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A meta-analysis of plant responses to light intensity for 70 traits ranging from molecules to whole plant performance

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Contents

Summary	1073	VII. Relation to field conditions	1089
I. Introduction	1074	VIII. Concluding remarks	1091
II. Concepts and methodology	1074	Acknowledgements	1091
III. Dose–response curves	1076	References	1091
IV. The overall response of plants to DLI	1085	Appendix A1	1094
V. Molecular response and regulation	1088		
VI. Shade-tolerant and light-demanding species	1089		

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Summary

By means of meta-analyses we determined how 70 traits related to plant anatomy, morphology, chemistry, physiology, growth and reproduction are affected by daily light integral (DLI; mol photons m^{−2} d^{−1}). A large database including 500 experiments with 760 plant species enabled us to determine generalized dose–response curves. Many traits increase with DLI in a saturating fashion. Some showed a more than 10-fold increase over the DLI range of 1–50 mol m^{−2} d^{−1}, such as the number of seeds produced per plant and the actual rate of photosynthesis. Strong decreases with DLI (up to three-fold) were observed for leaf area ratio and leaf payback time. Plasticity differences among species groups were generally small compared with the overall responses to DLI. However, for a number of traits, including photosynthetic capacity and realized growth, we found woody and shade-tolerant species to have lower plasticity. We further conclude that the direction and degree of trait changes adheres with responses to plant density and to vertical light gradients within plant canopies. This synthesis provides a strong quantitative basis for understanding plant acclimation to light, from molecular to whole plant responses, but also identifies the variables that currently form weak spots in our knowledge, such as respiration and reproductive characteristics.

I. Introduction

Almost all plant species are able to capture light and convert it to chemical energy by reducing CO₂. This photosynthetic process not only supports plant growth and productivity, but also supplies the energy for whole food webs at the ecosystem level, and directly or indirectly affects carbon (C), nutrient and water cycles at the global scale. We now have detailed insight into the mechanisms of both the light reactions – down to the femtosecond scale – and the dark reactions of photosynthesis (Niyogi *et al.*, 2015). By means of fluorescence or gas-exchange measurements, we can readily assess how leaf-level photosynthesis changes when photosynthetic photon flux density (PPFD) is altered (Long & Bernacchi, 2003). However, downstream from these short-term responses, there are a myriad of long-term responses of plants to light availability, which occur at the subcellular and cellular level (e.g. the composition of light-harvesting complexes) and at the organ or whole-plant level (e.g. leaf thickness and biomass allocation). Such phenotypic changes are commonly referred to as ‘plasticity’ (Valladares *et al.*, 2007; Nicotra *et al.*, 2010).

Hundreds of experiments have been carried out by (eco-) physiologists, horticulturists, agronomists, foresters and ecologists to study the long-term effects of light on plants, by growing them for weeks until years at two, three or more light levels (Gottschalk, 1994; Soustani *et al.*, 2014). Various reviews have placed these studies in perspective (Björkman, 1981; Anderson *et al.*, 1995; Poorter & Van der Werf, 1998; Veneklaas & Poorter, 1998; Valladares & Niinemets, 2008). Most of those reviews have been narrative, but others have used a meta-analytical approach, comparing ‘high-light-grown’ plants with ‘low-light-grown’ ones (Poorter & Nagel, 2000; Liu *et al.*, 2016). A relatively recent approach is the meta-phenomics concept, where a range of experiments is summarized by dose–response curves (DRCs) (Poorter *et al.*, 2010; Esteban *et al.*, 2015). The concept of DRCs is more than a century old (Mitscherlich, 1909), and well engrained in photosynthesis research, where short-term light, CO₂ and temperature responses have improved insights into cellular mechanisms (Von Caemmerer, 2000). However, DRCs would also be very helpful in understanding the *long-term* responses of plants to growth light intensity. The meta-phenomics approach combines information from many different experiments, taking into account the fact that ‘low light’ and ‘high light’ may be unlike in different experiments. The resulting DRCs summarize a wide variety of research efforts, enabling development of a concise picture of how plants respond to their environment. Moreover, they offer a basis for identifying species with exceptional characteristics and provide quantitative information that allows further analyses and modeling.

In this synthetic review, we focus on how higher plants respond to different light intensities in the photosynthetically active range of wavelengths. For effects of other aspects of light, such as spectral quality (e.g. ultraviolet (UV), red-to-far-red ratio (R:FR)), photoperiod and dynamics on plants, the reader is referred to reviews like Pearcy (1990), Ballaré *et al.* (2011), Casal (2013) and Ballaré & Pierik (2017). Reviews on leaf responses to

vertical light gradients in plant canopies are provided by Niinemets *et al.* (2015) and Pons (2016). Here, we first discuss the various metrics to quantify light availability and our methodology for processing published data. Second, we establish DRCs for a total of 70 eco-physiological traits, ranging from the subcellular to the whole-plant level. Do the trait values increase or decrease with light, is the form of the DRC linear or saturating, and what is the overall degree of plasticity? Third, we briefly discuss some of the molecular mechanisms underlying these long-term responses to light. Finally, we take an ecological perspective and consider to what extent these DRCs differ for shade-tolerant and light-demanding species.

II. Concepts and methodology

1. Characterizing light intensity

The amount of light available for plants can be characterized in various ways. For energy budgets of plants, the total incoming energy over all wavelengths of (sun)light is the relevant variable. It is commonly referred as ‘irradiance’ and measured in watts per square meter. The wavelengths that energetically drive photosynthesis are in the 400–700 nm range. Although photons in this range contain different energy levels, each can excite Chl to the same extent. Therefore, for photosynthesis-related processes, the flux of photons in the 400–700 nm range is the most relevant variable (Percy, 2000). This PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$) comprises about half the energy of solar radiation and (when expressed per second) scales well with the time frame at which photosynthesis responds to changes in light intensity. However, for longer term processes and structural traits, instantaneous values are less informative, as light intensity varies strongly both diurnally and among days. On cloudless days, PPFD at the top of a canopy progresses in a sinusoidal way, with maxima reaching $2200 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Ritchie, 2010), the actual value depending on latitude and time of year and day. With partially clouded skies, strong temporal changes in light will occur above the canopy, whereas PPFD changes within canopies are even more frequent and dynamic due to mutual shading by wind-moved plants. Many plant traits are found to be better related to daily light integral (DLI), which is the PPFD integrated over a day ($\text{mol m}^{-2} \text{d}^{-1}$), than to instantaneous PPFD values at any specific moment in time (Monteith, 1977; Chabot *et al.*, 1979; Poorter & Van der Werf, 1998; Niinemets *et al.*, 2015). For this review, we will therefore use average DLI during the experimental treatment as the quantifier for the light intensity experienced by the plants. Note that DLI may also change because of differences in day length.

To characterize monthly averaged DLI values world-wide, we used an extended climate database of daily irradiance (New *et al.*, 1999). As expected, DLI values in December in the Northern Hemisphere are strongly and almost linearly dependent on latitude, with levels saturating at latitudes between 0 and 20° (Fig. 1a). In June, however, when plants in many ecosystems are actively growing, latitude per se only explains

1% of the total variation in DLI, with maximum values occurring between 30° and 40° latitude. At this time of year, the lower solar angle at higher latitudes is almost fully compensated by longer day lengths. Local variation is substantial, with the Negev Desert, for example, receiving twice the DLI as the Tokyo region, although both are situated at the same latitude. Variation in cloudiness is the strongest driver for this difference, with additional effects of pollution and atmospheric dust (Stanhill *et al.*, 2014). Cloudiness is also the reason that highest DLI values over the year are found at *c.* 20° north and south rather than at the equator, and the cause of substantial day-to-day variation in DLI (Fig. 1b,c). Although most of this day-to-day variation is averaged out over longer

time scales, variation in DLI between years can still be substantial (Fig. 1d). Finally, the DLI as perceived by plants may be reduced due to external or internal shading, such that leaves and plants positioned low in the canopy may receive only 1–5% of the DLI present above the canopy (Chazdon & Fetcher, 1984; Pons, 2016).

Unfortunately, most reports of field and glasshouse experiments on light availability effects do not provide data on DLI (Niinemets & Keenan, 2012). We strongly recommend that DLI is measured for the duration of an experiment or, alternatively, that values are taken from the nearest weather station and, in the case of glasshouses, corrected for the fraction of daily irradiance reaching the plants (Poorter *et al.*, 2012).

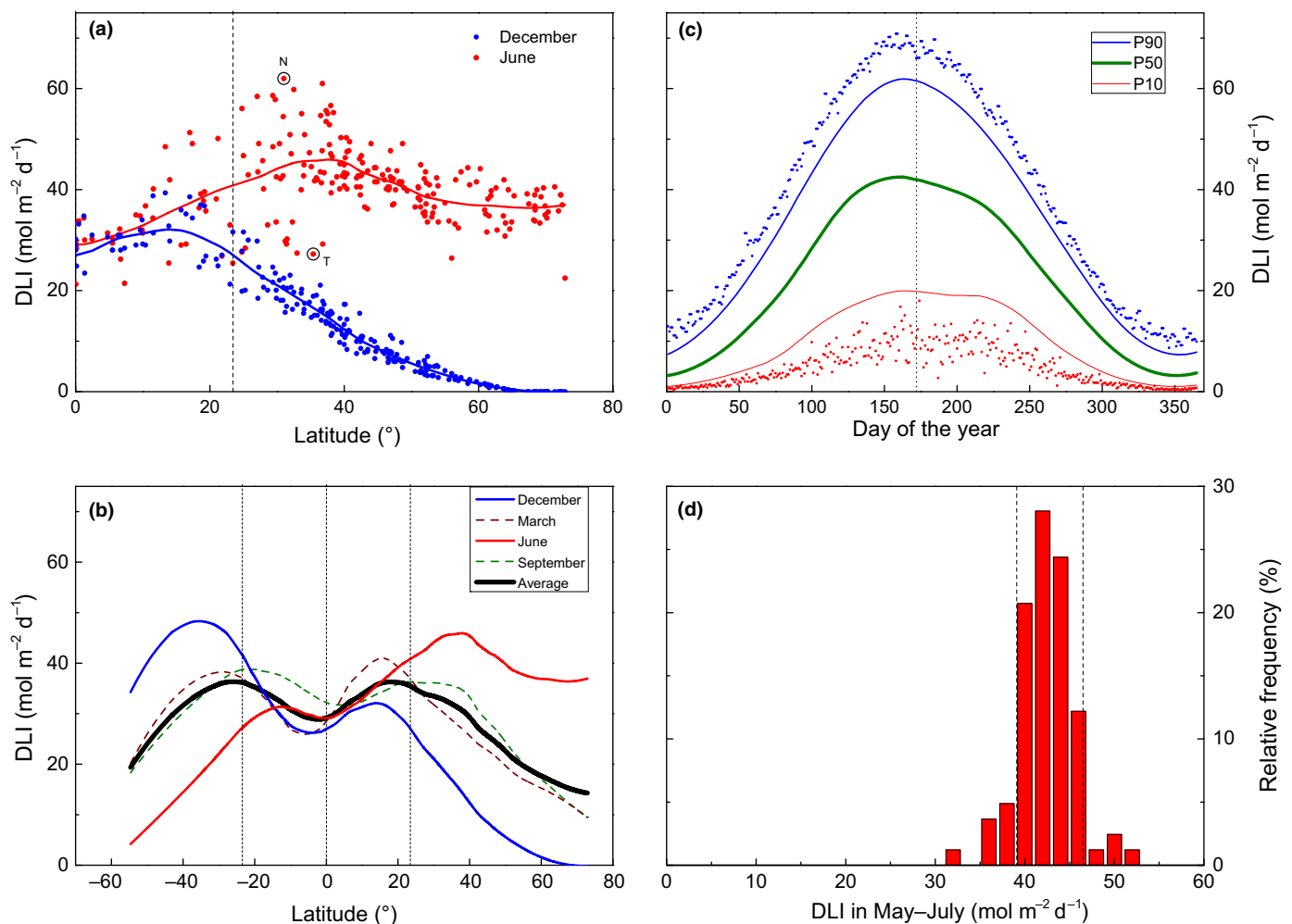


Fig. 1 Variation in time and space of the daily light integral (DLI). (a) Average DLI in the months of December (blue circles) and June (red circles) as dependent on latitude for a wide range of locations (230) in the Northern Hemisphere. The dotted line indicates the latitude of the Tropic of Cancer. Data are average values over the 1960–1990 period derived from New *et al.* (1999). Lines are fitted with a loess function. 'N' and 'T' mark observations for the Negev (31.0°N, 34.8°E) and Tokyo (35.4°N, 139.5°E), respectively. (b) Trends of DLI with latitude at different times of the year and the yearly average. Data based on the aforementioned database at 340 locations world-wide, trends smoothed with a loess curve. (c) Range of DLI as measured for every day of the year over a 60 yr period in De Bilt, the Netherlands (52.5°N, 5.2°E). The bold green line connects the median values at a specific day measured over the 60 yr period, the red and blue lines connect the 10th and 90th percentiles. All trends are smoothed with a loess function. The red and blue points give the minimum and maximum values, respectively, observed per day in this 60 yr period. The dotted line indicates the longest day of the year. Source: <https://www.knmi.nl/nederland-nu/klimatologie/daggegevens>, accessed 30 October 2017). (d) Distribution of the average DLI values in the main growing season (period May–July) as measured over an 82 yr period in Potsdam, Germany (52.4°N, 13.1°E). The dashed lines indicate the 10th and 90th percentiles. Source: <https://www.pik-potsdam.de/services/klima-wetter-potsdam/klimazeitreihen/globalstrahlung>, accessed 2 January 2019).

