betula nana</i>	Growing season length:	Long	0.55	122.86	Long → short	+1.69 (± 7.13)a	+1.86 (± 9.49)a	-0.16	8.85	Sites of long vs. short GSL	Short	0.61	124.94	<i>Diapensia lapponica</i>	Growing season length:	Long	0.07	48.79	Long → short	+52.34 (± 4.31)a	+52.15 (± 93.1)a	+0.19	0.36	Sites of long vs. short GSL	Short	0.07	74.34	<i>Empetrum hermaphroditum</i>	Growing season length:	Long	0.04	54.25	Long → short	+51.28 (± 3.33)a	+51.10 (± 13.4)a	+0.18	0.36	Sites of long vs. short GSL	Short	0.03	82.07	<i>Pedicularis lapponica</i>	Growing season length:	Long	0.69	105.94	Long → short	+10.54 (± 8.78)a	+8.79 (± 64.2)a	+1.75	19.91	Sites of long vs. short GSL	Short	0.62	117.11	<i>Salix herbacea</i>	Growing season length:	Long	0.88	110.26	Long → short	+5.05 (± 6.42)a	+3.57 (± 10.2)a	+1.48	41.62	Sites of long vs. short GSL	Short	0.81	115.82	<i>Vaccinium vitis-idaea</i>	Growing season length:	Long	0.20	54.99	Long → short	-13.2 (± 4.14)a	-13.31 (± 86.2)a	+0.11	41.62	Sites of long vs. short GSL	Short	0.18	47.72	<i>Betula pendula</i>	Light environment:	Long	7.38	118.66	High → low	+43.35 (± 8.15)a	+49.72 (± 19.9)a	-6.37	12.81	High vs. low incoming light	Short	9.38	170.10	<i>Populus tremula</i>	Light environment:	High	32.14	128.83	High → low	+12.43 (± 4.12)a	+14.73 (± 5.77)a	-2.29	15.57	High vs. low incoming light	Low	37.93	144.86	<i>Erythrophleum chlorostachys</i>	Rainfall:	High	22.34	108.50	High → low	-30.6 (± 5.91)a	-28.6 (± 14.4)a	-1.99	6.96	Sites of high vs. low precipitation	Low	22.34	75.28	<i>Eucalyptus tetradonta</i>	Rainfall:	High	94.84	46.15	High → low	+38.20 (± 3.97)a	+33.84 (± 12.2)a	+4.36	12.87	Sites of high vs. low precipitation	Low	60.53	63.78	<i>Viburnum tinus</i>	Rainfall:	High	16.75	112.66	High → low	-32.12 (± 4.16)a	-44.24 (± 16.1)a	+12.11	27.38	Sites of high vs. low precipitation	Low	7.18	76.46	<i>Rhamnus alaternus</i>	Rainfall:	High	4.14	102.26	High → low	-33.27 (± 4.59)a	-64.57 (± 45.8)a	+31.29	48.46	Sites of high vs. low precipitation	Low	0.55	68.23	<i>Arbutus unedo</i>	Leaf age:	Young	4.33	113.90	Young → old	-56.78 (± 4.83)a	-51.45 (± 12.4)a	-5.33	10.36	Young vs. old leaves	Old	5.82	49.22								
<i>Bromus erectus</i>	Atmospheric CO ₂ level:	Elevated	18.11	232.36	Elevated → ambient	-1.71 (± 6.69)a	-1.25 (± 17.3)a	-0.45	35.80																																																																																																																																																																																																																																																																				
	Elevated vs. ambient	Ambient	15.07	228.39						<i>Dactylis glomerata</i>	Atmospheric CO ₂ level:	Elevated	32.14	257.42	Elevated → ambient	+5.28 (± 6.65)a	+4.85 (± 12.2)a	+0.43	35.80	Elevated vs. ambient	Ambient	27.10	271.02	<i>Andropogon gerardi</i>	Fire frequency:	High	16.83	126.36	High → low	+59.70 (± 15.7)a	+57.77(± 829)a	+1.93	3.35	High vs. low	Low	11.09	201.80	<i>Aster azureus</i>	Fire frequency:	High	10.35	151.51	High → low	+64.11 (± 32.6)a	+64.08 (± 64.7)a	+0.0	0.04	High vs. low	Low	10.86	248.65	<i>Panicum praecociosum</i>	Fire frequency:	High	2.77	233.18	High → low	+33.13 (± 21.5)a	+31.90 (± 46.9)a	+1.22	3.83	High vs. low	Low	2.22	310.43	<i>Betula nana</i>	Growing season length:	Long	0.55	122.86	Long → short	+1.69 (± 7.13)a	+1.86 (± 9.49)a	-0.16	8.85	Sites of long vs. short GSL	Short	0.61	124.94	<i>Diapensia