Plant Soil
https://doi.org/10.1007/s11104-022-05391-8

REGULAR ARTICLE

MetaPhenomics: quantifying the many ways plants respond to their abiotic environment, using light intensity as an example

Hendrik Poorter · **Xinyou Yin** ·
Nouf Alyami · **Yves Gibon** · **Thijs L. Pons**

Received: 12 January 2022 / Accepted: 16 March 2022

Abstract Thousands of scientific papers have described how plants responded to different levels of a given environmental factor, for a wide variety of physiological processes and morphological, anatomical or chemical characteristics. There is a clear need to summarize this information in a structured and comparable way through meta-analysis. This paper describes how to use relative trait responses from many independent experiments to create generalized dose-response curves. By applying the same methodology to a wide range of plant traits, varying from the molecular to the whole plant level, we can achieve an unprecedented view on the many ways that plants are affected by and acclimate to their environment. We illustrate this approach, which we refer to as 'MetaPhenomics', with a variety of previously published and unpublished dose-response curves of the effect of light intensity on 25 plant traits. Furthermore, we discuss the need and difficulties to expand this approach to the transcriptomics and metabolomics level, and show how the generalized dose-response curves can be used to improve simulation models as well as the communication between modelers and experimental plant biologists.

Keywords Abiotic environment · Dose-response curve · Light intensity · Modeling · Normalization

Introduction

'Unlike most animals, plants are sessile organisms and therefore must have the ability to cope with wide fluctuations in their physical environment'.

Responsible Editor: Martin Weih.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11104-022-05391-8.

H. Poorter (✉)
Plant Sciences (IBG-2), Forschungszentrum Jülich GmbH, D-52425 Jülich, Germany
e-mail: h.poorter@fz-juelich.de

H. Poorter
Department of Natural Sciences, Macquarie University, North Ryde, NSW 2109, Australia

H. Poorter · T. L. Pons
Plant Ecophysiology, Institute of Environmental Biology, Utrecht University, 3512 PN Utrecht, The Netherlands

X. Yin
Centre for Crop Systems Analysis, Department of Plant Sciences, Wageningen University & Research, P.O. Box 430, 6700 AK Wageningen, the Netherlands

N. Alyami
College of Science, King Saud University, Riyadh, Saudi Arabia

Y. Gibon
UMR1332, Université de Bordeaux, INRAE Bordeaux Metabolome, MetaboHUB, PHENOME, Villenave d'Ornon, France

Words to this effect are popular starting sentences in scientific papers (e.g. Queitsch et al. 2000; Zhang and Friml 2020). To fully oversee its consequences, this general plant characteristic has to be coupled to another essential aspect, in which plants and animals also differ. Where body size of animals of a given age is often only marginally dependent on the external environment, variation is far more pronounced for plants: depending on environmental conditions, plant size can vary tremendously (Tardieu et al. 2017). In controlled experiments, the variation in biomass among equally-aged plants of different treatments may well be 3–10 fold, and sometimes differ more than 30-fold (Pons and Poorter 2014). In nature, over 100-fold differences in biomass can occur for even-aged plants, depending on site conditions (Portsmuth et al. 2005 vs. Ovington 1957; Lu et al. 2017 and Forrester et al. 2017). Although less variable than plant size, strong plasticity is also found for a diverse range of traits related to plant morphology, chemistry and physiology (Valladares and Niinemets 2008). To a certain extent these differences are merely physiological consequences of the environmental conditions: if light levels are low, the photosynthetic rates are necessarily also low. However, plants can also actively (re)program their development to acclimate to different levels of an environmental variable, by adjusting traits in a way that improves their performance under specific conditions as compared to when they had not reprogrammed themselves (Nicotra et al. 2010).

Analyzing the responses of plants to the range of environmental factors they experience is one of the main fields of focus of plant ecophysiology (Lambers and Oliveira 2019). An often-used experimental approach is to challenge seedlings or saplings for a period of time with two or more levels of a specific abiotic factor, such as light, water or nutrients. Subsequent plant measurements can have a focus on variables related to morphology and allocation, such as leaf size or thickness, chemical traits such as nitrogen or phosphorus concentration, physiological traits such as photosynthesis and transpiration, or variables describing growth and development, such as biomass or flowering time (Perez-Harguindeguy et al. 2016; Freschet et al. 2021). Over the last 30 years this approach has been extended by analyzing specific cellular messengers such as hormone or mRNA levels, and broad profiling of the transcriptome, proteome and metabolome (Sahoo et al. 2020).

Hundreds to thousands of such experimental studies on the environmental effects on plant growth and trait acclimation appear each year in the scientific literature, for a wide range of different species. The challenge for the scientific community is how to fruitfully handle and incorporate this enormous source of scientific data. Textbooks such as Lambers and Oliveira (2019) and Nobel (2020) or narrative reviews can help to structure this information to some extent. However, they will necessarily remain the author's personal impression of a field that gets more and more difficult to oversee, due to its breadth and the ever-increasing body of data. In this paper, we discuss how meta-analysis can help to digest this vast amount of information in a structured way. First, we focus on the need for generalized dose-response curves and explore some of the advantages and limitations of an approach we refer to as 'MetaPhenomics'. Second, we illustrate this methodology with 13 updated and 12 previously unpublished dose-response curves, focusing on the effects of light intensity on plants. We then go a step beyond and ask to what extent interaction between two or more environmental factors can be quantified. Finally, we discuss some possible options to expand this approach to the fields of molecular sciences and show how dose-response curves could be advantageously used for improving crop or ecosystem modeling.

Meta-analyses of plant responses to the environment

The need for generalization

Meta-analyses are quantitative analyses of a range of primary studies (Harrer et al. 2021). They were initially developed in the medical field, to evaluate results of various clinical trials. The integrative power of the meta-analytical approach subsequently has led to wide applications in other biological disciplines (Hedges et al. 1999). Meta-analyses in the botanical field sometimes target the environmental response of one specific species (e.g. Ainsworth et al. 2002), but are generally broader: They often focus on a range of species with common characteristics (crop species, conifers; e.g. Kimball 2016) or plants investigated with a specific methodology (such as CO_2 enrichment with FACE technology; Ainsworth and Long 2021).

In the broadest sense, they may even target responses of hundreds of species (Van Kleunen et al. 2010; Liang et al. 2020). In almost all of these compilations, conditions among experiments will be variable: physiologists preferably study treatments in growth chambers where all other conditions are controlled, horticultural scientists predominantly use glasshouses that mimic horticultural practice, whereas agronomists and ecologists rely mostly on field studies. All of these scientists grow plants under a specific set of environmental conditions, yet try to unravel principles, which are hopefully appliccable to plants of more species, and grown at a wider range of conditions. Experiments that have been carried out at a range of background conditions will likely allow for more general conclusions (Richter et al. 2009), and such a generality applies even stronger to meta-analyses where a range of experiments is combined (Harrer et al. 2021).

An important requirement in science is to discuss results in relation to ‘what is known already’. Citation of papers that confirm the results presented in a given paper help to achieve a sense of generality. With the myriad of published papers, it is often not difficult to find one or more publications where similar results have been observed. If this happens not to be the case, then simple ‘explanations’ can be suggested for observed discrepancies: e.g., other experiments were done with another species, at a different growth stage, or in a different growth environment. However, it is not easy to achieve firmer ground without a more systematic approach. Meta-analysis could be helpful to judge how general an observed difference between two treatments, for example low and high light, is. At the same time, it enables to test whether phylogeny (e.g. species from different families) or functional type of species (e.g. C_3 vs. C_4 plants) are relevant factors explaining variation in response among the range of compiled experiments.

There is another source of variation among experiments that is often not taken into account when comparing data. Using the example of light again, two experiments may show different phenotypic responses to light intensity (e.g. a strong positive effect vs. no effect, Fig. 1a). Where plant biologists often study the performance of a species like *Arabidopsis thaliana* at relatively low light intensities (say, 100 and 200 µmol.m^{-2}.s^{-1}), agronomists may prefer to compare light effects on a given crop species at much higher light levels (say 600 and 1200 µmol.m^{-2}.s^{-1}), because that bears more relevance to field conditions. Therefore, it could well be that differential results between these two experiments for a given phenotypic trait are only found because the effects of light were studied at different and non-overlapping ranges of an overall non-linear dose-response curve (Fig. 1b). Consequently, it would be very helpful if meta-analyses focusing on the effects of a specific environmental factor on plants would include the actual quantitative levels of the environmental factor of interest. Not only that, rather than asking whether two specific levels of a given environmental factor have differential effects on the plant phenotype, it would be far more instructive to derive dose-response curves from these data, as they

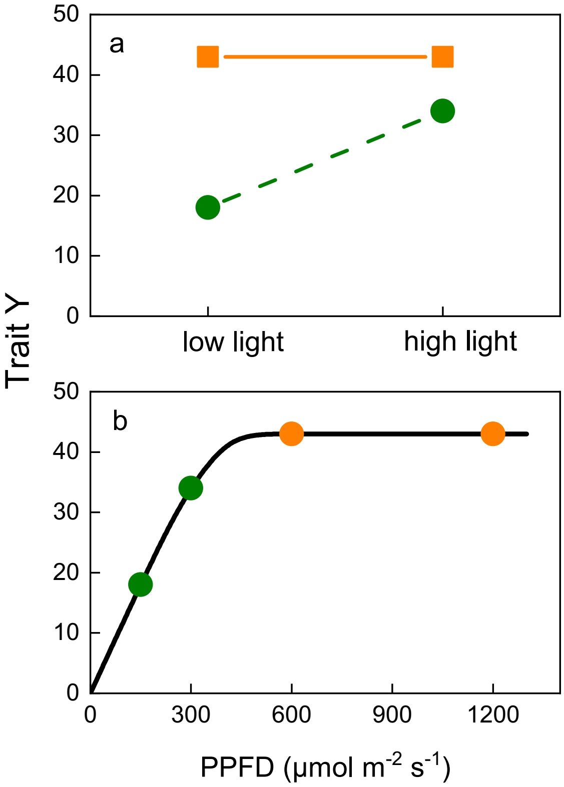


Fig. 1 Hypothetical example of how contrasting results from two experiments (colour-coded orange and green) can be interpreted. Differences in the response of a given phenotypic trait Y to, for example, a low and high light intensity could be due to **a** contrasting species or different growth facilities, or **b** due to rather different light levels used across experiments, with the two species actually following exactly the same dose-response curve

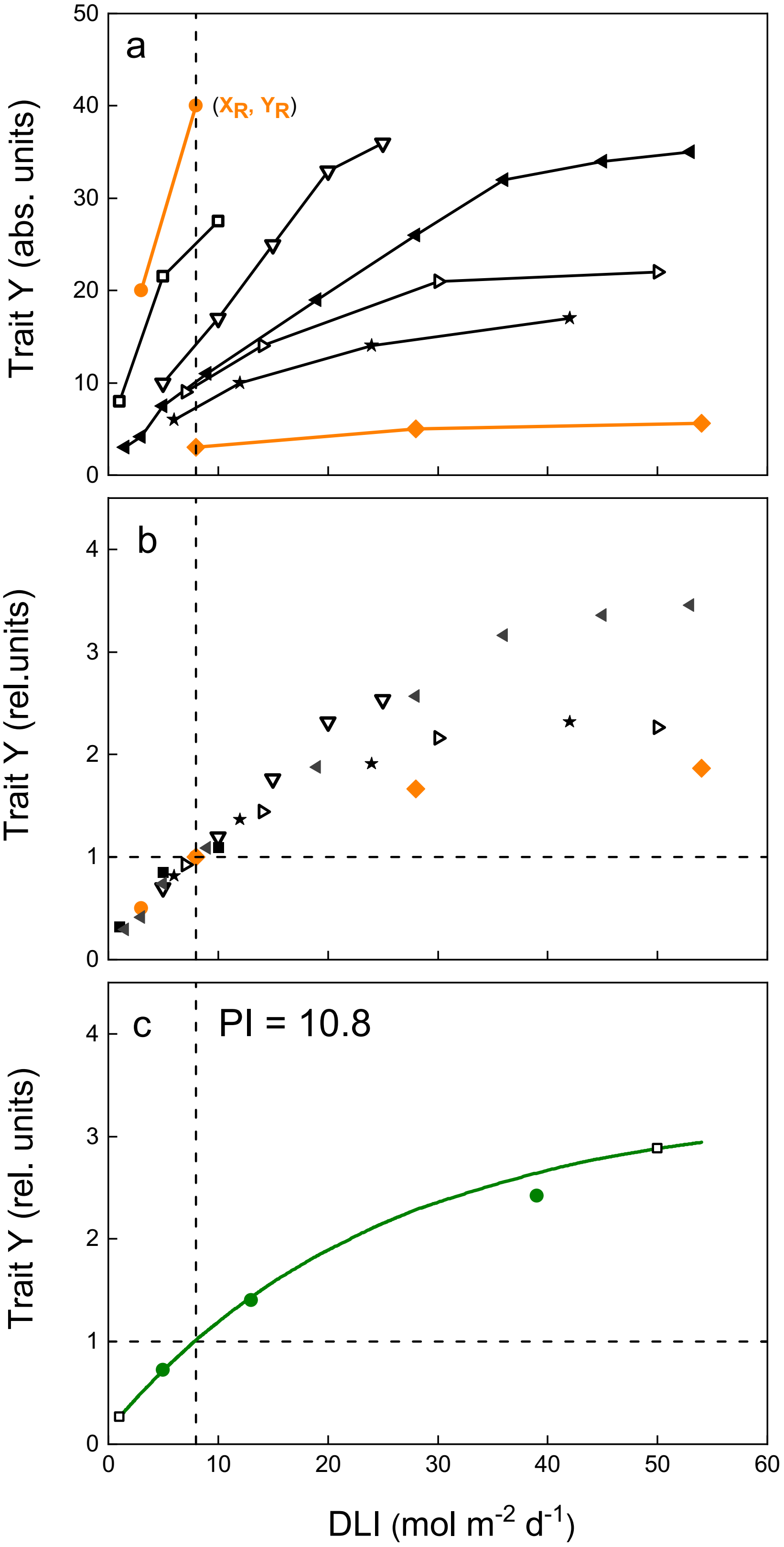
bear information over a wide range of levels and are therefore more informative to analyze and compare plant responses. The derivation of generalized dose-response curves by means of meta-analysis is the main focus of this paper.

Compiling and scaling data

For the MetaPhenomics database we compile environmental and phenotypic data, mainly from published experiments, where plants were exposed (for most of their life) to different levels of a specific environmental factor. The choice of the measure for characterization of the environmental factor requires careful consideration. On the one hand, this measure should be sufficiently relevant and precise to adequately capture the plant's responses. On the other hand, it should not require far more detail than what is usually described in literature, as this would result in the exclusion of too many experiments from the meta-analysis, making the results less broadly applicable (Harrer et al. 2021). Therefore, this choice is a balancing act between precision on the one hand and generality on the other. For example, in the case of light, 'photosynthetic photon flux density' (PPFD; μmol.m^{-2}.s^{-1}) would seem a logical first choice, as it is widely used in the plant biology literature. However, this is problematic, as glasshouse and field experiments are carried out at PPFDs that fluctuate continuously within and among days. In many of those experiments authors report 'PPFD measured at 12 o'clock under clear sky' or 'percentage of full light measured under an overcast sky' to characterize light levels. However, such characterizations are not well-defined and incomparable across experiments, as the maximum light intensity varies with season, latitude, shade from surrounding trees or buildings and - in the case of glasshouses - with roof transparency. Moreover, both measures ignore the frequency of sunny and cloudy days and duration of the light period. An alternative measure to characterize light intensity, which is applicable across all experimental platforms, is the Daily Light Integral (DLI, mol.m^{-2}.day^{-1}), the flux of quanta integrated over the day and averaged over the experimental period. This measure has the additional advantage that many of the longer-term morphological and plant growth responses are known to be better correlated with DLI per se than with photon flux density at any moment in time or duration of the light period (Poorter and Van der Werf 1998; Kjaer and Ottosen 2011; Niinemets and Keenan 2012). However, using the average DLI over the experimental period will unavoidably miss out on details such as variability that may occur within the day between temporarily low-light and high-light periods, or similar variation among cloudy and sunny days during the experimental period (Wayne and Bazzaz 1993; Matsubara 2018). Another source of error more specific for growth chambers is that there is often moderate variation in light intensity depending on the horizontal position of a plant, but strong vertical variation within the growth chamber (Poorter et al. 2012a, 2012b). With some researchers measuring light intensity at pot level, others at plant height, and with most of these values determined only once during the experiment, also those DLI values are approximations of the actual light levels received by the plants.

As much as for the environmental characterization, there is uncertainty and/or variability in the determination of phenotypic traits. Part of this is random variation, due to well-known biological variability. Part is systematic, and may relate to the development of phenotypic traits with age or size, or to systematic differences among measurement procedures (Quentin et al. 2015). Additional difficulties are that experiments are often carried out with different species, and dissimilar environmental backgrounds, such as pot size or watering frequency and duration of the experiment. These all preclude direct absolute comparisons of data among experiments. However, it is feasible to compare *relative* responses among experiments, by normalizing all phenotypic data within each experiment to the trait value observed at a predefined level of a given environmental factor (Poorter et al. 2010; see Box 1 for a summary of the methodological steps followed). The advantage of using a scaling approach is that it is very flexible, and works even for experiments with only two or three levels of a given environmental factor. Poorter et al. (2019), for example, normalized phenotypic data to a reference DLI level of 8 mol.m^{-2}.d^{-1}. If an experiment contains this level as one of the treatments, the calculations are straightforward (see Fig. 2a, b, orange lines). If two DLI levels are applied where one level is below and the other above that predefined value, normalization can be achieved after

Fig. 2 Calculation of dose-response curves from various experiments. **a** Response of plants to light, as observed for a given trait Y, expressed in absolute units. In this case, results of 7 independent experiments with 2–9 light levels are shown. For one of the orange experiments the Y-level at the reference light level for scaling is also indicated by (X_R,Y_R). **b** The same response for the 7 experiments, when all values are expressed in relative units, scaling to the absolute phenotypic value at the reference DLI of 8 mol. $m^{-2}.d^{-1}$. **c** Summary graph, showing the median values for the 10 points with the lowest DLI values, the 10 intermediate points and the 10 with the highest DLI value (green dots) as well as the fitted curve over the range of DLI data (green line). In cases where >100 data are available, points will not be grouped per 10, but per decile. The ratio of the fitted phenotypic values at a DLI of 50 and 1 (these points on the curve are indicated by black open squares) is called the plasticity index (PI) and has a value of 10.8 in this case. In case of negative trends, the ratio is inversed and multiplied by −1, to maintain the same size of scaling, but clearly indicating the negative direction of response



Box 1 Methodology of the MetaPhenomics approach

1. Collect the trait and environmental data from the literature.

- Each trait entry Y in the database is the average value over one or more measurement days.