2. Methodology followed in sampling and processing the data

The following presents a synopsis of our methodological procedures. A more extensive description is provided in Supporting Information Methods S1.

We screened the literature for experiments on higher plants subjected to different light intensities, but similar spectrum, during their full life or a substantial part thereof. These reports included studies in growth rooms, glasshouses, gardens or experimental field plots. Mean values per experiment, plant species (or genotype) and light level were collected for >70 different physiological, anatomical, morphological, chemical or growth-related traits. DLI levels were taken as specified by the authors, or estimated from the given light levels relative to daylight and the average DLI for the time of year of the experiment and location as derived from New *et al.* (1999). Based on the data for all light levels for a given species in a given experiment (further referred to as 'case'), we interpolated what the value of the phenotypic trait would have been at a DLI of $8 \text{ mol m}^{-2} \text{ d}^{-1}$, and subsequently scaled all data for that trait and species to this reference value (Poorter *et al.*, 2010). Avoiding *a priori* assumptions about data distribution and form of the relationship, we first summarized overall relationships by dividing all observations into 10 equally numbered classes, for data ranked with respect to DLI. Subsequently, we calculated the median DLI over all points in each light class, as well as the scaled median trait values per class (see Fig. S1 for an example). We also derived smoothed DRCs from the full point cloud by means of quantile regression, differentiating between linear, saturating (monomolecular) and exponential relationships. For three traits, underlying data often showed local maxima. In those instances, we fitted the scaled point cloud with a second-order polynomial.

From the smoothed DRCs we computed a plasticity index (PI) following Poorter *et al.* (2010) as the ratio between the highest and lowest phenotypic trait value in the $1\text{--}50 \text{ mol m}^{-2} \text{ d}^{-1}$ range, multiplied by -1 in the case of negative relationships. Note that this PI deviates somewhat from the classical plasticity concept, as it does not focus on one genotype but approximates the response of a whole group of species. The DLI range was deliberately chosen to encompass a wide span of conditions: $1 \text{ mol m}^{-2} \text{ d}^{-1}$ represents a heavily shaded habitat, whereas $50 \text{ mol m}^{-2} \text{ d}^{-1}$ embodies a very high light environment, which only occur across a whole growing season at a limited number of locations on Earth (Fig. 1a). The consistency of the direction of response (positive or negative) was computed by calculating the percentage of cases where the trait value was higher at the highest DLI than at the lowest DLI. To evaluate plasticity differences among groups of species we fitted the same type of equation to subgroups of interest. The ecological niche of species was characterized as being in the low-light range (shade-tolerant species), in the high-light range (light-demanding species) or intermediate (see Notes S1). Within the herbaceous and woody groups, we analyzed plasticity differences for this low light/high light preference rating as well as for some other categorizations, such as deciduousness and photosynthetic pathway.

3. Description of the database

In total, we analyzed DLI levels and phenotypic trait data for 500 experiments and 70 phenotypic traits. The traits are defined in Table 1. The database has 4010 records and 1380 cases (species \times experiment combinations for a set of different light levels), with each record containing the mean value for all of the phenotypic traits measured for a given species at a given DLI as reported in an experiment. The total number of observations in the database for a given trait ranges from *c.* 20 for the concentration of some constituents in stems to >2100 for specific leaf area (SLA). Note that not all phenotypic traits are independent of one another, for example, photosynthetic capacity is analyzed both on a leaf area, leaf mass and Chl basis. For one trait we used two alternative expressions: leaf mass per area (LMA) when analyzing leaf traits, and SLA when analyzing variation in growth-related traits ($\text{SLA} = 1/\text{LMA}$). Since we are primarily interested in relative responses, we combined closely related traits that bear more or less similar information (e.g. leaf density and leaf dry matter content). We also combined variables for which only a limited number of observations were present (e.g. total and organic root nitrogen (N); see Table 1). The database contains information for 760 species, 39% of which are herbaceous. References to all papers used are listed in Appendix A1.

III. Dose–response curves

We grouped the 70 traits into four thematic clusters, related to structure, chemical composition, physiology and growth. Specific graphs with more detailed information per trait are given in Figs S2–S72. The summary diagram presented in Fig. 6 (see Section IV) may also be helpful to place responses of individual traits in perspective.

1. Anatomy and morphology

A range of anatomical leaf traits are positively affected by DLI, with a plasticity index (PI) up to 2.0 (Table 2a). Changes are generally strongest in low light, and approach saturation at high light (Fig. 2). It is instructive to relate these traits to leaf mass per area (LMA), which shows leaf dry mass invested per leaf area and has a PI of 2.6 (Fig. 2a). Leaf thickness (LeaThi) almost doubles over the light range considered ($\text{PI} = 1.9$) and is one of the most consistent leaf responses to DLI, found in 99% of the cases we analyzed. Herbaceous species are more plastic than woody species in this respect (Table S1), but these differences cause only subtle variations in the overall dose–response curve (DRC). Increased leaf thickness is accompanied by a doubling in the cross-sectional area of mesophyll per unit leaf area (A_{mes}/A). The fraction of leaf volume occupied by mesophyll (including airspaces) also increases significantly, but with a marginal PI (1.1). The PI for the volumetric fraction of mesophyll occupied by palisade parenchyma is larger (1.3), but these are relatively small modulations on top of a large overall increase in thickness. Interestingly, the number of palisade cell layers (#PaCeLa; Table 2a) increases with DLI in only half of

Table 1 Plant traits and other variables used in this review.

Abbreviation	Variable name	Units	Explanation
1. Anatomy/morphology			
A_{mes}/A	Area of mesophyll/leaf area	$m^2 m^{-2}$	Includes both observations for total mesophyll area and for mesophyll area adjacent to intercellular spaces
DrMaCo _S	Stem dry matter content	%	Stem dry mass/fresh mass × 100
DrMaCo _R	Root dry matter content	%	Root dry mass/fresh mass × 100
InLeAr	Individual leaf area	cm ²	Can be either for a specific leaf or average over all leaves
IntLen	Internode length	cm	Length between two nodes
LeaDen	Leaf density	g ml ⁻¹	Leaf dry mass/leaf volume (combined with data for leaf dry matter content)
LMA	Leaf mass per area	g m ⁻²	Inverse of SLA, scales positively with leaf thickness and area-based photosynthetic rates
LeaThi	Leaf thickness	μm	Total leaf thickness
StoDen	Stomatal density	number mm ⁻²	Based on both sides, or on abaxial if adaxial is not provided
PlaHei	Plant height	cm	Height from ground level to the shoot apex or highest leaf tip
SpStLe	Specific stem length	m g ⁻¹	Stem length/stem mass
SRL	Specific root length	m g ⁻¹	Root length/root mass
VoFrMe	Fraction of leaf volume in mesophyll	ml ml ⁻¹	Derived from mesophyll thickness/total leaf thickness in cross-sections
VoFrPa	Fraction of palisade cell volume in total mesophyll volume	ml ml ⁻¹	Derived from palisade mesophyll thickness/palisade plus spongy mesophyll thickness in cross-sections
#PaCeLa	Number of palisade cell layers	—	Generally taken from single cross-sections per treatment in published papers
#BraTil	Number of branches or tillers	—	Number of tillers (grasses) or first-order side branches (dicots), plus the main tiller/axis
2. Chemical composition			
[C] _L	[C] leaf	mg g ⁻¹	No SPAD measurements
[C] _R	[C] root	mg g ⁻¹	
[C] _S	[C] stem	mg g ⁻¹	
Chl/A	Chl content/leaf area	μmol m ⁻²	Minerals or ash
Chl a : b	Chl a : Chl b	mol mol ⁻¹	
Chl/N	Chl to N ratio	mmol mol ⁻¹	
[Mine] _L	[Minerals] leaf	mg g ⁻¹	Total N, excluding NO ₃ ⁻
[NO ₃] _L	[Nitrate] leaf	mg g ⁻¹	
[Norg] _L	[Organic N] leaf	mg g ⁻¹	
Ntot/A	Leaf total N content/leaf area	g m ⁻²	Total N, including NO ₃ ⁻
[Ntot] _L	[Total N] leaf	mg g ⁻¹	Total N, including NO ₃ ⁻
[N] _R	[N] root	mg g ⁻¹	Total N or organic N
[N] _S	[N] stem	mg g ⁻¹	Total N or organic N
[P] _L	[P total] leaf	mg g ⁻¹	Only for leaves
[P] _R	[P total] root	mg g ⁻¹	
[P] _S	[P total] stem	mg g ⁻¹	
[SolPhe] _L	[Soluble phenolics] leaf	mg g ⁻¹	Violaxanthin + antheraxanthin + zeaxanthin
SolSug/TNC _L	Soluble sugar fraction in TNC	g g ⁻¹	
[TNC] _L	[Nonstructural carbohydrates] leaf	mg g ⁻¹	
[TNC] _R	[Nonstructural carbohydrates] root	mg g ⁻¹	
[TNC] _S	[Nonstructural carbohydrates] stem	mg g ⁻¹	
Xant/Chl	Xanthophylls/Chls	mmol mol ⁻¹	
3. Physiology			
Abso	Absorptance leaf	%	Absorptance of incident light
$c_i : c_a$	Intercellular/atmospheric CO ₂ concentration	mol mol ⁻¹	Measured at growth light conditions and ambient CO ₂
F_v/F_m-d	Fluorescence variable F_v/F_m		Measured during the diurnal period
F_v/F_m-n	Fluorescence variable F_v/F_m		Measured during the nocturnal period (predawn)
$J_{MAX}/V_{C_{MAX}}$	Electron transport capacity/ carboxylation capacity	mol mol ⁻¹	Measured at saturating light and CO ₂ levels
Phot/A ^{GL}	Photosynthesis at growth light/leaf area	μmol m ⁻² s ⁻¹	Measured at growth light conditions and ambient CO ₂
Phot/A ^{SL}	Photosynthesis at saturating light/ leaf area	μmol m ⁻² s ⁻¹	Measured at saturating light conditions and ambient CO ₂

Table 1 (Continued)

Abbreviation	Variable name	Units	Explanation
Phot/Chl ^{SL}	Photosynthesis at saturating light/Chl	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Measured at saturating light conditions and ambient CO ₂
Phot/M ^{GL}	Photosynthesis at growth light/leaf mass	$\text{nmol g}^{-1} \text{s}^{-1}$	Measured at growth light conditions and ambient CO ₂
Phot/M ^{SL}	Photosynthesis at saturating light/leaf mass	$\text{nmol g}^{-1} \text{s}^{-1}$	Measured at saturating light conditions and ambient CO ₂
Refl	Reflectance leaf	%	
Resp/M _{L+S}	Shoot respiration/shoot mass	$\text{nmol g}^{-1} \text{s}^{-1}$	Can be both on oxygen (O ₂) or CO ₂ basis; whole shoots
Resp/M _R	Root respiration/root mass	$\text{nmol g}^{-1} \text{s}^{-1}$	Can be both on O ₂ or CO ₂ basis
Resp/M _L	Leaf respiration/leaf mass	$\text{nmol g}^{-1} \text{s}^{-1}$	Can be both on O ₂ or CO ₂ basis; generally single leaf
Rubi/A	Rubisco enzyme/leaf area	$\mu\text{mol m}^{-2}$ or $\mu\text{mol m}^{-2} \text{s}^{-1}$	Only for leaves, estimates of both content and activity
StoCon	Stomatal conductance	$\text{mmol m}^{-2} \text{s}^{-1}$	Measured at growth light conditions for a single leaf in a leaf chamber
Trsm	Transmittance leaf	%	
V _C MAX/A	Carboxylation capacity/leaf area	$\mu\text{mol m}^{-2} \text{s}^{-1}$	
WatPot-d	Water potential	MPa	Measured during the diurnal period, absolute values
WatPot-n	Water potential	MPa	Measured during the nocturnal period (predawn), absolute values
4. Growth and reproduction			
ConCos _L	Construction costs leaf	g glucose g^{-1}	Glucose mass required to build 1 g of leaf
InSeMa	Individual seed mass	g	
LAR	Leaf area ratio	$\text{m}^2 \text{kg}^{-1}$	Leaf area/unit total vegetative plant mass
LMF	Leaf mass fraction	g g^{-1}	Leaf mass/unit total vegetative plant mass
PaBaTi _L	Payback time	d	Time required for a leaf to fix as much C (net) as was required to construct that leaf
RepEff	Reproductive effort	g g^{-1}	Reproductive mass/total plant mass (also: seed mass/total or above-ground mass)
RGR	Relative growth rate	$\text{mg g}^{-1} \text{d}^{-1}$	Rate of increase in biomass/unit total plant biomass
RMF	Root mass fraction	g g^{-1}	Root mass/total vegetative plant mass
SLA	Specific leaf area	$\text{m}^2 \text{kg}^{-1}$	Leaf area/leaf mass
SMF	Stem mass fraction	g g^{-1}	Stem mass/total vegetative plant mass
TDM	Total vegetative dry mass of the plant	g	Reproductive structures excluded
ULR	Unit leaf rate	$\text{g m}^{-2} \text{d}^{-1}$	Rate of increase in biomass/unit leaf area
#SeeFru	Number of seeds or fruits per plant	—	Excluded are complicated cases where species have fruits with many seeds (like tomato). Included are some observations on number of flowers
5. Other abbreviations			
DLI	Daily light integral	$\text{mol m}^{-2} \text{d}^{-1}$	Daily photosynthetic photon flux density averaged over the period of active growth

Abbreviations are alphabetically ranked within each overall category. Units are given as well as a further explanation of the variable and its specifications. All concentrations and ratios are on a dry mass basis, unless stated otherwise.

the cases, implying that this is not as standard a response as taught in text books.