lapponica</i>	Growing season length:	Long	0.07	48.79	Long → short	+52.34 (± 4.31)a	+52.15 (± 93.1)a	+0.19	0.36	Sites of long vs. short GSL	Short	0.07	74.34	<i>Empetrum hermaphroditum</i>	Growing season length:	Long	0.04	54.25	Long → short	+51.28 (± 3.33)a	+51.10 (± 13.4)a	+0.18	0.36	Sites of long vs. short GSL	Short	0.03	82.07	<i>Pedicularis lapponica</i>	Growing season length:	Long	0.69	105.94	Long → short	+10.54 (± 8.78)a	+8.79 (± 64.2)a	+1.75	19.91	Sites of long vs. short GSL	Short	0.62	117.11	<i>Salix herbacea</i>	Growing season length:	Long	0.88	110.26	Long → short	+5.05 (± 6.42)a	+3.57 (± 10.2)a	+1.48	41.62	Sites of long vs. short GSL	Short	0.81	115.82	<i>Vaccinium vitis-idaea</i>	Growing season length:	Long	0.20	54.99	Long → short	-13.2 (± 4.14)a	-13.31 (± 86.2)a	+0.11	41.62	Sites of long vs. short GSL	Short	0.18	47.72	<i>Betula pendula</i>	Light environment:	Long	7.38	118.66	High → low	+43.35 (± 8.15)a	+49.72 (± 19.9)a	-6.37	12.81	High vs. low incoming light	Short	9.38	170.10	<i>Populus tremula</i>	Light environment:	High	32.14	128.83	High → low	+12.43 (± 4.12)a	+14.73 (± 5.77)a	-2.29	15.57	High vs. low incoming light	Low	37.93	144.86	<i>Erythrophleum chlorostachys</i>	Rainfall:	High	22.34	108.50	High → low	-30.6 (± 5.91)a	-28.6 (± 14.4)a	-1.99	6.96	Sites of high vs. low precipitation	Low	22.34	75.28	<i>Eucalyptus tetradonta</i>	Rainfall:	High	94.84	46.15	High → low	+38.20 (± 3.97)a	+33.84 (± 12.2)a	+4.36	12.87	Sites of high vs. low precipitation	Low	60.53	63.78	<i>Viburnum tinus</i>	Rainfall:	High	16.75	112.66	High → low	-32.12 (± 4.16)a	-44.24 (± 16.1)a	+12.11	27.38	Sites of high vs. low precipitation	Low	7.18	76.46	<i>Rhamnus alaternus</i>	Rainfall:	High	4.14	102.26	High → low	-33.27 (± 4.59)a	-64.57 (± 45.8)a	+31.29	48.46	Sites of high vs. low precipitation	Low	0.55	68.23	<i>Arbutus unedo</i>	Leaf age:	Young	4.33	113.90	Young → old	-56.78 (± 4.83)a	-51.45 (± 12.4)a	-5.33	10.36	Young vs. old leaves	Old	5.82	49.22																						
<i>Dactylis glomerata</i>	Atmospheric CO ₂ level:	Elevated	32.14	257.42	Elevated → ambient	+5.28 (± 6.65)a	+4.85 (± 12.2)a	+0.43	35.80																																																																																																																																																																																																																																																																				
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	High vs. low	Low	11.09	201.80						<i>Aster azureus</i>	Fire frequency:	High	10.35	151.51	High → low	+64.11 (± 32.6)a	+64.08 (± 64.7)a	+0.0	0.04	High vs. low	Low	10.86	248.65	<i>Panicum praecociosum</i>	Fire frequency:	High	2.77	233.18	High → low	+33.13 (± 21.5)a	+31.90 (± 46.9)a	+1.22	3.83	High vs. low	Low	2.22	310.43	<i>Betula nana</i>	Growing season length:	Long	0.55	122.86	Long → short	+1.69 (± 7.13)a	+1.86 (± 9.49)a	-0.16	8.85	Sites of long vs. short GSL	Short	0.61	124.94	<i>Diapensia lapponica</i>	Growing season length:	Long	0.07	48.79	Long → short	+52.34 (± 4.31)a	+52.15 (± 93.1)a	+0.19	0.36	Sites of long vs. short GSL	Short	0.07	74.34	<i>Empetrum hermaphroditum</i>	Growing season length:	Long	0.04	54.25	Long → short	+51.28 (± 3.33)a	+51.10 (± 13.4)a	+0.18	0.36	Sites of long vs. short GSL	Short	0.03	82.07	<i>Pedicularis lapponica</i>	Growing season length:	Long	0.69	105.94	Long → short	+10.54 (± 