- Data are only considered for plants that had ample time to acclimate to their environment, which we define as being at least 2 weeks under those conditions and achieving preferably >80% of their biomass during the experimental treatment.

- Physiological measurements are considered for the vegetative and early flowering phase, vegetative biomass at the end of the growth experiment, generative traits at the end of the generative phase.

2. Double-check data for possible mistakes in numbers or units.

- Trait data are checked against the normal ranges (5th - 95th percentiles) of the data already in the database.

3. Scaling data for each species in each experiment.

- For every trait and each species (or genotype) within a given experiment, calculate by means of interpolation what estimated value Y_R they have at the predefined reference level X_R of the environmental factor of interest.

- Scale all observed data for that species and experiment by dividing their trait values Y by Y_R.

- To constrain the weight of an individual experiment in the overall compilation, consider a maximum of 10 species and 3 genotypes per experiment. If selection is necessary, choose species in a way that maximises phylogenetic or ecotypic diversity.

4. Scale the trait data from experiments where the range of levels X for the environmental factor of interest did not contain X_R.

- Fit all scaled Y vs X data as calculated in point 3 by a smoothed regression.

- For each of the traits of species and experiments that did not include X_R, take the treatment level X_C which is closest to X_R, and consider what the average Y'-value is as given by the smoothed regression.

- Scale all other Y data in that experiment with respect to the Y-value at X_C and multiply all with the Y'-value.

- After the previous step, remove the (X_C,Y_C) data point of each experiment that did not contain X_R in their environmental range from the data, as they do not contain independent information anymore after the scaling.

5. Establish unsmoothed dose-response curves and normal ranges.

- Order all data points by their X-value and divide them in 10 decile groups.

- Calculate median values for X and Y for each decile group.

- 10th, 25th, 75th and 90th percentiles for Y in each decile group indicate the normal ranges to be expected.

6. Fit smoothed dose-response curves.

- Fit each of the four following equations through all scaled data:

● The null model of no response:
$Y = 1$

● A linear equation:
$Y = a + bX$

● A saturating equation (monomolecular function):
$Y = a.\ (1 - b.\ \exp^{-cX})$

where parameter *a* reflects the a-symptotic value, *a* and *b* co-determine the trait value at $X = 0$ and *b* and *c* co-determine how quickly saturation is reached.

● A quadratic equation with or without a local minimum or maximum:

$Y = a + bX + cX^2$

- Test the most appropriate of these 4 equations by means of the Akaike Information Criterion

7. Calculate Plasticity index (PI).

- Take the ratio of Y_H and Y_L, for a predetermined X_H and X_L., as caluclated from the dose-response curve selected in step 6. For light intensity we chose X_H and X_L to be 50 and 1 $mol.m^{-2}.d^{-1}$. If Y_H is smaller than Y_L, then calculate the inverse and multiply by -1, to indicate negative responses with increasing X.

8. Calculate the Consistency index (CI).

- For every species x experiment combination, deduct the phenotypic value observed at the lowest level of the environmental variable from the phenotypic value observed at the highest level of the environmental variable.

Box 1 (continued)

- Determine the % of cases in which the difference is positive, and add to that half of the % of cases in which the difference is exactly 0.

9. Evaluate differences in the dose-response curves between species groups.

- Carry out repeated bootstrapping for observations of each group of interest and calculate for each iteration the PI. Statistical evaluation can be obtained by evaluating the distribution of the calculated PI values for the different species groups.

10. More details.

- More specific details on test procedures can be found in the supplement of Poorter et al. (2022).

---

interpolation (Fig. 2a, b; black lines). By applying this normalization, variation across species and experiments can largely be partialled out (Fig. 2c).

Establishing dose-response curves

Having computed relative responses for a given trait in each species x experiment combination of the data compiled, the next step then is to mathematically describe the relationship with the environmental factor of interest by establishing the appropriate dose-response curve. This can be done by fitting one of a variety of functions. Of the four options we use, the null model is that the trait of interest Y is not affected by the level of the environmental factor X at all. The second is a linear relationship. Another frequently-occurring relationship is a saturating curve, which approaches a maximum or minimum. For this we use a monomolecular function with three parameters (France and Thornley 1984; Box 1). More rarely, dose-responses will show a quadratic relationship, with or without a local optimum or minimum. These curves are characterized by a 2nd-degree polynomial. Out of these four, the best-fitting curve is selected statistically.

Based on the data and the selected equation, three descriptors of the established dose-response curve can be calculated:

- Plasticity Index (PI). This is the ratio of trait values at a predefined high and low value of the environmental factor of interest. In case of a ratio less than 1, the inverse is taken and multiplied by −1, to clarify that the relationship is negative while keeping plasticity values in the same range (>1). The advantage of the plasticity index is that the extent of plasticity for a wide range of dose-response curves for different traits or species groups can easily be compared.
- Consistency Index (CI). This value indicates in what percentage of the species × experiment combinations the plants exposed to the highest level of the environmental factor of interest do have a higher value for the trait of interest than those exposed to the lowest level. Values close to 0% or 100% indicate a high consistency across experiments, whereas a value close to 50% indicates a highly variable response. The consistency index is particularly informative when discriminating traits that change marginally but do so in a very consistent manner from those that change marginally and variably.
- Reliability Index (RI). Based on the number of observations per trait, the number of species on which the observations are based, the range of the environmental factor of interest over which traits are present in the database, and the inverse of the variability around the fitted dose response curve, the reliability of the dose-response curve is quantified on a scale from 1 to 10. The reliability index can be used to judge how much a dose-response curve could change when data of new experiments are included in the database.

The different steps to arrive at dose-response curves and their descriptors are described in more detail in Box 1.

Data distribution

The MetaPhenomics approach is flexible and can accommodate information from both small- and large-scale experiments, carried out over both narrow or wider ranges of values for environmental factors of interest. But to what extent is such information available from the literature? Taking the example of light again, most experiments in growth chambers, or glasshouses outside the summer season, will achieve DLI levels that are at best intermediate as compared

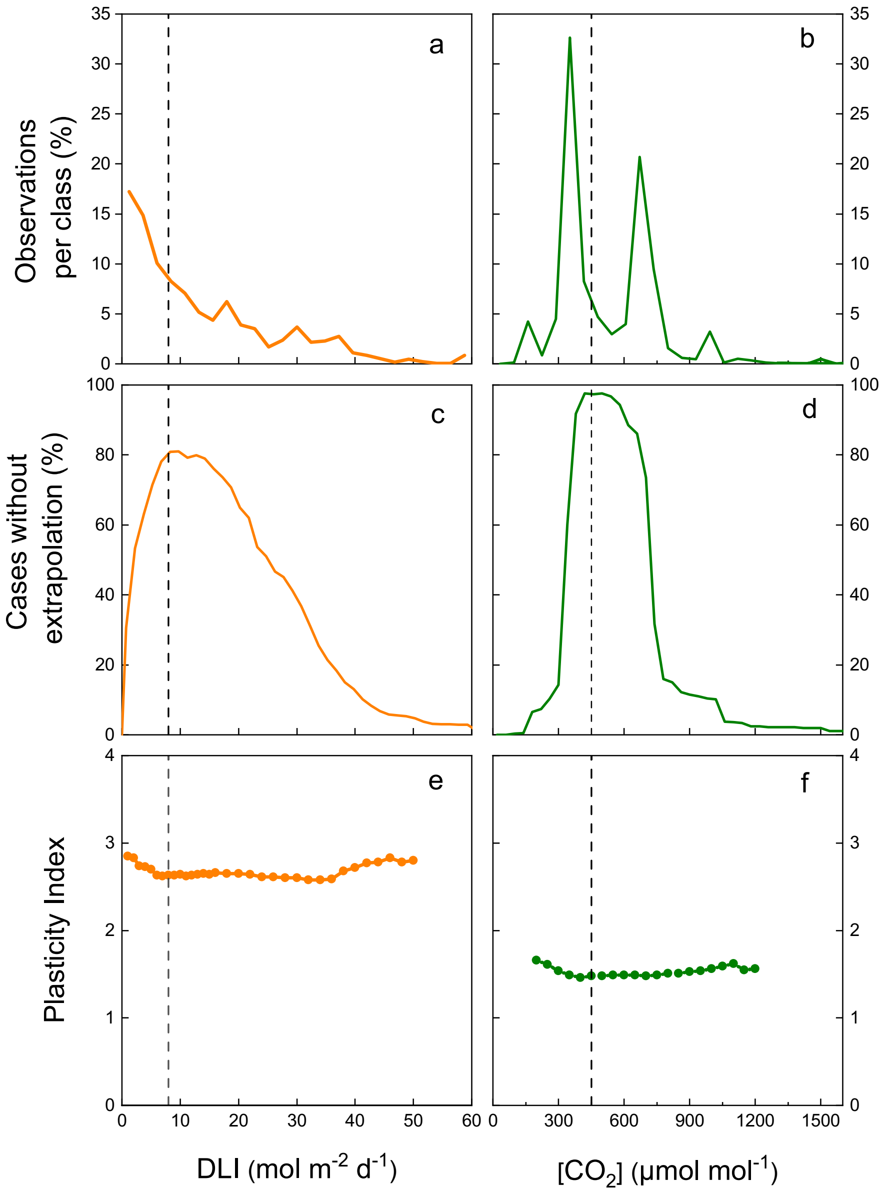


Fig. 3 Characterization of the MetaPhenomics database with respect to data for light (DLI) (**a**, **c**, **e**) and [CO$_2$] (**b**, **d**, **f**). **a**, **b** Distribution of Leaf Mass per Area (LMA) data over the full range of the environmental factor considered, for **a** DLI and **b** [CO$_2$]. **c**, **d** Percentage of the experimental LMA data where normalization can be done by interpolation, as dependent on the exact level of the environmental factor of interest used for the normalization (X_R), for **c** DLI and **d** [CO$_2$]. **e**, **f** Estimated Plasticity Index (PI) for LMA as dependent on the level of the environmental factor of interest used for the normalization (X_R), for **e** DLI values ranging from 1 to 50 mol.m^{-2}.d^{-1} and **f** [CO2] between 50 and 1200 µmol.mol^{-1}. Vertical lines denote the normalization values X_R, 8 mol.m^{-2}.d^{-1} for DLI and 450 µmol.mol^{-1} for [CO$_2$]. The data pertaining to these distributions and the nomenclature followed are from Poorter et al. (2019, 2022)

to those prevailing in the field during the growing season. Some experiments specifically focus on low-light acclimation (e.g. Bloor and Grubb 2003), or plant responses at high-light levels (e.g. Pendleton et al. 1967). Overall, the range of experimentally-applied light levels is wide, but the distribution is clearly skewed, with less information at high DLI levels (Fig. 3a). In the case of atmospheric CO$_2$ experiments, the distribution of [CO$_2$] applied is different. Most experiments so far have focused on the effect of future CO$_2$-concentrations, using ambient CO$_2$ as a control, and twice-ambient as a treatment. Consequently, there are clear peaks in the number of experiments carried out between 350 and 400 µmol.mol^{-1} and 700–800 µmol.mol^{-1}, with far less information outside these regions (Fig. 3b). Note that these distributions vary among traits, implying that dose-response curves for less-frequently measured traits may only be derived over a more limited range.

The non-uniform distribution of experimental data for the environmental factor of concern has two consequences. Firstly, the reference value of the environmental factor that is chosen to determine the trait value applied for scaling within each experiment should preferably encompass as many experiments as possible. The best choice in the case of DLI is a value of around 8 $mol.m^{-2}.d^{-1}$, as this yields a maximum of 81% of the cases where interpolation is possible (Fig. 3c). In the case of CO_2, where almost all experiments use ambient values as 'control' and 1.5x or 2x that value as 'treatment', any value between 400 and 550 $\mu mol.mol^{-1}$ will imply that almost 100% of the experiments are amenable to scaling (Fig. 3d). Secondly, information at the outer ends of the curves is generally scarce, but highly relevant for establishing the dose-response curve over a wide range. Some experiments focus only on various low-light or high-light levels and do not contain 8 $mol.m^{-2}.d^{-1}$. We therefore developed a procedure to link those data sets to all other scaled data, be it with a loss in the degrees of freedom (see point 4 in Box 1). Although this helps to add some additional data at the outer ends of the curves, data for these 'extreme' conditions remain limited. In the case of DLI, we were able – for most traits - to construct dose-response curves over a 50-fold range (1–50 $mol.m^{-2}.day^{-1}$; Poorter et al. 2019), whereas for [CO_2] for most traits it was only feasible to derive curves over a six-fold range (200–1200 $\mu mol.mol^{-1}$; Poorter et al. 2022).

Although it intuitively makes sense to choose the level of the environmental factor used for scaling the trait values such that it is common to many experiments, it is still relevant to know how sensitive the resulting dose-response curve is for the reference level chosen. We therefore calculated the plasticity index (PI) of the observed dose-response curve, using Leaf Mass per Area as an example, for which we took the ratio between the fitted LMA values at a DLI of 50 and 1 $mol.m^{-2}.d^{-1}$, or a [CO_2] of 1200 and 200 $\mu mol.mol^{-1}$. We did so for a wide range of reference values for the environmental factor of interest. As expected, the choice for an extreme level that is hardly contained in any experiment may yield a somewhat deviating estimate. However, over a wide range of values for DLI and CO_2, the resulting Plasticity Index is stable, as illustrated in Fig. 3e, f.

Further analyses

As a first approximation, we assume that the data we found in the compilation underlay a universal trend, valid for all plant species, and can be captured with one dose-response curve. This may often be sufficient. However, it cannot be excluded that different species groups have different dose-response curves. For example, photosynthetic responses to [CO_2] are generally different for C_3 and C_4 species, and this may have consequences for many more traits. Similarly, species from low- and high-light environments or cold and warm habitats may have different optima for various traits. Fitting one dose-response curve through all those data could then easily lead to oversimplification. Therefore, it is good to make the additional step to see whether species from different functional or phylogenetic groups show dose-response curves that deviate from the main trend, or have different plasticity. (See point 9 in Box 1).

Another application of the dose-response curves is that normal ranges can be calculated: By ranking all data from a low to a high value for the environmental factor of interest, and then dividing them into ten equally-sized decile groups, we can not only calculate the median X (environmental factor) and Y (scaled trait), but also calculate, for example, the 10th and 90th percentiles of the scaled trait in each of the ten decile groups. In this way we have the opportunity to check whether any specific experiment is indeed deviating from the majority of all other experiments, which could be an error, or an interesting case of a species that responds genuinely different from the majority of plants.

The effects of light intensity

Poorter et al. (2019) quantified the response of 70 plant traits employing dose-response curves, focusing on anatomy/morphology, chemical composition, and physiology of leaves, stems and roots, as well as growth/reproductive characteristics of whole plants. To illustrate the potential of generalized dose-response curves we first present here trait dependencies on Daily Light Integral (DLI) for 13 of the 70 previously published traits, using an extended data set containing >20% more experiments. We then present DLI dose-response curves for 12 other traits, which were not included in the Poorter et al. (2019) analysis. DLI varies tremendously, depending on location, cloud cover, time of the year and the presence of structures that cast shade. For plants present in a

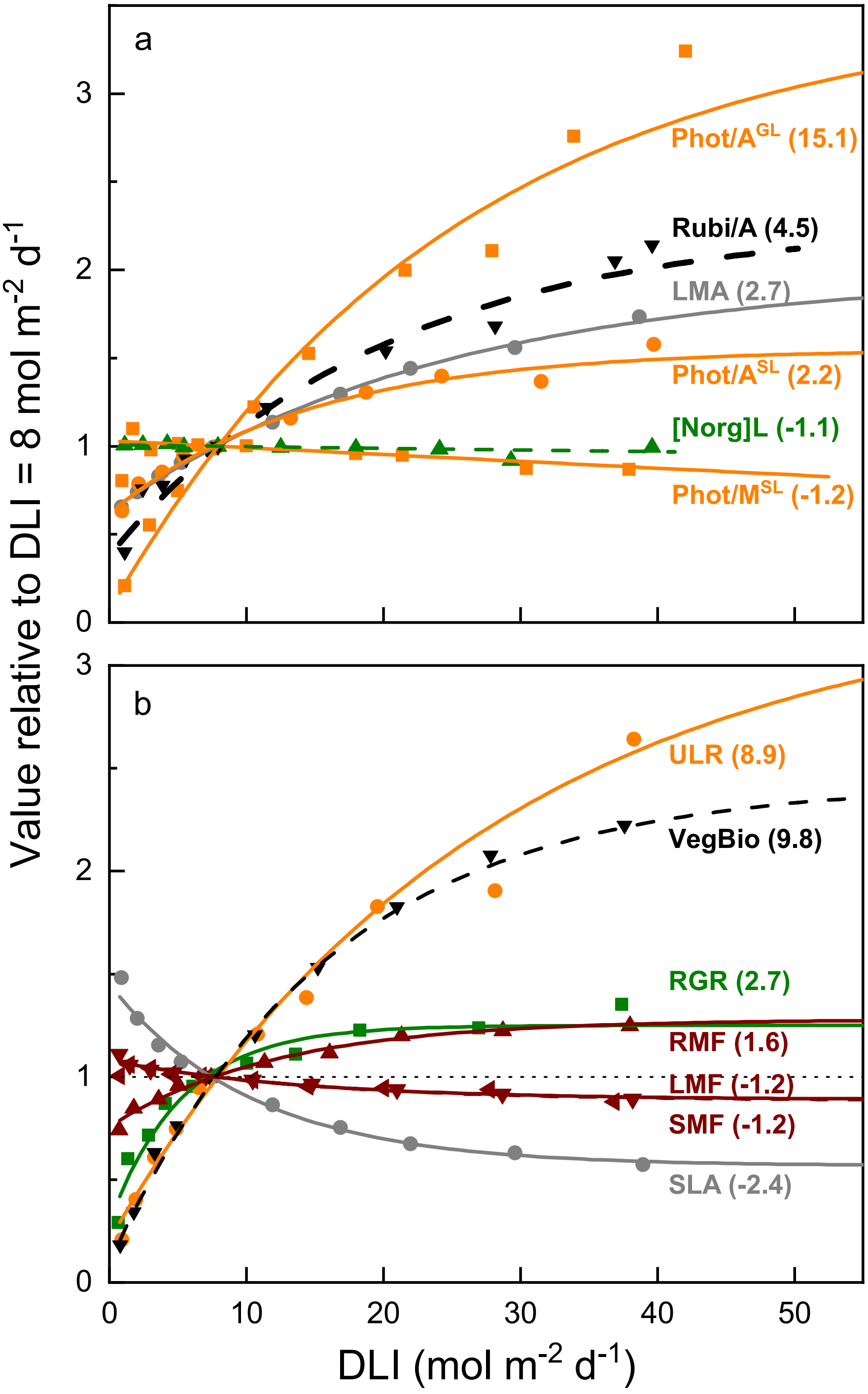


Fig. 4 Generalised dose-response curves with respect to light for **a** six photosynthesis-related traits and **b** seven growth-related traits. Abbreviations are as follows: **a** Phot/A^{GL}, rate of photosynthesis per unit area and measured at growth light conditions; Rubi/A, amount and/or activity of the enzyme Rubisco per unit leaf area; LMA, leaf mass per area; Phot/A^{SL}, rate of photosynthesis per unit leaf area measured at a saturating light level; $[Norg]_L$, leaf organic nitrogen per unit leaf mass; Phot/M^{SL}, rate of photosynthesis per unit leaf mass and measured at a saturating light level. **b** ULR, unit leaf rate; VegBio, vegetative biomass per plant; RGR, relative growth rate; RMF, root mass fraction; LMF, leaf mass fraction; SMF, stem mass fraction; SLA, specific leaf area. Data are based on Poorter et al. (Poorter et al. 2019; a compilation of 500 experiments), complemented with data from an additional 110 papers

vegetation, shading will typically be caused by neighboring plants. Light intensity then critically depends on the leaves' vertical position in the canopy, with subordinate leaves/plants experiencing values that could be less than 1 mol.m^{-2}.d^{-1}. On a monthly basis, high values sometimes exceeding 50 mol.m^{-2}.d^{-1} are experienced in summer in arid regions around the Tropics of Cancer and Capricorn. For the plasticity index, we therefore decided to focus on the DLI range of 1–50 mol.m^{-2}.d^{-1}.