Leaf thickness is not the only factor driving the 2.6-fold increase in LMA with DLI, as leaf density (LeaDen) plays a quantitatively similar role (PI = 1.7; Fig. 2g; Table 2a). Higher density may reflect more tightly packed small cells with a relatively low volume of airspaces, thicker cell walls, a larger proportion of vascular and sclerenchyma tissue and/or thicker cuticle (Niinemets, 2001; Poorter *et al.*, 2009; Villar *et al.*, 2013). Palisade cells of high-light-grown plants are actually larger rather than smaller (Wild & Wolf, 1980), but most of the other anatomical changes are found to change in the expected direction (Ivanova *et al.*, 2006; Tosens *et al.*, 2012). Tissue density of stems, as represented by stem dry matter content (DrMaCo_S), follows a similar response as leaf density and increases in 96% of the cases (Table 2a). Root dry matter content,

on the other hand, does not respond to light at all, suggesting little anatomical or chemical changes.

Whereas most of the traits we analyzed follow a saturating response to DLI or a linear relationship, there are three morphological traits that show a local maximum (Fig. 2i,j,l). Individual leaf area (InLeAr) and internode length (IntLen) decrease with increasing DLI between 2 and 50 $\text{mol m}^{-2} \text{d}^{-1}$, but they also decrease when DLI drops below 2 $\text{mol m}^{-2} \text{d}^{-1}$. For plants that experience low light due to shading by more or less similarly sized neighbors, production of longer internodes and larger leaves would enable better light capture. The fact that these variables, which are related to plant size, decrease also at low DLI is likely due to problems with a deteriorating C-budget. In that sense they behave differently from traits that embody ratios, such as LMA and specific stem length (SpStLe; stem length per unit stem biomass), which

generally change monotonously with DLI. Together with a small rise in stem mass fraction (SMF; Table 2b), the large changes in SpStLe enable plants to achieve roughly similar total plant height (PlaHei) over a wide range in DLI, be it with decreases at both ends of the DRC. Light responses for herbs were not different from woody species (Table S1).

Specific root length (SRL, root length per root mass) also decreases with DLI in a linear fashion (Fig. 2m), with relatively large plasticity ($PI = -2.3$). SRL is determined by root thickness and density. Since root dry matter content does not change (Table 2a), it is likely that roots of high-light-grown plants become thicker. This aspect is not often studied, but thicker roots may partly be a consequence of the fact that high-DLI plants have larger root systems anyway (Wahl *et al.*, 2001).

This is not only due to the higher root mass fraction, but also to the much greater plant size at high DLI (Table 2b). Alternatively, through increased xylem volume, thicker roots may more easily accommodate the higher transpirational demand that goes with increased stomatal conductance (StoCon; Table 2b). Maintaining adequate root length may be more important than thickness in low light, considering the reduced investment in roots (Table 2b). However, as far as we know, the various trade-offs involved here have never been thoroughly analyzed. In low light, plants make few branches (eudicots) or tillers (grasses), as a result of increased apical dominance. Branch or tiller number (#BraTil) is the only trait considered here that increases more than linearly with light availability, with an overall PI of 5.0.

Table 2 Summary of the dose–response curve (DRC) analysis for 70 plant traits as dependent on the daily light integral (DLI).

Trait	DLI range	No. observations	No. species	Fit	r^2	PI	Increases (%)	Reliability	<i>a</i>	<i>b</i>	<i>c</i>
(a)											
1. Anatomy and morphology											
LMA	0.1–75	2190	520	S***	0.74	2.6	98	8	1.955	0.6748	0.04143
LeaThi	0.2–75	540	160	S***	0.73	1.9	99	8	1.717	0.5423	0.03388
A_{mes}/A	0.7–69	60	25	S***	0.81	2.0	93	4	1.688	0.5469	0.04334
#PaCeLa	0.4–75	110	45	L*	0.35	1.5	52	4	0.9528	0.00882	
VoFrMe	0.4–75	190	75	L***	0.30	1.1	78	7	0.985	0.00165	
VoFrPa	0.4–75	180	65	L***	0.12	1.3	70	6	0.9501	0.00539	
LeaDen	0.4–75	540	150	S***	0.66	1.7	94	7	1.420	0.4565	0.05614
DrMaCo _S	0.4–43	130	35	S**	0.70	1.7	96	5	1.321	0.4502	0.07686
DrMaCo _R	0.4–43	140	40	L ^{ns}	0.04	1.1	59	5	0.991	0.00150	
InLeAr	0.2–72	480	130	M ^{ns}	0.00	−1.7	38	6	1.043	−0.00671	0.00004
IntLen	0.7–62	110	35	L***	0.16	−1.7	37	4	1.051	−0.00669	0.00004
SpStLe	0.3–48	160	50	S*	0.41	−2.6	2	4	0.877	−2.638	0.5089
PlaHei	0.3–59	830	225	M***	0.00	−1.3	54	7	0.918	0.0090	−0.00026
SRL	0.3–42	90	45	L**	0.29	−2.3	30	4	1.087	−0.01229	
StoDen	0.4–72	200	65	S***	0.51	1.8	94	6	1.503	0.5013	0.05446
#BraTil	0.4–50	140	35	E*	0.57	5.0	96	3	0.7494	0.02218	0.00080
2. Chemical composition											
Ntot/A	0.2–50	250	90	S***	0.68	2.0	92	6	1.597	0.5554	0.05121
[Ntot] _L	0.5–52	480	160	S***	0.34	−1.3	20	7	0.8394	−0.3287	0.07421
[Norg] _L	1.0–41	130	45	L ^{ns}	0.02	−1.1	42	5	1.007	−0.00093	
[NO ₃] _L	2.2–50	80	20	S***	0.64	−2.3	8	3	0.5645	−1.502	0.08579
[Mine] _L	0.7–40	70	20	S***	0.69	−1.6	0	4	0.7679	−0.6362	0.09375
[N] _S	0.6–36	40	15	L**	0.50	−2.1	20	2	1.093	−0.01157	
[N] _R	0.5–71	120	55	L***	0.24	−1.4	26	5	1.049	−0.00634	
[P] _L	0.8–38	140	45	L***	0.18	−1.8	23	4	1.019	−0.00996	
[P] _S	1.3–36	30	10	L***	0.52	−2.1	13	2	1.107	−0.01168	
[P] _R	1.1–39	30	15	L ⁺	0.13	−1.5	32	2	1.061	−0.00735	
[C] _L	0.7–40	190	65	S**	0.20	1.1	85	7	1.033	0.0571	0.07398
[C] _S	0.7–32	20	10	L*	0.30	1.0	75	3	0.9952	−0.00060	
[C] _R	0.7–71	50	25	L*	0.00	1.0	48	4	0.9951	−0.00074	
[TNC] _L	0.8–38	70	25	L***	0.54	2.5	91	3	0.7938	0.02502	
[TNC] _S	0.6–46	20	5	L*	0.77	4.0	89	1	0.6869	0.04514	
[TNC] _R	0.6–38	40	15	L**	0.45	1.7	89	2	0.8823	0.01263	
SolSug/TNC _L	0.8–46	60	20	L ^{ns}	0.00	−1.0	45	2	1.005	−0.00073	
[SolPhe] _L	0.7–43	40	20	L***	0.66	3.4	86	1	0.6521	0.03387	
Chl/A	0.2–82	740	195	L ^{ns}	0.00	−1.1	45	7	1.005	−0.00112	
Chl <i>a</i> : <i>b</i>	0.2–82	540	145	S***	0.43	1.2	82	7	1.175	0.2040	0.04165
Chl/N	0.9–50	180	55	S***	0.79	−2.5	4	6	0.4667	−1.828	0.0623
Xant/Chl	0.6–82	110	35	L***	0.57	3.0	100	4	0.7567	0.03042	

Table 2 (Continued)

Trait	DLI range	No. observations	No. species	Fit	r^2	PI	Increases (%)	Reliability	<i>a</i>	<i>b</i>	<i>c</i>
(b)											
3. Physiology											
Abso	0.2–40	80	30	L ^{ns}	0.00	−1.0	41	5	1.002	−0.00031	
Refl	0.8–40	50	20	L*	0.39	1.4	79	3	0.9393	0.00759	
Tran	0.8–82	50	25	L***	0.20	−1.9	19	3	1.085	−0.0106	
Rubi/A	0.4–50	100	30	S***	0.73	4.6	98	3	2.287	0.8388	0.05013
V_{CMAX}/A	0.8–42	110	35	L***	0.70	2.9	98	3	0.7449	0.02921	
$J_{\text{MAX}}/V_{\text{CMAX}}$	0.8–40	100	35	L*	0.00	1.1	60	5	0.9866	0.00166	
Phot/ A^{SL}	0.4–75	990	280	S***	0.53	2.2	89	7	1.529	0.5891	0.0707
Phot/ M^{SL}	0.4–53	440	150	L***	0.00	−1.3	38	6	1.033	−0.00417	
Phot/ Chl^{SL}	0.4–75	430	125	S***	0.57	2.3	93	6	1.567	0.6048	0.06954
Phot/ A^{GL}	0.4–69	330	95	S***	0.73	17.4	97	6	3.838	0.9872	0.03652
Phot/ M^{GL}	0.4–53	150	55	S***	0.59	3.4	91	4	1.688	0.7711	0.08054
$F_v/F_m\text{-n}$	0.2–82	140	50	L*	0.04	−1.0	30	6	1.003	−0.00042	
$F_v/F_m\text{-d}$	0.9–82	130	50	L***	0.53	−1.2	5	6	1.022	−0.00269	
StoCon	0.6–69	150	55	L***	0.39	2.2	85	4	0.7963	0.02193	
WatPot-n	0.9–69	30	10	L ^{ns}	0.00	1.0	50	2	1.000	0.00000	
WatPot-d	0.4–69	40	20	L ^{ns}	0.02	1.4	73	2	0.9441	0.00672	
$c_i : c_a$	0.9–50	50	25	L***	0.59	−1.2	8	4	1.029	−0.00363	
Resp/ M_L	0.3–45	300	105	L*	0.02	1.2	60	5	0.9663	0.00432	
Resp/ M_{L+5}	0.4–33	50	15	L***	0.41	2.2	67	2	0.7818	0.01911	
Resp/ M_R	0.5–32	30	10	L ^{ns}	0.00	−1.0	47	2	1.011	−0.00049	
4. Growth and reproduction											
RGR	0.1–69	1060	250	S***	0.66	2.7	94	7	1.248	0.7674	0.1899
ULR	0.2–64	690	165	S***	0.75	8.9	99	6	3.235	0.9384	0.03878
LAR	0.1–65	1380	335	S***	0.51	− 2.8	5	7	0.5522	−2.013	0.1236
SLA	0.1–75	2190	520	S***	0.69	− 2.4	2	8	0.5723	−1.517	0.09576
LMF	0.1–65	1410	360	S***	0.17	−1.2	27	8	0.8848	−0.2232	0.06975
SMF	0.1–65	1240	325	L***	0.07	−1.3	33	8	1.036	−0.0044	
RMF	0.1–71	1530	390	S***	0.40	1.6	85	8	1.275	0.4042	0.08225
ConCos _L	0.5–40	100	30	L***	0.21	1.1	74	6	0.9860	0.001628	
PaBaTi _L	1.0–40	70	25	S***	0.51	− 2.9	4	2	0.615	−2.264	0.16206
TDM	0.1–75	1520	385	S***	0.37	9.8	96	7	2.345	0.9633	0.06686
InSeMa	1.9–62	90	20	S***	0.02	1.6	76	3	1.164	0.4409	0.1557
#SeeFru	0.4–62	120	30	S***	0.14	> 50	96	3	3.736	1.053	0.04738
RepEff	1.9–52	40	10	L**	0.24	2.1	59	1	0.8406	0.0199	

Columns 2 and 3 indicate the range of DLI for which records are present and the total number of observations (equal to number of averaged values per species and light intensity over all experiments; rounded to the nearest 10). Column 4 shows the number of species for which we have observations for the various traits. The fit refers to the form of the dose–response curve. Fitted equations were either linear (L; $Y = a + bX$, where Y is the scaled value of the phenotypic trait of interest and X is the DLI), saturating (S; $Y = a[1 - b \exp(-cX)]$), exponential (E) or with a local maximum (M), both of which were fitted with a second-order polynomial ($Y = a + bX + cX^2$). The plasticity index (PI) as used here is the highest fitted value in the DLI range of 1–50 mol m^{−2} d^{−1} divided by the lowest fitted value, with positive values indicating positive trends with DLI and negative values decreasing trends; bold numbers indicate a $|PI| \geq 2.0$. The r^2 refers to the approximate fit in the previous column. The percentage increases refers to the percentage of all cases (species/experiment combinations) where the phenotypic value at the highest DLI was larger than at the lowest. Values close to 0 or 100 indicate highly consistent responses. The next column indicates the reliability level of the data, given the number of records in the database, the number of species, the range of DLI levels at which is measured and the average deviation from the median response, with a scale from 0 (low) to 9 (high reliability level). The last three columns give the values for parameters *a*, *b* and (if relevant) *c* for the equations mentioned.

Significance of the linear term (for linear relationships) and the quadratic term (for all other relationships) are indicated as follows: ns, nonsignificant; +, 0.05 < P < 0.10; *, P < 0.05; **, P < 0.01; ***, P < 0.001.