8.78)a	+8.79 (± 64.2)a	+1.75	19.91	Sites of long vs. short GSL	Short	0.62	117.11	<i>Salix herbacea</i>	Growing season length:	Long	0.88	110.26	Long → short	+5.05 (± 6.42)a	+3.57 (± 10.2)a	+1.48	41.62	Sites of long vs. short GSL	Short	0.81	115.82	<i>Vaccinium vitis-idaea</i>	Growing season length:	Long	0.20	54.99	Long → short	-13.2 (± 4.14)a	-13.31 (± 86.2)a	+0.11	41.62	Sites of long vs. short GSL	Short	0.18	47.72	<i>Betula pendula</i>	Light environment:	Long	7.38	118.66	High → low	+43.35 (± 8.15)a	+49.72 (± 19.9)a	-6.37	12.81	High vs. low incoming light	Short	9.38	170.10	<i>Populus tremula</i>	Light environment:	High	32.14	128.83	High → low	+12.43 (± 4.12)a	+14.73 (± 5.77)a	-2.29	15.57	High vs. low incoming light	Low	37.93	144.86	<i>Erythrophleum chlorostachys</i>	Rainfall:	High	22.34	108.50	High → low	-30.6 (± 5.91)a	-28.6 (± 14.4)a	-1.99	6.96	Sites of high vs. low precipitation	Low	22.34	75.28	<i>Eucalyptus tetradonta</i>	Rainfall:	High	94.84	46.15	High → low	+38.20 (± 3.97)a	+33.84 (± 12.2)a	+4.36	12.87	Sites of high vs. low precipitation	Low	60.53	63.78	<i>Viburnum tinus</i>	Rainfall:	High	16.75	112.66	High → low	-32.12 (± 4.16)a	-44.24 (± 16.1)a	+12.11	27.38	Sites of high vs. low precipitation	Low	7.18	76.46	<i>Rhamnus alaternus</i>	Rainfall:	High	4.14	102.26	High → low	-33.27 (± 4.59)a	-64.57 (± 45.8)a	+31.29	48.46	Sites of high vs. low precipitation	Low	0.55	68.23	<i>Arbutus unedo</i>	Leaf age:	Young	4.33	113.90	Young → old	-56.78 (± 4.83)a	-51.45 (± 12.4)a	-5.33	10.36	Young vs. old leaves	Old	5.82	49.22																																																		
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	Sites of long vs. short GSL	Short	0.62	117.11						<i>Salix herbacea</i>	Growing season length:	Long	0.88	110.26	Long → short	+5.05 (± 6.42)a	+3.57 (± 10.2)a	+1.48	41.62	Sites of long vs. short GSL	Short	0.81	115.82	<i>Vaccinium vitis-idaea</i>	Growing season length:	Long	0.20	54.99	Long → short	-13.2 (± 4.14)a	-13.31 (± 86.2)a	+0.11	41.62	Sites of long vs. short GSL	Short	0.18	47.72	<i>Betula pendula</i>	Light environment:	Long	7.38	118.66	High → low	+43.35 (± 8.15)a	+49.72 (± 19.9)a	-6.37	12.81	High vs. low incoming light	Short	9.38	170.10	<i>Populus tremula</i>	Light environment:	High	32.14	128.83	High → low	+12.43 (± 4.12)a	+14.73 (± 5.77)a	-2.29	15.57	High vs. low incoming light	Low	37.93	144.86	<i>Erythrophleum chlorostachys</i>	Rainfall:	High	22.34	108.50	High → low	-30.6 (± 5.91)a	-28.6 (± 14.4)a	-1.99	6.96	Sites of high vs. low precipitation	Low	22.34	75.28	<i>Eucalyptus tetradonta</i>	Rainfall:	High	94.84	46.15	High → low	+38.20 (± 3.97)a	+33.84 (± 12.2)a	+4.36	12.87	Sites of high vs. low precipitation	Low	60.53	63.78	<i>Viburnum tinus</i>	Rainfall:	High	16.75	112.66	High → low	-32.12 (± 4.16)a	-44.24 (± 16.1)a	+12.11	27.38	Sites of high vs. low precipitation	Low	7.18	76.46	<i>Rhamnus alaternus</i>	Rainfall:	High	4.14	102.26	High → low	-33.27 (± 4.59)a	-64.57 (± 45.8)a	+31.29	48.46	Sites of high vs. low precipitation	Low	0.55	68.23	<i>Arbutus unedo</i>	Leaf age:	Young	4.33	113.90	Young → old	-56.78 (± 4.83)a	-51.45 (± 12.4)a	-5.33	10.36	Young vs. old leaves	Old	5.82	49.22																																																																																																																																						
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Table 3. Continued

