Tansley review

Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control

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Contents

Summary

We quantified the biomass allocation patterns to leaves, stems and roots in vegetative plants, and how this is influenced by the growth environment, plant size, evolutionary history and competition. Dose–response curves of allocation were constructed by means of a meta-analysis from a wide array of experimental data. They show that the fraction of whole-plant mass represented by leaves (LMF) increases most strongly with nutrients and decreases most strongly with light. Correction for size-induced allocation patterns diminishes the LMF-response to light, but makes the effect of temperature on LMF more apparent. There is a clear phylogenetic effect on allocation, as eudicots invest relatively more than monocots in leaves, as do gymnosperms compared with woody angiosperms. Plants grown at high densities show a clear increase in the stem fraction. However, in most comparisons across species groups or environmental factors, the variation in LMF is smaller than the variation in one of the other components of the growth analysis equation: the leaf area : leaf mass ratio (SLA). In competitive situations, the stem mass fraction increases to a smaller extent than the specific stem length (stem length : stem mass). Thus, we conclude that plants generally are less able to adjust allocation than to alter organ morphology.

I. Allocation in perspective

Aquatic environments permit a wide range of unicellular and multicellular plants to coexist and thrive without extensive morphological specialization (Niklas, 2000). By contrast, the physical separation of resources in terrestrial environments has forced a much stronger division of functions within most vascular land plants. The archetypal vascular plant has leaves that fix carbon (C), stems that provide mechanical support and a hydraulic pathway, and roots that absorb nutrients and water, and provide anchorage. The relative amount of biomass present in the various organs, which we term 'biomass allocation' for convenience (see Section III for a discussion on this issue), is not fixed but may vary over time, across environments and among species. A quantitative understanding of such patterns is of fundamental importance to plant ecology and evolution, and has many uses in agricultural practice and implementation, as these patterns, and the extent to which they vary among species, set limits on biomass production and utilization (Niklas, 1994; Reich, 2002).

Our knowledge of the physiological basis underlying the variation in biomass allocation is poor, but should start with an understanding of the regulation of sugar transport from the leaves to metabolic sinks (Farrar & Jones, 2000). Unfortunately, the instantaneous transport rate and partitioning of sugars can only be measured with isotopically labelled C and magnetic resonance imaging-positron emission tomography (MRI-PET) (Minchin & Thorpe, 2003; Jahnke *et al.*, 2010), both of which are not readily available to most researchers. In addition, it is also necessary to know how much C is allocated to the synthesis of C-rich and C-poor compounds (Poorter & Villar, 1997), and how much is lost from the various organs, either in the form of respiration (Lambers *et al.*, 2002) and retranslocation (Brüggemann *et al.*, 2011), or – in an ecological framework – how much is lost in the form of volatiles, root exudates, through mycorrhizal

associations, consumption by animals and as dissociated dead parts (Reich, 2002). None of these fluxes is easily measured, especially in a whole-plant context. Nevertheless, the end result of all of these processes can be easily assessed in terms of the biomass present in each of the three organs. The actual distribution pattern among these organs is the main focus of this review.

There are basically two schools of thought when it comes to the description and analysis of allocation to the different plant organs. In the first, biomass allocation at any given time is considered to be a strong driver of the capacity of plants to take up C, water and nutrients for future use (Evans, 1972). As such, it plays an important role in the growth of plants. Under the assumption that photosynthesis takes place only in the leaves, the C economy of the whole plant can be modelled as the net result of whole-plant photosynthesis and respiration per unit leaf area (which is roughly the unit leaf rate, ULR), the ratio of leaf area to leaf mass (specific leaf area, SLA) and the fraction of total plant biomass allocated to leaves (leaf mass fraction, LMF; see Table 1 for definitions). The relative growth rate (RGR) of the plants is then given by the product of these three traits (Evans, 1972):

$$RGR = ULR \times SLA \times LMF \qquad \text{Eqn 1}$$

In a rather similar way, growth can be analysed from a nutrient perspective (Garnier, 1991). RGR is then given by the product of the net uptake rate of nitrogen (N) per unit root mass (NIR, nitrogen intake rate), the concentration of N in the plant (PNC) and the fraction of biomass invested in roots (RMF, root mass fraction):

$$RGR = NIR \times 1/PNC \times RMF \qquad \text{Eqn 2}$$

Table 1 Abbreviations used in this article, together with a definition and the units applied here (note that mass fractions also appear in the literature as weight ratios (e.g. LWR), mass ratios (LMR) or weight fractions (LWF))

Abbreviation	Variable	Definition	Units
DPI	Daily photosynthetic photon irradiance	Flux of quanta in the 400–700-nm range/area/time	mol m^{-2} d^{-1}
LAR	Leaf area ratio	Leaf area/total plant dry mass	m^2 kg^{-1}
LMF	Leaf mass fraction	Leaf dry mass/total plant dry mass	g g^{-1}
NIR	Nitrogen intake rate	Nitrogen uptake/root dry mass/day	mmol N g^{-1} d^{-1}
PNC	Plant nitrogen concentration	Nitrogen/plant dry mass	mmol N g^{-1}
PI	Plasticity index	(highest value of a trait along the range of an environmental factor considered/lowest value) (* – 1 if the slope is negative)	Dimensionless
RGR	Relative growth rate	Increase in plant mass/unit plant mass/time	mg g^{-1} d^{-1}
R/FR ratio	Red to far-red ratio	Flux of quanta in the 660–670-nm range/flux of quanta in the 725–735-nm range	mol mol^{-1}
RMF	Root mass fraction	Root dry mass/total plant dry mass	g g^{-1}
SLA	Specific leaf area	Leaf area/leaf dry mass	m^2 kg^{-1}
SMF	Stem mass fraction	Stem dry mass/total plant dry mass	g g^{-1}
S/R ratio	Shoot to root ratio	(leaf + stem dry mass)/root dry mass	g g^{-1}
SSL	Specific stem length	Stem length/stem dry mass	m g^{-1}
TDM	Total dry mass	Dry mass of leaves, stems plus roots	g
ULR	Unit leaf rate	Increase in total plant dry mass/leaf area/time	g m^{-2} d^{-1}

In the end, the plant has to balance the allocation to leaves, stems and roots in a way that matches the physiological activities and functions performed by these organs.

The second perspective is that of the allometric approach (Huxley, 1932; Niklas, 1994). Rather than considering ratios at specific times, it describes the overall relationship between the total amount of one organ (say, shoot mass) and another (say, root mass). These relationships are often described as:

$$\log M_Y = \log \beta + \alpha \cdot \log M_X \qquad \text{Eqn 3}$$

where M_Y and M_X represent the masses of organs Y and X, respectively. The parameter α reflects the RGR ratio between organs X and Y (Ledig & Perry, 1966), which equals 1.0 when plant growth is in the steady state (Ingestad & Ågren, 1991), but can deviate from unity because of environmental perturbation or ontogenetic development, or as a consequence of interspecific variation when the data come from multiple species.

Allometric plots based on Eqn 3 are very instructive in understanding the observed relationships between organs, and powerful in summarizing plant development over time. Mass fractions have the advantage that they can be directly related to the actual RGR and physiology (see Eqn 1). The best insight is gained by analysing data in both ways.

II. Topics of this review

In this review, we focus on the allocation of biomass in plants during the vegetative phase. The investment in reproductive structures is outside the scope of this review (see Niklas & Enquist, 2003; Reekie & Bazzaz, 2005; Weiner *et al.*, 2009). We first consider some methodological issues and explain why we use LMF, SMF (stem mass fraction) and RMF as the state variables to describe plant allocation (Section III). We then ask the following questions:
- How is allocation – in a quantitative sense – affected by a plant's abiotic environment? To this end, we construct dose–response curves of allocation for 12 environmental factors, based on experiments with plants that were grown individually and conducted under controlled conditions. Moreover, taking the perspective of Eqn 1, how plastic is LMF in comparison with SLA (Section IV)?
- Allocation may also depend on plant size and ontogeny. How large are the size-related changes and to what extent can they explain the environmentally induced allocation differences considered above (Section V)?
- Are there systematic differences in allocation between 'functional groups' of plant species (Section VI)?
- What is our knowledge about the physiological and molecular regulation of biomass allocation (Section VII)?
- How is allocation affected when plants are grown in competition? And what are the differences in allocation patterns across different biomes (Section VIII)?

III. Methodology

1. Growth and measurements of biomass

Although the concept of allocation is straightforward, the actual determination may not be. Experiments in pots with single plants allow for relatively easy retrieval of most roots, but cleaning the roots is a challenge, and just a few grains of sand attached to roots during weighing can lead to erroneous estimates. Ashing and weighing of the remaining organic fraction can overcome this (Oliveira *et al.*, 2000), but require additional time investment. Another frequently overlooked problem is that larger and faster growing plants generally have larger demands for nutrients and water. In the case of light treatment, for example, for plants grown in small pots, the supply of nutrients and water may not be able to keep up with a plant's demand, especially for faster growing high-light-treated plants. These may then easily encounter a strong nutrient or water limitation (Walters & Reich, 1989), with concomitant changes in LMF and RMF as secondary consequences (see Section IV). Unfortunately, there is no objective way a posteriori to separate these treatment effects from pot size effects, although strongly pot-bound roots are a good sign of potential problems. Small pots limit both shoot and root growth but, interestingly, the shoot is inhibited more strongly and RMF generally increases (Thomas & Strain, 1991; Loh *et al.*, 2003; Climent *et al.*, 2011).

In the field, retrieval of all roots is even more of a challenge (Robinson, 2004). Typically, the root biomass of individual plants is estimated by taking a soil core of a relatively small area around a plant to a particular and often limited depth (often 1 or 2 m). This is especially tricky in cases in which root systems extend over long distances (> 30 m), either horizontally or vertically (e.g. Jackson *et al.*, 2007). Fine roots below a specific root diameter (<< 1 mm) are often undersampled during sieving because of time constraints. In addition, the separation of live from dead roots is likely to be more challenging than is commonly assumed (Comas *et al.*, 2000). Therefore, reliable estimates of root biomass are difficult to obtain, seriously hampering an objective analysis of allocation patterns in the field. The separation of roots between individuals, or even species, is also challenging. Several methods have been used in controlled experiments to separate roots, based on, for example, ^{13}C discrimination (competition of C_3 and C_4 species; Wong & Osmond, 1991), colour infiltration (Holzapfel & Alpert, 2003), presence of a fluorescent protein (Faget *et al.*, 2009) or the relative proportion of chemical or DNA markers in roots (Roumet *et al.*, 2006; Mommer *et al.*, 2008). However, none of these techniques is particularly fast and easy. The last two seem to be promising for field application, provided that markers are available for all species present in the plots.