2. Chemical composition

Total leaf N content per unit leaf area (N_{tot}/A) increases two-fold over the DLI range considered (Fig. 3a; Table 2a) and scales well with leaf thickness and A_{mes}/A (Fig. 2b,c). However, LMA increases more, and consequently the concentration of leaf total N declines ($[N_{\text{tot}}]_L$; $PI = -1.3$). Interestingly, this is different from the concentration of organically bound N in leaves, which is not significantly affected by DLI. This difference is explained by the leaf

nitrate concentration, which is high in low light and decreases with increasing DLI in nitrate-accumulating species ($PI = -2.3$). Nitrate serves as an N-source for constructing proteins, Chl and DNA/RNA. However, especially for herbaceous species, nitrate may also be a readily available and cheap vacuolar osmoticum, particularly at low DLI. At high DLI, when photosynthesis and growth rate are faster, the demand for organic N is higher, and so is the supply of sugars. Under the latter conditions, vacuolar nitrate is exchanged for soluble sugars and organic acids (Blom-Zandstra &

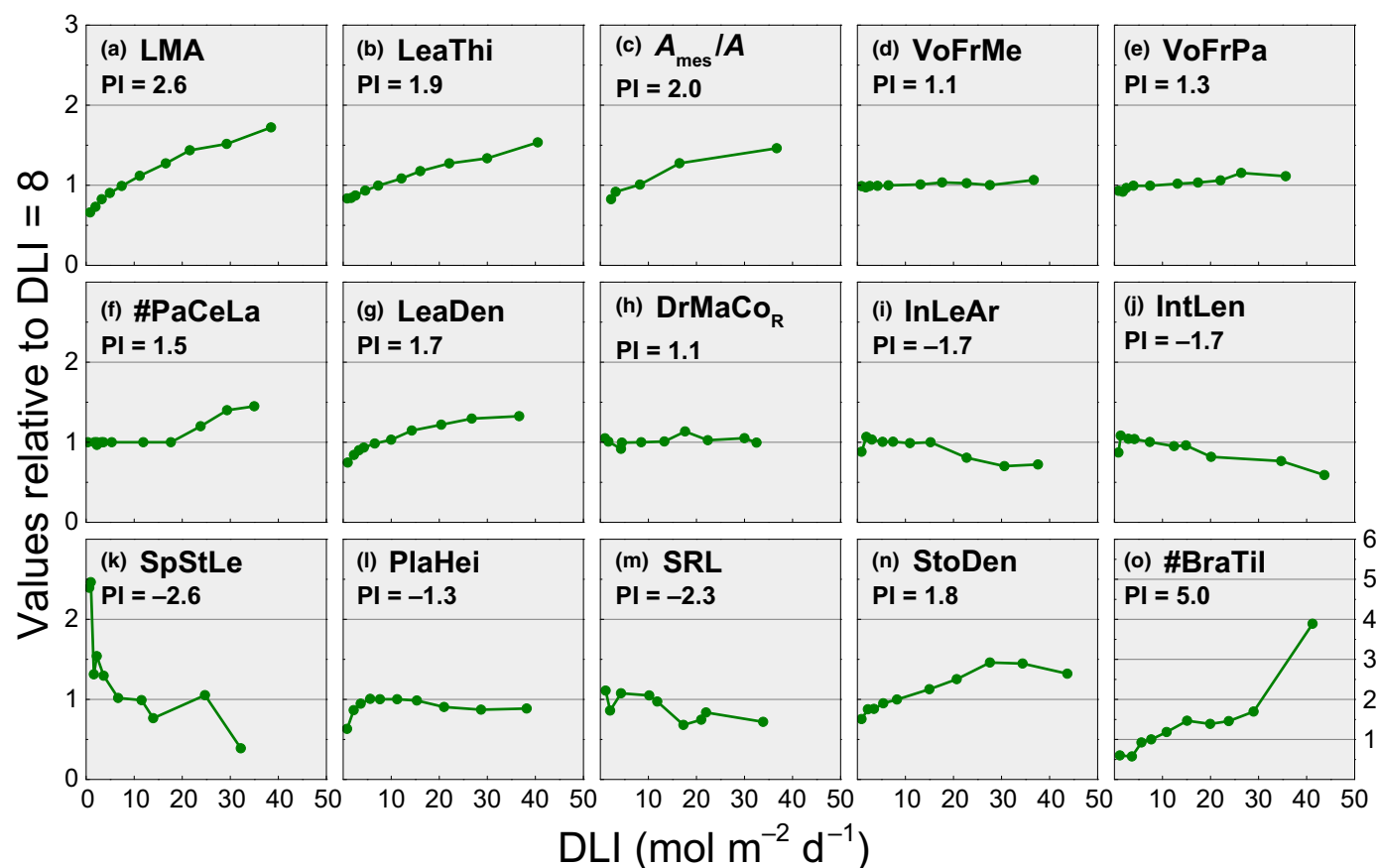


Fig. 2 Overall response of 15 anatomical and morphological plant traits to the daily light integral (DLI) during growth, as well as their plasticity index (PI) values. All data in the database for a given trait were normalized to the value plants in a specific experiment had at a DLI of $8 \text{ mol m}^{-2} \text{ d}^{-1}$ and grouped into 10 groups on the basis of deciles for the actual DLI during growth, or less so if the minimum number of observations would become < 10 . For each group, the median value for DLI and the scaled plant trait of interest was calculated. The closer the points are in the x-direction, the denser the information in that part of the curve. The total number of observations for each trait and extended definitions are listed in Table 2. Graphs with more details per trait can be found in Supporting Information Figs S2–S72. Note that the PI values are calculated for the $1\text{--}50 \text{ mol m}^{-2} \text{ d}^{-1}$ range based on the fitted lines, and therefore will be larger than the ratio of lowest and highest points in these graphs. Traits listed are (a) LMA, leaf dry mass per area; (b) LeaThi, leaf thickness; (c) A_{mes}/A , area of mesophyll relative to leaf area; (d) VoFrMe, fraction of leaf volume occupied by mesophyll, including air spaces; (e) VoFrPa, fraction of mesophyll volume occupied by palisade parenchyma, airspaces included; (f) #PaCeLa, number of palisade parenchyma cell layers; (g) LeaDen, leaf density; (h) DrMaCo_R, root dry mass per area; (i) InLeAr, individual leaf area; (j) IntLen, internode length; (k) SpStLe, specific stem length; (l) PlaHei, plant height; (m) SRL, specific root length; (n) StoDen, stomatal density; (o) #BraTil, number of branches or tillers.

Lampe, 1985). Information on nitrate concentrations in stems and roots is almost absent, so it remains unclear whether they respond similarly to DLI as leaves do. As we also found little information on N in stems and roots, we merged estimates of organic and total N concentrations. In both organs, N concentration decreased with DLI, but more so for stems.

Leaf C concentration increases slightly ($[C]_L$, $\text{PI} = 1.1$) but consistently with DLI (Fig. 3f), in 85% of the cases considered. This relates at least partly to decreases in nitrate and other minerals, but it may also be due to increases in compounds with high concentrations of C, such as lipids, lignin, or soluble phenolics. The limited data on C concentration in stems and roots revealed minor increases with DLI (Table 2a). Leaf phosphorus concentration ($[P]_L$), on the other hand, decreased surprisingly strongly ($\text{PI} = -1.8$), more than total leaf N. This would imply that P uptake cannot keep up with increased growth at higher light. We have tried to find supportive evidence from reported N : P ratios in leaf biomass grown at different

light levels (Güsewell, 2004), but so far little information is available, and this is true for stems and roots as well.

The concentration of nonstructural carbohydrates in the leaves measured for the second half of the diurnal period ($[TNC]_L$) more than doubles in a linear manner with increasing DLI (Fig. 3h). There is wide variability among species in the form of nonstructural carbohydrates accumulated, but generally plants accumulate a mix of soluble sugars (sucrose, short-chain fructans) and large polymers (starch, long-chain fructans). DLI does not affect the fraction of total nonstructural carbohydrates present as soluble sugars (SolSug/TNC_L , $\text{PI} = -1.0$). The very limited amount of data on the nonstructural carbohydrate concentration of stems and roots suggests that the effect of DLI is of similar magnitude as for leaves (Table 2a). This is interesting, as most other chemical constituents in roots, as well as root dry matter content, are hardly affected by light availability. Of all groups of compounds considered here, the one with the strongest response observed

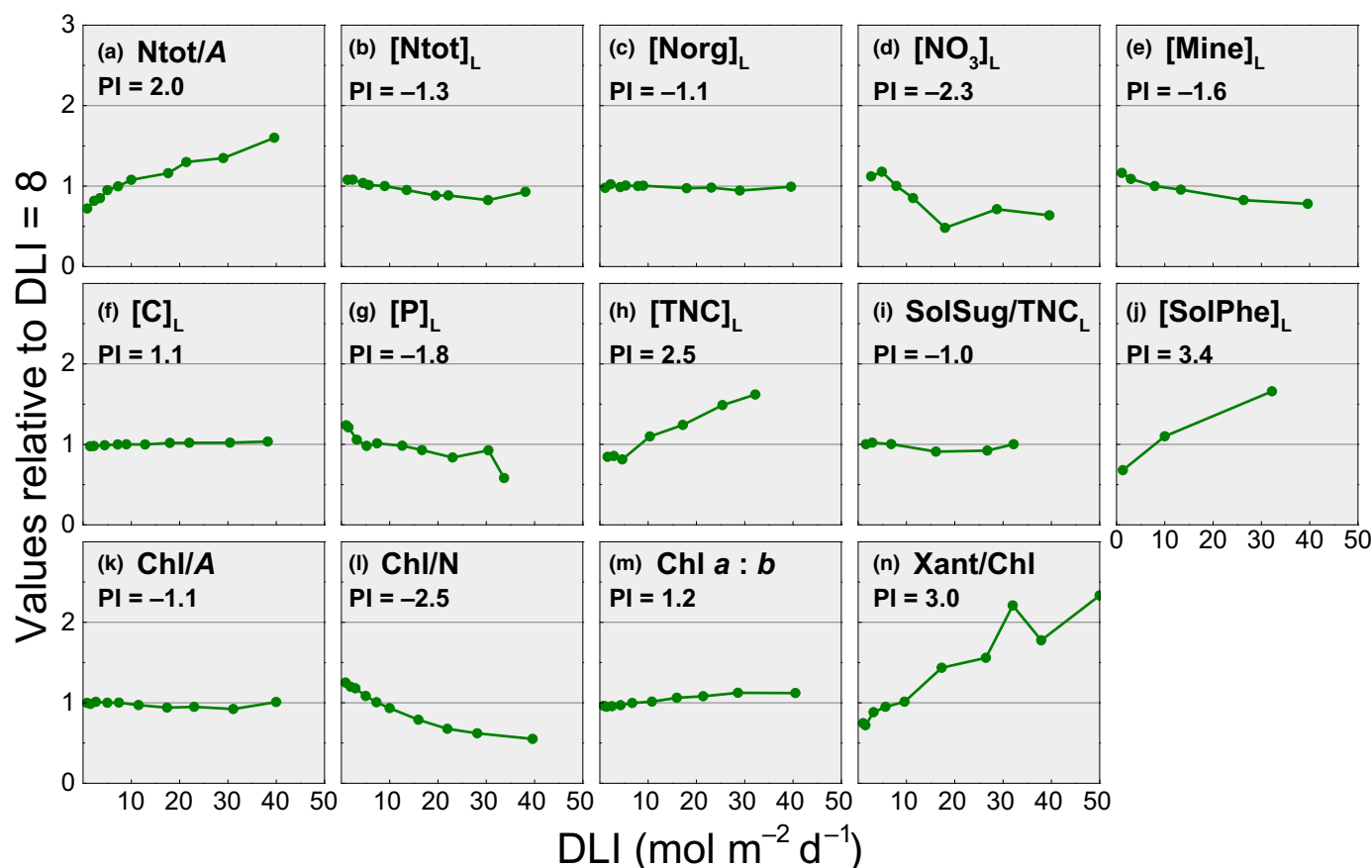


Fig. 3 Overall response of 14 chemical plant traits to the daily light integral (DLI) during growth, as well as their plasticity index (PI) values. Traits listed are (a) N_{tot}/A , content of total nitrogen (N) in the leaves expressed per unit leaf area; (b) $[N_{tot}]_L$, concentration of total N in leaves; (c) $[N_{org}]_L$, concentration of organic N in leaves; (d) $[NO_3]_L$, concentration of nitrate in leaves; (e) $[Mine]_L$, concentration of minerals in leaves; (f) $[C]_L$, leaf carbon concentration; (g) $[P]_L$, concentration of total phosphorus in leaves; (h) $[TNC]_L$, concentration of nonstructural carbohydrates in the leaves; (i) $SolSug/TNC$, fraction of leaf nonstructural carbohydrates present as soluble sugars; (j) $[SolPhe]_L$, concentration of soluble phenolics in leaves; (k) Chl/A , Chl per unit leaf area; (l) Chl/N , Chl per unit leaf N; (m) $Chl\ a : b$, $Chl\ a : Chl\ b$ ratio; (n) $Xant/Chl$, xanthophylls (violaxanthin + antheraxanthin + zeaxanthin) per unit Chl. For more information, see the legend of Fig. 2.

has been measured only occasionally. This is the group of soluble phenolics ($[SolPhe]_L$), which more than triples as DLI increases from 1 to $50\ mol\ m^{-2}\ d^{-1}$. Their phenolic ring absorbs UV radiation, which makes them useful protectors against DNA damage, especially in the upper epidermis of the leaves (Ballaré *et al.*, 2011).