Species	Type of contrast	Treatment level or placement along gradient	A (cm ²)	SLA (cm ² g ⁻¹)	Arbitrarily considered direction of change	SLA _{Δm} (measured effect, % change)	SLA _{Δt} (treatment effect, % change)	SLA _{Δs} (leaf size effect, % change)	(SLA _{Δs} /SLA _{Δt}) * 100
<i>Buxus sempervirens</i>	Leaf age:	Young	0.97	67.67	Young → old	-25.05 (± 3.00)a	-22.27 (± 6.52)a	-2.78	12.48
	Young vs. old leaves	Old	1.13	50.72					
<i>Quercus ilex</i>	Leaf age:	Young	2.64	62.62	Young → old	-27.24 (± 4.15)a	-13.21 (± 7.47)a	-14.03	106.22
	Young vs. old leaves	Old	2.36	45.56					
<i>Cistus laurifolius</i>	Leaf age:	Young	5.70	60.89	Young → old	-10.29 (± 4.07)a	-13.21 (± 7.47)a	-7.60	282.81
	Young vs. old leaves	Old	8.28	54.62					
<i>Quercus coccifera</i>	Leaf age:	Young	1.24	55.43	Young → old	-15.21 (± 3.63)a	-17.38 (± 7.61)a	+2.18	12.52
	Young vs. old leaves	Old	0.93	47.00					
<i>Quercus faginea</i>	Leaf age:	Young	3.27	165.88	Young → old	-39.33 (± 7.34)a	-17.88 (± 10.1)a	-21.45	119.92
	Young vs. old leaves	Old	3.08	100.64					
<i>Leontodon hispidus</i>	Plant age:	Juvenile	7.18	218.23	Juv → post-reprod.	-7.95 (± 30.2)a	-1.58 (± 326)a	-6.37	403.01
	Juvenile vs. post-reproductive plants	Post-reproductive	11.25	200.89					