2. Expressions used

Various expressions have been used to capture the biomass allocation in whole plants. Among these, the shoot : root ratio and its inverse, the root : shoot ratio, are the most frequently employed

(e.g. Brouwer, 1962; Wilson, 1988; Kruse *et al.*, 2010). These expressions have the advantage that they condense the biomass allocation of the whole plant into one parameter, whose numerator and denominator are statistically independent of one other. The main disadvantage of both parameters is that they bulk all above-ground biomass into one compartment, despite the fact that leaves and stems have very different functionalities (Körner, 1994; Pearcy *et al.*, 2005). A somewhat different approach is taken by the Japanese school, where the ratio between the biomass of nonphotosynthetic and photosynthetic organs is considered ('C/F'; Monsi & Saeki, 2005). Other investigators have used the leaf : root, root : leaf or leaf : fine root ratio as an alternative (Kirschbaum *et al.*, 1992; Shipley & Meziane, 2002; Osone & Tateno, 2005), thereby more clearly acknowledging that leaves and roots, when compared with stems, are generally the resource-acquiring organs. These expressions, however, ignore the variation in the contribution of stems which, for many species, can be significant. In the end, it is impossible to encapsulate all information about the three fractions into one ratio. Moreover, all of these ratios have the mathematical characteristic that numbers vary strongly when above 1.0, but seemingly very little when below 1.0, which makes their use less straightforward for generalizations.

Indeed, we will show that more insights are gained by analysing the biomass allocation fractions of leaves (LMF), stems (SMF) and roots (RMF) individually. Mathematically, this has been criticized, as the biomass of the organ of interest is present in both the numerator and denominator (Müller *et al.*, 2000). Moreover, similar to the quotients mentioned above, fractions can change because either the numerator or the denominator differs, or both. However, the concept is biologically clear and well grounded in the plant growth theory discussed above (Eqns 1, 2). Moreover, this approach retains a maximum of information, as all other ratios can be calculated from these three variables. In several cases, as in larger woody species, it could be useful to separate the plant body into even more categories (Körner, 1994). The concept of fractions provides an easy understandable basis for this.

Some authors have tried to distinguish semantically between the actual momentary allocation of photosynthates and the final distribution of biomass (Section I) by using terms such as 'partitioning', 'allocation' and 'distribution' (Reich, 2002); however, these distinctions have not been widely adopted in the scientific community. Throughout this article, we use 'assimilate partitioning' for the actual process and 'biomass allocation' or 'allocation' in reference to the resulting biomass fractions.

IV. Environmental effects

Plants that have part of their leaves or roots removed show remarkable resilience, in that they restore their allocation pattern quickly to control levels (Brouwer, 1963; Poorter & Nagel, 2000). On the other hand, plants grown at low light show increased allocation to the shoot relative to control plants, whereas plants with a low nutrient supply show increased allocation to roots (Brouwer, 1963). The combination of these observations has led to the concept of a 'functional equilibrium' of

biomass allocation (Brouwer, 1963; Thornley, 1972; Iwasa & Roughgarden, 1984). That is, plants will allocate relatively more biomass to roots if the limiting factor for growth is below ground (e.g. nutrients, water), whereas they will allocate relatively more biomass to shoots if the limiting factor is above ground (e.g. light, CO_2). The 'functional' aspect of this response is that it probably increases plant growth by enhancing the uptake of the most limiting factor. Plants allocate their biomass in an optimal pattern if all above- and below-ground resources that a plant requires are limiting growth to an equal extent (Bloom *et al.*, 1985). This concept is also referred to in the literature as the 'balanced growth hypothesis' (Shipley & Meziane, 2002) or the 'optimal partitioning theory' (Gedroc *et al.*, 1996). From a theoretical perspective, 'optimal partitioning' is a well-defined special case of 'functional partitioning', but, as optimality is more difficult to prove than functionality, we use 'functional equilibrium' throughout this review.

Numerous authors have provided wide-ranging reviews of biomass allocation patterns among plants (see, for example, Ledig & Perry, 1966; Wilson, 1988; Cannell & Dewar, 1994; Poorter & Nagel, 2000; Reich, 2002). Most of these reviews made qualitative assessments of observed responses. Some quantitative evaluations in the form of meta-analyses have been carried out, generally focusing on the effect of one environmental factor (nutrients, Reynolds & D'Antonio, 1996; light, Poorter & Van der Werf, 1998; Veneklaas & Poorter, 1998; CO_2, Poorter & Navas, 2003; Wang & Taub, 2010; ozone, Grantz *et al.*, 2006). In an effort to evaluate the functionality of allocation changes, Poorter & Nagel (2000) carried out a meta-analysis, relating the change in biomass allocation between 'high' and 'low' levels of four environmental factors to the change in growth rates. They concluded that the responses in allocation are generally modest, or even absent, providing only little support for the importance of allocation in the adjustment of plants to their environment. Although this conclusion has been corroborated by others (Reich, 2002), the actual approach has been criticized, because of a failure to scale for the level of the environmental factors across experiments (De Groot *et al.*, 2001). This criticism also applies to most of the other mentioned meta-analyses, as generally only a distinction between 'high' and 'low' levels of an abiotic factor was made within each of the analysed experiments.

The issue could be solved by establishing dose–response curves rather than effect sizes. Dose–response curves capture the relationship between a biological trait and an environmental factor in a continuous manner, thereby providing an excellent way to quantify the strength, sign and form of the effect of a given factor on the trait of interest over the full relevant range of that factor. The approach has been pioneered by, for example, Mitscherlich (1909). Recently, methodology has become available to derive dose–response curves from a range of different experiments (Poorter *et al.*, 2010). We use this approach here to establish, for the first time, general dose–response curves of biomass allocation for 12 of the most important abiotic factors in a plant's life. The analysis is based on an initiative to set up a comprehensive database of ecophysiologically relevant traits measured on plants that have been experimentally challenged with different levels of an

abiotic stress factor (http://www.metaphenomics.org). So far, we have compiled the results of *c.* 800 experiments on *c.* 850 different species, studied in growth chambers, glasshouses, open-top chambers or experimental gardens. The method not only estimates a general dose–response curve for the 'average' plant, but also allows us to analyse whether ecologically or phylogenetically diverging groups of species within the database show different dose–response curves. A summary of the procedures followed is given in Appendix A1.

The most simple and straightforward experiment to test the effect of a given environmental factor on the growth and performance of plants is to apply two or more different levels of this factor to different subgroups of a given species and harvest plants of each subgroup after a given period of time. Detailed measurements can then help to understand how traits, such as photosynthesis, respiration, SLA and allocation, are affected by the treatment, and how these changes subsequently affect the plant's growth. The remaining part of this section therefore deals with a meta-analysis of allocation data for plants subjected to different treatments and compared at similar ages.

1. Light and atmospheric composition

Plants grown at low irradiance fix only relatively small amounts of C in photosynthesis. They also require less nutrients than high-light plants, because of slower growth, and use less water, because of decreased stomatal conductance. According to the functional equilibrium hypothesis, they therefore should show higher allocation to stems and, especially, leaves at the expense of roots. Averaged over all species and experiments, this is actually what was found, with changes being most evident over the 1–5 mol quanta m^{-2} d^{-1} range (Fig. 1a), and becoming saturated above 20 mol m^{-2} d^{-1}. The dose–response curve does not differ between sun- and shade-tolerant species, or between woody and herbaceous species ($P > 0.05$). Under field conditions, lower light availability is often associated with a decrease in the red to far-red (R/FR) ratio. However, averaged over the experiments in which the R/FR ratio is decreased independently from the amount of photosynthetic irradiance, there is a significant *increase* in the proportion of stems and a slightly decreased LMF (Fig. 1b). These responses, however, are generally small (< 0.05 g g^{-1}). A similar conclusion holds for the effect of various UV-B radiation loads, with negligible differences in response among functional groups (Fig. 1c).

Most plants respond to elevated CO_2 by an increase in photosynthesis – at least in the short term – which presumably should lessen the above-ground limitation for growth. Decreased limitation below ground could be expected for water, because of lower stomatal conductance, but, as a result of accelerated growth, there will be an increased demand for nutrients. Overall, we might possibly expect an increased allocation to roots, but less so than for light. The data show little support for a functional equilibrium here, as allocation is remarkably unaffected, with only minor allocation shifts in the expected direction at very low CO_2 concentrations (Fig. 1d). A similar conclusion was reached by Bernacchi *et al.* (2000). LMF increases with increasing ozone

concentration, as reported by Grantz *et al.* (2006), but again the change is small, with no obvious differences among groups of species (Fig. 1e).

2. Nutrients and water

Nutrients and drought are the most complicated factors for the construction of dose–response curves, because there is no simple objective way to characterize the severity of the treatment. Therefore, we have used the reduction in plant biomass relative to the nutrient and water levels that yield the largest plants within each experiment as the indicator of stress severity. The variability of responses across experiments is relatively large (Supporting Information Fig. S1). Nonetheless, the changes in allocation when nutrients are limiting are the strongest of all allocation responses, with a large increase in roots at the expense of stem and, especially, of leaf biomass (Fig. 1f). This clearly supports the idea of functional biomass allocation. There was no statistically detectable difference in the dose–response curve between species from nutrient-poor and nutrient-rich habitats, in accordance with conclusions from Reynolds & D'Antonio (1996).

The response to drought is remarkable, because plants subjected to moderate water stress are often very nearly the same size as control plants (data not shown; Padilla *et al.*, 2009), with only a small increase in RMF (Fig. 1g). Only when plants are subjected to severe drought – that is when biomass is reduced by > 50% of that of control plants – is a strong increase in RMF found, at the expense of stems. Possibly, plants do not respond very strongly to relatively short time periods of drought, as water availability often depends on rain events that are unpredictable by nature. Changing allocation too quickly might then result in a suboptimal growth after restoration of the water supply. Interestingly, LMF hardly changes over the entire trajectory of the drought dose–response curve. Waterlogged plants show a decrease in RMF (Fig. 1h), which may partly be a reflection of dying root tissue. The reduced RMF could contribute to the reduced stomatal conductance observed during waterlogging experiments in intolerant species (Parent *et al.*, 2008). There was a difference here between woody species, which increased LMF on waterlogging, and herbaceous species, which did not ($P < 0.05$). Full submergence of land plants is a special case, as they will not gain in biomass after the onset of this treatment. A number of specialist species can survive if they are able to restore contact with the air. To this end, they strongly elongate (Bailey-Serres & Voesenek, 2008), partly by re-allocating biomass (especially starch) to stems and petioles (Fig. 1i). The change in RMF, however, is not stronger in species generally found in submergence-prone habitats.