Chl content per unit leaf area (Chl/A) shows almost as many increasing as decreasing trends, and therefore the overall response to DLI is nonsignificant ($PI = -1.1$; Fig. 3k). Interestingly, there is a significant interaction: woody species often show decreasing Chl per area with DLI, whereas herbaceous species generally show increases ($P < 0.001$; Table S1). We expect the Chl concentration per unit mass to decrease as LMA more than doubles. This is also true for the Chl-to-N ratio, which has a similar PI to that for LMA (-2.5). The decrease is highly consistent across cases, without strong plasticity differences between herbaceous and woody species. Simultaneously, the amount and/or activity of Rubisco per unit leaf area increases strongly with DLI (Fig. 4d). Altogether, this indicates a coordinated shift in N-investment patterns in the photosynthetic machinery from light harvesting (Chl) at low light towards C

fixation (Rubisco) at high light (Anderson *et al.*, 1995; Niinemets & Tenhunen, 1997; Evans & Poorter, 2001). Furthermore, there is a small increase in the $Chl\ a : Chl\ b$ ratio with DLI, although this is less consistent as we expected, being found in 82% of the cases.

Three carotenoids, violaxanthin, antheraxanthin and zeaxanthin, together constitute the xanthophyll cycle and do play a specific role in dissipating excitation energy at moments when light levels exceed the plant's capacity for photosynthetic electron transport and C fixation. As expected, they increase strongly with light level ($Xant/Chl$, $PI = 3.0$, Fig. 3n). Although other carotenoids, like lutein and β -carotene, may also be involved in mitigating excess excitation energy and electrons, they are less responsive to DLI (Esteban *et al.*, 2015).

3. Physiology

Light absorbance by leaves is partly dependent on compounds such as anthocyanins, internal light scattering, and leaf pubescence, but Chl content is the dominant factor, with absorbance increasing asymptotically with Chl per area (Evans,

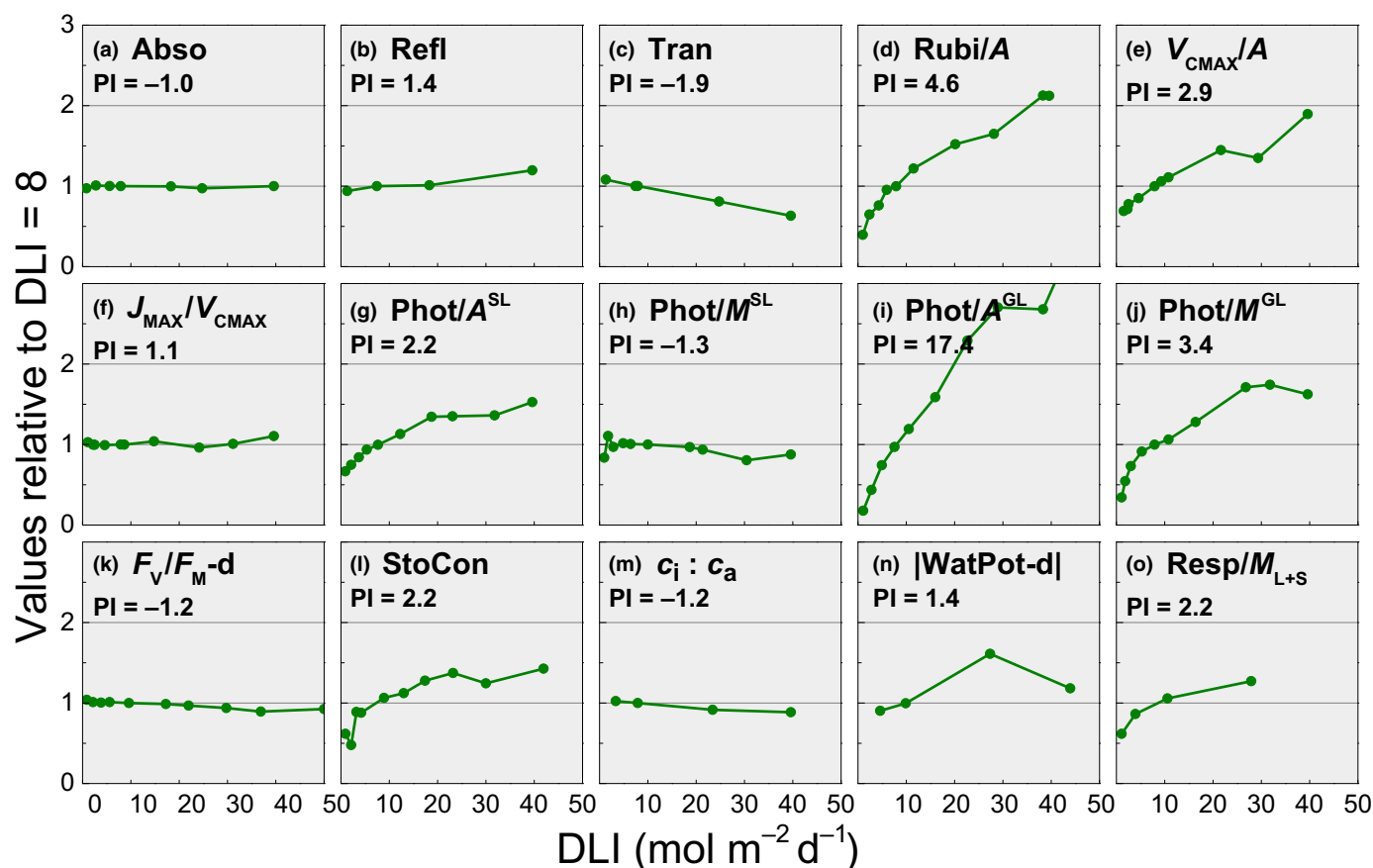


Fig. 4 Overall response of 15 physiological plant traits to the daily light integral (DLI) during growth, as well as their plasticity index (PI) values. Traits listed are (a) Abso, leaf absorbance; (b) Refl, leaf reflectance; (c) Tran, leaf transmittance; (d) Rubi/A, Rubisco content or activity per unit leaf area; (e) V_{CMAX}/A , maximum rate of carboxylation per unit leaf area; (f) $J_{\text{MAX}}/V_{\text{CMAX}}$, ratio between maximum rate of electron transport and maximum rate of carboxylation; (g) $\text{Phot}/A^{\text{SL}}$, rate of photosynthesis per unit leaf area at saturating light levels; (h) $\text{Phot}/M^{\text{SL}}$, rate of photosynthesis per unit leaf mass at saturating light levels; (i) $\text{Phot}/A^{\text{GL}}$, rate of photosynthesis per unit leaf area at growth light conditions; (j) $\text{Phot}/M^{\text{GL}}$, rate of photosynthesis per unit leaf mass at growth light conditions; (k) $F_V/F_M\text{-d}$, ratio of dark-adapted variable fluorescence to maximum fluorescence measured for plants during the diurnal period; (l) StoCon, stomatal conductance in growth conditions; (m) $c_i : c_a$, CO_2 concentration in the intercellular air spaces relative to the concentration in ambient air; (n) $|\text{WatPot-d}|$, water potential during the diurnal period; (o) $\text{Resp}/M_{\text{L+S}}$, rate of shoot respiration per unit shoot dry mass. For more information, see the legend of Fig. 2.

1996). The fact that absorbance does not change across DLI (Abso; Fig. 4a) is therefore in line with Chl content being unaffected (Fig. 3k). Reflectance, on the other hand, increases with DLI in a linear manner ($\text{PI} = 1.4$), likely by increased reflection at the leaf surface or internally. Transmittance, therefore, decreases with increasing light.

The maximum RuBP-carboxylase activity of Rubisco derived from gas exchange (V_{CMAX}/A), an *in vivo* estimate of Rubisco activity, increases with DLI (Fig. 4d), in agreement with the even stronger increase in *in vitro* measured Rubisco content. J_{MAX}/A , the capacity to regenerate RuBP, generally increases in parallel with V_{CMAX}/A , resulting in a $J_{\text{MAX}}/V_{\text{CMAX}}$ ratio that increases marginally across the full DLI range. The increase in V_{CMAX}/A scales reasonably in form and extent with the observed photosynthetic rate at saturating light ($\text{Phot}/A^{\text{SL}}$), which more than doubles. The increase also scales quantitatively with the increases in A_{mes}/A and LMA; consequently, the light-saturated rate of CO_2 fixation expressed per unit leaf dry mass ($\text{Phot}/M^{\text{SL}}$) is not affected by light. The importance of changes in leaf and mesophyll thickness, and consequently LMA, for high-light-induced increases in

photosynthetic capacity is also reflected in plasticity differences between woody and herbaceous species. The smaller plasticity of woody species for leaf thickness and LMA is also observed in lower plasticity for light-dependent alterations in area-based photosynthetic capacity, Rubisco, and (although nonsignificant) in V_{CMAX}/A (Table S1).

How do all these changes work out on the most relevant photosynthetic variable for growth: the area-based rate of photosynthesis under growth light conditions ($\text{Phot}/A^{\text{GL}}$)? This variable is highly responsive to DLI, with only a modest curvature at high light levels (Fig. 4i). The PI (17.4) is the second highest observed in this analysis, with a similar plasticity difference between woody and herbaceous species as was found for other area-based photosynthetic characteristics (Table S1). The photosynthetic rate per unit leaf mass increases far less, indicating that intracellular physiology probably responds more similarly across different plant functional types than leaf anatomy. Regarding photochemistry, F_V/F_M measured predawn is not affected by DLI (Table 2b), but there is a small decrease in F_V/F_M measured during the diurnal period. This indicates absence of photoinhibition in the majority of experiments

and some downregulation of photosynthetic efficiency at high DLI. However, because photosynthesis is more constrained by the Calvin cycle than by electron transport under high light conditions, C fixation generally is not hampered.

Stomatal conductance (StoCon; Fig. 4l) under growth conditions increases to a similar extent with DLI as stomatal density does (Fig. 2n). However, the increase is not sufficient to keep up with the increasing demand for CO₂ by photosynthesis. Consequently, the intercellular to ambient CO₂ concentration ratio ($c_i : c_a$) declines with increasing DLI. Although the fold-change is small, the decrease is highly consistent and seen in 92% of the cases (Table 2b). A lower StoCon decreases the transpirational costs per C fixed (Flexas *et al.*, 2016), but might – due to increased photorespiration at low c_i – negatively affect photosynthesis. However, this is more than compensated by the direct positive effect of high light on C fixation. Increased StoCon, in combination with higher leaf temperatures, enhances the transpiration rate per unit leaf area. As plants are also larger at high DLI, this results in a substantial increase in the demand for water. Particularly when grown in pots, but probably also in the field, this may increase the probability of drought stress. Indeed, the few measurements on leaf water potential during the day show more negative values at high DLI (Table 2b), although the effect of DLI was nonsignificant.

Much information is available on photosynthetic variables, especially under light-saturated conditions, but we understand little of what happens at the respiratory side, although this comprises 30–70% of gross C gain at the whole-plant level (Raich *et al.*, 2014). Most of the respiratory information comes from photosynthetic light-response curves, measured on (part of) a single fully mature leaf. Mass-based leaf respiration shows a modest increase with DLI in these cases (PI = 1.2; Table 2b), which is consistent with larger maintenance costs and higher transport rates of assimilates at high DL. However, estimating low CO₂ fluxes in small leaf cuvettes can be problematic for various reasons (Pons & Welschen, 2002; Rodeghiero *et al.*, 2007), so reported respiration rates are potentially inaccurate. Moreover, measurements in fully mature leaves do not provide good estimates for whole-plant C budgets because the high respiration rates of actively growing tissues are not included. Measurements of whole shoots (Resp/ M_{L+S}) show that mass-based respiration doubles across the DLI range (Fig. 4o). This fits better with the notion that faster growing plants (Fig. 5b) have higher respiration rates as a result of increased growth-related metabolism. Therefore, we also expected higher root respiration, but this is not supported by the limited data.

4. Growth and reproduction

Whereas photosynthesis measurements provide detailed insights into the C gain of (part of) a specific leaf, the growth parameter unit leaf rate (ULR, the rate of increase in biomass per unit leaf area) yields a time-integrated growth estimate over all leaves of a plant. ULR is generally well correlated with whole-plant average daily net photosynthesis (Poorter & Van der Werf, 1998; Pons & Poorter, 2014). It has an 8.9-fold increase over the DLI range considered

(Fig. 5a), with increases in 99% of cases, and is only slightly more curved than the area-based photosynthetic rate (Phot/ A_{GL} , Fig. 4i). Short-term measurements in field experiments are not necessarily representative of daily C gain, so a perfect correlation may not be expected. Nonetheless, the relative changes of ULR and *in situ* photosynthesis do show similar responses. Like area-based photosynthesis, there is a larger plasticity difference between species groups, with the ULR of woody species increasing less with DLI than for herbs (Table 2b). Differences in the ability to adjust leaf structure may play a role here.

Whereas the rates of photosynthesis and growth per unit leaf area increase strongly with DLI, we found the response in relative growth rate (RGR) to be much weaker (PI = 2.7, Fig. 5b). There are modest decreases in mass fractions of leaves and stems, whereas the mass fraction of roots increases. This change in allocation of biomass is considered to be functional with respect to the higher requirements for water and nutrients by faster-growing and -transpiring plants at high DLI (Bloom *et al.*, 1985). A more dominant 2.4-fold decrease occurs for specific leaf area (SLA), the inverse of LMA (Fig. 2a). Relationships between these growth-related variables are discussed in the next section.