Estimated effects of variation in SLA as measured in the original study, without controlling for leaf size effects (SLA_{Δm}); effect of variation in treatment once leaf size-driven variability has been removed (SLA_{Δs}); and effect of leaf size variation (SLA_{Δt}). Different letters in the same row for SLA_{Δm} and SLA_{Δt} mean significant differences between originally-measured and size-dependency corrected effects. See Methods for details on calculations of the above effects and significance testing. Also arithmetic means of A (leaf area, cm²), and SLA for each species and treatment.

reproductive branches had significantly greater SLA than leaves from short and vegetative branches. Finally, young leaves, and leaves from juvenile plants, showed higher SLA than mature leaves, or leaves from old individuals.

The aim of this paper is to investigate whether and to what extent the responses described above, as measured in the original studies, stand after the influence of leaf size correlates are removed. The correction for size-dependency did not modify the sign and significance of the SLA response in any of the contrasts considered here. However, several of the effects changed noticeably in magnitude (rightmost column in Table 3). For instances, much of the decline of SLA as water availability decreases was hindered by the fact that (i) leaves were smaller in the low water availability sites, and (ii) smaller leaves *per se* had higher SLA (β of (log) *A* vs. (log) *M* > 1). Thus, treatment and leaf size effects pushed in opposite directions in rainfall contrasts. Consequently, when the leaf size effect is accounted for, the treatment effect becomes larger in magnitude. Similarly, changes in *A* among treatments for *Bupleurum fruticosum*, *B. erectus*, *Leontodon hispidus* or *Salix herbacea*, had a relevant effect on the magnitude of SLA change due to environmental–developmental modifications.

The responses measured here, both in the original studies and in our re-analyses, are composed of two sources of variation: phenotypic plasticity among closely related individuals, and genotypic differences between genetically and geographically distinct individuals of the same species. We cannot formally assess which of the above levels was more responsive, since each type of contrast was evaluated at a single level in the original studies. However, one may think on field studies involving different locations as at least a rough proxy for the genetic component, and seeding experiments under greenhouse-like conditions as proxy for the plasticity component. We only compiled one seeding experiment (elevated vs. ambient CO₂), which arose as one of the most sensitive treatments to the leaf size effect, since both treatments differed in scaling slope, and in average leaf size. This may indicate a higher relevance of the phenotypic plasticity component in terms of responsiveness to leaf size effects.

To illustrate the three possible outcomes of our analyses, in Fig. 3 we show three examples where the change in environment–development and the change in leaf size had contrasting consequences on SLA response measured in the original investigation (graphs for all other species analysed here are in Supplementary Material, Fig. S1):

1. No leaf size effect: in *Aster azureus*, leaf size did not change remarkably from high fire frequency treatments to low fire frequency treatments. Also, when averaged between treatments, *M* scaled isometrically to *A*. Thus, there was no dependency of SLA on leaf size.
2. Leaf size and rainfall effects pushing in opposite directions: *Viburnum tinus* leaves were much smaller in low compared to high rainfall sites. Moreover, β was 1.135, averaged among treatments. Taken together, those two facts exerted a remarkable size-dependency effect on this particular SLA response. Given the correlated direction of change,