3. Temperature, salinity and mechanical perturbation

Low temperatures decrease the fraction of stems and leaves and increase RMF (Fig. 1j). A range of plant functions are impaired by low temperature (photosynthesis, nutrient uptake, growth), but reduced rates of water uptake are a probable cause of increased allocation to roots (Lambers *et al.*, 2008). The changes are more modest above 18°C. Salinity negatively affects both
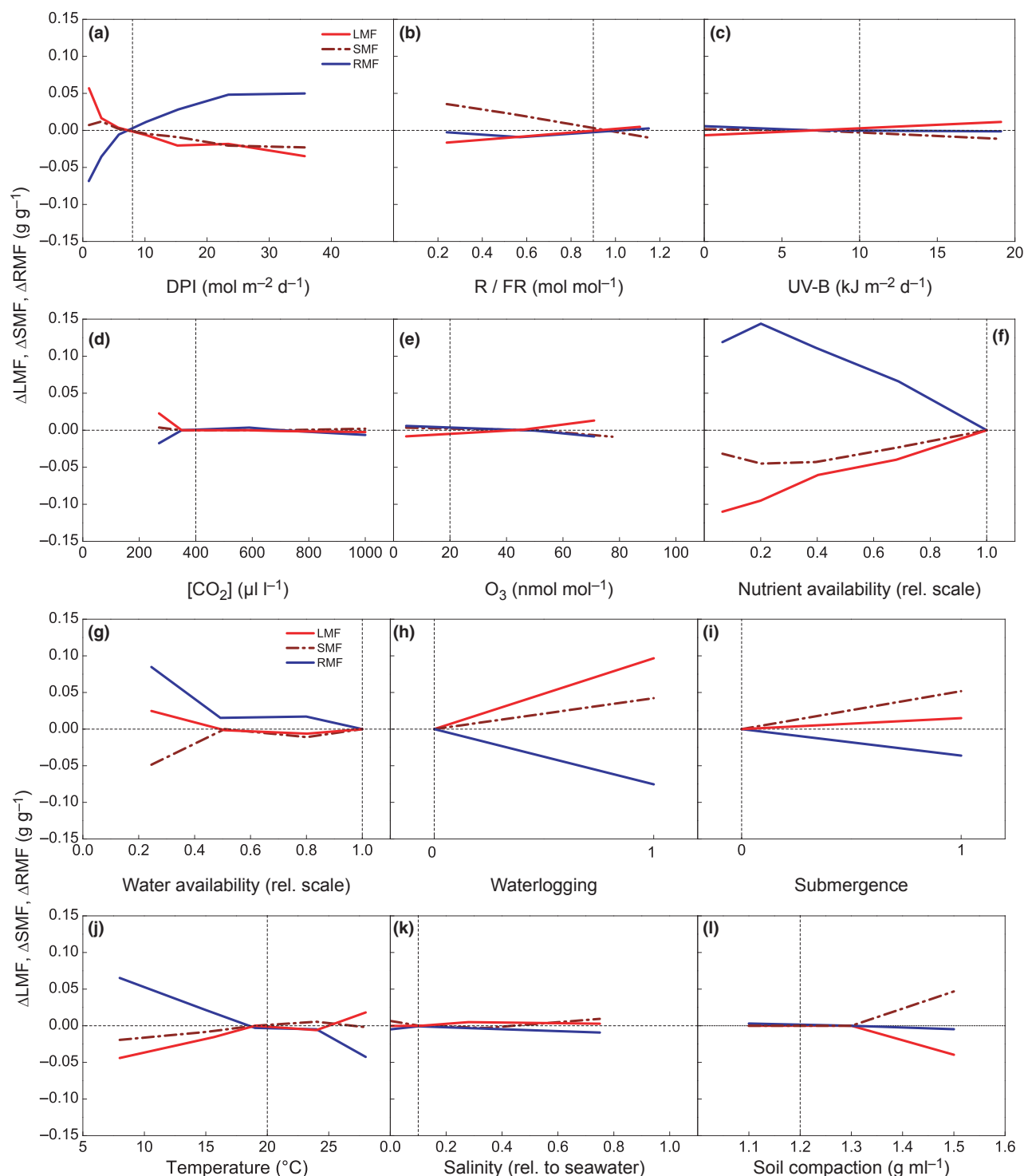
Fig. 1 Dose–response curves of the absolute response of the fraction of whole plant mass represented by leaves (LMF; red line), stems (SMF; brown line) and roots (RMF; blue line) to 12 environmental factors: (a) daily photon irradiance (DPI); (b) red : far-red (R/FR) ratio; (c) UV-B; (d) CO_2 concentration; (e) ozone; (f) nutrient availability; (g) water availability (drought stress); (h) waterlogging; (i) submergence; (j) temperature; (k) salinity; (l) soil compaction. Data are a compilation of the literature. For each environmental factor, a reference condition was chosen (indicated by a vertical line; values listed in Table 2), and data for each species in each experiment were subtracted from the allocation values observed or interpolated for that reference level. For more information on the methodology followed, see Appendix A1 and Poorter *et al.* (2010). References are listed in Table S1. Additional data were obtained from Chapin *et al.* (1989), Barrett & Ash (1992), Wong *et al.* (1992), Searles *et al.* (1995), Canham *et al.* (1996), Veenendaal *et al.* (1996), Ryser *et al.* (1997), Anderson & Tomlinson (1998), Funnell *et al.* (1998), Tjoelker *et al.* (1998), Glimskär & Ericsson (1999), De Pinheiro Henriques & Marcelis (2000), Dias-Filho & De Carvalho (2000), Franzaring *et al.* (2000), Schulte auf'm Erley *et al.* (2001), Taub (2002), Veneklaas *et al.* (2002), Krauss & Allen (2003), Poot & Lambers (2003), Reich *et al.* (2003), Jansen *et al.* (2005), Bloomberg *et al.* (2008), Debez *et al.* (2008), Luo *et al.* (2009) and K. Nagel (pers. comm.).

photosynthesis and transpiration, and minimally affects alloca-
tion (Fig. 1k). Soil compaction has a strong effect on allocation,
but only at severe levels, in which case RMF increases strongly
(Fig. 1l). Other abiotic factors have also been reported to affect
biomass allocation. For example, RMF generally increases and
SMF decreases with wind exposure, stem flexure and other
mechanical effects on shoots (Niklas, 1998; Puijalon & Bornette,
2006; Coutand *et al.*, 2008).

4. Plasticity in LMF and SLA

In the above section, we discussed the form (linear/nonlinear)
and sign (positive/negative) of the dose–response curves. Now,
we wish to quantify and compare the extent to which various
environmental factors affect allocation. To confine this analysis
to the ecologically relevant parts of the dose–response curves, we
previously defined for 10 of the 12 abiotic factors considered here
in what range plants in nature are normally found to show active
growth (Poorter *et al.*, 2010; Table 2). For these 10 defined
ranges, plus waterlogging and submergence, we fitted the LMF
values to either a linear or nonlinear regression curve, whichever
was most appropriate (for estimates of parameters, see Table 2).
To make these values comparable with previous analyses, we
scaled all individual data relative to the reference value, rather
than considering absolute differences (Fig. S1). We subsequently
determined the 'plasticity index' as the ratio of the highest and
lowest LMF value of the fitted equation within the defined range.
When the slope of the fitted line was negative, we gave this ratio
a negative sign. The plasticity indices of LMF for the 12 environ-
mental factors are shown in Table 3. The largest changes
observed are for irradiance, nutrients and soil compaction, com-
mensurate with the results in the previous paragraphs. Yet, even
these changes are modest and amount to *c.* 30% for light and
nutrients. Changes in LMF with temperature and CO_2 are much
smaller. Thus, although we agree with the criticism of De Groot

et al. (2001) regarding meta-analyses that ignore the severity of
the stress factor, the order in the strength of the responses among
the various environmental factors considered here is basically the
same as in Poorter & Nagel (2000).

Another interesting point is how plasticity in LMF relates to
plasticity in the other components of the RGR equation (Eqn 1).
Here, we compare the fitted curves for LMF with those for SLA
(cf. Poorter *et al.*, 2010), and analyse for each abiotic factor
which component varies most strongly. This is important to
know as the product of the two traits, LAR (leaf area ratio, leaf
area : total dry mass), determines how much leaf area is present
for one unit of plant mass, and, as such, co-determines with the
rate of photosynthesis and respiration what will be the RGR of
the plant. The results show that, for six environmental factors,
plasticity in SLA is clearly larger than in LMF (Table 3). For
example, in the case of light, shaded plants increase LAR far more
by adjusting leaf morphology (increasing SLA by 200% over the
full light range) than by allocation (increasing LMF by 30%).
Only in the case of nutrient limitation is the change in biomass
allocation stronger than the change in SLA.

V. Ontogeny

1. The principle of size correction

The analyses in Section IV focused on the allocation patterns that
plants realize after growing for a certain period of time in a given
environment. This is, by itself, valuable and objective information
(Coleman *et al.*, 1994), relevant in a range of agricultural and eco-
logical settings. However, it is clear that plant ontogeny may also
have a strong effect on allocation patterns (Evans, 1972; Poorter
& Pothmann, 1992; Coleman *et al.*, 1994). These changes could
be related to shifts in the developmental stage of the plants under
study (e.g. from vegetative to generative in annual herbs), but will
also depend on plant size (e.g. developing trees; Niklas & Enquist,

Table 2 The 12 environmental factors studied in this article, the range considered for each environmental factor to be ecologically relevant for physio-
logically active (nondormant) plants, the reference value used to normalize data within each experiment and the coefficients for the response curves of
scaled leaf mass fraction (LMF) values as affected by the various environmental factors

Environmental factor	Range considered	Reference level	Units	*a*	*b*	*c*	df	r^2
Irradiance	1–50	8	mol m^{-2} d^{-1}	1.007	−0.818	0.099	850	0.21
R/FR ratio	0.2–1.2	0.9	mol mol^{-1}	−0.138	0.157	–	80	0.35
UV-B	1–20	7	kJ m^{-2} d^{-1}	–	–	–	20	–
CO_2	200–1200	400	µmol mol^{-1}	–	–	–	670	–
O_3	5–100	35	nmol mol^{-1}	−0.037	0.001	–	120	0.19
Nutrients	0.02–1	1	rel. units	−0.343	0.339	1.587	820	0.26
Water	0.05–1	1	rel. units	–	–	–	300	–
Waterlogging	Absent/present	Absent	–	0.014	0.169	–	90	0.12
Submergence	Absent/present	Absent	–	–	–	–	60	–
Temperature	5–35	20	°C	−0.146	0.007	–	270	0.08
Salinity	0–1	0.1	Fraction of seawater	–	–	–	130	–
Compaction	1.0–1.6	1.2	g ml^{-1}	0.541	−0.480	–	40	0.17

R/FR ratio, red to far-red ratio.
For each factor, we test whether there is a linear relationship ($y = a + bx$), a nonlinear relationship ($y = a + bx^c$; fitted if the quadratic component of a sec-
ond-degree polynomial is significant) or no relationship at all, with *x* being the value of the environmental factor. To allow for the logarithmic nature of
ratios, all scaled LMF values were $\log_2$-transformed prior to the regression analysis. For each relationship, the degree of freedom (df) and the r^2 value are
indicated.