Growth can also be analyzed as a function of construction costs, the amount of glucose required to build 1 g of plant biomass, taking into account the biosynthetic pathways and chemical composition (Penning de Vries *et al.*, 1974; Cavatte *et al.*, 2012) and the time for a plant to recoup these costs by photosynthesis (payback time; Williams *et al.*, 1989). Leaf construction costs per unit mass (ConCon_L) increase only marginally with DLI (Fig. 5h), partly because the concentrations of two relatively cheap groups of compounds, minerals and nonstructural carbohydrates, change in opposite direction with increasing DLI. Biosynthetically more expensive compounds, like proteins, hardly change, or increase but are present in low concentrations anyway (soluble phenolics; Fig. 3j). Leaf payback time (PaBaTi_L), on the other hand, strongly increases at low light, due to the low mass-based rate of photosynthesis. There is little knowledge on construction costs of stems and roots, but they are likely not much affected either. Since the payback time of a whole plant equals doubling time, and therefore is another expression of RGR (Poorter, 1994), we expect that the plasticity of payback time at the whole-plant level is in the same range as that of leaves and the inverse of RGR.

Whole-plant dry mass is one of the few traits presented here that is not normalized by area, mass or in another way. Biomass accumulation over time often starts exponentially; and as different experiments had different duration, this may well interfere with the strength of the proportional light response. We nevertheless included total biomass in the analysis because it is such an important variable, under the assumption that variation in duration of experiments is unrelated to the DLI applied. Total Dry Mass saturates as a function of DLI, with a PI of 9.8 (TDM; Fig. 5j). The increase in biomass with DLI in herbaceous plants is much greater than in woody species (Table S1). Many shade-tolerant species do not thrive well at DLI levels > 15–20 mol m⁻² d⁻¹. Semchenko *et al.* (2012) concluded from an experiment with a range of herbaceous monocots and eudicots that

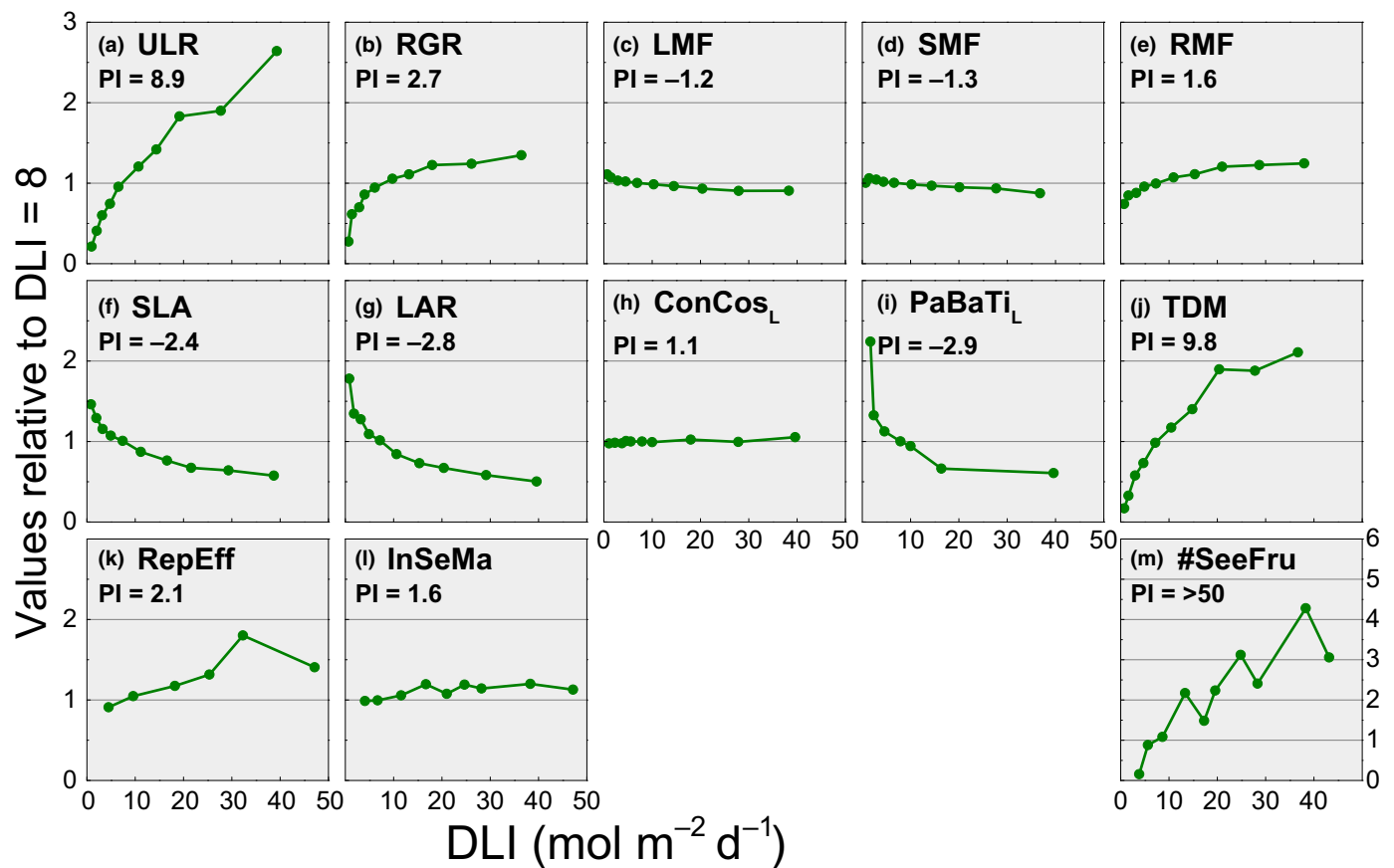


Fig. 5 Overall response of 13 growth- and reproduction-related plant traits to the daily light integral (DLI) during growth, as well as their plasticity index (PI) values. Traits listed are (a) ULR, unit leaf rate; (b) RGR, relative growth rate; (c) LMF, leaf mass fraction; (d) SMF, stem mass fraction; (e) RMF, root mass fraction; (f) SLA, specific leaf area; (g) LAR, leaf area ratio; (h) ConCos_L, construction costs of the leaves; (i) PaBaTi_L, payback time of leaves; (j) TDM, total vegetative dry mass; (k) RepEff, reproductive effort; (l) InSeMa, individual seed mass; (m) #SeeFru, number of seeds or fruits per plant. For more information, see the legend of Fig. 2.

this would be true for herbaceous species in general, as plants from 100% light in their garden experiment produced on average 35% less dry mass than at 50% light. However, considered over all experiments in our analysis, we do not see this to be a general trend. Inability to respond to high light might be indicative of other stress factors at high light, such as limited nutrient availability or drought (Osmond, 1983).

Reproductive effort, which is the fraction of total biomass invested in generative organs, doubles over the DLI range (RepEff; Fig. 5k; Table 2b). This variable is known to depend positively on plant size (Weiner *et al.*, 2009). Total reproductive output of an individual plant is determined by the number of seeds produced and the mass per seed. Individual seed mass (InSeMa) increases in a saturating fashion, with a PI of 1.6. Seeds from high-light-grown plants therefore have a larger embryo size and/or more seed reserves, which gives them a head start after germination. However, the main variable affected by light availability is the number of seeds or fruits produced (#SeeFru), which shows a strong response to DLI. Unfortunately, our PI approach falls short here, as most experimental plants grown at a DLI $< 3\text{--}4\text{ mol m}^{-2}\text{ d}^{-1}$ do not reproduce. Such plants may indeed not reproduce at low DLI at all or take longer to initiate reproduction than the duration of most

experiments (Kachi, 2012; Poorter *et al.*, 2016). We cannot, therefore, precisely calculate its PI, but the response is the strongest of all 70 traits discussed here.

IV. The overall response of plants to DLI

1. A whole-plant perspective

Fig. 6 summarizes the responses to light of many of the 70 variables analyzed, and also shows our conceptual model of the most important relationships between these traits, if variation in all other traits were to be controlled for. The main chain of events, indicated by a central vertical axis with bold arrows in Fig. 6, starts with the effect of light intensity on leaf anatomy, which then affects photosynthetic capacity, actual C gain, growth and eventually seed production. Different traits in this chain are differently stimulated by DLI, which in part can be understood by the modulating effects by traits shown to the left or right of this central axis. Based on the plasticity indices (PIs; Table 2), the overall response to a 50-fold increase in DLI is a 50% increase in palisade parenchyma cell layers (#PaCeLa, PI = 1.5). The increase in leaf thickness and A_{mes}/A is *c.* 100% (PI = 2.0), as (palisade) cells also become larger (Ivanova

et al., 2006). The increase in the amount of Rubisco and $V_{\text{C}_{\text{MAX}}}$ per unit leaf area are even stronger (PIs of 4.6 and 2.9), at least partly due to a preferential investment of N into compounds related to the dark reactions of photosynthesis. The increase in area-based light-saturated photosynthesis, therefore, is somewhat higher than the increase in A_{mes}/A . All of these light-induced changes are modest compared with the PI for the area-based rate of photosynthesis at growth light intensity, which is 17.4. This value is so much higher partly because photosynthetic capacity increases with DLI, but also because the actual photon flux driving the C fixation differs 50-fold. The main reason why the actual rate of photosynthesis is not stimulated more than 17-fold is that the photosynthetic capacity of the leaves largely plateaus above a DLI of $20 \text{ mol m}^{-2} \text{ d}^{-1}$. Additionally, as can be derived from the lower $c_i : c_a$ under high light conditions, the intercellular CO_2 concentration drops, with negative impacts on photosynthesis through decreased substrate supply and increased photorespiration.

ULR, the daily growth rate per unit leaf area, shows only half the response to DLI of the actually measured photosynthetic rates (PI = 8.9). ULR differs from actual short-term photosynthetic measurements in three ways: (1) it integrates C fixation over the full light period and all leaves; (2) it includes the C losses through respiration, exudation and volatilization of the whole plant; and (3) it incorporates how much biomass is built with one unit of C (Pons & Poorter, 2014). There is a small increase in leaf [C] with DLI (PI = 1.1; Fig. 3f), but stem and root [C] are hardly affected, and consequently whole-plant [C] will only have a minor negative effect on ULR. Shoot respiration increases with DLI, and root respiration – though unaffected in our analysis by DLI on a root mass basis – may still increase whole-plant respiration rate because respiratory rates of roots are generally higher than for shoots (Lambers *et al.*, 2008) and high-DLI plants invest relatively more of their biomass in roots. The few reports available where C budgets for whole plants were made indicate respiration to be a constant fraction of whole-plant photosynthesis across a wide DLI range (McCree & Troughton, 1966; Pons & Poorter, 2014). Therefore, losses through respiration could not explain the difference in PI either, unless respiration were to become a much larger fraction of photosynthesis at DLIs close to 1, which is to be expected. As yet, there are too few measurements on C budgets to make firm conclusions on the PI differences. However, since our database contains a large number of short-term photosynthetic and respiratory measurements on one individual leaf, the quantitative discrepancy we observe here between photosynthetic rates and ULRs may well be caused by challenges in scaling up individual leaf measurements to whole plants.

The PI of relative growth rate (RGR) is again much lower (2.7) than the one for ULR. RGR is a mass-based rate. Since the higher area-based photosynthetic and biomass gains are realized with leaves that are much heavier (and hence have a much lower SLA), and with preferential investment in roots (and hence a lower leaf mass fraction; LMF), the biomass gain is actually much more modest on a whole-plant mass than a leaf-area basis. Nevertheless, TDM again shows a high PI (9.8), due to the fact that, through a higher RGR, plants accrue exponentially more biomass. A negative feedback will be that plants of larger size

invest more biomass in stems and thereby less in leaves (lower LMF). Another negative feedback is that increasing plant size causes increased internal shading, thus reducing whole-plant area-based C fixation.

The effect on TDM is crucial, as it has strong positive effects on reproduction. Plant reproduction depends on a wide range of factors, including vegetative biomass, the number of tillers or flowering stalks, number of inflorescences and actual sugar availability. All of these increase with DLI, and so do individual seed mass (PI = 1.6) and reproductive effort (PI = 2.1). However, the most important factor determining seed production is the DLI effect on TDM.

2. The shape of the DRCs

Approx. 40% of traits considered show a saturating response to light. However, full saturation at the highest DLI most plants are ever likely to encounter ($50 \text{ mol m}^{-2} \text{ d}^{-1}$) was achieved for only a few traits. Of the phenotypic changes over the light range from 1 to $50 \text{ mol m}^{-2} \text{ d}^{-1}$, 25% already was realized at a DLI of 5, and 76% at a DLI of $20 \text{ mol m}^{-2} \text{ d}^{-1}$. The reason why a number of traits saturate may be related to restrictions in leaf anatomy. For area-based processes to increase requires thicker leaves with more cell layers. There may be an organizational limit to the number of palisade layers that can function properly on top of each other, and therefore also to the photosynthetic machinery. Linear relationships were found for c. 55% of the traits. Most of these traits have a low PI, except soluble phenolics and xanthophylls, which fulfill important photoprotective roles at high light levels. Especially for several root and physiological traits, data for high-light-grown plants (DLI > 30) are scarce; if more information becomes available, these relationships might be found to be saturating as well.

Only three traits have a DRC with a maximum at intermediate light levels (Fig. 2i,j,l). As already discussed, individual leaf area and internode length generally decrease with DLI, but also decrease at low C availability. In the short time frame of most experiments, total plant height follows internode length. However, integrated over many growing seasons, high-light-grown trees may achieve greater length than low-light ones. The only variable that responds exponentially to DLI is the number of branches and tillers. They increase especially at DLI levels larger than $25 \text{ mol m}^{-2} \text{ d}^{-1}$ (Fig. 2o).