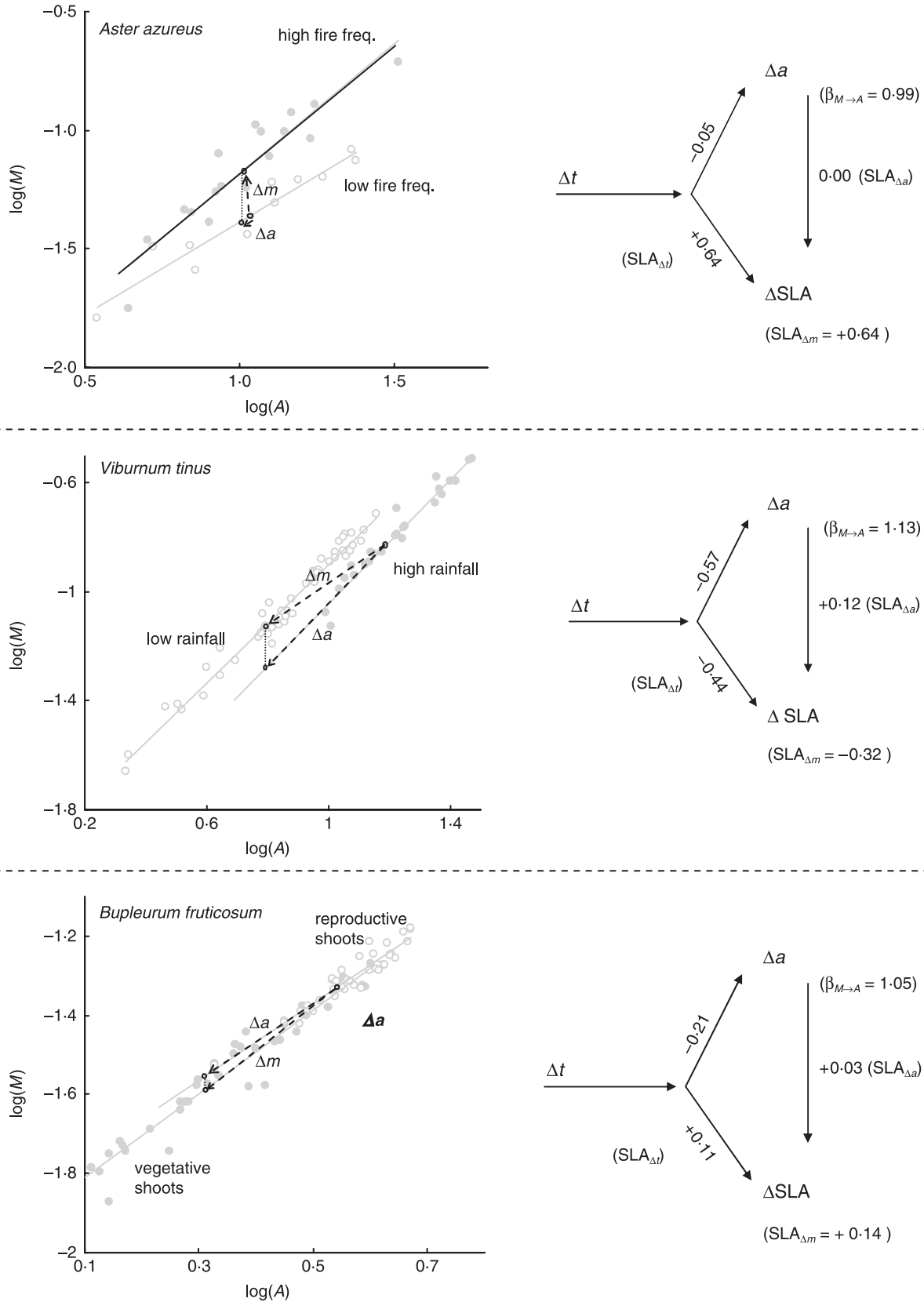


Fig. 3. Three contrasting examples of the relative impact of the measured variation in SLA as a consequence of a change in treatment ($SLA_{\Delta m}$), compared to that of a change in leaf size ($SLA_{\Delta a}$). Magnitude of treatment, leaf size, and measured effects, and β , taken from Tables 2 and 3.

the decrease of SLA in response to low water availability was buffered in magnitude by the increase in SLA imposed by leaf size reduction.

3. Leaf size and leaf age effects pushing in the same direction: in *B. fruticosum* we compared leaves from functionally different types of shoots: vegetative and reproductive. Those from vegetative shoots were smaller, and similarly to the above case, *M* scaled faster than *A*. Since vegetative shoots bore higher SLA leaves, leaf-size dependency inflated the response ratio of SLA. Once corrected, the difference in SLA for hypothetical leaves of the same size that was attributable to the developmental change from reproductive to a vegetative branch decreased from approximately 14% to 11% (see Table 3).