Table 3 The plasticity index (PI) of the leaf mass fraction (LMF), specific leaf area (SLA) and total dry matter (TDM), calculated over the range given in Table 2

Environmental factor	PI LMF	PI SLA	PI TDM	PI LMF herbs size-corrected	PI LMF trees size-corrected
Irradiance	**−1.31**	**−3.03**	**12.4**	−1.14	−1.09
R : FR ratio	1.12	1.00	1.2	1.12	1.12
UV-B	1.00	1.00	1.0	1.00	1.00
CO_2	1.00	−1.41	2.3	1.04	1.05
O_3	1.07	1.00	−1.4	1.06	1.05
Nutrients	**1.26**	1.10	**49.1**	**1.43**	**1.49**
Water	1.00	1.27	19.9	1.13	1.18
Waterlogging	1.12	−1.12	−1.7	1.10	1.09
Submergence	1.00	**1.58**	−3.2	−1.07	−1.08
Temperature	1.14	**2.10**	**19.5**	**1.28**	**1.32**
Salinity	1.00	−1.16	−2.6	−1.05	−1.07
Compaction	−1.22	−1.18	−1.02	**−1.22**	**−1.22**

R/FR ratio, red to far-red ratio.
PI is defined as the highest phenotypic value in the response curve divided by the lowest value. Thus, a PI value of unity indicates no change. To indicate the direction of the response, PIs were given a minus sign if an increase in the environmental factor is associated with a decreased value in the trait of interest. The last two columns show the plasticity of LMF after correcting for the environmentally induced changes in plant size (see Appendix A3). For each PI, the three largest changes are indicated in bold.

2002), with increasingly larger investments in support tissues expected for larger plants. Hence, if we want to know whether plants *actively* alter their assimilate partitioning to adjust to a given environment, it has to be shown whether the allocation differences persist if plants are compared at a common size (Coleman *et al.*, 1994; Reich, 2002). The case of light serves as an example: low-light-grown plants have a higher LMF than high-light-grown plants, but are also smaller when compared after a similar growth period. If LMF decreases during development simply because of size constraints, the observed differences in LMF may disappear when plants are compared at a common size. Thus, if we want to evaluate whether the differences in allocation pattern between plants that experience different environments are a result of active reprogramming of assimilate partitioning, correction for size is the best available option.

2. Ontogenetic trends in allocation

What actually is the extent to which ontogenetic trends in allocation occur? The general pattern according to Ledig & Perry (1966) is that the shoot : root ratio increases with size for herbaceous plants (see also Wilson, 1988), but decreases for woody species. These generalizations were made on the basis of qualitative impressions and do not distinguish between leaf and stem fractions. Moreover, we are interested in the magnitude of these changes, whether they occur over the full-size trajectory of plants and whether they differ between herbaceous monocots and eudicots, and between woody angiosperms and gymnosperms.

To quantify the general changes in allocation, we carried out an allometric analysis similar to that of Niklas & Enquist (2004a). We used their dataset (*c.* 600 average values) and extended it with data gathered from the primary literature pertaining to a range of controlled experiments as well as tree stands from forest communities (Table S2). Collectively, the extended dataset consists of *c.* 5300 records (generally average values per treatment) covering a broad range of herbaceous and woody species. We carried out an

allometric analysis on the overall relationship between leaves and roots, and between stem and roots (Fig. S2), and did so separately for herbaceous monocots, herbaceous eudicots, woody angiosperms and gymnosperms. In most cases, the log–log relationships were not linear, but were best fitted by quadratic polynomials, for which the coefficients are given in Table 4. For comparative purposes, log–log linear estimates are also provided. These data show that leaves generally have lower growth rates than roots ($\alpha_{RMA} < 1$; Niklas & Enquist, 2002), which may imply that older, larger root systems have a nutrient uptake rate that increasingly lags behind the C fixation of the leaves (Shipley & Meziane, 2002). Stems, on the other hand, show higher growth rates than roots. However, the α_{RMA} values do not show us the actual allocation patterns of the plants. To this end, we used the quadratic formulae when appropriate and calculated the leaf, stem and root fractions over the full range of total plant mass for which observations are available. Considered over this range, which spans from 3 mg to 100 g, vegetative herbaceous plants show a decrease in LMF and an increase in both SMF and RMF (Fig. 2a–c). Compared with the environmentally induced shifts in allocation (Section IV), these changes are large, with LMF decreasing from an average of 0.54 to 0.35. Remarkably, when considered over the same size range, the allocation values for woody species largely overlap with those of herbs (0.60–0.28). However, the LMF decreases more strongly and the SMF increases more rapidly for the tree seedlings, which is probably caused by stronger stem development. At sizes over 100 g (shaded area in Fig. 2), for which we only have tree data, the proportion of stem increases even further, reaching over 82% of total biomass at a size of 1000 kg. At this mass, the proportion of leaves drops to 2% (Fig. 2d), and that of roots to *c.* 16% (Fig. 2e). Most of the shift in allocation is between the leaf and stem fraction, with RMF decreasing moderately after a plant size of 1 kg.

These results are dissimilar to those mentioned by Ledig & Perry (1966) for trees. However, our allometric analysis is based on a mixed dataset consisting of numerous species from very

Table 4 Allometric scaling coefficients for different groups of plant species.

Species	Regression	a	b_1	b_2	r^2
Herbaceous monocots	Leaf vs root	0.031**	0.951***	–	0.94
	Stem vs root	−0.107***	1.098***	0.0216*	0.93
Herbaceous eudicots	Leaf vs root	0.259***	0.916***	–	0.93
	Stem vs root	−0.111***	1.029***	–	0.87
Woody gymnosperms	Leaf vs root	0.243***	0.924***	−0.0282***	0.95
	Stem vs root	−0.070***	1.236***	−0.0186***	0.98
Woody angiosperms	Leaf vs root	0.090***	0.889***	−0.0254***	0.97
	Stem vs root	−0.097***	1.071***	0.0179***	0.98

Species	Regression	α_{RMA}	Log β_{RMA}	r^2
Herbaceous monocots	Leaf vs root	0.981	0.048	0.94
	Stem vs root	1.11	−0.070	0.93
Herbaceous eudicots	Leaf vs root	0.953	0.274	0.93
	Stem vs root	1.10	−0.081	0.87
Woody gymnosperms	Leaf vs root	0.814	0.207	0.95
	Stem vs root	1.16	−0.081	0.98
Woody angiosperms	Leaf vs root	0.806	0.047	0.96
	Stem vs root	1.15	−0.092	0.98

Data were calculated from $\log_{10}$-transformed leaf biomass or stem biomass vs $\log_{10}$-transformed root biomass, with masses expressed in grams. Data were derived from a combined database of Niklas & Enquist (2004b) and J. Oleksyn & P. B. Reich (unpublished) on mainly large trees, and the Meta-Phenomics database of Poorter *et al.* (2010) (plants exposed for some time to different environmental treatments), supplemented with data on young herbaceous and woody plants from a range of comparative growth experiments. The total number of observations (generally average values per harvest) for herbaceous monocots was 650, for herbaceous eudicots 850, woody gymnosperms 1500 and woody angiosperms 2200. The top part of the table gives data for a stepwise regression with quadratic polynomials of the form $y = a + b_1x + b_2x^2$, where y is the $\log_{10}$-transformed leaf or stem mass and x is the $\log_{10}$-transformed root mass. The bottom part shows the results of a reduced major axis (linear) regression with slope α_{RMA} and intercept log β_{RMA}. Statistical significance: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

different habitats and grown under very different conditions. Therefore, it is possible that the trends shown in Fig. 2 are unrepresentative of individually grown plants of a given species. To address this possibility, we collected data from a number of experiments, carried out in growth chambers, glasshouses or under more or less controlled field conditions where plants were harvested over time. The trends in these data, which are shown as thin black lines in Fig. 2, are roughly similar to those produced from the allometric dataset. In accordance with Wilson (1988), most herbaceous species show a trend towards a decreased RMF with size. SMF generally increases, whereas LMF seems to be least affected. Trends in young woody species are more variable, but, especially in larger seedlings (1–100 g), SMF invariably increases at the expense of LMF and RMF.

We have insufficient insight into the reasons why species respond so variably, especially for tree seedlings. First, the direction of response may differ because of inherent differences. Another explanation is that some of these species were grown under conditions in which nutrient and/or water supply became relatively more restricted over time, with secondary increases in RMF as a consequence (Section IV).

3. Environmental effects

The dose–response curves described in Section IV are based on data obtained from plants treated differently for an equal period of time. If plants actively adjust their biomass allocation (Nicotra *et al.*, 2010), the observed differences should (still) be present after size correction. Most data included in our database are from experiments in which no size correction was considered. In most of the remaining publications, a statistical test was used to correct for size, but the authors did not provide quantitative estimates of allocation patterns at a common size. Consequently, the number of quantitative size-corrected data is too small for an appropriate meta-analysis. Therefore, we estimated the environmental effects on allocation independent of size in a different way. We also collated data for total biomass and calculated how much this variable is affected by the 12 treatments. Subsequently, we used the allometric relationships shown in Fig. 2 to derive the change in LMF expected because of such a size difference. The plasticity indices for LMF, given in Section IV, were then corrected for the changes that would be expected by the difference in biomass alone. A more detailed description of this approach is given in Appendix A2.