3. Reliability of the DRCs

The current meta-analyses summarize existing data into an average DRC per trait. However, the number and quality of underlying data vary largely among traits. We therefore rated each trait with a 'Reliability' score with a value from 0 to 9 (Table 2), based on (1) the total number of observations, (2) the number of species for which information is present, (3) the DLI range over which we have data and (4) the overall degree of variability around the fitted line. More than half of the traits have a value < 6, with especially low values for physiological characteristics like shoot and root respiration, reproductive characteristics, and for stem and root chemical composition. These variables are essential to understand whole-

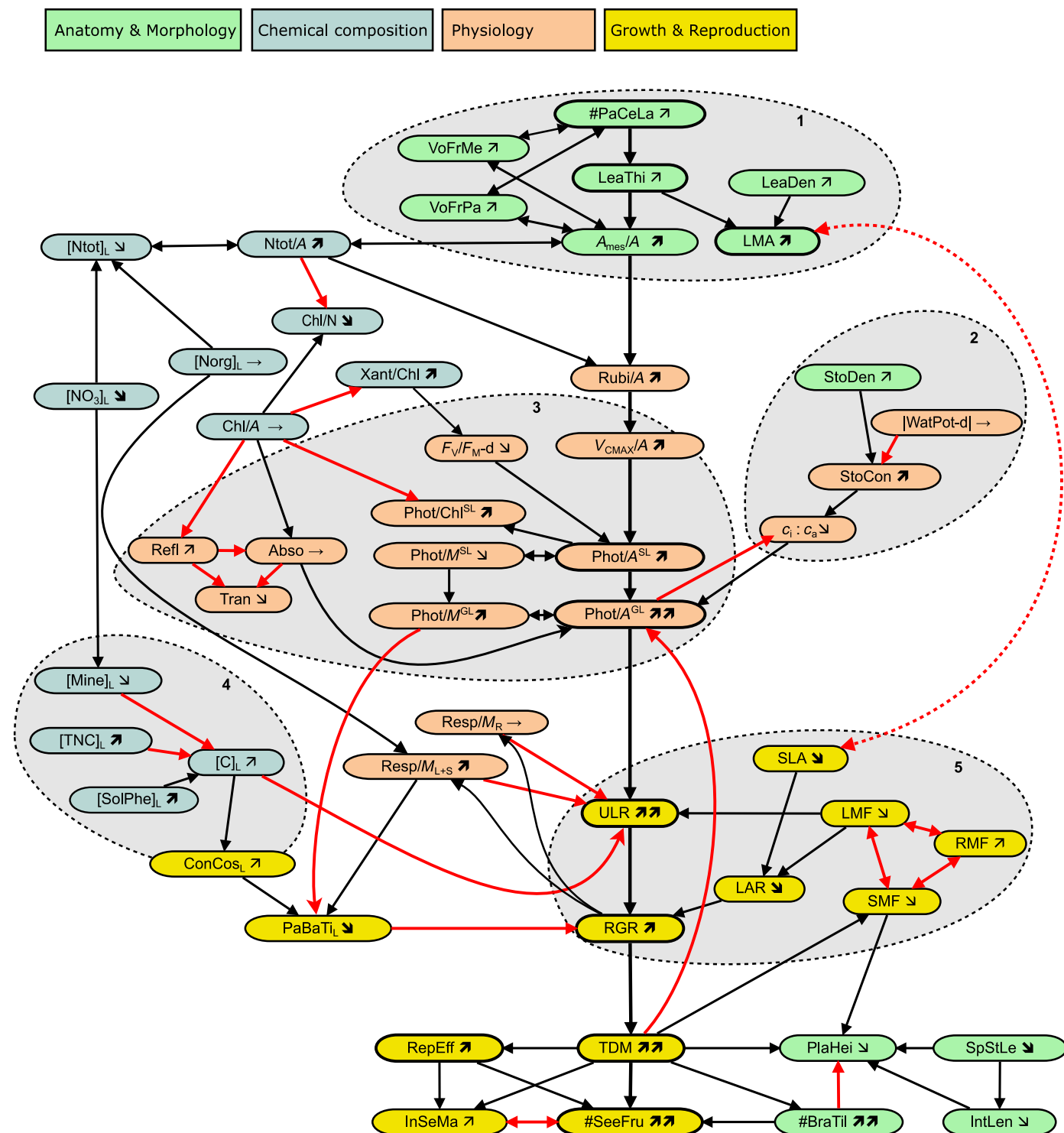


Fig. 6 Relation diagram of plant traits and how they are affected by daily light integral (DLI). The lines with arrows between boxes indicate positive (black) or negative (red) relationships between two traits when all other traits would remain constant. Arrows behind each trait indicate whether the effect of light on that trait is positive (upward arrows), neutral (horizontal arrows) or negative (downward arrows). Bold arrows indicate that the plasticity index (PI) is > 2 or < -2 , respectively; double upward bold arrows indicate a $PI > 5$. The color of the boxes indicates to which of the four categories used in the paper the trait belongs. The traits arranged vertically in the middle of the diagram, connected with thicker arrows, are considered the most basic chain of events in light acclimation: more cell layers in the leaf leads to thicker leaves, with higher photosynthetic capacity, resulting in faster growth, higher biomass and greater seed production. Explanation of all variables can be found in Table 1. The gray areas indicate traits that form logical groups, and are only for clarity. 1, leaf morphology; 2, water relations; 3, photosynthetic traits; 4, chemical composition other than nitrogen compounds; 5, growth analysis traits. Also, for clarity reasons, only those traits were included that have clear relationships with other traits in the present analysis. See Table 1 for explanation of all trait abbreviations.

plant responses to shade. It is our hope that plant biologists will pay more attention to quantifying the light response of these traits. Other traits have a high reliability score, which gives more confidence in the DRC, and will also allow easier identification of species groups with a particularly low or high PI.

V. Molecular response and regulation

Given the myriad of phenotypic responses already discussed, an interesting question is how the acclimation of plants to DLI is regulated. Molecular regulation is a field in its own right, and for recent reviews the reader is referred to Dietz (2015) and Ballaré & Pierik (2017). Most of what we know about light effects actually pertains to short-term responses of photosynthesis. Here, we discuss some of the long-term responses that are relevant given the observed DRCs.

A simple straightforward light regulation for plants would be to measure available photosynthates and accommodate the DLI responses accordingly. Starch accumulation over the day and breakdown during the night is well regulated (Graf *et al.*, 2010), although the actual sensing mechanism is unknown. More is understood about the sensing of soluble sugars, where trehalose 6-phosphate, target of rapamycin kinase and Snf1-related kinase are playing a role (Lastdrager *et al.*, 2014). Is it starch and sugar sensing that informs the plant about the prevailing DLI and sets the growth machinery in motion? An interesting experiment of Ludwig *et al.* (1975) showed that the nocturnal respiration of a given tomato leaf was directly related to its rate of photosynthesis during the preceding diurnal period. As far as increased respiratory activity implies enhanced metabolic activity, this could indeed accord with sugar-sensing mechanisms triggering downstream growth responses. However, they also showed that respiration responded more strongly when photosynthesis was altered by varying light intensity than by changing atmospheric CO₂. Similarly, DRCs for allocation, leaf morphology and growth are rather different for light and CO₂, and so is the growth response if light and CO₂ stimulate photosynthesis to the same extent (Poorter *et al.*, 2013). Given the strong interactions of light with other environmental factors, we assume that regulation by various mechanisms will allow for more adequate responses anyway.

Photoreceptors are logical candidates to co-regulate the response of plants to light. Three different groups of light receptors are well-known: the R : FR photoreceptor phytochrome, the blue light and UV-A receptor cryptochrome (Casal, 2013; Ballaré & Pierik, 2017) and the blue light and UV-A receptor phototropin (Christie *et al.*, 2018). Stem elongation is the classical response that involves light receptors. When the R : FR of the light that reaches the plant is low, the active (Pfr) form of phytochrome B (phyB) is transformed to the inactive one (Pr). This releases the negative feedback of phyB on basic helix–loop–helix transcription factors (PIFs, phytochrome interacting factors) which lead to the downstream production of auxin and gibberellins, and ultimately to cell elongation (Casal, 2013; Ballaré & Pierik, 2017), with longer internodes and higher specific stem length as a consequence. At the same time, auxin will suppress shoot branching. By doing so, plants may overtop their neighbors, which ensures better access to light at the expense of

reduced stem thickness. Interestingly, this classical shade-avoidance response does also occur when DLI per se is reduced (Fig. 2k), so without affecting light quality. It is becoming increasingly clear that phytochromes are not the only sensors that play a role in this network. Cryptochromes also negatively control various PIFs. They are sensitive in the blue light region and can sense differences in light intensity. Limited availability of blue light may thus attenuate cryptochrome–PIF interaction (Ma *et al.*, 2016; Pedmale *et al.*, 2016) with induced elongation growth as a consequence. However, it has been shown that phyB is also sensitive to overall light intensity (Trupkin *et al.*, 2014). It would be interesting to see what the changes in R : FR and DLI have to be to achieve a quantitatively similar increase in (specific) stem length.

Most studies so far have investigated phytochrome and cryptochrome function at low DLI rather than in the intermediate or high range. Photoreceptors and light signal transduction were shown to affect photosynthetic capacity and pigment composition (Chl content and Chl *a* : Chl *b* ratio) in *Arabidopsis* mutants grown under DLIs of 3–12 mol m⁻² d⁻¹ (Walters *et al.*, 1999). In fact, a number of nuclear-encoded photosynthetic genes are directly regulated by light via photoreceptors (Terzaghi & Cashmore, 1995; Toledo-Ortiz *et al.*, 2014), and so is transcription of plastid-encoded genes like D1 and D2 proteins of photosystem II (Thum *et al.*, 2001; Tsunoyama *et al.*, 2004). Coordinated regulation of nuclear- and plastid-encoded genes would be essential to maintain $V_{\text{F}}/F_{\text{M}}$ and $J_{\text{MAX}}/V_{\text{CMAX}}$ across a wide DLI range (Fig. 4f,k). This points to the necessity of signaling between the nucleus and chloroplasts in both directions (anterograde and retrograde) to ensure efficient photosynthesis at all DLI levels (Nott *et al.*, 2006). At high DLI, responses may be confounded by other factors that accompany or result from strong irradiance, such as growing demands for water and nutrients, high temperature or photo-oxidative stress. High-light acclimation thus encompasses various signals generated in chloroplasts and cytosol, including changes in redox state, metabolites, hormones and hydrogen peroxide to benefit from high light availability while protecting from excessive light (Dietz, 2015).

A key trait in light acclimation is LMA, with thicker (LeaThi) and denser (LeaDen) leaves ensuring higher area-based photosynthetic capacity at high DLI (Fig. 6). There is a role for phototropins here, as phototropin-2 promotes cell-autonomous development of cylindrical palisade cells which are so typical for high-light-grown dicotyledonous leaves (Kozuka *et al.*, 2011). Formation of additional palisade cell layers (Fig. 2f), on the other hand, is triggered systemically by increased supply of sucrose from source leaves (Terashima *et al.*, 2006; Mohammed *et al.*, 2018). Again, signals from light, cytoplasmic and mitochondrial energy status and probably also hormones (auxin, cytokinin) converge (Mohammed *et al.*, 2018). The photoreceptor regulation network can even affect root functioning: in *Arabidopsis*, the basic leucine zipper transcription factor elongated hypocotyl5, which mediates transcriptional outputs in both phytochrome and cryptochrome signaling pathways, travels from shoot to root where it activates gene expression of a high-affinity nitrate transporter, resulting in enhanced root nitrate uptake with increasing DLI (Chen *et al.*, 2016).

In summary, rather than operating as individual actors, there is a whole network of different players (sugars, photoreceptors,

hormones, etc.) that together regulate the long-term response of plants to light. Some responses are related to C limitation at low light, whereas others are associated with oxidative or other stresses at high light. So far, our insights into the regulation of long-term responses of phenotypic traits are poor, and this is especially true for responses to high light.

VI. Shade-tolerant and light-demanding species

To this point we have discussed how plants in general acclimate to light. However, some species are predominantly growing in shaded habitats, whereas others are largely located in light-exposed places. What are the key traits for adaptation to these different habitats? To answer this question, we categorized the species in the database into three groups: shade tolerators, light-demanding species and an intermediate category. Since herbaceous and woody species differ in so many traits, we also analyzed this question for herbaceous and woody species separately (Table S1).

Studies have reported a lower plasticity of shade-tolerant compared with light-demanding species (Valladares *et al.*, 2000; Portsmouth & Niinemets, 2007; Chmura *et al.*, 2017). In our database, this is found for a limited number of variables, with significant or near-significant lower plasticity for LMA, area-based N content (N_{tot}/A), photosynthetic capacity ($Phot/A^{SL}$), ULR, leaf area ratio and TDM (Table S1). Lower plasticity for these variables would be consistent with the idea of Jackson (1967) that shade-tolerant species have less ability to increase the number of palisade layers at high light. However, we could not confirm all of these differences when herbaceous and woody species were considered separately. It should be borne in mind that differences in plasticity are statistically challenging to prove: first, because they are often small changes on top of a larger overall effect; second, because shade tolerators often are not grown at high light and light-demanding species not at low light; and third, because there are not many shade-tolerating species in the database. Information on their DRCs at the ranges where we expect them most contrasting is therefore scarce.