Discussion

GENERAL PATTERN

We set out to clarify whether future research on responses of SLA to changes in the environment or in plant development needs to correct for leaf size dependency. We examined this in a diverse set of environmental and endogenous contrasts and in 26 different species. In most cases, we observed a significant effect of leaf size, though generally much smaller than the effect of treatments. The sole previous assessment, we are aware of, is in agreement with our general pattern: Poorter & de Jong (1999) found that the effect on SLA of changing leaf size among sites of contrasting productivity was negligible as compared to the effect of productivity in itself.

In Milla & Reich (2007), we showed that, on average, large leaves of a given species tend to have lower SLA than small leaves of the same species, which also occurs at the interspecific level, though in a less intense manner (Niklas *et al.* 2007). Also, we proposed that this allometric tendency might influence the interpretation of previous work on SLA. In the current paper, the overall scaling exponent of *A* to *M* was also allometric ($\beta = 1.08$ here; $\beta = 1.10$ in Milla & Reich, 2007; $\beta = 1.02$ in Niklas *et al.* 2007). Therefore, even if we got an overall modest effect of leaf size, for those experiments where among-treatment changes in leaf size are important, attention should still be paid to the scaling exponent of *A* to *M* before discarding leaf size correlates.

THE EFFECT OF CHANGING LEAF SIZE AMONG TREATMENTS ON SLA IS CONTEXT-DEPENDENT

The tendency of large leaves to show lower SLA is general, but not obligate, since we previously found a wide range of variation in *A* to *M* scaling exponents among species (Milla & Reich 2007). Here, we show that leaf size effects are not solely dependent on the species, but also on the sort of contrast under study, ranging from almost no effect of leaf size variation in fire frequency contrasts, to very strong variation in magnitude of effect for several of the leaf age comparisons.

Leaf size (defined here as area) responded differently to the several contrasts compiled here. In general, leaves were larger

in the shade, and in well-watered environments. The leaves from CO₂-impoverished atmosphere, and short and vegetative shoots, were smaller; and the response to growing season length, fire frequency, and leaf or plant age was species-dependent. Part of these patterns agree with previous literature (e.g. leaves under low water availability are consistently smaller, Cunningham, Summerhayes & Westoby 1999), others disagree (e.g. leaf size decreases in low temperature environments in a consistent manner across previous studies, Körner 1999), while for others there is no substantial specific previous information (e.g. fire frequency).

SLA reflects a resource allocation strategy within the individual leaf (Westoby *et al.* 2002), and thus reacts strongly when changes in internal or external cues are perceived by the plant. Consequently, SLA was lower in long and reproductive branches, under low fire frequency, long growing season length, and high irradiance, and in old leaves and plants. Response to CO₂ treatments and to water availability was species-dependent. This is, for the most part, consistent with previous literature, when available for the factor under study (e.g. Reich, Walters & Ellsworth 1991; Körner 1999; Cornelissen *et al.* 2003; Poorter *et al.* 2006).

Therefore, since leaf size and SLA frequently react differently to different types of environmental–developmental changes, it is reasonable to expect that the effect of size–correlates would be different between types of contrasts. This, further, interacts with the fact that leaf size effects are frequently species-specific, making size-dependency difficult to predict. We comment on leaf age contrasts hereon to illustrate the above point (detailed graphs on leaf age contrasts can be found in Supplementary Fig. S1). It is common knowledge that, as leaves become older, more carbon-rich compounds are stored in a fixed surface area per leaf, leading to the well-known pattern of decreasing SLA with leaf age (Reich *et al.* 1991). However, it is less well-known whether leaves of different size have contrasting life spans within a given crown (but see studies on heterophyllous species, e.g. Kypris, Grammatikopoulos & Manetas 1997). In this compilation we found that the old leaves of the three species of *Quercus* were smaller than the young leaves, whereas the opposite was true for the *Cistus*, *Arbutus* and *Buxus* species. This suggests a species-specific pattern of survival of leaves of different sizes across leaf ontogeny, and/or that leaves born at different times in the season are of different size. Together with the decrease of SLA with leaf age, and with the fact that β was remarkably different among leaf ages (see Table 2), this leads to leaf size change accounting for most of the SLA decrease in old compared to young *Cistus laurifolius* leaves, but leaf size change obscuring the negative response ratio of SLA to leaf aging in *Quercus coccifera*.