The plasticity indices corrected for size are given in the last two columns of Table 3. As far as we know, these are the first general estimates of the quantitative effect of size correction on biomass fractions. For most treatments, the correction does not alter the conclusions dramatically, with allocation differences because of a differential treatment effect being ≤ 5 percentage points. However, the effect of irradiance is much smaller when size differences are accounted for, which suggests that a substantial part of the observed allocation response is, in fact, a passive consequence of differences in plant size. This is probably more so in tree seedlings (Reich, 2002) than in herbaceous species (Shipley & Meziane, 2002). In contrast with irradiance, size-corrected changes in LMF are much stronger than uncorrected ones (> 15 percentage points) in the case of water, nutrient and temperature stress.
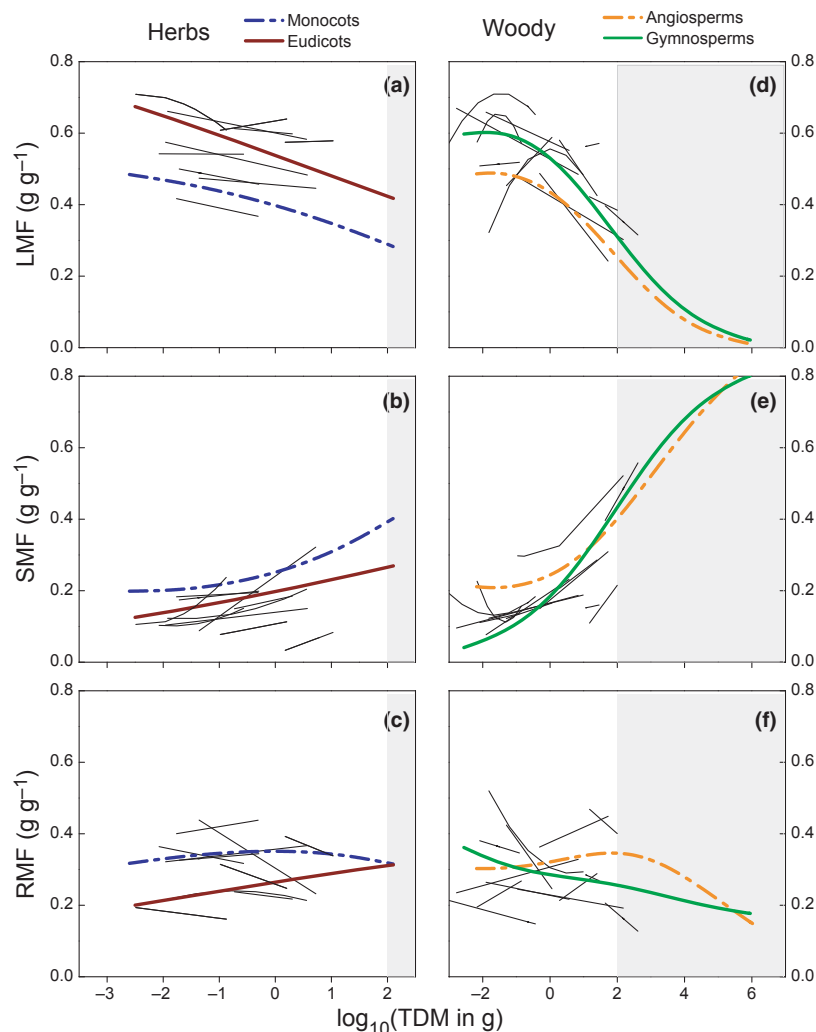
Fig. 2 Allocation in relation to total plant dry mass (TDM). (a–c) The fractional allocation to leaves (LMF), stems (SMF) and roots (RMF), respectively, for herbaceous species. (d–f) The fractional allocation to leaves, stems and roots, respectively, for woody species. The bold lines indicate the main trend derived from an allometric analysis carried out with a dataset that combined growth data for a range of young herbaceous and woody plants used in growth analyses, the Meta-Phenomics database, which deals with somewhat older plants, and the databases of Niklas & Enquist (2004b) and J. Oleksyn & P. B. Reich (unpublished), which mainly consist of data on adult trees growing in the field (see Table S2 for a full list of references). Data for herbaceous plants were analysed separately for monocots and eudicots. Data for woody species separated gymnosperms and angiosperms. Relationships between log-transformed leaf mass or stem mass and $\log_{10}$-transformed root mass was tested for linear and quadratic components and subsequently fitted with the relevant polynomial. From these relationships, total plant mass, as well as LMF, SMF and RMF, were calculated over the full range of data. The shaded area indicates plants > 100 g. For comparison, thin black lines show progressions of allocation for a range of experiments with individually grown vegetative plants. These data are for the herbaceous species *Achillea millefolium*, *Arabidopsis thaliana*, *Cirsium vulgare*, *Deschampsia flexuosa*, *Galinsoga parviflora*, *Geum urbanum*, *Holcus lanatus*, *Hordeum vulgare*, *Hypericum perforatum*, *Lycopersicon esculentum* and *Plantago major*, followed repeatedly over a longer period of time. Data for woody species include *Acacia saligna*, *Acacia tetragonaphylla*, *Alnus glutinosa*, *Betula papyrefera*, *Chamaerops humilis*, *Eucalyptus grandis*, *Olea europea*, *Pinus banksiana*, *Pinus halepensis*, *Quercus suber* and *Washingtonia robusta*. For better visibility of trends, progressions were smoothed. References are listed in Table S3. Additional data were obtained from Pons (1977), Kirschbaum *et al.* (1992), Reich *et al.* (1998), Atkin *et al.* (1999), Antunez *et al.* (2001), Tholen *et al.* (2004) and Nieves *et al.* (2011).

Thus, we conclude that these three factors are clear cases in which plants actively reprogram assimilate partitioning in order to acclimate to a specific environment.

A final issue in relation to ontogeny involves the question of whether a difference in biomass allocation can only be considered to be functionally relevant if it is shown to be independent of plant size. We wonder whether this is necessarily always true. Let us consider the case of tree seedlings growing under low-light conditions. When small, they have a high LMF, which could allow

them to maintain a positive C budget through a relatively large amount of photosynthetic tissue. Plants of larger size may have difficulties in surviving in the same environment (Lusk *et al.*, 2008), partly because of higher self-shading (Lusk *et al.*, 2011), partly because each unit of leaf having to maintain a larger amount of nonphotosynthetic biomass (Givnish, 1988). Small and large plants differ in other aspects, but it should not be excluded a priori that the ontogenetically determined difference in LMF contributes to the better survival of younger, smaller plants.

VI. Differences between species

One way to investigate inherent differences in allocation among physiologically, ecologically and/or phylogenetically contrasting species is to analyse broad allometric relationships between leaf, stem and root biomass for different species groups (e.g. Enquist *et al.*, 1999; Enquist & Niklas, 2002; Niklas, 2004; Section V). This approach, where data typically originate from plants grown under various environmental conditions, focuses on size as the main driver of allocation changes. The analysis proceeds under the assumption that all species of a given group face the same size constraints and that environmental effects are negligible. Another approach is to compare species belonging to different species groups that are grown simultaneously under the same conditions. This minimizes the risk of allocation being confounded with environmentally induced variation. We followed the latter approach and performed a meta-analysis of experiments in which the LMF of species of two groups of interest was measured. The average value for LMF was then calculated per species group within each experiment, and the distribution of the resulting ratios was analysed across a range of experiments. If the geometric mean of this ratio deviates statistically from unity across a wider range of experiments, there is reason to consider this difference for further analysis (see Appendix A3 for a more extensive explanation). A possible drawback could be that many data were not corrected for possible size differences. However, all plants included in the analysis are < 10 g, and thus in a size range in which the shifts in allocation are relatively small (Fig. 2).

1. Woody species

Based on the analyses in Section V, a difference is expected between larger sized plants of herbaceous and woody species, particularly given the substantial investment in stems in the latter. Indeed, most herbs in the vegetative phase of growth have an LMF of *c.* 0.50, whereas the LMF of full-grown trees is < 0.03 (Fig. 2). As noted, however, our allometric analysis showed that these differences are nearly completely absent for seedlings and saplings (Fig. 2). The same conclusion is reached when we consider a range of experiments that included herbs as well as juvenile shrubs and trees. Notwithstanding the variation among experiments, the overall picture is that the LMF of woody seedlings and saplings is remarkably similar to that of herbs (Fig. 3a; Poorter & Nagel, 2000).

Within the group of woody species, there is strong phenological contrast between deciduous and evergreen species. If plants of higher leaf longevity are associated with infertile and/or dry sites (Givnish, 2002), we may expect evergreens to have higher allocation to roots and lower allocation to leaves. However, such a difference is not found between seedlings of the two groups of species when grown under controlled conditions (Fig. 3a). It should be noted that the number of experiments on which this conclusion is based is rather limited. A greater contrast is found when, within each experiment, the average of the 33% fastest growing species and the average of the 33% slowest growing

species are compared. In this case, faster growing species have a somewhat higher LMF (Fig. 3a).

Biomass allocation patterns for adult trees are generally known only from data in forest stands and thus are confounded with a possible density effect (see Section VIII). On average, there is no difference in allocation to roots between conifers and angiosperm trees. Allocation to leaves is significantly higher in conifers ($P < 0.001$), a difference that becomes approximately two-fold at a total plant biomass of 1000 kg (0.021 vs 0.010). These differences are also reflected in the allometric slope and intercept (Table 2) and are fully in line with the observations, for example, of Körner (1994), Enquist & Niklas (2002) and McCarthy *et al.* (2007). It should be pointed out that most conifers retain leaves
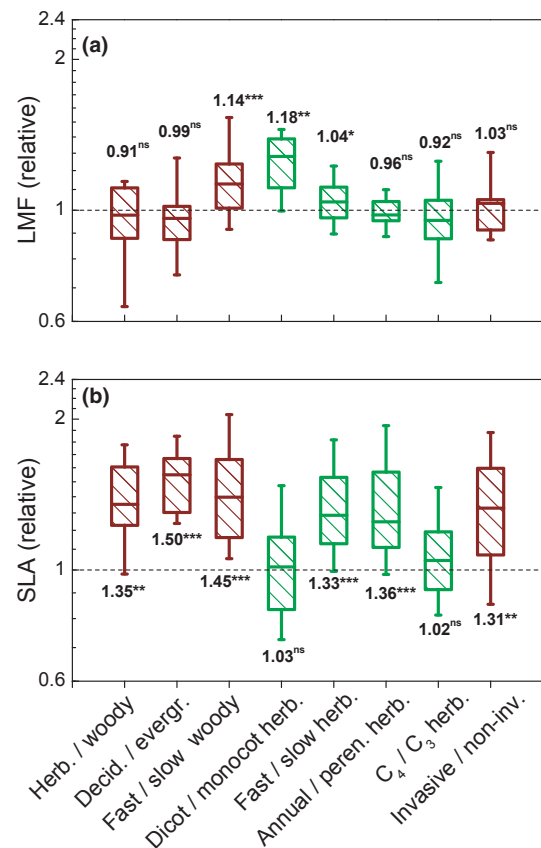
Fig. 3 Interspecific variation in biomass allocation (a) and specific leaf area (b) for plants grown under the same experimental conditions. The box plots give the distribution of ratios, where each ratio represents an experiment with the average value of group *x* (for example, herbaceous species in the first contrast) relative to the average value of group *y* (woody species in the first contrast). The average response ratio (based on the back-transformed mean of the log-transformed ratios) is given above or below each box plot. Contrasts including woody species are shown in brown, contrasts with herbaceous species only in green. The rounded numbers of experiments considered for the fraction of the whole plant mass represented by leaves (LMF) and the leaf area : leaf mass ratio (SLA), respectively, are as follows: herbaceous/woody, 20/20; deciduous woody/evergreen woody, 15/10; fast-growing/slow-growing woody, 30/30; eudicotyledonous/monocotyledonous herbs, 20/20; fast-growing/slow-growing herbs, 70/70; annual/perennial herbs, 15/20; C_4/C_3 herbs, 30/30; invasive/noninvasive species, 10/20. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. References are listed in Table S4.

for two or more years. Thus, the higher LMF may simply be the consequence of leaf longevity rather than higher assimilate partitioning *per se*. In this way, conifers are able to compensate for their lower physiological activity per gram of leaf.