Dose-response curves for photosynthetic and growth parameters

It is well-known that photosynthetic capacity per unit leaf area (Phot/A^{SL}) increases with the light intensity plants experience during growth (Björkman and Holmgren 1966; Sims and Pearcy 1989), which happens to occur in a saturating fashion (see Fig. 4a; also for other traits discussed). On average, the capacity more than doubles over the 1–50 mol.m^{-2}.d^{-1} trajectory (PI = 2.2). Leaf mass per area (LMA) increases even more strongly (PI = 2.7), with a high consistency index (99%), and so does the nitrogen content per unit leaf area (PI = 2.0; Poorter et al. 2019) as well as the amount or activity of the enzyme Rubisco expressed per unit area (PI = 4.5). Although it is clear that large changes occur in the N-allocation within the photosynthetic apparatus, the total organic N content per unit leaf dry mass ([Norg]$_L$) remains remarkably constant. The resulting PI has a value of −1.1, indicating that the N concentration may decrease marginally over the DLI range considered. Photosynthetic capacity per unit leaf dry mass (Phot/M^{SL}) even decreases somewhat more strongly over the trajectory considered (PI = -1.2). Therefore, for this set of traits, light responses expressed on an area-basis are all strong, but small or absent when expressed on a leaf dry mass basis. Clearly, the increased thickness of palisade and spongy parenchyma form the main drivers of the increased photosynthetic capacity.

How then does the actual performance of the leaves change with DLI? Next to leaf structure, photosynthetic compounds, and stomatal conductance, this is co-determined by the prevailing light intensity. Photosynthetic activity per unit leaf area under growth light conditions (Phot/A^{GL}) increases strongly, with a PI of 15.1 (Fig. 4a). This is the largest increase over the 1–50 mol.m^{-2}.day^{-1} range for all traits considered here. Most of the increase is the result of a direct effect of light intensity on photosynthetic rate. Part of the increase in Phot/A^{GL}, however, is enabled by the increase in photosynthetic capacity (Phot/A^{SL}) with DLI, which enables better exploitation of light at the high-intensity range.

At the whole-plant level, a simple model to factorize growth is RGR = ULR * SLA * LMF (Evans 1972; Lambers and Poorter 1992), where RGR is the Relative Growth Rate, ULR the biomass increase per unit leaf area (Unit Leaf Rate), SLA the leaf area/leaf biomass ratio (Specific Leaf Area) and LMF the fraction of biomass invested in leaves (Leaf Mass Fraction). Among the growth-related traits, ULR is the variable most strongly related to photosynthesis per unit leaf area, and increases over the light trajectory considered with a PI of 8.9 (Fig. 4b; also for the next traits discussed). However, that value is only little more than half the increase in photosynthetic activity per unit area. This could be partly explained by the fact that photosynthesis is typically measured on the 'youngest fully-developed leaf' exposed to the prevailing light intensity. Many of the plant's other leaves are subject to self-shading and thus have lower photosynthetic rates, making whole-plant C-gain lower than estimated from these single leaf measurements. Self-shading is more pronounced at high DLI compared to low, due to larger plant size. A decrease in photosynthetic capacity in older and/or shaded leaves may also contribute. Furthermore, in field and glasshouse experiments, photosynthesis is typically measured at noon when light intensity is highest, which may also overestimate the daily C-gain differences between light treatments. Additionally, we anticipate an increased respiratory load, especially because the allocation to leaves and stems (PI = -1.2) decreases in favor for biomass allocation to the roots (PI = 1.6). A somewhat higher [C] in high-light plants (PI = 1.1; Poorter et al. 2019) may also contribute to the observed difference in PI between Phot/A^{GL} and ULR. Next to the biomass shift towards roots, there is also a decrease in SLA (inverse of LMA). Consequently, the increase in RGR is much more modest than the increases in photosynthesis or ULR. How this then results in changes in vegetative biomass will depend partly on the duration of growth and how plant size feeds back on the trajectory of growth stimulation. For the data compiled for these 610 experiments, the median response for vegetative biomass is almost 10-fold (PI = 9.8).

Dose-response curves for 12 additional traits

Next to the dose-response curves for 70 plant traits as presented in Poorter et al. (2019), we have compiled data for 12 more traits, for which we present the response curves here (Fig. 5, Table 1, see also the Suppl. Figs. S1-S12 for detailed graphs per trait). The first variable is the volumetric fraction of airspaces

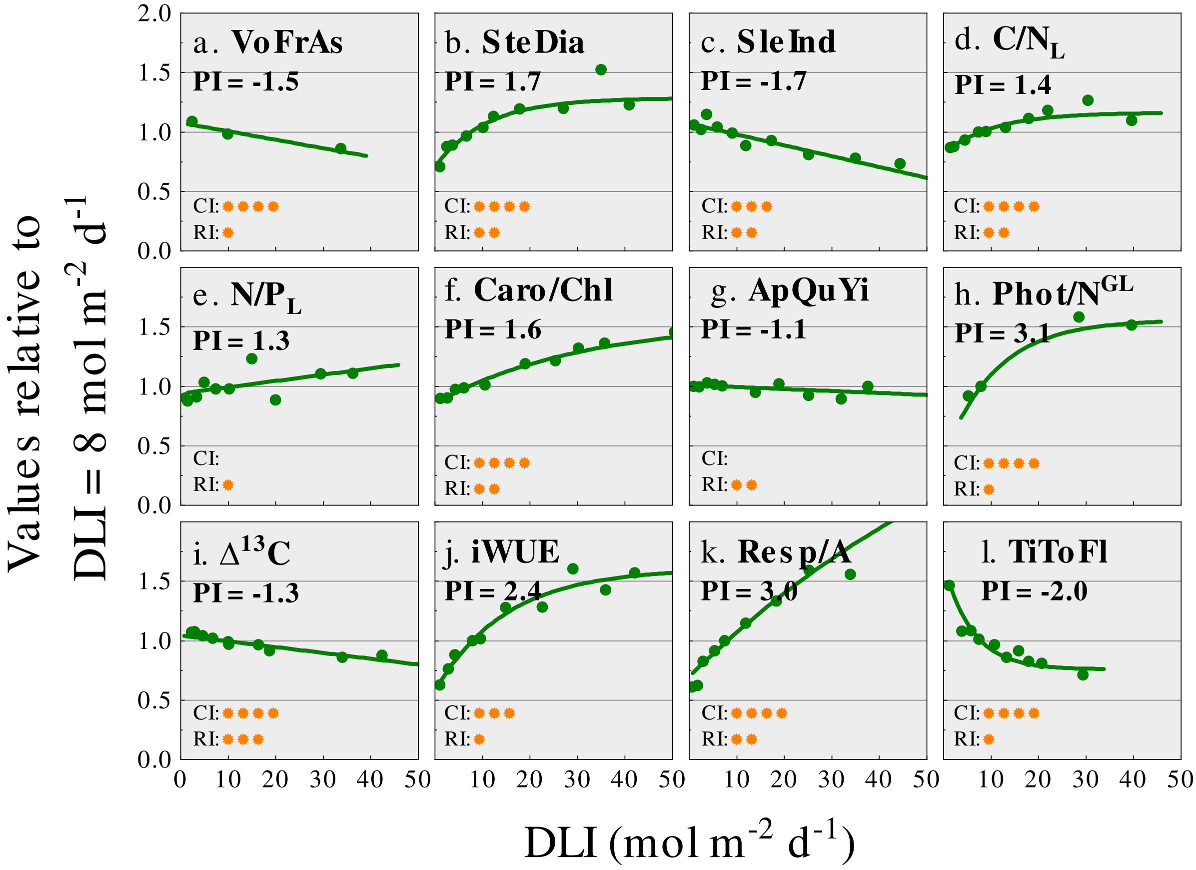


Fig. 5 Dose-response curves of 12 plant variables in relation to the daily light integral (DLI, mol m^{-2} d^{-1}), as well as the Plasticity Index (PI) over the 1–50 mol m^{-2} d^{-1} range, the Consistency Index (CI) and the Reliability Index (RI). The traits given are **a** SteDia, stem diameter; **b** SleInd, slenderness index; **c** C/N$_L$, carbon to nitrogen ratio of the leaves; **d** N/P$_L$, nitrogen to phosphorous ratio of the leaves; **e** ApQuYi, apparent quantum yield; **f** Phot/N^{GL}, rate of photosynthesis per unit leaf N measured under growth light conditions; **g** Δ^{13}C, ^{13}C discrimination as measured in leaf biomass relative to atmospheric conditions; **h** iWUE, intrinsic water use efficiency; **i** Resp/A, leaf respiration rate per unit leaf area; **j** TiToFl, time to flowering. All scaled values for a given trait were grouped into deciles based on the DLI level during growth, and median values for each decile group are indicated as green dots in the panels. The closer the points are in the x-direction, the denser the information in that DLI range. The line is the smooth curve fitted through all data points present in the 0–60 mol.m^{-2}.d^{-1} range, and given over the DLI range over which observations were present in the database. The strength of the Consistency Index is indicated by the number of orange symbols: none: % increases in the trait value with increasing DLI: 40–60%; ✷: 30–40% or 60–70%; ✷✷: 20–30% or 70–80%; ✷✷✷: 10–20% or 80–90%; ✷✷✷✷: 0–10% or 90–100%. The strength of the Reliability Index: none: RI = 1–2; ✷: 3–4; ✷✷: 5–6; ✷✷✷: 7–8; ✷✷✷✷: 9–10

in the leaf (VoFrAs). This variable is not frequently reported, but there is a highly consistent decrease with increasing light intensity. Although a densely packed leaf will increase the photosynthetic machinery per unit leaf area, it may at the same time complicate the diffusion of CO$_2$ from the stomates to the chloroplasts (Oguchi et al. 2018). Stem diameter (SteDia), generally measured at the base of the plant, or otherwise at breast height for trees, increases with light intensity in a saturating fashion, and with a very high consistency (Fig. 5b; CI = 98). Of all the morphological traits measured, plant height was on average one of the least affected by light (Poorter et al. 2019). Consequently, the slenderness index, the ratio between plant height and stem diameter, decreases with DLI (SleInd, Fig. 5c). We therefore presume that plants growing in the shade have a higher chance of mechanical failure (Peltola et al. 1999).

Table 1 Summary of the dose-response curve analysis for 12 plant traits as dependent on the daily light integral (DLI) during growth

Trait	DLI range (mol.m^{-2}.d^{-1})	# of observations	# of species	fit	Pseudo r^2	Plasticity (PI)	Consistency (CI)	Reliability (RI)	a	b	c
VoFrAs	0.9–40	30	10	L***	0.61	−1.5	**0**	3	1.077	−7.13e-3	
SteDia	0.7–52	200	65	S***	0.54	1.7	**99**	6	1.285	0.4504	9.39e-2
SleInd	0.7–52	170	60	L***	0.37	−1.7	20	6	1.070	−9.12e-3	
C/N$_L$	1.0–46	200	75	S***	0.30	1.4	**91**	5	1.163	0.2952	9.56e-2
N/P$_L$	0.8–46	120	40	L	0.14	1.3	57	4	0.9396	5.28e-3	
Caro/Chl	0.5–70	110	40	S**	0.52	1.6	**94**	5	1.549	0.4471	3.24e-2
ApQuYi	0.4–70	270	85	–	0.00	−1.1	41	6	1.011	−1.66e-3	
Phot/N^{GL}	3.0–46	40	20	S***	0.67	**3.1**	**100**	3	1.560	0.7476	9.24e-2
Δ^{13}C	0.2–64	160	45	L***	0.60	−1.3	**0**	7	1.044	−4.90e-3	
iWUE	0.4–70	120	45	S***	0.41	**2.4**	84	4	1.607	0.6415	6.73e-2
Resp/A	0.4–70	330	120	S*	0.60	**3.0**	**96**	6	3.865	0.8198	1.25e-2
TiToFl	1.2–34	140	35	S***	0.73	**−2.0**	**7**	4	0.7588	−1.185	1.68e-1

Columns 2 and 3 indicate the range of daily light integrals for which records are present in the database and the total number of observations (= number of averaged values per species and DLI 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 no relationship (–; Y = a where Y is the scaled value of the phenotypic trait of interest and a is the overall average of Y values); linear (L; Y = a + bX where X is the DLI), or saturating (S; Y = a (1 - b. e(−cX))). The Plasticity Index (PI) as used here is the fitted value at DLI = 50 divided by the fitted value at DLI = 1, with positive values indicating positive trends with DLI and negative values decreasing trends; bold numbers indicate a $|PI| \geq 2.0$. The pseudo r^2 refers to the approximate fit of the selected equation. The Consistency Index refers to the percentage of all cases (species x experiment combinations) where the phenotypic value at the highest DLI was larger than at the lowest DLI, indicating the consistency of the response. Values close to 0 or 100 indicate highly-consistent positive or negative responses. The next column shows the reliability index, based on the number of records in the database for that trait, the number of different species, the range of DLI levels at which it is measured and the average deviation from the median response, with a relative scale from 1 (low) to 10 (high reliability level). The last 3 columns give the values for parameters a, b and - if relevant - c for the equations mentioned above. Trait abbreviations: VoFrAs, Volumetric Fraction of Airspaces; SteDia, Stem Diameter; SleInd, Slenderness Index; C/N$_L$, Carbon to Nitrogen ratio of the Leaves; N/P$_L$, Nitrogen to Phosphorous ratio of the Leaves; Caro/Chl, carotenoid content per unit chlorophyll; ApQuYi, Apparent Quantum Yield; Phot/N^{GL}, rate of Photosynthesis per unit leaf N as measured under Growth Light conditions; Δ^{13}C, discrimination against ^{13}C in the leaves of whole plant; iWUE, instantaneous Water Use Efficiency; Resp/A, leaf Respiration per unit leaf Area; TiToFl, Time To Flowering. The relative weight w_i of the model selected by the AICc-test is given by: *, $0.70 < w_i < 0.90$; **, $0.90 < w_i < 0.98$; ***, $w_i > 0.98$, but only indicated in case the Consistency Index is <40% or > 60%

The C-concentration of the leaves generally slightly increases (PI = 1.1; Poorter et al. 2019), whereas [N] decreases (PI = −1.3), and consequently the C/N ratio of the leaves is increasing, with a PI of 1.4 and a high consistency index (Fig. 5d; CI = 91). Preliminary data show that the C/N ratio of roots is increasing as well. Accumulation of starch and soluble sugars (Rodríguez-López et al. 2014), higher levels of C-rich secondary compounds (Poorter et al. 2006) as well as the exchange of nitrate for soluble sugars (Blom-Zandstra et al. 1988) may all contribute to this increase in C/N ratio. Leaf phosphorous concentration decreases more (PI = -1.8; Poorter et al. 2019) than the leaf nitrogen concentration, and hence the N/P ratio of the leaves increases with increasing DLI (Fig. 5e, PI = 1.3), be it with a low consistency. This mirrors the effect of [CO$_2$], where leaf N/P decreases with increasing CO$_2$ levels (Poorter et al. 2022), also with relatively low consistency. It would be interesting to test whether the opposing effects of light and [CO$_2$] on the transpiration rate differentially affects mass flow around the roots, thereby affecting the uptake of nitrate more than of phosphorous compounds. Leaf carotenoid concentration generally scales well with chlorophyll content, but using the investment in carotenoids relative to chlorophyll, we see that carotenoid presence is favored at higher light levels (Fig. 5f, PI = 1.6). This response is predominantly due to increases in the three carotenoids involved in the xanthophyll cycle, although lutein and β-carotene increase with DLI as well (Esteban et al. 2015).