ULTRASTRUCTURAL BASIS FOR LEAF SIZE-RELATED SLA DIFFERENCES

Ultrastructural traits that trigger variation in leaf size and in SLA can also help explain why our general pattern was so varied between types of treatments and species. Large leaves invest

up to 40% more in midribs and other support tissues than small leaves (Niinemets *et al.* 2007). This leads to a lower percentage of photosynthetically active compounds per unit mass, and thus to lower metabolic rates for large leaves (Niinemets *et al.* 2006). Small leaves, on the other hand, have lower support needs, and thus a higher fraction of productive tissue. Leaf temperature and evaporative demand also scale positively with leaf size, possibly constraining leaf size variation (Gates 1980).

Variation in SLA, on the other hand, is achieved through modifications in its two components: leaf density and leaf thickness. Changes in tissue composition leading to changes in leaf density can be quite different than those leading to leaf thickness variation. Increasing thickness by augmenting number of layers of spongy or palisade mesophyll produce thicker and lower SLA leaves, though it may not modify, or even decrease, leaf density. This occurs, for instance, under high light or temperature conditions (Oguchi, Hikosaka & Hirose 2003). Water scarcity, as a contrasting example, selects for leaves with denser cell walls or more sclerenchyma, leading to denser and lower SLA, but not obligately thicker, leaves (Niinemets 2001). The above modifications in leaf ultrastructure have nearly opposite effects for leaf functioning than an increase of thickness, although they can yield similar SLA scores (Castro-Díez, Puyravaud & Cornelissen 2000).

Thus, whether changes in SLA are predominantly due to thickness or density variation, and whether support needs of increasing leaf size are met by increasing support within the leaf lamina, or by stronger petioles, or by increasing branch-level resistance, can lead to large heterogeneity as regards leaf size dependency of environmental and developmental effects on SLA. For instance, reconsidering the above example on leaf age contrasts, decreases in SLA are more dependent on increases in leaf density for the species of *Quercus* studied here, whereas *Cistus*, *Arbutus* and *Buxus* species modify leaf thickness instead (Milla, unpublished data). More mesic leaves of the latter group may have enabled survival for longer for large leaves, thus leading to longer survival of larger leaves. The opposite might have occurred for the more xeric leaves of *Quercus* species.

Conclusion

The fact that size-dependency profoundly affects leaf function through trade-offs between construction of support or productive tissue has recently been proposed as one of the chief missing links that can account for unexplained worldwide variation in leaf traits (Niinemets *et al.* 2007). For example, leaves sharing similar SLA and leaf longevity can show widely different photosynthetic rates (Wright *et al.* 2004). This variation might be related to changes in leaf size. However, the results and patterns found in the original papers and data compiled here stand after re-analysis including leaf size effects. The magnitude of measured effects, though, was remarkably modified in several of the study cases. Consideration of leaf size effects requires large sample sizes to develop reliable allometric relationships between leaf area

and mass, which may be costly. This has important implications for designing experiments. Our results here should help guide expert criteria to evaluate *a priori* whether a given design with SLA as a response variable is likely to exhibit leaf size dependency. As a rule of thumb, experiments considering factors that tend to affect leaf size (e.g. water availability), should be prepared to implement protocols to control for leaf size dependency, because, generally, M and A will relate allometrically within species.

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Supplementary material

The following supplemental material is available for this article:

Appendix S1. Calculation of 95% confidence intervals (CI) of the SLA change induced by a change in treatment as measured in the original source without leaf size corrections (measured effect, SLA_{Δm}), and the effect of the environmental–developmental change in SLA, after the effect of changing leaf size had been removed (treatment effect, SLA_Δ)

Fig. S1. Extension of Fig. 3 for all the species compiled here. Relative impact of the measured variation in SLA as a consequence of a change in treatment (SLA_{Δm}), compared to that of a change in leaf size (SLA_Δ). Magnitude of treatment, leaf size, and measured effects, and β, taken from Tables 2 and 3.

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