2. Herbaceous species

The majority of comparative experiments published are restricted to either monocotyledonous or eudicotyledonous species. However, for the experiments that comprised both, a higher LMF was found for eudicots (Fig. 3a), paralleling the allometric analysis above (Fig. 2). In fact, this is the largest difference observed among the groups compared. Therefore, we analysed the other contrasts within the herbaceous species separately for both clades. In most cases, comparisons among the different functional groups failed to identify differences, either between annuals or perennials, or between C_3 and C_4 species (Fig. 3a). Fast-growing species hardly differed from slow-growing species. There was, however, a small difference between monocots and eudicots in this respect. For monocots, variation in LMF was not associated with variation in RGR, but there was a small but significant contribution of LMF to variation in RGR for eudicots ($P < 0.01$). These differences were still present in experiments that were corrected for size (Poorter & Remkes, 1990). A comparison that extended over woody and herbaceous species showed that invasive species did not differ from noninvasive plants in LMF.

3. Other comparisons

Darwin (1867) advanced the idea that climbing species are mechanical parasites that do not require large allocation to stems relative to species with self-supporting stems. In a growth analysis of eight climbing and 28 nonclimbing herbs, climbing species were much taller, with a *higher* SMF and a lower LMF relative to their self-supporting counterparts (Den Dubbelden & Verburg, 1996). Young woody lianas – at least the light-demanding ones – had higher SMFs than tree seedlings (Cai *et al.*, 2007), and the same applied to a climbing *Hydrangea* relative to three shrubs from the same genus (Kaneko & Homma, 2006). Thus, it seems that climbing species are specialists that gear for additional height gain not only by increasing specific stem length (length realized per unit stem mass), but also by stronger investment in stems. However, evidence is still fragmentary and larger datasets are required. A final group of interesting species is the Crassulacean acid metabolism (CAM) group. Given that they generally function under very dry conditions, one might expect inherently large investment in roots. However, field-grown studies report RMF values that are average (*c.* 0.3; Martínez-Berdeja & Valverde, 2008) to very low (< 0.15; Winter *et al.*, 1997). We are not aware of systematic species comparisons under controlled conditions.

Following the same approach as here for LMF, Poorter *et al.* (2009) investigated the differences in SLA. An updated summary is shown in Fig. 3(b). In all contrasts considered, with the exception of monocots vs eudicots, and of C_3 vs C_4 species, inherent differences in SLA were much larger than those in LMF. Thus,

similar to the case of environmentally induced plasticity, variation in LAR, the total amount of leaf area per unit plant mass, is mainly determined by variation in leaf morphology.

VII. Physiology and molecular regulation

In both Section IV, where the response to environmental factors was analyzed, and Section VI, where we quantified the inherent variation amongst functional groups, we found that the extent of variation in LMF is often much smaller than the variation in SLA. An intriguing question is why this is so. Partly, this might be a consequence of the mathematical way in which allocation is expressed: fractions always range between zero and unity, so that plants with an LMF of 0.5 can, at most, change LMF by 100%. However, all values found were much lower. Therefore, it is likely that there is a strong biological constraint on shifts in biomass allocation, caused by the intrinsic dependence of photosynthesis on the uptake of nutrients and water in the root, and the dependence of roots and stems on carbohydrates from the leaves. Moreover, plants of a given size will always need a root system to obtain proper anchorage. Thus, even with an unlimited supply of nutrients or photosynthates, plants have to maintain a balance in investment such that all functions and organs are limiting performance (e.g. growth) to the same degree (Bloom *et al.*, 1985). In this context, mathematical models have been used to provide a more integrative perspective on plant growth. The emerging picture from these models does not always comply with our notion of constraints, as optimal growth levels can be achieved over a fairly broad range of allocation patterns (Sugiura & Tateno, 2011). One confounding factor which may complicate such an analysis is that many models presume organ functionality to be proportional to organ mass (Iwasa & Roughgarden, 1984), which is not necessarily true. For example, split-root experiments, wherein nutrients are suddenly withdrawn from half of the root system, show that reduced nutrient uptake by the deprived part can be compensated by a doubled uptake rate in the other half (Jeudy *et al.*, 2010). Analogous phenomenology has been shown for N_2 fixation by nodules and for photosynthesis of the leaves that remain on the plant after other leaves have been removed (Kasai, 2008). Over longer time frames, plants can compensate with morphological changes, such as, for example, increases in SLA and specific root length (Aerts & Chapin, 2000) or changes in root architecture (Fitter & Stickland, 1991). Notwithstanding this array of alternative physiological and morphological adjustments, perturbation experiments with leaf or root removal have shown that plants have a strong resilience, in that, with time, biomass allocation returns to the allometric relationships before disturbance (Brouwer, 1963; Eshel *et al.*, 2001). How do plants achieve such control?

Farrar & Jones (2000) provided an insightful discussion, in which they discriminated between the control of assimilate partitioning residing in the sugar-producing source leaves or in sugar-consuming sinks, such as roots. For the analysis of the source part, it is required to obtain an insight into the total amount of sugars available for sinks and the rate at which they are translocated from the leaves. Techniques have now been developed to

follow the momentary translocation of sugars on fine time scales using isotopically labelled CO_2 and NMR, as discussed in Section I. Interesting questions that need to be answered are where and how plants gauge the availability of soluble sugars, and whether they are also able to determine the amount of starch they accumulate. Another fundamental question is why it makes such a difference to a plant whether additional carbohydrates are gained by increasing photosynthesis by additional light or by elevated CO_2, not only for processes such as night respiration (Ludwig *et al.*, 1975), but also for biomass allocation (compare Fig. 3a,d). Apparently, part of the control of assimilate partitioning resides in the sinks and, if the translocation of sugars to the roots and stems cannot be increased, the accumulation of starch in source leaves will occur (Paul & Pellny, 2003).

The actual physiological mechanisms that control assimilate partitioning and, ultimately, biomass allocation are key to plant growth and performance. Levels of soluble sugars and nitrate are important in this mechanism, in part because they may affect the expression of a wide range of genes (Scheible *et al.*, 1997; Stitt & Feil, 1999; Hermans *et al.*, 2006). Hormone signalling is involved, with a range of mutants/transformants showing changed allocation (Table 5). Indeed, part of the success of the Green Revolution was based on gibberellic acid insensitivity, with decreased allocation to stems and increased investments to seed as a consequence (Hedden, 2003). Given that the phloem is a long-distance transport system by which a variety of small and larger molecules may travel, it could constitute another level of regulation (Pant *et al.*, 2008). However, with regard to the available evidence, there is no central gene or compound that determines assimilate translocation and biomass allocation. Rather, control is diffuse and shared by various processes in different locations (Farrar & Jones, 2000; Yang & Midmore, 2009).

## VIII. Ecological aspects

1. Effect of competition

The above analyses were all for plants that had presumably been grown individually. The situation becomes more challenging in competition, when neighbouring individuals compete for the same above- and below-ground resources (Donald, 1958; Tilman, 1988; Aerts, 1999; Dybzinski *et al.*, 2011). If increased density mainly leads to a depletion of nutrients, we would – based on the dose–response curve of Fig. 1(f) – expect an increased allocation to roots in plants grown at high densities, at the cost of SMF and, especially, LMF. Decreased SMF and increased RMF would similarly be expected if competition reduced water availability (Fig. 1g). If increased density simply equated to a lower light availability per plant, one might predict a decrease in RMF and an increase in LMF (Fig. 1a). In reality, however, none of the expected responses is empirically observed. From the moderate number of experiments (18) found in the literature that considered all three organs separately for vegetative plants, the average response to increasing plant density was a small *decrease* in LMF and RMF, and an *increase* in SMF (Fig. 4a). An increased RMF with density may be observed in cases in which the availability of

Table 5 Allocation of biomass, as affected by a range of mutations

Transgene or mutation	Physiological effect	Change in LMF	Change in SMF	Change in RMF	Species	Reference
Sugar-related						
Anti-sense Rubisco	Reduced photosynthesis	+0.15	−0.05	−0.10	*Oryza sativa*	Makino *et al.* (2000)
Overexpressed SBPase (sedoheptulose-1,7-bisphosphatase)	Increased regeneration of RUBP in the Calvin cycle	+0.03	+0.02	−0.05	*Nicotiana tabacum*	Lefebvre *et al.* (2005)
Anti-sense MDH (malate dehydrogenase)	Decreased mitochondrial respiration	−0.02	+0.07	−0.05	*Lycopersicon esculentum*	Nunes-Nesi *et al.* (2005)
Overexpressed levansucrase	Fructan accumulation	+0.01	0.00	−0.01	*Nicotiana tabacum*	Pilon-Smits *et al.* (1995)
N-related						
nia1 and nia2 transformed with NIA2 gene	Very low nitrate reductase	+0.13	x	−0.13	*Nicotiana tabacum*	Scheible *et al.* (1997)
Overexpressed NIA	Increased nitrate reductase	+0.02	x	−0.02	*Nicotiana tabacum*	Gojon *et al.* (1998)
Hormone-related						
Overexpressed GA20-oxidase	Increased GA production	+0.01	+0.10	−0.11	*Populus* sp.	Eriksson *et al.* (2000)
gib-1	Decreased GA production	−0.04	−0.06	+0.10	*Lycopersicon esculentum*	Nagel & Lambers (2002)
etr-1	Ethylene insensitive	+0.04			*Petunia × hybrida*	Tholen *et al.* (2004)
Sitiens	ABA deficient	−0.03	+0.02	+0.03	*Lycopersicon esculentum*	Nagel *et al.* (1994)
Other						
Anti-sense 4CL (4-coumarate:CoA ligase	Decreased lignin production	+0.01	+0.05	−0.05	*Populus tremuloides*	Hancock *et al.* (2007)