We also determined response curves related to the physiology of the plants. The apparent quantum yield is the CO_2 fixed per photons incident on a leaf measured in the linear light-limited part of the photosynthesis-light response. Theoretically, we would not expect this variable to be affected by growth light conditions (Evans 1987), and indeed, taken over all experiments the apparent quantum yield remains virtually constant (ApQuYi, Fig. 5g). However, there is a remarkable amount of variability across experiments (Suppl. Fig. 7), probably reflecting the different ways the apparent quantum yield is calculated, in combination with the difficulty to measure close-to-zero CO_2 fluxes in leaf cuvettes that contain a small leaf area (Pons and Welschen 2002). Photosynthetic Nitrogen Use efficiency, the rate of photosynthesis per unit leaf N determined under growth light intensities, increases with DLI, with a very high consistency (Phot/N^{GL}; Fig. 5h). There is a slight but consistent decrease in the intercellular to ambient [CO_2] ratio (ci/ca) of the leaves in plants grown at higher DLI (Poorter et al. 2019), and so we expect a long-term indicator of the ci/ca ratio, $\Delta^{13}C$, to decrease as well. This is indeed what happens, with high consistency (Fig. 5i). With the large increase in photosynthesis under growth light levels (PI = 15.1), and a 2.7 fold increase in stomatal conductance we expected the intrinsic Water Use Efficiency (iWUE), the ratio of the two, to increase as well. This is indeed what is found (Fig. 5j), but the increase is less than the expected 6-fold increase calculated from the PI's of the components. We have as yet no explanation for this discrepancy.

Leaf respiration per unit leaf mass is slightly affected by the light level during growth (Poorter et al. 2019), but as LMA increases (Fig. 4a), we may expect respiration per unit leaf area to increase strongly with DLI. This happens to be the case, with a PI just slightly larger than the one for LMA (Resp/A; PI = 2.9; Fig. 5k). Also for this variable the CI is high. Finally, generative development is strongly retarded in low light, which shows up in a strongly increased time before plants flower (TiToFl; Fig. 5l). This is especially true for DLI levels lower than 10 mol. $m^{-2}.d^{-1}$. Low-light plants are also much smaller in biomass. For some species, at least monocarpic perennials, it is known that flowering only occurs when plants reach a certain biomass (Klinkhamer et al. 1987; Pons and During 1987).

Further applications of MetaPhenomics

Interaction between environmental factors

So far, we have been able to construct dose-response curves for 12 abiotic environmental factors (Poorter et al. 2009, 2012a, 2012b). For most factors, such as light and CO_2, it is relatively easy to objectively quantify the levels plants are exposed to. However, for others -notably nutrients and water- it is more complex, as the growth restriction imposed by these soil resources depends not only on the level or amount applied, but also on additional factors such as pot and plant size. An alternative way to express the strength of the environmental limitation could then be to use the biomass of low-resource plants relative to those growing at optimal conditions.

Having established these dose-response curves, an interesting next step would be to calculate dose-response *surfaces*, where the combined effect of two environmental factors on plant traits is visualized. These dose-response surfaces are particularly interesting to analyze how strong the interaction between two environmental factors can be, and where in the environmental space the interactions occur. For example, is the relative response to environmental factor X_1 similar over a wide range of levels for environmental factor X_2 and vice-versa? The Sprengel-Liebig Law of the Minimum assumes that plant growth is determined by only one environmental constraint at a time (Van der Ploeg et al. 1999). Assuming this would also be true for other plant traits than biomass, we would for each of them expect simple dose-response curves consisting of two parts: a relatively linear increase (or a decrease) and a plateau. Dose-response surfaces would show similarly abrupt changes. However, exactly because of the acclimatory changes plants realize, such as a change in biomass allocation, two or more environmental factors can be co-limiting at the same time (Bloom et al. 1985; Gorban et al. 2011). Consequently, dose-response curves and surfaces will change smoothly rather than showing abrupt alterations. If interactions are largely absent, then the dose-response surface could simply be composed by information from the two individual response curves.

Two problems arise which hinder the construction of dose-response surfaces. First, this analysis requires experiments where a factorial combination of two environmental factors is studied. Although factorial experiments are not uncommon, they comprise less than 30% of the data in the MetaPhenomics database. Thus, construction of these surfaces has to be done with ~70% less data than are available for simple dose-response curves. A second challenge is that trait scaling now has to be carried out with respect to *two* environmental factors. The chance that the trait scaling value Y_R for this combination of reference levels X_{1R} and X_{2R} can be obtained by interpolation is lower, and extrapolation is more complicated due to the 3-dimensional characteristic of the dose-response surfaces.

Dose-response curves for gene expression, enzyme activities and metabolites

In principle, environmentally-induced changes in the levels of specific mRNA transcripts, proteins or metabolites are not different from changes in any classical phenotypic trait. We therefore can see a clear future for the MetaPhenomics approach in these areas, although the sheer amount of information makes the analyses more challenging. An additional complication is that most experiments in this field focus on the short-term consequences of changing a specific environmental factor from level L_1 to L_2, with measurements typically concentrating on the first 3–48 h after a shift (e.g. Liu et al. 2019). Often, many time-specific changes will occur over that period, on top of diurnal effects on gene expression. This makes it rather different from ecophysiological traits, where we sought to select experiments and harvests where plants had ample time to fully acclimate to the new environment. Bringing in time after a change as an additional factor in the analysis will allow for a more complete picture, but also make the calculations more complicated. The simplest first step would be to avoid the strong temporal fluctuations after a switch and focus on the transcriptome of plants that have fully acclimated to the new growth conditions. This kind of data, however, is very scarce in the literature (but see Walters 2005).

We carried out an experiment where *A. thaliana* plants were grown at five light intensities and sampled for RNA transcripts as well as capacities of various enzymes after plants had ample time to fully acclimate to their light environment. The experimental design allowed a first impression of a dose-response curve, with specifics of this experiment summarized in the legend of Fig. 6. The mRNA expression of early light-induced protein 1 and 2 strongly increased with light (Fig. 6a). They are thought to play a role in photoprotection. There was no change whatsoever in Rubisco activase and the gene encoding the small subunit of Rubisco. This may be surprising at first sight, as Rubisco strongly increases with DLI (Fig. 4a), but this is when expressed per unit leaf area. The increase on a dry mass basis is much smaller, due to the increase in leaf mass per area (LMA) and this measure may be more comparable to total mRNA. Expressions of elip2 and especially elip1 showed strong increases with increasing DLI, as is also observed during shorter-term high-light exposure (Huang et al. 2019). A consistent decrease was found for pal4, which encodes a protein involved in lignin synthesis. We actually expected mRNA levels for this protein to *increase* with light, as lignin concentrations generally increase with light levels (Waring et al. 1985; Niinemets and Kull 1998). The discrepancy could be due to the timing of expression, post-translational modification in enzyme levels, or degradation processes.

One aspect which deserves attention is that expression of a given gene is generally calculated relative to the expression in all other genes. Integrating such data into the MetaPhenomics approach makes that in fact *two* different steps of normalization are carried out, which may complicate the interpretation of the link between mRNA data and ecophysiological traits. It is in principle possible to calculate the absolute concentration of a given mRNA, but for this, it is necessary to use spikes (internal standards of synthetic RNA added at the start of RNA extraction), a practice which is still very little used in the plant sciences (e.g., Belouah et al. 2019).

Other fields where meta-analyses of data could yield instructive dose-response curves include the activity of enzymes ('activome'), proteins in general (proteome) and metabolites (metabolome). Enzymes are major engines of cell metabolism, and the different chemical compounds produced may reflect the physiological status plants are in. So far, we have only been able to include Rubisco amount or activity as an

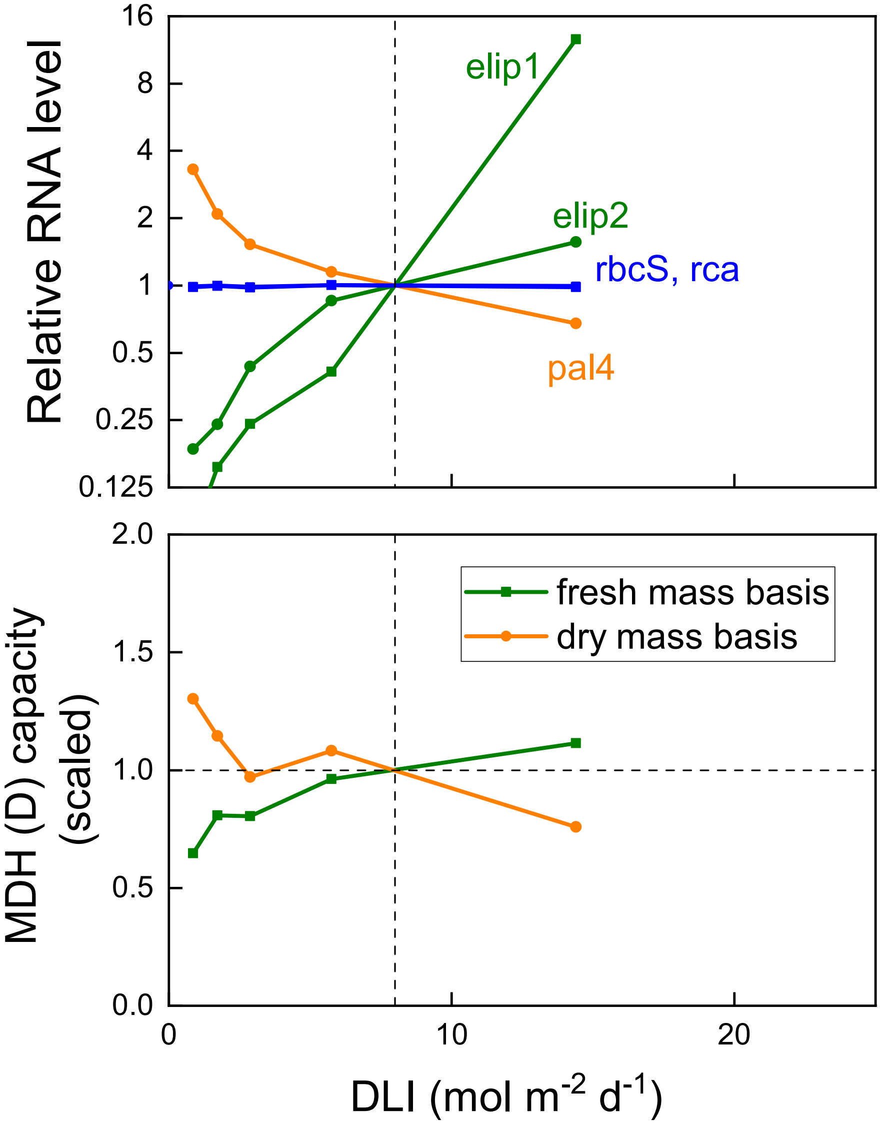


Fig. 6 Responses of (a) relative mRNA levels and (b) the capacity of the malate dehydrogenase enzyme (MDH) as dependent on the daily light integral (DLI). Genes shown are early light-induced protein 1 (elip1) and 2 (elip2), Rubisco small subunit (rbcS), Rubisco activase (rca), phototropin 1 (phot1), and phenylalanine ammonia-lyase (pal4). All values are expressed relative to the total amount of mRNA expressed. Enzyme capacity of MDH is expressed per unit leaf fresh mass and dry mass, respectively. Data fare for *Arabidopsis thaliana* plants grown in a growth chamber in pots with a PPFD of 25, 50, 100, 200, and 500 µmol.m^{-2}.s^{-1} for 8 h a day, at a day/night temperature of 20 °C

important enzymatic factor in C-fixation, and chlorophyll, xanthophylls and other carotenoids, and soluble phenolics as relevant groups of specific metabolic compounds (Poorter et al. 2019, 2022). However, there is a wide range of enzymes and compounds that could be instructive for the physiological status of plants. For the same *A. thaliana* plants for which we showed some gene expression levels, we also measured various enzymes and metabolites, of which we show the capacity of NAD-dependent Malate Dehydrogenase (MHD) as an example. MDH, whose activity is much higher than that of other enzymes of the TCA cycle (Gibon et al. 2009), plays a central role in metabolism, i.e. in the assimilation of nitrogen (Hanning and Heldt 1993), in photorespiration (Journet et al. 1981), but also in cellular redox homeostasis (Scheibe 2004; Shameer et al. 2019). It seems logical that this activity would increase when increasing light intensity, since this generates more metabolic activity and growth, but also more reactive oxygen species. However, our expectation was not confirmed, as enzyme capacities expressed per unit dry mass decreased with light levels during growth (Fig. 6b).

Clearly, we need a more holistic understanding of changes in capacity and activity of enzyme levels and their products. With time, more and more datasets become available for an increasing diversity of environments and species. A problem of metabolome data is that they are almost always expressed semi-quantitatively and making them interoperable via absolute quantification remains a considerable challenge (Ferreira et al. 2021; Røst et al. 2020).

The basis of normalization for plant processes and compounds

As plants or plant organs vary in size, it is common to normalize measured rates of physiological processes or chemical content by the size of the biological sample taken. However, there is a hidden problem here. Plant biologists studying photosynthesis generally consider leaf area as the 'logical' basis for normalization of photosynthetic and transpiration rates (Lloyd et al. 2013). Eco(physio)logists often express data on a dry mass basis, which helps to avoid variation due to time-dependent fluctuations in water availability, especially in the field. Cell biologists who grow their plants generally under controlled conditions express their data per unit dry mass, fresh mass or chlorophyll, depending on the nature of the study or sometimes on the lab's habits. For example dry mass is often used in water stress studies (e.g. Ahmadi and Baker 2001), whereas fresh mass or chlorophyll are preferred in other cases (e.g. Sicher and Bunce 1997). If data for different traits are normalized in different ways, then it is complicated to compare them. For example, the MDH capacity which did not follow our hypothesis when expressed per unit dry mass, confirms our hypothesis when data are expressed per unit fresh mass (Fig. 6b), simply because the water content per unit dry mass decreases strongly with increasing DLI (Poorter et al. 2019). Unfortunately, conversion factors are rarely reported in papers, as they are often not relevant for the research question of interest. However, without knowing the conversion factor between leaf area, dry mass, fresh mass and chlorophyll for a specific species in a specific experiment at a specific environmental level, these data cannot be matched with those from other reports, hindering reuse of data for purposes such as meta-analyses. To bridge the 'cultural' gaps among the different subdisciplines, and allow integration across fields, we strongly recommend that all plant biologists report the conversion factors among the four variables mentioned above as a standard routine in their papers. This should not just be a dutiful exercise. They are relatively easy to achieve, and there is highly relevant insight to be gained from comparing physiological rates and amounts of chemical compounds on different bases (McMillen and McClendon 1983; Garnier et al. 1999; Terashima et al. 2005; Poorter et al., 2014).

Use of dose-response curves in modeling

Modeling is a great way to integrate knowledge of different plant processes and is used advantageously to understand and forecast growth and productivity, both for crops (Keating et al. 2003) and worldwide vegetation (Keenan et al. 2021). Most of these models are based on a 'radiation use efficiency' (RUE), multiplied by the prevailing light intensity and some factor depending on temperature, or on Farquhar-Von-Caemmerer-Berry type of equations to predict photosynthesis depending on light intensity and CO_2 concentration (Boote et al. 2013). However, acclimation of plants to different levels of an environmental factor is generally not an intrinsic part of these simulation models. They do not necessarily form an integral part of ecosystem models that focus on global change either, even though these models often attain a high level of complexity.

How could the present information on dose-response curves be used advantageously to improve plant growth models? We suggest two different options, using the light-response of SLA as an example. First, acclimation could be explicitly simulated using the generalized dose-response curve as we derived before. As an illustration we used an old crop model (SUCROS; Kropff et al. 1994), and either assumed a constant SLA, or allow SLA to acclimate to light as derived from the generalized dose-response curve of MetaPhenomics (Fig. 7a). For simplicity, we only considered plant biomass 40 days after germination, when plants are still vegetative and assumed a constant temperature. We then challenged the model with DLI levels between 8 and 50 $mol.m^{-2}.d^{-1}$, admittedly a broader range than most crop plants would ever experience outside. For clarity, the data of this analysis were normalized for a DLI of 35 $mol.m^{-2}.d^{-1}$, a typical light level crops experience under field conditions. As shown in Fig. 7b, total vegetative biomass after 40 days varied strongly with light, increasing 220-fold when SLA was kept constant. In

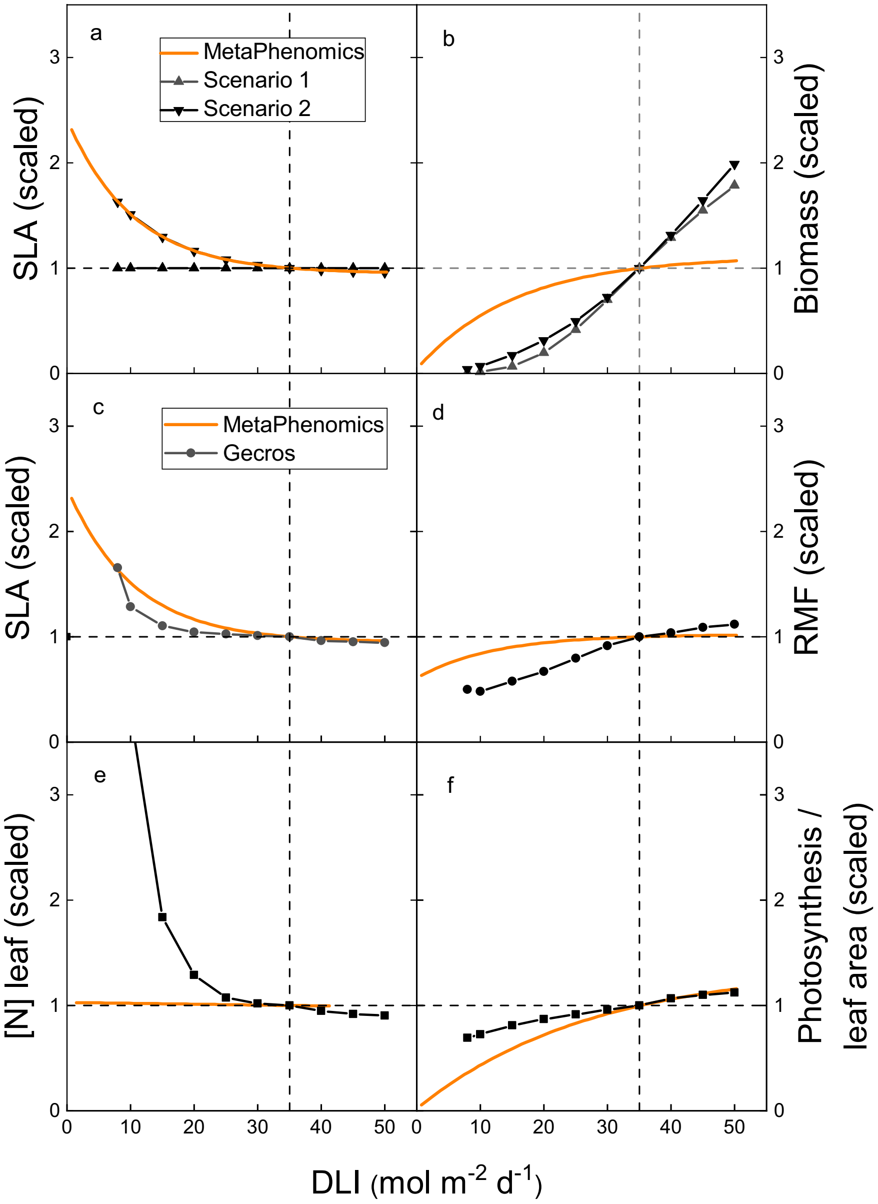


Fig. 7 Comparing the dose-response curves as found for MetaPhenomics, with results from different crop models (a-b: SUCROS; c-f, GECROS). **a** The two SUCROS simulated scenarios, keeping specific leaf area (SLA) constant (scenario 1), or applying SLA following the dose-response curve derived in MetaPhenomics (scenario 2). **b** Simulated total dry mass of the crop after 40 days of growth, scaled to 1 at a DLI of 35 mol. m^{-2}.d^{-1}. **c** Dose-response curve for SLA as output of the model GECROS (black line), compared to the dose-response curve observed for MetaPhenomics. **d** Idem for root mass fraction (RMF). **e** Idem for leaf nitrogen concentration. **f** Idem or the rate of photosynthesis per unit leaf area under actual light conditions, averaged for all leaves in the canopy. All MetaPhenomics dose-response curves are shown in orange. For reasons of clarity, all trait data in this figure were normalized to the value observed at a DLI of 35 mol.m^{-2}.d^{-1}. Dashed lines indicate the scaling DLI at the x-axis, and the resulting scaled phenotypic trait value (=1) in the y direction

contrast, variation was less than 50-fold when incorporating the 2-fold change in SLA into the model, showing the principle that the acclimation in leaf morphology is improving plant C-gain under low-light conditions, and presumably also plant fitness under these conditions. Considerable differences in output of a vegetation-climate model were also found when the well-known decrease in SLA with increasing atmospheric [CO$_2$] was included in the simulations (Kovenock and Swann 2018).