Although plasticity per se can be useful for a given species to cope with various environmental conditions (Nicotra *et al.*, 2010), we expect selection to work on *absolute* values of traits rather than on the scaled ones. We therefore tested the differences in the original trait values between shade tolerators and light-demanding species, for a low DLI range ($1\text{--}6\text{ mol m}^{-2}\text{ d}^{-1}$) and a high range ($20\text{--}50\text{ mol m}^{-2}\text{ d}^{-1}$). As we used bootstrapping, we could not directly test the interaction, but rather examined the differences in PI, for herbaceous and woody species separately. At high DLI, comparative studies indicate that light-demanding species have a more favorable C balance and growth rates in high light (Valladares & Niinemets, 2008; Pons & Poorter, 2014). What is the evidence in our database? Again, for most traits there are too little data available to test differences. At high light, herbaceous shade tolerators generally have thinner leaves than light-demanding species, with lower LMA and lower LMF (Table S1). For woody species, we found no difference in LMA, but area-based photosynthetic capacity is lower for shade-tolerating species, and so are Chl content and LMF. At low light, leaf density stands out as being much higher

for shade-tolerating herbaceous species. For woody species, LMA and leaf thickness are higher for shade tolerators, whereas photosynthetic capacity, leaf respiration, ULR and RGR are lower.

Two mechanisms have been proposed for shade tolerance, one which maximizes C gain at low DLI (Givnish, 1988) and another that achieves a high stress tolerance in shade (Kitajima, 1994). Maximization of C gain could be expected if shade tolerators are inherently better than light-demanding species in ways that accord with the suite of acclimatory responses discussed in Section III: lower LMA, higher $Chl a : Chl b$ ratio, and so on (Evans & Poorter, 2001). However, this is *not* the case, as low-light-grown herbaceous shade tolerators do not have lower LMAs, and in fact do not differ in many other relevant traits (Table S1; Liu *et al.*, 2016). Also, no evident difference in C budget at low DLI was found between the two groups (Pons & Poorter, 2014). Although this is not invariably the case (Walters & Reich, 1996), we found that, overall, woody shade tolerators were even found to have lower ULR and RGR than light-demanding species at low light.

The other mechanism suggested is that shade tolerators are better guarded against mechanical damage, herbivores and pathogens, thereby increasing the longevity of their organs at low DLI. A leaf lifetime beyond payback time is essential for survival and contributes to the formation of a large leaf area and a positive C balance in shade (Lusk *et al.*, 2008; Niinemets, 2010). Leaf longevity is not regularly measured in controlled experiments, but some traits may provide indirect evidence. The high LMA and tissue density of shade-tolerant species was associated with greater tissue strength in evergreen trees (Lusk *et al.*, 2010; Houter & Pons, 2014). Shade-tolerant herbs do have high leaf tissue density (Table S1), which also may reflect tougher leaves possibly with different chemical composition. Specific stem length of woody shade tolerators is lower than for light demanders, which likely confers greater strength of stems in shade. Unfortunately, insufficient data are available for shade-tolerant herbs, but reduced stem extension is known from spectral canopy shade (Gommers *et al.*, 2013). Note that the observed characteristics, such as high LMA and leaf density, actually may come at the expense of short-term C gain (growth–survival trade-off; Valladares & Niinemets, 2008) which was indeed found for woody species.

In conclusion, the combined data provide little evidence for maximization of C gain per unit time as the principal mechanism of shade tolerance. Rather, high LMA and/or tissue density in shade-tolerant species support the stress tolerance hypothesis. A positive C balance in shade at the longer timescale remains, of course, essential. This may also be determined by factors not analyzed here, such as leaf angle (Hikosaka & Hirose, 1997), plant architecture (Sterck *et al.*, 2013) and – in the understory of deciduous forests – leaf phenology (Kwit *et al.*, 2010).

VII. Relation to field conditions

Our analyses are based on experiments that are predominantly carried out with spaced plants grown individually in pots. Although some sensing of other plants will have occurred in those experiments (Gommers *et al.*, 2013), the overall light quality was not altered and there was little or no competition with neighbors.

By growing plants under (semi-)controlled conditions with exclusion of most herbivores, pathogens and often without UV-B, the question is relevant to what extent these experimental results can be generalized to field conditions (Poorter *et al.*, 2016; Fraser *et al.*, 2017).

One important issue is that most experiments have been carried out with young, small seedlings, whereas shade tolerance is also highly relevant for saplings and larger subdominant individuals in the vegetation. It is known that various traits change with ontogeny, which may have consequences for their growth and shade tolerance (Niinemets, 2006; Gibert *et al.*, 2016). This comes on top of an overall decrease in LMF and increased risk on self-shading (Givnish, 1988). A second caveat is that trait plasticity differences among species with different shade tolerance can become increasingly smaller at lower nutrient availability (Portsmouth & Niinemets, 2007). This is relevant for putting the results into a natural context, as soil nutrient availability and plant nutrient requirement often change throughout succession in parallel with changes in light availability.

However, there are also indications that the presented DRCs have wider validity. Within a vegetation there is not only a strong gradient in light intensity, but also a strong decrease in the R : FR ratio (Pons, 2016). Given the known importance of phytochromes in shade-avoidance syndromes (Section V), how well do the DRCs from Section III represent responses of plants or leaves growing low in the canopy? First, for at least some traits, such as RGR, ULR and SLA, we observe similar responses for plants that were grown in differently sized gaps, which reduce both light intensity and R : FR, as we reported here for DLI per se (data not shown), indicating that, for those traits, light intensity is far more important than light quality (cf. DRCs for SLA in Poorter *et al.*, 2009). Second, Niinemets *et al.* (2015) analyzed light gradients within tree canopies and herbaceous stands from top to bottom in a similar manner as we did here for individually grown plants. For the traits studied in common we observed a very similar ranking and size of PI values as in the present report (Fig. 7a). Finally, we have previously analyzed how competition affects traits of individual plants by quantifying how much they changed when plant density was doubled (Poorter *et al.*, 2016). Since a doubling of plant density implies a 50% reduction in the light available per plant, we compared the density response with the changes expected when halving light intensity for individually grown plants from 20 to 10 mol m⁻² d⁻¹. For most traits we found strong concordance between the two gradients, supporting the idea that light availability is a dominant factor in plant competition. However, there is a clear exception for specific stem length, which responds hardly to halving the DLI, but strongly to increasing density (Fig. 7b). It is very likely that this trait, although sensitive to light intensity at low DLI (Fig. 2k), is more responsive to the decreases in R : FR occurring during competition (Morgan & Smith, 1981). For the other traits considered, we expect the observed responses to DLI to have validity beyond the current experiments.

Finally, what does this imply for the light compensation point of growth, as integrator of the many underlying trait responses (Craine *et al.*, 2012)? Laboratory measurements of C budgets at low light levels are scarce but indicate that young plants can achieve a

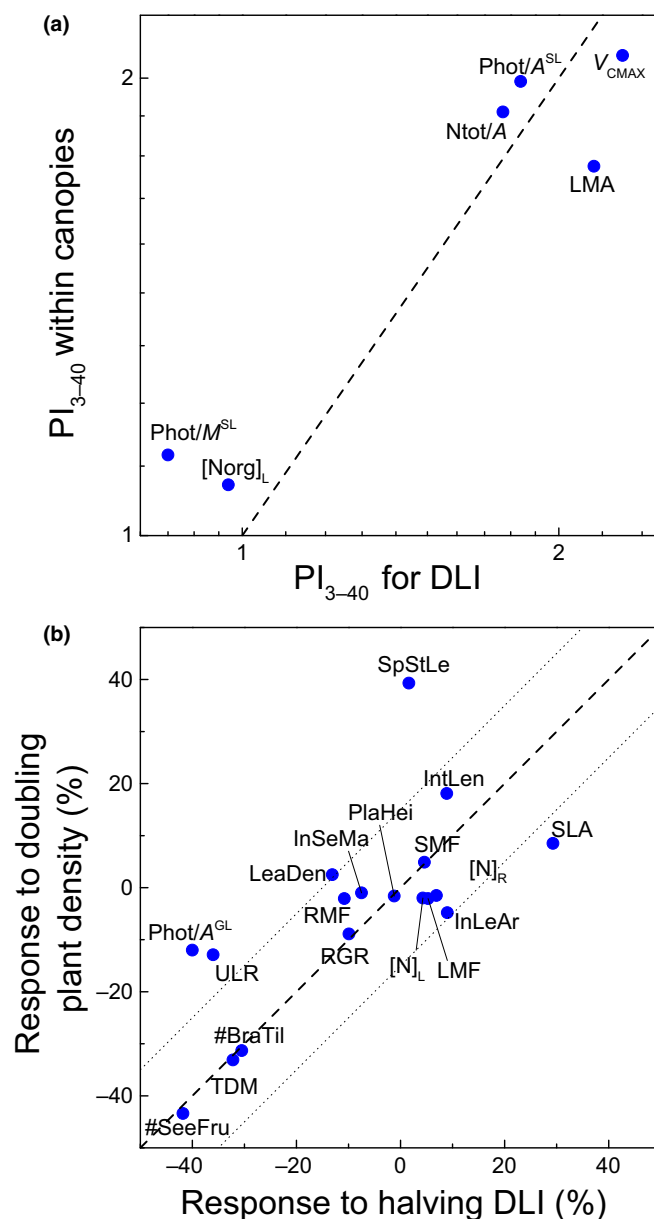


Fig. 7 (a) Relation between the plasticity index (PI) observed by Niinemets *et al.* (2015) for traits depending on light gradients within plant canopies and the PI derived in this paper from species grown at different daily light integral (DLI). (b) Relation between the percentage response of traits to a doubling of plant density as shown by Poorter *et al.* (2016) and the percentage response of traits to halving DLI from 20 to 10 mol m⁻² d⁻¹, as derived from the dose-response curves presented in this paper. Broken lines indicate a 1 : 1 relationship; dotted lines in (b) indicate a 15% deviation from the percentage response in the negative or positive direction. See Table 1 for explanation of all trait abbreviations.

positive C balance at DLI levels of *c.* 1 mol m⁻² d⁻¹ or lower, depending on species (McCree & Troughton, 1966; Baltzer & Thomas, 2007; Pons & Poorter, 2014). Similar results are found in growth analyses where the DLI for which RGR is zero is assessed (Poorter, 1999). Light compensation points for whole-plant growth are generally higher in the field (Baltzer & Thomas, 2007). Partly, this will be an effect of size, especially for trees where

leaf area ratio strongly decreases during development (Givnish, 1988; Sterck *et al.*, 2013). However, the compensation point in the field is also higher due to additional stress from fungi, insects, competition and/or limited soil resources (Emborg, 1998). This lends further support to the concept of shade tolerance being more a matter of stress tolerance than short-term maximization of C gain (Section VI).

VIII. Concluding remarks

1. Outlook

The effect of light intensity on plants has been studied experimentally for > 100 yr now (e.g. Lubimenko, 1908). The accumulated information provides us with an accurate picture on how various plant traits change with DLI. However, there are still substantial gaps in our knowledge. In the following, we outline five topics that would progress the field.

1 *The 'dark side' of light acclimation.* As much as we know about photosynthesis and shoot growth parameters, we know little about the effects of DLI on reproduction, respiration, chemical composition and belowground organs (Table 2).

2 *Scaling up in time and size.* Physiological processes are well studied on the standard 'youngest full-grown' leaves of plants. What the effects are on whole plant physiology and how this changes when plants age and/or mature is highly relevant but far less known. This issue is also relevant for comparisons of characteristics of low-light- and high-light-grown plants, as the latter will inevitably become much larger during the growth period, which then may have indirect effects on a range of other plant traits.

3 *Molecular regulation of plasticity.* We begin to understand the cellular regulation of responses to light for various photosynthetic compounds that respond in the short term. However, many of the traits discussed here develop over longer time periods, for which the plants probably make decisions based on light availability over the longer term. What are the molecular mechanisms behind these changes and what are the cellular integrators that determine the strength of the response? To what extent is the response to shade for different traits determined by DLI or by the R : FR ratio, and to what degree can these two stimuli be mutually exchanged to achieve the same phenotypic effect?

4 *Interaction between traits.* So far, we have analyzed each trait separately. However, *in planta*, where plant parts and processes function in dependency (Fig. 6), environmental or genetic changes in one trait will have consequences for other traits. Trait correlation networks are at their infancy (Poorter *et al.*, 2013; Messier *et al.*, 2017; Kleyer *et al.*, 2018), but they can become an important tool to gain quantitative insight in how plants can optimally acclimate to a given light environment.

5 *Fundamental and realized niches.* What makes the ecological niche of plants with respect to light smaller than what they can achieve in controlled environments? Although the available evidence indicates that (a)biotic interactions play an important role, we have few insights into the actual mechanisms. What exactly makes light-demanding species succumb at low light, and what are the reasons that shade species do so much better?

2. Conclusions

1 We quantified the effects of light intensity on 70 plant traits by deriving generalized DRCs. They provide a concise picture of how plants respond to light and can be used for further analyses and modeling.








2 Differences in plasticity among traits were large, but there was clear co-variation for LMA, area-based photosynthetic capacity and ULR.

3 Although shade-tolerant and light-demanding species showed differences in the plasticity to light intensity, differences in DRCs were generally small relative to the overall DRC.

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Appendix A1

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Example showing how dose-response curves are calculated based on scaled data from various experiments.

Figs S2–S72 Specific figures per trait, showing all data for woody and herbaceous species as well as dose-response curves and 10th, 25th, 50th, 75th and 90th percentiles.

Methods S1 Extended materials and methods.

Notes S1 List of all herbaceous and woody species used, classified into the categories Shade-Tolerant, Intermediate and Light-Demanding.

Table S1 Parameter values of the fitted dose-response curves as well as contrasts between functional groups in plasticity indices

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