ABA, abscisic acid; GA, gibberellic acid; RUBP, ribulose-1,5-bisphosphate.
Values are given for leaf mass fraction (LMF), stem mass fraction (SMF) and root mass fraction (RMF) of the transgene minus the values for the wild-type plants.
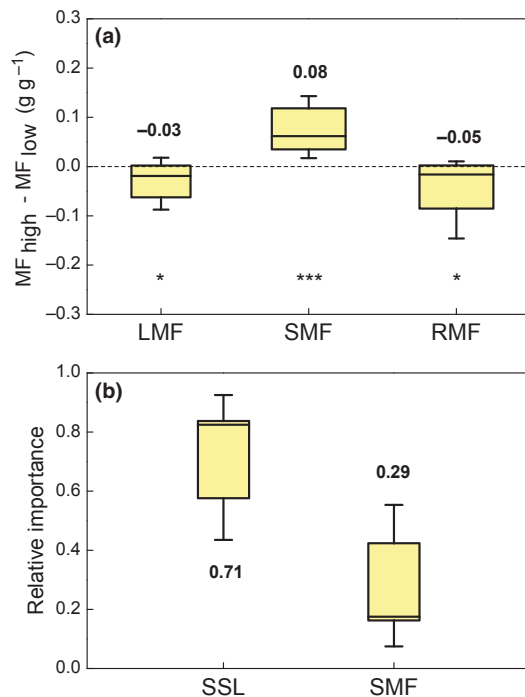
Fig. 4 (a) Increase in the fraction of whole plant mass represented by leaves (LMF), stems (SMF) and roots (RMF) for plants grown at a high density relative to plants grown at a low density. (b) The relative importance of specific stem length (SSL) and SMF in explaining the difference in height per unit total plant mass between plants grown at high and low density. In some experiments, a 'low density' pertains to individually grown plants. All observations (18 studies, 20 species) are for intraspecific competition and, in all but two studies, below-ground competition was part of the experiment. Herbaceous species include *Abutilon theophrasti*, *Amaranthus quitensis*, *Amaranthus hybridus*, *Atriplex prostrata*, *Brassica cernua*, *Fagopyrum esculentum*, *Glycine max*, *Hordeum vulgare*, *Impatiens capensis*, *Impatiens parviflora*, *Nicotiana tabacum* and *Xanthium pensylvanicum*. Woody species are *Acacia implexa*, *Alnus glutinous*, *Betula pendula*, *Betula pubescens*, *Pinus sylvestris* and *Populus deltoides*. Literature references are listed in Table S5. Additional data were obtained from Casper *et al.* (1998), Pierik *et al.* (2004), Forster *et al.* (2011) and A. Jagodzinski (pers. comm.). *, $P < 0.05$; ***, $P < 0.001$.

nutrients is low (Berendse & Möller, 2009). The increase in SMF, however, occurred systematically in all crowding experiments considered. We speculate that these responses are connected to the near-unidirectional nature of light in a closed canopy, where the positioning of leaves at the top of the canopy is of utmost importance for light interception. Gaining stem length is then essential. It is well known that, under crowding conditions, plants increase the length per unit stem mass (specific stem length, SSL; Schmitt *et al.*, 1999). One of the most important triggers here is the R/FR ratio, sensed by the phytochrome system (Keuskamp & Pierik, 2010). Interestingly, the allocation response to crowding is remarkably similar to the response of individually grown plants treated with low R/FR (Fig. 1b), suggesting that light quality is also the trigger for altered allocation. In this sense, increased stem allocation could be seen as an additional response variable of the shade avoidance syndrome (Franklin, 2008).

It is worth noting that, given the ontogenetic increase in SMF with size (Fig. 2), we would expect the density effect on SMF to

be even more pronounced after allometric correction. In one of the few reports in which an allometric analysis was carried out (Casper *et al.*, 1998), no size-corrected effects for shoot vs root allocation were found, confirming that the shoot : root ratio does not always change with competition. However, this experiment showed a clear allometric effect, in that dense plants had *c.* 35% lower leaf mass for any given stem mass. A second point of interest is that, in all cases, the available data from plant density experiments indicate a reduction in average plant body mass (often at two- to five-fold levels). Crowded plants generally achieve similar heights as plants at low densities, which implies that their height expressed per unit total plant mass is much higher. This ratio is mathematically the product of SSL and SMF. A log–log scaling slope analysis (Appendix A4) showed that increased SSL explained the largest part of the variation (71%) in height per mass, but the increased allocation to stem still explained 29% (Fig. 4b). Thus, in this case also, morphology is more plastic than allocation.

Interspecific vs intraspecific competition, as the result of the depletion of resources, can affect allocation patterns differently. The analysis of plants competing for nutrients in split-root designs has shown that RMF increases when two plants rather than one are grown in twice the volume (Gersani *et al.*, 2001; O'Brien *et al.*, 2005). This increased root investment comes at the expense of investments in reproduction, and could thus be considered as an overinvestment triggered by competition. However, some workers claim that the 'overproduction' of roots can also be the result of larger rooting volumes *per se*, independent of nutrient supply (Schenk, 2006; Hess & De Kroon, 2007). Currently, more evidence is accumulating that root interactions affect allocation patterns. Mommer *et al.* (2010) reported a three-fold increase in RMF in *Anthoxanthum* in response to interspecific relative to intraspecific neighbours. These effects may even work via other organisms: non-native *Chromolaena* plants increased SMF and height growth depending on the soil organisms present (Te Beest *et al.*, 2009). Ninkovic (2003) showed that one *Hordeum* cultivar increased RMF when exposed to volatiles of another cultivar. Clearly, the signal transduction pathways determining biomass allocation are diverse and complex.

2. Allocation in natural habitats

Most of the preceding analyses were based on experiments with vegetative plants grown under controlled conditions. What is known about the realized biomass allocation patterns in the field? As mentioned in Section III, reliable estimates of root biomass of individual species and vegetation types are difficult to obtain, hampering an objective analysis of allocation patterns in the field. It is also clear that there is a large amount of variation within vegetation types (Jackson *et al.*, 1996), among species within specific communities and among individuals of the same species (King *et al.*, 2007). Variation among species is illustrated by the study of Pate & Bell (1999), who analysed biomass allocation in 40 of each of the most common species in a *Banksia* woodland in Australia. Woody shrubs and small tree species had an average RMF of 0.32, but values ranged from 0.16 to 0.63. Further

examination showed that approximately one-half of the variance in RMF was associated with a species fire strategy, with resprouters having almost double the RMF of fire-killed reseeders (0.39 vs 0.23, respectively). However, even among the reseeders, the variance in RMF was large, with values ranging from 0.16 to 0.45. As this variation was not related to plant size either, biomass allocation *per se* does not seem to be a good predictor for species success in this particular community.

Keeping the above limitations in mind, it would still be very interesting to determine how the biomass allocation patterns differ among biomes. Several reviews (e.g. Jackson *et al.*, 1996; Mokany *et al.*, 2006) have attempted to address this issue by analysing the literature on root and shoot biomass as recorded in different vegetation types. We further examined this question by looking at the allocation to leaves, stems and roots. Although most investigations of woody species generally distinguish between leaves and stems, this is not a tradition among ecologists working with nonwoody vegetation. In this respect, there is a paucity of data for grasslands, but also for savannahs and deserts. Nevertheless, some general patterns in biomass allocation can be observed (Fig. 5). In a one-way ANOVA of biomass allocation data drawn from field studies, vegetation type accounts for 24%, 66% and 67% of the total variation across observations in LMF, SMF and RMF, respectively. Although this number is lowest for leaf allocation, the LMF values themselves are probably most remarkable, as they differ strongly from those of laboratory-grown plants, not only for trees but also for herbs. Whereas both herbaceous and tree seedlings in laboratory experiments often allocate > 50% of their biomass to leaves (Fig. 2), allocation in the field is, on average, just 5%. This difference, caused by both size and environment, may have a strong impact on the C budget of these plants and, as far as C is limiting growth, may explain the generally much lower growth rate of field plants.

With leaves often representing only a small fraction of the plant, the strong differentiation seems to be between stems and roots. In woody species, allometric constraints cause plants to increasingly invest in stems when size increases (see Section V; Ruark & Bockheim, 1987; Litton *et al.*, 2003). The largest SMF values are therefore found in forest stands, which are dominated by large trees (Fig. 5b), with only small differences between forests from different latitudes. Woodland and shrubland show intermediate values, probably because woody species are less dominant in biomass in these systems, and because they are of smaller sizes. Large within-group variation is seen for various other biomes. In the case of tundra vegetation, this variation is largely a result of differences between shrubby tundra, where plants have larger stem biomass allocation, and tundra consisting of herbaceous species, which predominantly show large allocation to roots. Shrubs in deserts strongly invest in roots, presumably because of low water availability. This contrasts with the strategy of succulents, which generally have a low RMF, and quickly produce new but shallow roots at the onset of the rainy season (Werger, 1983).