The second way we see dose-response curves to be used advantageously, is in comparing and analyzing the dose-response curves of different variables simulated in the model with those found for experimental plants or vegetation. Modelers need to keep their models simple and tractable, which makes them selective in the processes and detail included in their models. Experimentalists often have a different background, and find it difficult to understand what exactly is or is not included in the wide variety of simulation models and what consequences this has for the output of these models. A model that seeks to incorporate some form of acclimation at a tractable level is GECROS (Yin and Struik 2017). It includes photosynthesis and respiration as the main processes for growth. Biomass allocation is governed by the sugar-allocation to shoots and roots that maximizes growth. Leaf area expansion at each time step is derived from the amount of sugar allocated to leaf growth, but co-limited by N availability for new growth. Again calculating model output for a wider range of light levels than ever anticipated, average SLA responded in a manner very similar to what was found in the MetaPhenomics analysis (Fig. 7c). The root mass fraction (RMF) in the model increased, as also found for experimental plants, but the change was stronger for the modeled plants (Fig. 7d). Modeled leaf N concentration was constant over a broad range of DLI's, but increased strongly below a DLI of 15 $\mathrm{mol.m^{-2}.d^{-1}}$ (Fig. 7e). Photosynthesis per unit total leaf area was less plastic in the model, which may also be because the experiments compiled in MetaPhenomics often measure the youngest full-grown and full-light exposed leaf, whereas the model considers all leaves of a crop. Clearly, GECROS is not able to fully simulate crop response down to what are very low light levels for a crop (< 15 $\mathrm{mol.m^{-2}.d^{-1}}$). However, it is able to show acclimation as an intrinsic property of the model much the way that plants actually acclimate to light. This illustrates that the comparison of model output with the dose-response curves from MetaPhenomics may provide a good focal point for communication between modelers and experimentalists.

Conclusions

a. In this paper we have shown the power of generalized dose-response curves in summarizing plant responses to the environment. Using a systematic approach across all kinds of subdisciplines, a quantitative and systematic overview on plant responses for many traits can be obtained from the literature.
b. The same information can be used to assess whether functional groups of species do behave similarly or differently in their acclimation to a given environmental factor.
c. Although there are challenges based on different ways of normalization, the approach could also be advantageously used to describe mRNA, enzyme activities or metabolite concentrations. Another field of applications is the inclusion of the derived dose-response curves into plant models, or in the communication between modelers and experimental biologists. Dose-response curves in MetaPhenomics could be exploited as a yardstick to guide the future effort of improving models.

Appendix A1

Citations used in the meta-analysis

Abrams MD, Kloeppel BD, Kubiske ME (1992) Ecophysiological and morphological responses to shade and drought in two contrasting ecotypes of *Prunus serotina*. Tree Physiol 10:343–355. https://doi.org/10.1093/treephys/10.4.343

Ajmi A, Vázquez S, Morales F, et al (2018) Prolonged artificial shade affects morphological, anatomical, biochemical and ecophysiological behavior of young olive trees (cv. Arbosana). Sci Hortic 241:275–284. https://doi.org/10.1016/j.scienta.2018.06.089

Allard G, Nelson CJ, Pallardy SG (1991a) Shade effects on growth of tall fescue: II. Leaf gas exchange characteristics. Crop Sci 31:167–172. https://doi.org/doi.org/10.2135/cropsci1991.0011183X003100010037x

Allard G, Nelson CJ, Pallardy SG (1991b) Shade effects on growth of tall fescue: I. Leaf anatomy and dry matter partitioning. Crop Sci 31:163–167. https://doi.org/10.2135/cropsci1991.0011183X003100010037x

Ammer C (2003) Growth and biomass partitioning of *Fagus sylvatica* L. and *Quercus robur* L. seedlings in response to shading and small changesin the R/FR-ratio of radiation. Ann For Sci 60:163–171. https://doi.org/10.1051/forest:2003009

An H, Shangguan ZP (2008) Specific leaf area, leaf nitrogen content, and photosynthetic acclimation of *Trifolium repens* L. seedlings grown at different irradiances and nitrogen concentrations. Photosynthetica 46:143–147. https://doi.org/10.1007/s11099-008-0023-y

Andersen PC, Norcini JG, Knox GW (1991) Influence of irradiance on leaf physiology and plant growth characteristics of *Rhododendron* x 'Pink

Ruffles.' J Amer Soc Hortic Sci 116:881–887. https://doi.org/10.21273/JASHS.116.5.881

Anderson JM, Chow WS, Park Y-I, et al (2001) Response of *Tradescantia albiflora* to growth irradiance: Change versus changeability. Phot Res 67:103–112. https://doi.org/doi:10.1023/A:1010681721929.

Angmo P, Phuntsog N, Namgail D, et al (2021) Effect of shading and high temperature amplitude in greenhouse on growth, photosynthesis, yield and phenolic contents of tomato (*Lycopersicum esculentum* Mill.). Physiol Mol Biol Plants 27:1539–1546. https://doi.org/10.1007/s12298-021-01032-z

Aranda I, Pardos M, Puertolas J, et al (2007) Water-use efficiency in cork oak (*Quercus suber*) is modified by the interaction of water and light availabilities. Tree Physiol 27:671–677. https://doi.org/10.1093/treephys/27.5.671

Armitage AM (1995) Photoperiod, irradiance, and temperature influence flowering of *Hamelia patens* (Texas Firebush). HortSci 30:255–256. https://doi.org/10.21273/HORTSCI.30.2.255

Ashton PMS, Berlyn GP (1992) Leaf adaptations of some *Shorea* species to sun and shade. New Phytol 121:587–596. https://doi.org/10.1111/j.1469-8137.1992.tb01130.x

Bagnall DJ, King RW (1991) Response of peanut (*Arachis hypogaea*) to temperature, photoperiod and irradiance 1. Effect on flowering. Field Crops Res 26:263–277. https://doi.org/10.1016/0378-4290(91)90004-F

Bailey S, Horton P, Walters RG (2004) Acclimation of *Arabidopsis thaliana* to the light environment: the relationship between photosynthetic function and chloroplast composition. Planta 218:793–802. https://doi.org/10.1007/s00425-003-1158-5

Balaguer L, Martínez-Ferri E, Valladares F, et al (2001) Population divergence in the plasticity of the response of *Quercus coccifera* to the light environment: Plasticity of *Quercus coccifera* populations. Funct Ecol 15:124–135. https://doi.org/10.1046/j.1365-2435.2001.00505.x

Baligar VC, Elson MK, Almeida A-AF, et al (2021) The impact of carbon dioxide concentrations and low to adequate photosynthetic photon flux density on growth, physiology and nutrient use efficiency of juvenile cacao genotypes. Agronomy 11:397. https://doi.org/10.3390/agronomy11020397

Baloch J-U-D, Munir M, Abid M, Iqbal M (2012) Effects of varied irradiance on flowering time of facultative long-day ornamental annuals. Pak J Bot 44:111–117

Baltzer JL, Thomas SC (2007) Physiological and morphological correlates of whole-plant light compensation point in temperate deciduous tree seedlings. Oecologia 153:209–223. https://doi.org/10.1007/s00442-007-0722-2

Barbosa MAM, Chitwood DH, Azevedo AA, et al (2019) Bundle sheath extensions affect leaf structural and physiological plasticity in response to irradiance. Plant Cell Environ 42:1575–1589. https://doi.org/10.1111/pce.13495

Barros F de V, Goulart MF, Sá Telles SB, et al (2011) Phenotypic plasticity to light of two congeneric trees from contrasting habitats: Brazilian Atlantic Forest versus cerrado (savanna): Plasticity to light of congeneric trees from contrasting habitats. Plant Biol 14:208–215. https://doi.org/10.1111/j.1438-8677.2011.00474.x

Bartieres EMM, P.Q. Scalon S, Dresch DM, et al (2020) Shading as a means of mitigating water deficit in seedlings of *Campomanesia xanthocarpa* (Mart.) O. Berg. Not Bot Horti Agrobo 48:234–244. https://doi.org/10.15835/nbha48111720

Baruch Z, Pattison R, Goldstein G (2000) Responses to light and water availability of four invasive melastomataceae in the Hawaiian islands. Int J Plant Sci 161:107–118. https://doi.org/doi.org/10.1086/314233

Bellasio C, Griffiths H (2014) Acclimation of C_4 metabolism to low light in mature maize leaves could limit energetic losses during progressive shading in a crop canopy. J Exp Bot 65:3725–3736. https://doi.org/10.1093/jxb/eru052

Benvenuti S, Macchia M, Stefani A (1994) Effects of shade on reproduction and some morphological characteristics of *Abutilon theophrasti* Medicos, *Datura stramonium* L. and *Sorghum halepense* L. Pers. Weed Res 34:283–288. https://doi.org/10.1111/j.1365-3180.1994.tb01996.x

Brearley FQ, Scholes JD, Press MC, Palfner G (2007) How does light and phosphorus fertilisation affect the growth and ectomycorrhizal community of two contrasting dipterocarp species? Plant Ecol 192:237–249. https://doi.org/10.1007/s11258-007-9325-6

Buchmann N, Brooks JR, Rapp KD, Ehleringer JR (1996) Carbon isotope composition of C_4 grasses is influenced by light and water supply. Plant Cell Environ 19:392–402. https://doi.org/10.1111/j.1365-3040.1996.tb00331.x

Buisson D, Lee DW (1993) The developmental responses of papaya leaves to simulated canopy shade. Amer J Bot 80:947–952. https://doi.org/10.2307/2445515

Bunce JA, Patterson DT, Peet MM, Alberte RS (1977) Light acclimation during and after leaf expansion in soybean. Plant Physiol 60:255–258. https://doi.org/10.1104/pp.60.2.255

Bungard RA, McNeil D, Morton JD (1997) Effects of nitrogen on the photosynthetic apparatus of *Clematis vitalba* grown at several irradiances. Funct Plant Biol 24:205–214. https://doi.org/10.1071/PP96085

Caffarri S, Frigerio S, Olivieri E, et al (2005) Differential accumulation of *Lhcb* gene products in thylakoid membranes of *Zea mays* plants grown under contrasting light and temperature conditions. Proteomics 5:758–768. https://doi.org/10.1002/pmic.200402008

Cai ZQ (2011) Shade delayed flowering and decreased photosynthesis, growth and yield of Sacha Inchi (*Plukenetia volubilis*) plants. Industr Crops Prod 34:1235–1237. https://doi.org/10.1016/j.indcrop.2011.03.021

Campanello PI, Gatti MG, Goldstein G (2008) Coordination between water-transport efficiency and photosynthetic capacity in canopy tree species at different growth irradiances. Tree Physiol 28:85–94. https://doi.org/10.1093/treephys/28.1.85

Cantliffe DJ (1973) Nitrate accumulation in table beets and spinach as affected by nitrogen, phosphorus, and potassium nutrition and light intensity. Agron J 65:563–565. https://doi.org/10.2134/agronj1973.00021962006500040012x

Cao W, Tibbitts TW, Wheeler RM (1994) Carbon dioxide interactions with irradiance and temperature in potatoes. Adv Space Res 14:243–250. https://doi.org/10.1016/0273-1177(94)90304-2

Carelli MLC (1999) Carbon isotope discrimination and gas exchange in *Coffea* species grown under different irradiance regimes. Rev Bras Fisiol Veg 11:63–68

Carrión-Tacuri J, Rubio-Casal AE, de Cires A, et al (2011) *Lantana camara* L.: a weed with great light-acclimation capacity. Photosynthetica 49:321–329. https://doi.org/10.1007/s11099-011-0039-6

Casson SA, Franklin KA, Gray JE, et al (2009) Phytochrome B and pif4 regulate stomatal development in response to light quantity. Curr Biol 19:229–234. https://doi.org/10.1016/j.cub.2008.12.046

Castro-Diez P, Navarro J, Pintado A, et al (2006) Interactive effects of shade and irrigation on the performance of seedlings of three Mediterranean *Quercus* species. Tree Physiol 26:389–400. https://doi.org/10.1093/treephys/26.3.389

Cavatte PC, Oliveira ÁAG, Morais LE, et al (2012) Could shading reduce the negative impacts of drought on coffee? A morphophysiological analysis. Physiol Plant 144:111–122. https://doi.org/10.1111/j.1399-3054.2011.01525.x

Chagvardieff P, d'Aletto T, André M (1994) Specific effects of irradiance and CO_2 concentration doublings on productivity and mineral content in lettuce. Adv Space Res 14:269–275. https://doi.org/10.1016/0273-1177(94)90307-7

Chan SS, Radosevich SR, Grotta AT (2003) Effects of contrasting light and soil moisture availability on the growth and biomass allocation of Douglas-fir and red alder. Can J For Res 33:106–117. https://doi.org/10.1139/x02-148

Chen B, Liu X, Jia L, et al (2021) Effects of different light intensities on stem characters and mechanical traits of four Commelinaceae plants. Act Pratacult Sin 30:103–116. https://doi.org/DOI:10. 11686/cyxb2020466

Comstock JP, McCouch SR, Martin BC, et al (2005) The effects of resource availability and environmental conditions on genetic rankings for carbon isotope discrimination during growth in tomato and rice. Funct Plant Biol 32:1089. https://doi.org/10.1071/FP05117

Coopman RE, Reyes-Diaz M, Briceno VF, et al (2008) Changes during early development in photosynthetic light acclimation capacity explain the shade to sun transition in *Nothofagus nitida*. Tree Physiol 28:1561–1571. https://doi.org/10.1093/treephys/28.10.1561

Coste S, Roggy J-C, Schimann H, et al (2011) A cost–benefit analysis of acclimation to low irradiance in tropical rainforest tree seedlings: leaf life span and payback time for leaf deployment. J Exp Bot 62:3941–3955. https://doi.org/10.1093/jxb/err092

Danyagri G, Dang Q-L (2014) Effects of elevated carbon dioxide concentration and soil temperature on the growth and biomass responses of mountain maple (*Acer spicatum*) seedlings to light availability. J Plant Ecol 7:535–543. https://doi.org/10.1093/jpe/rtt061

De Groot CC, Marcelis LFM, Van Den Boogaard R, Lambers H (2001) Growth and dry-mass partitioning in tomato as affected by phosphorus nutrition and light: Growth and dry-mass partitioning. Plant Cell Environ 24:1309–1317. https://doi.org/10.1046/j.0016-8025.2001.00788.x

De Pinheiro Henriques AR, Marcelis LFM (2000) Regulation of growth at steady-state nitrogen nutrition in lettuce (*Lactuca sativa* L.): interactive effects of nitrogen and irradiance. Ann Bot 86:1073–1080. https://doi.org/doi:10.1006/anbo.2000.1268

Delpérée C, Kinet JM, Lutts S (2003) Low irradiance modifies the effect of water stress on survival and growth-related parameters during the early developmental stages of buckwheat (*Fagopyrum esculentum*). Physiol Plant 119:211–220. https://doi.org/10.1034/j.1399-3054.2003.00170.x

Dias-Filho MB, Chagas Júnior AF (2000) Growth, biomass allocation and photosynthesis of *Rolandra fruticosa* (Asteraceae) in response to shade. Planta Dan 18:71–80. https://doi.org/10.1590/S0100-83582000000100007

Díaz-Barradas MC, Zunzunegui M, Alvarez-Cansino L, et al (2018) How do Mediterranean shrub species cope with shade? Ecophysiological response to different light intensities. Plant Biol 20:296–306. https://doi.org/10.1111/plb.12661

Doley D (1978) Effects of shade on gas exchange and growth in seedlings of *Eucalyptus grandis* Hill ex Maiden. Aust J Plant Physiol 5:723–738. https://doi.org/10.1071/PP9780723