Thus, there is an overall increase in SMF with increasing standing crop of the system, which has been attributed to the accumulation of metabolically inert above-ground standing
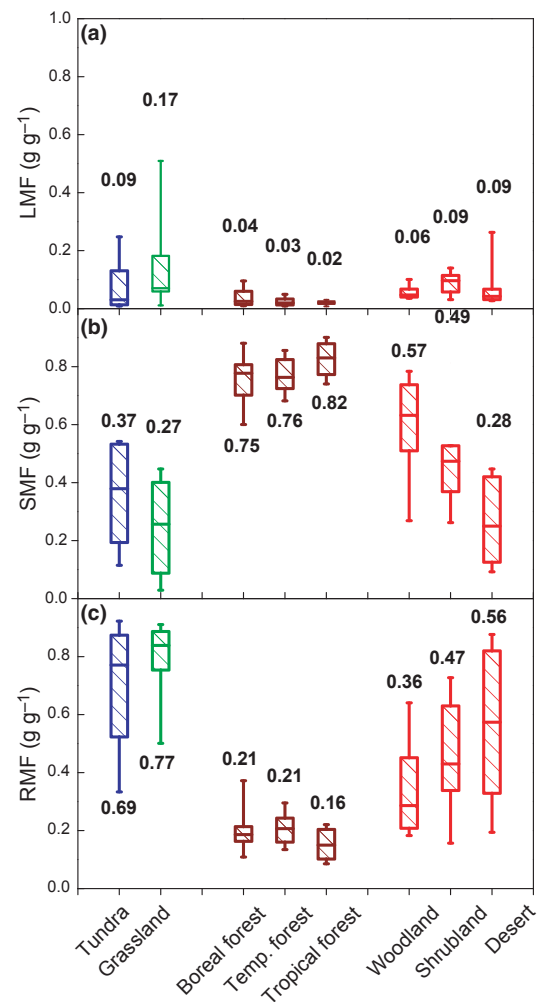
Fig. 5 Allocation to leaves (a), stems (b) and roots (c) in various biomes of the world. For some biomes, there is a paucity of studies distinguishing between leaf, stem and root biomass. In these cases, we added additional observations for which vegetation was separated into above- and below-ground biomass, from which the root mass fraction could be determined. In most cases, the biomass of whole plots of stands was measured; for forests, the biomass was sometimes estimated from allometric relationships determined from a number of trees. In cases in which stand data were scarce, such as deserts, we averaged the allocation data for the individual species measured there (e.g. Werger, 1983). In cases in which data were more readily available (mainly forests), we selected the observations on mature forests, taking care to spread observations over various geographical locations and different types of forest. Literature references are listed in Table S6. The numbers above or below the boxplots indicate the average value. The rounded numbers of observations for leaf mass fraction (LMF), stem mass fraction (SMF) and root mass fraction (RMF) in each biome are as follows: tundra, 15/15/40; grassland, 10/10/60; boreal forest, 40/40/40; temperate forest, 70/70/70; tropical forest, 40/40/40; woodland, 15/15/15; shrubland, 15/15/20; desert, 10/10/20.

biomass, such as stems, over time in forest and woodland ecosystems (see Fig. 2e). However, this may not be the only explanation, as vegetation types with higher standing biomass are often associated with higher temperatures, adequate soil moisture and ample nutrients, factors that are collectively associated with a lower RMF in individual plants (cf. Fig. 1f,g,j). Generally, colder biomes (i.e. tundra, cold deserts, temperate grasslands, cool

temperate arid shrublands) have the highest RMF values across all biomes (cf. Jackson *et al.*, 1996; Mokany *et al.*, 2006). This is likely to be partly related to their low standing biomass, but is also consistent with our analysis on temperature-induced changes in allocation patterns in experimental studies (cf Fig. 1j). Genotypic adaptation can also play a role, as *Picea abies* from high-altitude cold locations shows greater intrinsic root allocation (Oleksyn *et al.*, 1998). For both grass and shrubland ecosystems, as well as forest and woodland ecosystems, a decrease in precipitation is associated with an increase in RMF (Mokany *et al.*, 2006; but see Schenk & Jackson, 2002 who could only demonstrate this for herbaceous species). Similar to our analysis of individual species (Fig. 1g), the largest changes in RMF occur at the lowest precipitation levels. Thus, despite methodological issues, and a large range of relevant covariates that are unaccounted for in the many allocation studies (e.g. time since last disturbance, nutrient availability, soil type, depth to bedrock, etc.), whole communities, on average, show similar changes in response to several environmental factors (i.e. light, rainfall) as do individual plants in experimental studies (cf. McCarthy & Enquist, 2007).

IX. Perspectives

Irradiance has the strongest effect on the allocation of all environmental factors considered, but this change appears to be largely a result of size-induced differences between treatments. Nutrient levels also have a large effect, which becomes more pronounced after size correction, as does the effect of temperature. Inherently higher values for LMF are present in eudicots relative to monocots, and for gymnosperms relative to angiosperms. However, in most cases, important foliar functional traits (SLA) are far more variable than allocation traits (LMF) across species, a conclusion that, with the exception of nutrient stress, extends to most environmental effects. Clearly, we require deeper insights into the interrelationships between the activities and proportions of the three main organ types to understand why plant allocation patterns are relatively 'inert', when changes in allocation are truly functional, and whether changes in allocation achieve optimality.

Our knowledge about the mechanism by which allocation is regulated is poor, although more methods have become available to quantify assimilate partitioning nondestructively. Single measurements using these techniques are currently time consuming, but, if they become faster, would enable a comparative analysis of mutants and transformants. This is fundamental, as a better understanding of source : sink relationships and assimilate partitioning will enable us to improve the productivity of economically important organs. However, it is most likely that partitioning is not under the control of one gene, but rather under the control of the relative source and sink strengths of all organs.

Finally, our analyses indicate that high planting densities generally invoke increased allocation to stems at the expense of roots and/or leaves in ways that can, albeit modestly, contribute to the elevation of the canopies of individuals competing for light. Yet, as in many other cases, the variation in stem allocation is much smaller than the variation in stem morphology. Understanding the mechanisms responsible for density-dependent changes in biomass allocation, both in terms of signal transduction pathways as well as light and N distribution, will help us to achieve a more mechanistic understanding of plant competition.

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Appendix A1: Technical details of our methodology

Data collection

Our methodology is based on a wide range of experiments published in the literature in which individually grown plants were subjected to different levels of a specific environmental factor, and biomass data were collected separately for different biomass fractions. The literature comes from molecular, physiological, agricultural, ecological, horticultural and forestry journals (see Table S1). All vascular plant species were included, provided that they are autotrophic and have leaves and roots by nature. Data for plants that were dormant and had shed their leaves were excluded. We also excluded plants in the generative phase as, especially in (bi)-annuals, this takes place with a massive reprogramming in the plant's physiology and allocation patterns. However, in some experiments, only one harvest is reported, of plants just entering the generative phase. We decided to include these data if reproductive biomass represented < 5% of total biomass, but calculated allocation without taking into account the reproductive organs. When data for several harvests were reported, we chose data pertaining to the later part of the vegetative phase studied, averaging over two or three harvests in the case of experimental designs in which frequent small harvests were made.

In the best situation, LMF, SMF and RMF were reported. However, in a number of publications, only LMF was reported, or the shoot : root ratio (S/R), from which we derived RMF by:

$$RMF = \frac{1}{1 + S/R}$$

We included all available information from the database, with the consequence that the sum of the three response curves can sometimes deviate somewhat from unity, albeit not systematically.

If possible, we included petioles with the stem fraction, as they both functionally serve to place leaves in the light and to transport water, nutrients and sugars. However, in a number of experiments, petioles will have been included in the leaf fraction. One final remark is that a small percentage (< 5%) of the data for different treatments will have a correction for size, but by far the largest amount of data have no size correction.

Construction of dose–response curves

The collected allocation data can vary between species or experiments, and were therefore normalized with respect to the allocation value observed at a chosen reference level of a given environmental factor. The values of these reference levels are listed in Table 2. In the likely case that the experiment was not carried out at exactly the reference level, the allocation value for scaling was obtained by interpolation. Response curves were then constructed by summarizing data over different intervals of the environmental factor by percentiles, and by fitting response equations. Poorter *et al.* (2010) described this method considering proportional changes in the trait of interest. However, here, we also calculated absolute differences in allocation. The reason for this is that the young plants used in most experiments have, in general, more leaves than stems and roots (Fig. 2), which implies that proportional changes in two of the compartments will not

be balanced by a similar proportional change in the third. Absolute changes are then easier to interpret.

There are observations for *c.* 800 species in the Meta-Phenomics dataset. This could mean that an average response curve does not justify possible differences between species from contrasting functional groups. We therefore checked, with the help of regression trees (De'ath & Fabricius, 2000) what were the most contrasting biological groups.

Appendix A2: Correction of the plasticity in LMF as a result of the environment for differences caused by size

Plants grown in different environments may have a different allocation, partly as a result of differences in size. To estimate how strong is the size effect, we first analysed the data for final total dry matter (TDM) in our database, which was collected for the various experiments together with the information on biomass allocation. Similar to LMF (Fig. S1), we calculated the relative dose–response curves for TDM for each of the 12 environmental factors. Judging from the plasticity index for TDM (Table 3), some factors, such as UV-B, have hardly any effect on growth, whereas light and temperature affect TDM by more than 10-fold. Using a geometric mean value of biomass across treatments of 1 g, we calculated the expected TDM for both the lowest and highest level in the range considered for each environmental factor (e.g. 0.28 and 3.52, respectively, in the case of irradiance). These values were then used in conjunction with the trends from Fig. 2 to calculate the expected change in LMF solely as a result of the differences in plant size. (Note that, for LMF, the overall trends and those of individual experiments are rather similar.) The actual observed plasticity indices for LMF were then corrected for the size-related change. The analyses were performed separately for the four classes of species discerned, but subsequently averaged for herbaceous and woody species (Table 3).

Appendix A3: Analysis of inherent differences in LMF and SLA

Inherent differences in LMF and SLA between functional groups of species were taken from experiments described in the literature and listed in Supporting Information Table S4. For each experiment in which species from groups A and B were grown together, the average LMF and SLA were calculated per group of species, and the ratio between these two averages was computed. For comparisons of fast- and slow-growing species, where differences are not dichotomous, but continuous, we averaged the LMF and SLA of the 33% fastest growing species and of the 33% slowest growing species and calculated a ratio from these two average values. Monocots and eudicots were analysed separately. The ratios calculated per experiment were subsequently analysed over all experiments considered. Their distribution is characterized by

boxplots that indicate the 10th, 25th, 50th, 75th and 90th percentiles. The observed differences between groups were tested for significance with a *t*-test. Ratios were log-transformed before statistical analysis.

Appendix A4: Analysis of multiplicative relationships

A number of relationships considered in this article are multiplicative by nature. It is therefore of interest to analyse how variation in the 'dependent' variable is related to variation in the two or more 'independent' variables. One way to analyse this is the 'log–log scaling slope analysis', where all values are log-transformed and the slope is calculated of each of the 'independent' variables and the 'dependent' variable. These slopes indicate the extent of variation in each independent variable – taken over all data – responsible for the variation in the variable of interest. A value of unity indicates an exact proportional relationship, and a value of zero no relationship at all. The sum of all slopes is unity, giving an easy way to condense information. More detail can be found in Renton & Poorter (2011).

Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Dose–response curves of the *relative* response of the leaf mass fraction (LMF) to 12 environmental factors.

Fig. S2 Allometric relationships between leaf mass, stem mass and root mass for herbaceous and woody species.

Table S1 Literature for the compilation of environmental effects on biomass allocation

Table S2 Literature for the database on allometric relationships

Table S3 Literature for the compilation on ontogenetic trends in allocation

Table S4 Literature for the compilation on interspecific variation in the leaf mass fraction (LMF)

Table S5 Literature for the compilation on allocation under density-dependent competition

Table S6 Literature for the compilation on allocation in the field

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