Ducrey M (1992) Variation in leaf morphology and branching pattern of some tropical rain forest species from Guadeloupe (French West Indies) under semi-controlled light conditions. Ann For Sci 49:553–570. https://doi.org/10.1051/forest:19920601

Eng RYN, Tsujita MJ, Grodzinski B (1985) The effects of supplementary HPS lighting and carbon dioxide enrichment on the vegetative growth, nutritional status and flowering characteristics of *Chrysanthemum morifolium* Ramat. J Hortic Sci 60:389–395. https://doi.org/10.1080/14620316.1985.11515643

Euliss AC, Fisk MC, McCleneghan SC, Neufeld HS (2007) Allocation and morphological responses to resource manipulations are unlikely to mitigate shade intolerance in *Houstonia montana*, a rare southern Appalachian herb. Can J Bot 85:976–985. https://doi.org/10.1139/B07-104

Evans CA, Miller EK, Friedland AJ (2001) Effect of nitrogen and light on nutrient concentrations and associated physiological responses in birch and fir seedlings. Plant Soil 236:197–207. https://doi.org/DOI: 10.1023/a:1012772604362

Evans JR, Poorter H (2001) Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain: Photosynthetic acclimation of plants to growth irradiance. Plant Cell Environ 24:755–767. https://doi.org/10.1046/j.1365-3040.2001.00724.x

Falbel TG, Staehelin LA, Adams WW (1994) Analysis of xanthophyll cycle carotenoids and chlorophyll fluorescence in light intensity-dependent chlorophyll-deficient mutants of wheat and barley. Photosynth Res 42:191–202. https://doi.org/10.1007/BF00018262

Fausey BA, Heins RD, Cameron AC (2005) Daily light integral affects flowering and quality of greenhouse-grown *Achillea, Gaura*, and *Lavandula*. HortSci 40:114–118. https://doi.org/10.21273/HORTSCI.40.1.114

Feng L, Raza MA, Li Z, et al (2019) The influence of light intensity and leaf movement on photosynthesis characteristics and carbon balance of soybean. Front Plant Sci 9:1952. https://doi.org/10.3389/fpls.2018.01952

Feng YL, Cao KF, Zhang JL (2004) Photosynthetic characteristics, dark respiration, and leaf mass per unit area in seedlings of four tropical tree species grown under three irradiances. Photosynthetica 42:431–437. https://doi.org/10.1023/B:PHOT.0000046163.83729.e5

Fini A, Loreto F, Tattini M, et al (2016) Mesophyll conductance plays a central role in leaf functioning of *Oleaceae* species exposed to contrasting sunlight irradiance. Physiol Plant 157:54–68. https://doi.org/10.1111/ppl.12401

Ford MA, Thorne GN (1967) Effect of CO_2 concentration on growth of sugar-beet, barley, kale, and maize. Ann Bot 31:629–644. https://doi.org/10.1093/oxfordjournals.aob.a084168

Freschet GT, Violle C, Bourget MY, et al (2018) Allocation, morphology, physiology, architecture: the multiple facets of plant above- and below-ground responses to resource stress. New Phytol 219:1338–1352. https://doi.org/10.1111/nph.15225

Fu QS, Zhao B, Wang YJ, et al (2010) Stomatal development and associated photosynthetic performance of *Capsicum* in response to differential light availabilities. Photosynthetica 48:189–198. https://doi.org/10.1007/s11099-010-0024-5

Funayama S, Terashima I (1999) Effects of geminivirus infection and growth irradiance on the vegetative growth and photosynthetic production of *Eupatorium makinoi*. New Phytol 142:483–494. https://doi.org/10.1046/j.1469-8137.1999.00418.x

García-Plazaola JI, Hernández A, Artetxe U, Becerril JM (2002) Regulation of the xanthophyll cycle pool size in duckweed (*Lemna minor*) plants. Physiol Plant 116:121–126. https://doi.org/10.1034/j.1399-3054.2002.1160115.x

Giertych MJ, Karolewski P, Oleksyn J (2015) Carbon allocation in seedlings of deciduous tree species depends on their shade tolerance. Acta Physiol Plant 37:216. https://doi.org/10.1007/s11738-015-1965-x

Gleason SM, Ares A (2004) Photosynthesis, carbohydrate storage and survival of a native and an introduced tree species in relation to light and defoliation. Tree Physiol 24:1087–1097. https://doi.org/10.1093/treephys/24.10.1087

González AV, Gianoli E (2004) Morphological plasticity in response to shading in three *Convolvulus* species of different ecological breadth. Acta Oecol 26:185–190. https://doi.org/10.1016/j.actao.2004.05.001

Goulart MF, Lovato MB, de Vasconcellos Barros F, et al (2011) Which extent is plasticity to light involved in the ecotypic differentiation of a tree species from savanna and forest? Ecotypic differentiation in savanna and forest. Biotropica 43:695–703. https://doi.org/10.1111/j.1744-7429.2011.00760.x

Grace SC, Logan BA (1996) Acclimation of foliar antioxidant systems to growth irradiance in three broad-leaved evergreen species. Plant Physiol 112:1631–1640. https://doi.org/10.1104/pp.112.4.1631

Grassi G, Minotta G (2000) Influence of nutrient supply on shade-sun acclimation of *Picea abies* seedlings: effects on foliar morphology, photosynthetic performance and growth. Tree Physiol 20:645–652. https://doi.org/10.1093/treephys/20.10.645

Grechi I, Vivin Ph, Hilbert G, et al (2007) Effect of light and nitrogen supply on internal C:N balance and control of root-to-shoot biomass allocation in grapevine. Env Exp Bot 59:139–149. https://doi.org/10.1016/j.envexpbot.2005.11.002

Groninger JW, Seiler JR, Peterson JA, Kreh RE (1996) Growth and photosynthetic responses of four Virginia Piedmont tree species to shade. Tree Physiol 16:773–778. https://doi.org/10.1093/treephys/16.9.773

Groot CC de, Marcelis LFM, Boogaard R van den, Lambers H (2002) Interactive effects of nitrogen and irradiance on growth and partitioning of dry mass and nitrogen in young tomato plants. Funct Plant Biol 29:1319. https://doi.org/10.1071/FP02087

Guzmán Q. JA, Cordero S. RA, Corea A. E (2016) Biomass allocation and gas exchange are affected by light conditions in endangered *Cedrela salvadorensis* (Meliaceae) seedlings. Rev Biol Trop 64:1143–1154. https://doi.org/10.15517/rbt.v64i3.19606

Hanba YT, Kogami H, Terashima I (2002) The effect of growth irradiance on leaf anatomy and photosynthesis in *Acer* species differing in light demand: Light acclimation and leaf anatomy in *Acer*. Plant Cell Environ 25:1021–1030. https://doi.org/10.1046/j.1365-3040.2002.00881.x

Hao G-Y, Wang A-Y, Sack L, et al (2013) Is hemiepiphytism an adaptation to high irradiance? Testing seedling responses to light levels and drought in hemiepiphytic and non-hemiepiphytic *Ficus*. Physiol Plant 148:74–86. https://doi.org/10.1111/j.1399-3054.2012.01694.x

Hao X, Papadopoulos AP (1999) Effects of supplemental lighting and cover materials on growth, photosynthesis, biomass partitioning, early yield and quality of greenhouse cucumber. Sci Hortic 80:1–18. https://doi.org/10.1016/S0304-4238(98)00217-9

Heraut-Bron V, Robin C, Varlet-Grancher C, et al (1999) Light quality (red:far-red ratio): does it affect photosynthetic activity, net CO_2 assimilation, and morphology of young white clover leaves? Can J Bot 77:1425–1431

Hicklenton PR, Newman SM, Davies LJ (1993) Night temperature, photosynthetic photon flux, and long days affect *Gypsophila paniculata* flowering. HortSci 28:888–890. https://doi.org/10.21273/HORTSCI.28.9.888

Huber BM, Louws FJ, Hernández R (2021) Impact of different daily light integrals and carbon dioxide concentrations on the growth, morphology, and production efficiency of tomato seedlings. Front Plant Sci 12:615853. https://doi.org/10.3389/fpls.2021.615853

Hummel G, Kazda M The impact of different light conditions on growth and biomass allocation of the liana. Unpubl.

Israel WK, Watson-Lazowski A, Chen Z-H, Ghannoum O (2022) High intrinsic water use efficiency is underpinned by high stomatal aperture and guard cell potassium flux in C_3 and C_4 grasses grown at glacial CO_2 and low light. J Exp Bot 73:1546–1565. https://doi.org/10.1093/jxb/erab477

Israeli Y, Schwartz A, Plaut Z, Yakir D (1996) Effects of light regime on delta^{13}C, photosynthesis and yield of field-grown banana (*Musa* sp., Musaceae)*. Plant Cell Environ 19:225–230. https://doi.org/10.1111/j.1365-3040.1996.tb00244.x

James SA, Bell DT (2000) Influence of light availability on leaf structure and growth of two *Eucalyptus globulus* ssp. *globulus* provenances. Tree Physiol 20:1007–1018. https://doi.org/10.1093/treephys/20.15.1007

Jespersen E, Kirk GH, Brix H, et al (2021) Shade and salinity responses of two dominant coastal wetland grasses: implications for light competition at the transition zone. Ann Bot 128:469–480. https://doi.org/10.1093/aob/mcab089

Jha P, Norsworthy JK, Riley MB, et al (2008) Acclimation of palmer amaranth (*Amaranthus palmeri*) to shading. Weed Sci 56:729–734. https://doi.org/10.1614/WS-07-203.1

Johnston M, Onwueme IC (1998) Effect of shade on photosynthetic pigments in the tropical root crops: yam, taro, tannia, cassava and sweet potato. Exp Agric 34:301–312. https://doi.org/10.1017/S0014479798343033

Jurik TW, Chabot JF, Chabot BF (1982) Effects of light and nutrients on leaf size, CO_2 exchange, and anatomy in wild strawberry (*Fragaria virginiana*). Plant Physiol 70:1044–1048. https://doi.org/10.1104/pp.70.4.1044

Karlsson MG (2002) Flower formation in *Primula vulgaris* is affected by temperature, photoperiod and daily light integral. Sci Hortic 95:99–110. https://doi.org/10.1016/S0304-4238(02)00024-9

Karlsson MG, Heins RD, Erwin JE, et al (1989) Irradiance and temperature effects on time of development and flower size in *Chrysanthemum*. Sci Hortic 39:257–267. https://doi.org/doi.org/10.1016/0304-4238(89)90138-6

Kelly J, Jose S, Nichols JD, Bristow M (2009) Growth and physiological response of six Australian rainforest tree species to a light gradient. For Ecol Manage 257:287–293. https://doi.org/10.1016/j.foreco.2008.09.008

Kitajima K (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. Oecologia 98:419–428. https://doi.org/10.1007/BF00324232

Kitao M, Lei TT, Koike T, et al (2000) Susceptibility to photoinhibition of three deciduous broadleaf tree species with different successional traits raised under various light regimes. Plant Cell Environ 23:81–89. https://doi.org/10.1046/j.1365-3040.2000.00528.x

Knake EL (1972) Effect of shade on giant foxtail. Weed Sci 20:588–592. https://doi.org/10.1017/S0043174500078826

Kobayashi T, Hori Y (1999) Photosynthesis and seedling survival of weeds with different trampling susceptibilities under contrasting light and water conditions. J Weed Sci Techn 44:195–204

Königer M, Winter K (1991) Carotenoid composition and photon-use efficiency of photosynthesis in *Gossypium hirsutum* L. grown under conditions of slightly suboptimum leaf temperatures and high levels of irradiance. Oecologia 87:349–356. https://doi.org/10.1007/BF00634590

Krause GH, Winter K, Matsubara S, et al (2012) Photosynthesis, photoprotection, and growth of shade-tolerant tropical tree seedlings under full sunlight. Photosynth Res 113:273–285. https://doi.org/10.1007/s11120-012-9731-z

Kubiske ME, Pregitzer KS (1996) Effects of elevated CO_2 and light availability on the photosynthetic light response of trees of contrasting shade tolerance. Tree Physiol 16:351–358. https://doi.org/10.1093/treephys/16.3.351

Kurasova I (2002) Characterization of acclimation of *Hordeum vulgare* to high irradiation based on different responses of photosynthetic activity and pigment composition. Photosynth Res 72:71–83. https://doi.org/doi: 10.1023/A:1016018900535.

Kurasová I, Kalina J, Štroch M, et al (2003) Response of photosynthetic apparatus of spring barley (*Hordeum vulgare* L.) to combined effect of elevated CO_2 concentration and different growth irradiance. Photosynthetica 41:209–219. https://doi.org/10.1023/B:PHOT.0000011953.36956.a3

Lauerer M, Saftic D, Quick WP, et al (1993) Decreased ribulose-1,5-bisphosphate carboxylase-oxygenase in transgenic tobacco transformed with “antisense” rbcS. Planta 190:332–345. https://doi.org/doi.org/10.1007/BF00196962

Lawler IR, Foley WJ, Woodrow IE, Cork SJ (1997) The effects of elevated CO_2 atmospheres on the nutritional quality of *Eucalyptus* foliage and its interaction with soil nutrient and light availability. Oecologia 109:59–68. https://doi.org/10.1007/s004420050058

Lee DW, Oberbauer SF, Johnson P, et al (2000) Effects of irradiance and spectral quality on leaf structure and function in seedlings of two Southeast Asian *Hopea* (Dipterocarpaceae) species. Amer J Bot 87:447–455. https://doi.org/10.2307/2656588

Lee DW, Oberbauer SF, Krishnapilay B, et al (1997) Effects of irradiance and spectral quality on seedling development of two Southeast Asian *Hopea* species. Oecologia 110:1–9. https://doi.org/10.1007/s004420050126

Lee DW, Oberbauer SF, Krishnapillay B, et al (1999) Effects of irradiance and spectral quality on the seedling development of jelutong (*Dyera costulata*). J Trop For Sci 11:132–147. http://www.jstor.org/stable/43582519

Lehto T, Grace J (1994) Carbon balance of tropical tree seedlings: a comparison of two species. New Phytol 127:455–463. https://doi.org/10.1111/j.1469-8137.1994.tb03963.x

Leishman MR, Sanbrooke KJ, Woodfin RM (1999) The effects of elevated CO_2 and light environment on growth and reproductive performance of four annual species. New Phytol 144:455–462. https://doi.org/doi.org/10.1046/j.1469-8137.1999.00544.x

Lestari DP, Nichols JD (2016) Seedlings of subtropical rainforest species from similar successional guild show different photosynthetic and morphological responses to varying light levels. Tree Physiol 37:186–198. https://doi.org/10.1093/treephys/tpw088

Lewis CE, Peratoner G, Cairns AJ, et al (1999) Acclimation of the summer annual species, *Lolium temulentum*, to CO_2 enrichment. Planta 210:104–114. https://doi.org/10.1007/s004250050659

Li H, Radunz A, He P, Schmid GH (2002) Influence of different light intensities on the content of diosgenin, lipids, carotenoids and fatty acids in leaves of *Dioscorea zingiberensis*. Zeitschr Naturforsch 57:135–143. https://doi.org/10.1515/znc-2002-1-223

Li Y, Zhao H, Duan B, et al (2011) Effect of drought and ABA on growth, photosynthesis and antioxidant system of *Cotinus coggygria* seedlings under two different light conditions. Env Exp Bot 71:107–113. https://doi.org/10.1016/j.envexpbot.2010.11.005

Li Z, Shi K, Zhang F, et al (2019) Growth, physiological, and biochemical responses of tung tree (*Vernicia fordii*) seedlings to different light intensities. HortSci 54:1361–1369. https://doi.org/10.21273/HORTSCI14035-19

Liao JX, Ge Y, Huang CC, et al (2005) Effects of irradiance on photosynthetic characteristics and growth of *Mosla chinensis* and *M. scabra*. Photosynthetica 43:111–115. https://doi.org/10.1007/s11099-005-1115-6

Liu S, Yang R, Ren B, et al (2016) Differences in photosynthetic capacity, chlorophyll fluorescence, and antioxidant system between invasive *Alnus formosana* and its native congener in response to different irradiance levels. Botany 94:1087–1101. https://doi.org/10.1139/cjb-2016-0026

Logan BA, Demmig-Adams B, Iii WWA, Grace SC (2018) Antioxidants and xanthophyll cycle-dependent energy dissipation in *Cucurbita pepo* L. and *Vinca major* L. acclimated to four growth PPFDs in the field. J Exp Bot 49:1869–1879. https://doi.org/10.1093/jxb/49.328.1869

Lokhande SD, Ogawa K, Tanaka A, Hara T (2003) Effect of temperature on ascorbate peroxidase activity and flowering of *Arabidopsis thaliana* ecotypes under different light conditions. J Plant Physiol 160:57–64. https://doi.org/10.1078/0176-1617-00990

Lynch DJ, McInerney FA, Kouwenberg LLR, Gonzalez-Meler MA (2012) Plasticity in bundle sheath extensions of heterobaric leaves. Amer J Bot 99:1197–1206. https://doi.org/10.3732/ajb.1100525

Makoto K, Koike T (2007) Effects of nitrogen supply on photosynthetic and anatomical changes in current-year needles of *Pinus koraiensis* seedlings grown under two irradiances. Photosynthetica 45:99–104. https://doi.org/10.1007/s11099-007-0015-3

Manolaki P, Tooulakou G, Byberg CU, et al (2020) Probing the response of the amphibious plant *Butomus umbellatus* to nutrient enrichment and shading by integrating eco-physiological with metabolomic analyses. Front Plant Sci 11:581787. https://doi.org/10.3389/fpls.2020.581787

Marçal DMS, Avila RT, Quiroga-Rojas LF, et al (2021) Elevated [CO_2] benefits coffee growth and photosynthetic performance regardless of light availability. Plant Physiol Biochem 158:524–535. https://doi.org/10.1016/j.plaphy.2020.11.042

Marfo J, Dang Q-L (2009) Interactive effects of carbon dioxide concentration and light on the morphological and biomass characteristics of black spruce and white spruce seedlings. Botany 87:67–77. https://doi.org/10.1139/B08-114

Marler TE, Schaffer B, Crane JH (1994) Developmental light level affects growth, morphology, and leaf physiology of young carambola trees. J Amer Soc Hortic Sci 119:711–718. https://doi.org/10.21273/JASHS.119.4.711

Martins SCV, Galmés J, Cavatte PC, et al (2014) Understanding the low photosynthetic rates of sun and shade coffee leaves: bridging the gap on the relative roles of hydraulic, diffusive and biochemical constraints to photosynthesis. PLoS ONE 9:e95571. https://doi.org/10.1371/journal.pone.0095571

Matsuki S, Ogawa K, Tanaka A, Hara T (2003) Morphological and photosynthetic responses of *Quercus crispula* seedlings to high-light conditions. Tree Physiol 23:769–775. https://doi.org/10.1093/treephys/23.11.769

Mattson NS, Erwin JE (2005) The impact of photoperiod and irradiance on flowering of several herbaceous ornamentals. Sci Hortic 104:275–292. https://doi.org/10.1016/j.scienta.2004.08.018

Melick D (1990) Regenerative succession of *Tristaniopsis laurina* and *Acmena smithii* in riparian warm temperate rain-forest in Victoria, in relation to light and nutrient regimes. Aust J Bot 38:111. https://doi.org/10.1071/BT9900111

Milligan JN, Flynn AG, Wagner JD, et al (2021) Quantifying the effect of shade on cuticle morphology and carbon isotopes of sycamores: present and past. Amer J Bot 108:2435–2451. https://doi.org/10.1002/ajb2.1772

Miyazawa Y, Manythong C, Fukuda S, Ogata K (2014) Comparison of the growth traits of a commercial pioneer tree species, paper mulberry (*Broussonetia papyrifera* L. Vent.), with those of shade-tolerant tree species: investigation of the ecophysiological mechanisms underlying shade-intolerance. Agrofor Syst 88:907–919. https://doi.org/10.1007/s10457-014-9735-0

Mommer L, De Kroon H, Pierik R, et al (2005) A functional comparison of acclimation to shade and submergence in two terrestrial plant species. New Phytol 167:197–206. https://doi.org/10.1111/j.1469-8137.2005.01404.x

Moraes GABK, Chaves ARM, Martins SCV, et al (2010) Why is it better to produce coffee seedlings in full sunlight than in the shade? A morphophysiological approach. Photosynthetica 48:199–207. https://doi.org/10.1007/s11099-010-0025-4

Noda H, Muraoka H, Washitani I (2004) Morphological and physiological acclimation responses to contrasting light and water regimes in *Primula sieboldii*: acclimation responses in *Primula sieboldii*. Ecol Res 19:331–340. https://doi.org/10.1111/j.1440-1703.2004.00642.x

Noguchi K, Nakajima N, Terashima I (2001) Acclimation of leaf respiratory properties in *Alocasia odora* following reciprocal transfers of plants between high- and low-light environments: Respiratory acclimation after changes of light environment. Plant Cell Environ 24:831–839. https://doi.org/10.1046/j.1365-3040.2001.00728.x

Oberbauer SF, Strain BR (1985) Effects of light regime on the growth and physiology of *Pentaclethra macroloba* (Mimosaceae) in Costa Rica. J Trop Ecol 1:303–320. https://doi.org/10.1017/S0266467400000390

Oberbauer SF, Strain BR (1986) Effects of canopy position and irradiance on the leaf physiology and morphology of *Pentaclethra macroloba* (Mimosaceae)l. Amer J Bot 73:409–416. https://doi.org/doi.org/10.1002/j.1537-2197.1986.tb12054.x

Oguchi R, Hikosaka K, Hirose T (2003) Does the photosynthetic light-acclimation need change in leaf anatomy: Chloroplast volume change in photosynthetic light-acclimation. Plant Cell Environ 26:505–512. https://doi.org/10.1046/j.1365-3040.2003.00981.x

Oguchi R, Hikosaka K, Hirose T (2005) Leaf anatomy as a constraint for photosynthetic acclimation: differential responses in leaf anatomy to increasing growth irradiance among three deciduous trees. Plant Cell Environ 28:916–927. https://doi.org/10.1111/j.1365-3040.2005.01344.x

Oh W, Cheon IH, Kim KS, Runkle ES (2009) Photosynthetic daily light integral influences flowering time and crop characteristics of *Cyclamen persicum*. HortSci 44:341–344. https://doi.org/10.21273/HORTSCI.44.2.341

Onoda Y, Schieving F, Anten NPR (2008) Effects of light and nutrient availability on leaf mechanical properties of *Plantago major*: a conceptual approach. Ann Bot 101:727–736. https://doi.org/10.1093/aob/mcn013

Pan T, Wang Y, Wang L, et al (2020) Increased CO_2 and light intensity regulate growth and leaf gas exchange in tomato. Physiol Plant 168:694–708. https://doi.org/10.1111/ppl.13015

Pandey S, Kushwaha R (2005) Leaf anatomy and photosynthetic acclimation in *Valeriana jatamansi* L. grown under high and low irradiance. Photosynthetica 43:85–90. https://doi.org/10.1007/s11099-005-5090-8

Patterson DT, Duke SO, Hoagland RE (1978) Effects of irradiance during growth on adaptive photosynthetic characteristics of velvetleaf and cotton. Plant Physiol 61:402–405. https://doi.org/10.1104/pp.61.3.402

Pierson EA, Mack RN, Black RA (1990) The effect of shading on photosynthesis, growth, and regrowth following defoliation for *Bromus tectorum*. Oecologia 84:534–543. https://doi.org/10.1007/BF00328171

Plantenga FDM, Bergonzi S, Bachem CWB, et al (2019) High light accelerates potato flowering independently of the FT-like flowering signal StSP3D. Env Exp Bot 160:35–44. https://doi.org/10.1016/j.envexpbot.2019.01.004

Pons TL (1977) An ecophysiological study in the field layer of ash coppice. II Experiments with *Geum urbanum* and *Cirsium palustre* in different light intensities. Acta Bot Neerl 26:29–42. https://doi.org/10.1111/j.1438-8677.1977.tb01093.x

Pons TL (2012) Interaction of temperature and irradiance effects on photosynthetic acclimation in two accessions of *Arabidopsis thaliana*. Photosynth Res 113:207–219. https://doi.org/10.1007/s11120-012-9756-3

Pons TL, Pearcy RW (1994) Nitrogen reallocation and photosynthetic acclimation in response to partial shading in soybean plants. Physiol Plant 92:636–644. https://doi.org/doi.org/10.1111/j.1399-3054.1994.tb03034.x

Poorter H, Van der Werf AK (1998) Is inherent variation in RGR determined by LAR at low irradiance and by NAR at high irradiance? A review of herbaceous species. In: Inherent variation in plant growth. Physiological mechanisms and ecological consequences. Backhuys Publishers, Leiden, Leiden, pp 309–336

Poot P, Pilon J, Pons TL (1996) Photosynthetic characteristics of leaves of male-sterile and hermaphrodite sex types of *Plantago lanceolata* grown under conditions of contrasting nitrogen and light availabilities. Physiol Plant 98:780–790. https://doi.org/doi.org/10.1111/j.1399-3054.1996.tb06685.x

Portes Mt, Damineli Dsc, Ribeiro Rv, et al (2010) Evidence of higher photosynthetic plasticity in the early successional *Guazuma ulmifolia* Lam. compared to the late successional *Hymenaea courbaril* L. grown in contrasting light environments. Braz J Biol 70:75–83. https://doi.org/10.1590/S1519-69842010000100011

Portsmuth A, Niinemets Ü (2007) Structural and physiological plasticity in response to light and nutrients in five temperate deciduous woody species of contrasting shade tolerance. Funct Ecol 21:61–77. https://doi.org/10.1111/j.1365-2435.2006.01208.x

Puértolas J, Pardos M, Jiménez MD, et al (2008) Interactive responses of *Quercus suber* L. seedlings to light and mild water stress: effects on morphology and gas exchange traits. Ann For Sci 65:611–611. https://doi.org/10.1051/forest:2008044

Qiu Q, Wang J, Lin N, et al (2020) Effects of irradiance on growth and morphophysiology in *Catalpa bungei* plantlets. Pak J Bot 52:1899–1910. https://doi.org/10.30848/PJB2020-6(23)

Quinet M, Descamps C, Coster Q, et al (2015) Tolerance to water stress and shade in the invasive *Impatiens parviflora*. Int J Plant Sci 176:848–858. https://doi.org/10.1086/683276

Read J, Hill RS (1985) Photosynthetic responses to light of Australian and Chilean species of *Nothofagus* and their relevance to the rainforest dynamics. New Phytol 101:731–742. https://doi.org/10.1111/j.1469-8137.1985.tb02878.x

Rebbeck J, Gottschalk K, Scherzer A (2011) Do chestnut, northern red, and white oak germinant seedlings respond similarly to light treatments? I. Growth and biomass. Can J For Res 41:2219–2230. https://doi.org/10.1139/x11-124

Rebbeck J, Scherzer A, Gottschalk K (2012) Do chestnut, northern red, and white oak germinant seedlings respond similarly to light treatments? II. Gas exchange and chlorophyll responses. Can J For Res 42:1025–1037. https://doi.org/10.1139/x2012-057

Regnier EE, Salvucci ME, Stoller EW (1988) Photosynthesis and growth responses to irradiance in soybean (*Glycine max*) and three broadleaf weeds. Weed Sci 36:487–496. https://doi.org/10.1017/S004317450007524X

Retuerto R, Lema BF, Roiloa SR, Obeso JR (2000) Gender, light and water effects in carbon isotope discrimination, and growth rates in the dioecious tree *Ilex aquifolium*: Gender and carbon isotope discrimination in holly. Funct Ecol 14:529–537. https://doi.org/10.1046/j.1365-2435.2000.t01-1-00454.x

Rezazadeh A, Harkess R, Telmadarrehei T (2018) The effect of light intensity and temperature on flowering and morphology of potted red firespike. Horticulturae 4:36. https://doi.org/10.3390/horticulturae4040036

Roden JS, Farquhar GD (2012) A controlled test of the dual-isotope approach for the interpretation of stable carbon and oxygen isotope ratio variation in tree rings. Tree Physiol 32:490–503. https://doi.org/10.1093/treephys/tps019

Rodríguez-Calcerrada J, Pardos JA, Gil L, et al (2008) Light response in seedlings of a temperate (*Quercus petraea*) and a sub-Mediterranean species (*Quercus pyrenaica*): contrasting ecological strategies as potential keys to regeneration performance in mixed marginal populations. Plant Ecol 195:273–285. https://doi.org/10.1007/s11258-007-9329-2

Rodríguez-López NF, Martins SCV, Cavatte PC, et al (2014) Morphological and physiological acclimations of coffee seedlings to growth over a range of fixed or changing light supplies. Env Exp Bot 102:1–10. https://doi.org/10.1016/j.envexpbot.2014.01.008

Ryser P, Eek L (2000) Consequences of phenotypic plasticity vs. interspecific differences in leaf and root traits for acquisition of aboveground and belowground resources. Amer J Bot 87:402–411. https://doi.org/10.2307/2656636

Sack L, Grubb PJ (2002) The combined impacts of deep shade and drought on the growth and biomass allocation of shade-tolerant woody seedlings. Oecologia 131:175–185. https://doi.org/10.1007/s00442-002-0873-0

Santelices R, Espinoza S, Cabrera A (2015) Effect of four levels of shade on survival, morphology and chlorophyll fluorescence of *Nothofagus alessandrii* container-grown seedlings. iForest 8:638–641. https://doi.org/10.3832/ifor1321-007

Santiago LS, Lau TS, Melcher PJ, et al (2000) Morphological and physiological responses of Hawaiian *Hibiscus tiliaceus* populations to light and salinity. Int J Plant Sci 161:99–106. https://doi.org/10.1086/314236

Scoffoni C, Kunkle J, Pasquet-Kok J, et al (2015) Light-induced plasticity in leaf hydraulics, venation, anatomy, and gas exchange in ecologically diverse Hawaiian lobeliads. New Phytol 207:43–58. https://doi.org/10.1111/nph.13346

Scuderi D, Giuffrida F, Toscano S, Romano D (2012) Growth, physiological response, and quality characteristics of weeping fig in response to shading levels and climatic conditions. HortSci 47:1586–1592. https://doi.org/10.21273/HORTSCI.47.11.1586

Selzer LJ, Busso CA (2016) Pigments and photosynthesis of understory grasses: Light irradiance and soil moisture effects. Russ J Plant Physiol 63:224–234. https://doi.org/10.1134/S1021443716020126

Siebenkäs A, Schumacher J, Roscher C (2015) Phenotypic plasticity to light and nutrient availability alters functional trait ranking across eight perennial grassland species. https://doi.org/101086/314233 7:. https://doi.org/10.1093/aobpla/plv029

Sims DA, Pearcy RW (1992) Response of leaf anatomy and photosynthetic capacity in *Alocasia macrorrhiza* (Araceae) to a transfer from low to high light. Amer J Bot 79:449–455. https://doi.org/10.2307/2445158

Sims DA, Pearcy RW (1994) Scaling sun and shade photosynthetic acclimation of *Alocasia macrorrhiza* to whole plant performance - I. Carbon balance and allocation at different daily photon flux densities. Plant Cell Environ 17:881–887. https://doi.org/doi.org/10.1111/j.1365-3040.1994.tb00318.x

Sims DA, Pearcy RW (1989) Photosynthetic characteristics of a tropical forest understory herb, *Alocasia macrorrhiza*, and a related crop species, *Colocasia esculenta* grown in contrasting light environments. Oecologia 79:53–59. https://doi.org/10.1007/BF00378239

Sims DA, Pearcy RW (1991) Photosynthesis and respiration in *Alocasia macrorrhiza* following transfers to high and low light. Oecologia 86:447–453. https://doi.org/10.1007/BF00317615

Skillman JB, Garcia M, Virgo A, Winter K (2005) Growth irradiance effects on photosynthesis and growth in two co-occurring shade-tolerant neotropical perennials of contrasting photosynthetic pathways. Amer J Bot 92:1811–1819. https://doi.org/10.3732/ajb.92.11.1811

Sugiura D, Kojima M, Sakakibara H (2016) Phytohormonal regulation of biomass allocation and morphological and physiological traits of leaves in response to environmental changes in *Polygonum cuspidatum*. Front Plant Sci 7:. https://doi.org/10.3389/fpls.2016.01189

Sugiura D, Sawakami K, Kojima M, et al (2015) Roles of gibberellins and cytokinins in regulation of morphological and physiological traits in *Polygonum cuspidatum* responding to light and nitrogen availabilities. Funct Plant Biol 42:397. https://doi.org/10.1071/FP14212

Syvertsen JP, Smith ML (1984) Light acclimation in citrus leaves. I. Changes in physical characteristics, chlorophyll, and nitrogen content. J Amer Soc Hortic Sci 109:807–812

Tang J, Sun B, Cheng R, et al (2021) The effect of low irradiance on leaf nitrogen allocation and mesophyll conductance to CO_2 in seedlings of four tree species in subtropical china. Plants 10:2213. https://doi.org/10.3390/plants10102213

Thompson W, Kriedemann P, Craig I (1992a) Photosynthetic response to light and nutrients in sun-tolerant and shade-tolerant rainforest trees. I. Growth, leaf anatomy and nutrient content. Funct Plant Biol 19:1. https://doi.org/10.1071/PP9920001

Thompson WA, Huang LK, Kriedemann PE (1992b) Photosynthetic response to light and nutrients in sun-tolerant and shade-tolerant rainforest trees. II. Leaf gas exchange and component processes of photosynthesis. Funct Plant Biol 19:19–42. https://doi.org/10.1071/PP9920019

Thompson WA, Stocker GC, Kriedemann PE (1988) Growth and photosynthetic response to light and nutrients of *Flindersia brayleyana* f. Muell., a rainforest tree with broad tolerance to sun and shade. Funct Plant Biol 15:299. https://doi.org/10.1071/PP9880299

Tinoco-Ojanguren C, Pearcy RW (1995) A comparison of light quality and quantity effects on the growth and steady-state and dynamic photosynthetic characteristics of three tropical tree species. Funct Ecol 9:222–230. https://doi.org/10.2307/2390568

Tolley LC, Strain BR (1984) Effects of CO_2 enrichment on growth of *Liquidambar styraciflua* and *Pinus taeda* seedlings under different irradiance levels. Can J For Res 14:343–350. https://doi.org/10.1139/x84-063

Trouwborst G, Hogewoning SW, Harbinson J, van Ieperen W (2011) Photosynthetic acclimation in relation to nitrogen allocation in cucumber leaves in response to changes in irradiance. Physiol Plant 142:157–169. https://doi.org/10.1111/j.1399-3054.2011.01456.x

Turnbull MH (1991) The effect of light quantity and quality during development on the photosynthetic characteristics of six Australian rainforest tree species. Oecologia 87:110–117. https://doi.org/10.1007/BF00323788

Valladares F, Dobarro I, Sánchez-Gómez D, Pearcy RW (2004) Photoinhibition and drought in Mediterranean woody saplings: scaling effects and interactions in sun and shade phenotypes. J Exp Bot 56:483–494. https://doi.org/10.1093/jxb/eri037

Valladares F, Martinez-Ferri E, Balaguer L, et al (2000) Low leaf-level response to light and nutrients in Mediterranean evergreen oaks: a conservative resource-use strategy? New Phytol 148:79–91. https://doi.org/10.1046/j.1469-8137.2000.00737.x

Villar-Salvador P, Planelles R, Enríquez E, Rubira JP (2004) Nursery cultivation regimes, plant functional attributes, and field performance relationships in the Mediterranean oak *Quercus ilex* L. For Ecol Manage 196:257–266. https://doi.org/10.1016/j.foreco.2004.02.061

Vráblová M, Hronková M, Vrábl D, et al (2018) Light intensity-regulated stomatal development in three generations of *Lepidium sativum*. Env Exp Bot 156:316–324. https://doi.org/10.1016/j.envexpbot.2018.09.012

Walters MB, Kruger EL, Reich PB (1993) Growth, biomass distribution and CO_2 exchange of northern hardwood seedlings in high and low light: relationships with successional status and shade tolerance. Oecologia 94:7–16. https://doi.org/10.1007/BF00317294

Walters MB, Reich PB (2000) Trade-offs in low-light CO_2 exchange: a component of variation in shade tolerance among cold temperate tree seedlings: Trade-offs in whole-plant low-light CO_2 exchange. Funct Ecol 14:155–165. https://doi.org/10.1046/j.1365-2435.2000.00415.x

Walters RG, Horton P (1994) Acclimation of *Arabidopsis thaliana* to the light environment: Changes in composition of the photosynthetic apparatus. Planta 195:248–256. https://www.jstor.org/stable/23383331

Wang J-H, Cai Y-F, Li S-F, Zhang S-B (2020) Photosynthetic acclimation of rhododendrons to light intensity in relation to leaf water-related traits. Plant Ecol 221:407–420. https://doi.org/10.1007/s11258-020-01019-y

Wang ML, Jiang YS, Wei JQ, et al (2008) Effects of irradiance on growth, photosynthetic characteristics, and artemisinin content of *Artemisia annua* L. Photosynthetica 46:17–20. https://doi.org/10.1007/s11099-008-0004-1

Ward DA, Woolhouse HW (1986) Comparative effects of light during growth on the photosynthetic properties of NADP-ME type C_4 grasses from open and shaded habitats. I. Gas exchange, leaf anatomy and ultrastructure. Plant Cell Environ 9:261–270. https://doi.org/doi.org/10.1111/1365-3040.ep11611679

Wiebel J, Chacko EK, Downton WJS, Ludders P (1994) Influence of irradiance on photosynthesis, morphology and growth of mangosteen (*Garcinia mangostana* L.) seedlings. Tree Physiol 14:263–274. https://doi.org/10.1093/treephys/14.3.263

Winter K, Schmitt MR, Edwards GE (1982) *Microstegium vimineum*, a shade adapted C_4 grass. Plant Sci Let 24:311–318. https://doi.org/10.1016/0304-4211(82)90027-X

Woledge J (1971) The effect of light intensity during growth on the subsequent rate of photosynthesis of leaves of tall fescue (*Festuca arundinacea* Schreb.). Ann Bot 35:311–322. https://doi.org/10.1093/oxfordjournals.aob.a084480

Wu J, Li J, Su Y, et al (2017) A morphophysiological analysis of the effects of drought and shade on *Catalpa bungei* plantlets. Acta Physiol Plant 39:80. https://doi.org/10.1007/s11738-017-2380-2

Xie H, Yu M, Cheng X (2018) Leaf non-structural carbohydrate allocation and C:N:P stoichiometry in response to light acclimation in seedlings of two subtropical shade-tolerant tree species. Plant Physiol Biochem 124:146–154. https://doi.org/10.1016/j.plaphy.2018.01.013

Xu N, Wang R, Liu J, et al (2015) Hierarchy of plasticity traits in responses of *Quercus aliena* to light conditions and water availability. Dendrobiology 74:169–180. https://doi.org/10.12657/denbio.074.017

Xue W, Li X (2017) Moderate shade environment facilitates establishment of desert phreatophytic species *Alhagi sparsifolia* seedlings by enlarge fine root biomass. Acta Physiol Plant 39:7. https://doi.org/10.1007/s11738-016-2305-5

Yamashita N, Koike N, Ishida A (2002) Leaf ontogenetic dependence of light acclimation in invasive and native subtropical trees of different successional status: Light acclimation during leaf ontogeny. Plant Cell Environ 25:1341–1356. https://doi.org/10.1046/j.1365-3040.2002.00907.x

Yeh DM, Atherton JG (1999) Effects of irradiance on growth and flowering in the shade plant, *Cineraria*. Ann Appl Biol 134:329–334. https://doi.org/10.1111/j.1744-7348.1999.tb05272.x

Yu H, Ong B-L (2001) Responses of *Acacia mangium* seedlings to different irradiances. Photosynthetica 39:477–479. https://doi.org/10.1023/A:1015159100276

Zhang D, Armitage AM, Affolter JM, Dirr MA (1995) Environmental control of flowering and growth of *Lysimachia congestiflora* Hemsl. HortSci 30:62–64. https://doi.org/10.21273/HORTSCI.30.1.62

Zhang D, Armitage AM, Affolter JM, Dirr MA (1996) Environmental control of flowering and growth of *Achillea millefolium* l. `summer pastels'. HortSci 31:364–365. https://doi.org/10.21273/HORTSCI.31.3.364

Zhang LX, Guo QS, Chang QS, et al (2015a) Chloroplast ultrastructure, photosynthesis and accumulation of secondary metabolites in *Glechoma longituba* in response to irradiance. Photosynthetica 53:144–153. https://doi.org/10.1007/s11099-015-0092-7

Zhang S-B, Yin L-X (2012) Plasticity in photosynthesis and functional leaf traits of *Meconopsis horridula* var. *racemosa* in response to growth irradiance. Bot Stud 53:335–345

Zhang YJ, Yan F, Gao H, et al (2015b) Chlorophyll content, leaf gas exchange and growth of oriental lily as affected by shading. Russ J Plant Physiol 62:334–339. https://doi.org/10.1134/S1021443715030206

Zhang Z, Jiang C, Zhang J, et al (2009) Ecophysiological evaluation of the potential invasiveness of *Rhus typhina* in its non-native habitats. Tree Physiol

29:1307–1316. https://doi.org/10.1093/treephys/tpp065

Zhou SB, Liu K, Zhang D, et al (2010) Photosynthetic performance of *Lycoris radiata* var. *radiata* to shade treatments. Photosynthetica 48:241–248. https://doi.org/10.1007/s11099-010-0030-7

Acknowledgements We thank Angelika Portsmuth for providing additional biomass data for *Pinus sylvestris* plants, growing in the raised bog of Endla, and Bas Lerink for additional biomass estimates of *Pinus*. We thank Jouke Postma for discussions, and Kelvin Acebron as well as the reviewers for their comments on a previous version of this manuscript. HP is also grateful to Hans Lambers, for being the best supervisor a PhD student could wish for, and TP for Hans being an excellent head of the Plant Ecophysiology department at Utrecht University.

Funding Open Access funding enabled and organized by Projekt DEAL.

Declarations

HP received financial support from Utrecht University for the microarray analysis. The authors declare that no other funds, grants, or other support were received in relation to this manuscript. The authors have no competing financial or non-financial interests to disclose.

References

Ahmadi A, Baker DA (2001) The effect of water stress on the activities of key regulatory enzymes of the sucrose to starch pathway in wheat. Plant Growth Regul 35:81–91. https://doi.org/10.1023/A:1013827600528

Ainsworth EA, Long SP (2021) 30 years of free-air carbon dioxide enrichment (FACE): what have we learned about future crop productivity and its potential for adaptation? Glob. Change Biol. 27:27–49. https://doi.org/10.1111/gcb.15375

Ainsworth EA, Davey PA, Bernacchi CJ, Dermody OC, Heaton EA, Moore DJ et al (2002) A meta-analysis of elevated [CO_2] effects on soybean (*Glycine max*) physiology, growth and yield. Glob Change Biol 8:695–709. https://doi.org/10.1046/j.1365-2486.2002.00498.x

Belouah I, Nazaret C, Pétriacq P, Prigent S, Bénard C, Mengin V et al (2019) Modeling protein destiny in developing fruit. Plant Physiol 180:1709–1724. https://doi.org/10.1104/pp.19.00086

Björkman O, Holmgren P (1966) Photosynthetic adaptation to light intensity in plants native to shaded and exposed habitats. Physiol Plant 19:854–859. https://doi.org/10.1111/j.1399-3054.1966.tb07074.x

Blom-Zandstra M, Lampe JEM, Ammerlaan FHM (1988) C and N utilization of two lettuce genotypes during growth under non-varying light conditions and after changing the light intensity. Physiol Plant 74:147–153. https://doi.org/10.1111/j.1399-3054.1988.tb04955.x

Bloom AJ, Chapin FS, Mooney HA (1985) Resource limitation in plants—an economic analogy. Annu Rev Ecol Syst 16:363–392. https://doi.org/10.1146/annurev.es.16.110185.002051

Bloor JM, Grubb PJ (2003) Growth and mortality in high and low light: trends among 15 shade-tolerant tropical rain forest tree species. J Ecol 91:77–85. https://doi.org/10.1046/j.1365-2745.2003.00743.x

Boote KJ, Jones JW, White JW, Asseng S, Lizaso JI (2013) Putting mechanisms into crop production models. Plant Cell Environ 36:1658–1672

Esteban R, Barrutia O, Artetxe U, Fernández-Marín B, Hernández A, García-Plazaola JI (2015) Internal and external factors affecting photosynthetic pigment composition in plants: a meta-analytical approach. New Phytol 206:268–280. https://doi.org/10.1111/nph.13186

Evans GC (1972) The quantitative analysis of plant growth. Univ. of California Press

Evans JR (1987) The dependence of quantum yield on wavelength and growth irradiance. Aust J Plant Physiol 14:69–79. https://doi.org/10.1071/PP9870069

Ferreira M, Ventorim R, Almeida E, Silveira S, Silveira W (2021) Protein abundance prediction through machine learning methods. J Mol Biol 433:167267. https://doi.org/10.1016/j.jmb.2021.167267

Forrester DI, Tachauer IHH, Annighoefer P, Barbeito I, Pretzsch H, Ruiz-Peinado R et al (2017) Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate. For Ecol Manag 396:160–175. https://doi.org/10.1016/j.foreco.2017.04.011

France J, Thornley JHM (1984) Mathematical models in agriculture. Butterworths, London, p 335

Freschet GT, Pagès L, Iversen CM, Comas LH, Rewald B, Roumet ., ... & McCormack ML. (2021) A starting guide to root ecology: strengthening ecological concepts and standardising root classification, sampling, processing and trait measurements. New Phytol 232: 973–1122

Garnier E, Salager JL, Laurent G, Sonié L (1999) Relationships between photosynthesis, nitrogen and leaf structure in 14 grass species and their dependence on the basis of expression. New Phytol 143:119–129. https://doi.org/10.1046/j.1469-8137.1999.00426.x

Gibon Y, Pyl ET, Sulpice R, Lunn JE, Hoehne M, Günther M, Stitt M (2009) Adjustment of growth, starch turnover, protein content and central metabolism to a decrease of the carbon supply when Arabidopsis is grown in very short photoperiods. Plant Cell Environ 32:859–874. https://doi.org/10.1111/j.1365-3040.2009.01965.x

Gorban AN, Pokidysheva LI, Smirnova V, Tyukina TA (2011) Law of the minimum paradoxes. Bull Math Biol 73:2013–2044. https://doi.org/10.1007/s11538-010-9597-1

Hanning I, Heldt HW (1993) On the function of mitochondrial metabolism during photosynthesis in spinach (*Spinacia oleracea* L.) leaves (partitioning between respiration and export of redox equivalents and precursors for nitrate assimilation products). Plant Physiol 103:1147–1154. https://doi.org/10.1104/pp.103.4.1147

Harrer M, Cuijpers P, Furukawa TA, Ebert DD (2021) Doing Meta-analysis with R: a hands-on guide. Chapman & Hall/CRC Press, Boca Raton, FL and London. isbn:978-0-367-61007-4

Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156. https://doi.org/10.1890/0012-9658(1999)080[1150:TMAORR]2.0.CO;2

Huang J, Zhao X, Chory J (2019) The Arabidopsis transcriptome responds specifically and dynamically to high light stress. Cell Rep 29:4186–4199. https://doi.org/10.1016/j.celrep.2019.11.051

Journet EP, Neuburger M, Douce R (1981) Role of glutamate-oxaloacetate transaminase and malate dehydrogenase in the regeneration of NAD+ for glycine oxidation by spinach leaf mitochondria. Plant Physiol 67:467–469. https://doi.org/10.1104/pp.67.3.467

Keating BA, Carberry PS, Hammer GL, Probert ME, Robertson MJ, Holzworth D et al (2003) An overview of APSIM, a model designed for farming systems simulation. Eur JAgron 18:267–288. https://doi.org/10.1016/S1161-0301(02)00108-9

Keenan TF, Luo X, De Kauwe MG, Medlyn BE, Prentice IC, Stocker BD et al (2021) A constraint on historic growth in global photosynthesis due to increasing CO2. Nature 600:253–258. https://doi.org/10.1038/s41586-021-04096-9

Kimball BA (2016) Crop responses to elevated CO_2 and interactions with H_2O, N, and temperature. Curr Opin Plant Biol 31:36–43. https://doi.org/10.1016/j.pbi.2016.03.006

Kjaer KH, Ottosen CO (2011). Growth *of Chrysanthemum* in response to supplemental light provided by irregular light breaks during the night. Journal of the American Society for Horticultural Science 136: 3-9. 10.21273/JASHS.136.1.3

Klinkhamer PG, de Jong TJ, Meelis E (1987) Delay of flowering in the 'biennial' *Cirsium vulgare*: size effects and devernalization. Oikos 49:303–308. https://doi.org/10.2307/3565765

Kovenock M, Swann AL (2018) Leaf trait acclimation amplifies simulated climate warming in response to elevated carbon dioxide. Glob Biogeo Cycl 32:1437–1448. https://doi.org/10.1029/2018GB005883

Kropff MJ, Cassman KG, Van Laar HH (1994) Quantitative understanding of the irrigated rice ecosystem and yield potential. In Hybrid rice technology: new developments and future prospects (pp. 97-114). IRRI Los Banos, Philippines

Lambers H, Oliveira R (2019) Plant physiological ecology. Springer, New York

Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Adv Ecol Res 23:187–261. https://doi.org/10.1016/S0065-2504(08)60148-8

Liang X, Zhang T, Lu X, Ellsworth DS, BassiriRad H, You C et al (2020) Global response patterns of plant photosynthesis to nitrogen addition: a meta-analysis. Glob. Change Biol. 26:3585–3600. https://doi.org/10.1111/gcb.15071

Liu A, Xiao Z, Li MW, Wong FL, Yung WS, Ku YS et al (2019) Transcriptomic reprogramming in soybean seedlings under salt stress. Plant Cell Environ 42:98–114. https://doi.org/10.1111/pce.13186

Lloyd J, Bloomfield K, Domingues TF, Farquhar GD (2013) Photosynthetically relevant foliar traits correlating better on a mass vs an area basis: of ecophysiological relevance or just a case of mathematical imperatives and statistical quicksand? New Phytol 199: 311–321. https://DOI: https://doi.org/10.1111/nph.12281

Lu H, Jansen JJ, Oosterbaan A, Goudzwaard LG, Oldenburger JF, Mohren GMJ, Den Ouden J (2017) FEM growth and yield data monocultures - scots pine (revised version). Archived data at DANS. 10.17026/dans-x93-d59w

Matsubara S (2018) Growing plants in fluctuating environments: why bother? J Exp Bot 69:4651–4654. https://doi.org/10.1093/jxb/ery312

McMillen GG, McClendon JH (1983) Dependence of photosynthetic rates on leaf density thickness in deciduous woody plants grown in sun and shade. Plant Physiol 72:674–678. https://doi.org/10.1104/pp.72.3.674

Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F, van Kleunen M (2010) Plant phenotypic plasticity in a changing climate. Trends Plant Sci 15:684–692. https://doi.org/10.1016/j.tplants.2010.09.008

Niinemets Ü, Keenan T (2012) Measures of light in studies on light-driven plant plasticity in artificial environments. Front Plant Sci 3:156. https://doi.org/10.3389/fpls.2012.00156

Niinemets Ü, Kull O (1998) Stoichiometry of foliar carbon constituents varies along light gradients in temperate woody canopies: implications for foliage morphological plasticity. Tree Physiol 18:467–479. https://doi.org/10.1093/treephys/18.7.467

Nobel PS (2020) Physicochemical and environmental plant physiology. Academic Press

Oguchi R, Onoda Y, Terashima I, Tholen D (2018) Leaf anatomy and function. In: Adams WW, Terashima I (eds) The leaf: a platform for performing photosynthesis. Springer, Cham, pp 97–139

Ovington JD (1957) Dry-matter production by *Pinus sylvestris* L. Ann Bot 21:287–314. https://doi.org/10.1093/oxfordjournals.aob.a083565

Peltola H, Kellomäki S, Väisänen H, Ikonen VP (1999) A mechanistic model for assessing the risk of wind and snow damage to single trees and stands of scots pine, Norway spruce, and birch. Canadian J For Res 29:647–661. https://doi.org/10.1139/x99-029

Pendleton JW, Egli DB, Peters DB (1967) Response of *Zea mays* L. to a "light rich" field environment. Agron J 59:395–397. https://doi.org/10.2134/agronj1967.00021962005900050003x

Perez-Harguindeguy N, Diaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P et al (2016) Corrigendum to: new handbook for standardised measurement of plant functional traits *worldwide*. Austr J Bot 64:715–716. https://doi.org/10.1071/BT12225_CO

Pons TL, During HJ (1987) Biennal behaviour of *Cirsium palustre* in ash coppice. Holarct Ecol 10:40–44. https://doi.org/10.1111/j.1600-0587.1987.tb00736.x

Pons TL, Poorter H (2014) The effect of irradiance on the carbon balance and tissue characteristics of five herbaceous species differing in shade-tolerance. Front Plant Sci 5:12. https://doi.org/10.3389/fpls.2014.00012

Pons TL, Welschen RAM (2002) Overestimation of respiration rates in commercially available clamp-on leaf chambers. Complications with measurement of net photosynthesis. Plant Cell Environ 25:1367–1372. https://doi.org/10.1046/j.1365-3040.2002.00911.x

Poorter H, Van der Werf A (1998) Is inherent variation in RGR determined by LAR at low irradiance and by NAR at high irradiance? A review of herbaceous species. In: Lambers H, Poorter H, van Vuuren MMI (eds) Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences. Backhuys Publishers, Leiden, pp 309–336

Poorter H, Pepin S, Rijkers T, De Jong Y, Evans JR, Körner C (2006) Construction costs, chemical composition and payback time of high-and low-irradiance leaves. J Exp Bot 57:355–371. https://doi.org/10.1093/jxb/erj002

Poorter H, Niinemets Ü, Poorter L, Wright IJ, Villar R (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New Phytol 182:565–588. https://doi.org/10.1111/j.1469-8137.2009.02830.x

Poorter H, Niinemets Ü, Walter A, Fiorani F, Schurr U (2010) A method to construct dose–response curves for a wide range of environmental factors and plant traits by means of a meta-analysis of phenotypic data. J Exp Bot 61:2043–2055. https://doi.org/10.1093/jxb/erp358

Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012a) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytol 193:30–50. https://doi.org/10.1111/j.1469-8137.2011.03952.x

Poorter H, Fiorani F, Stitt M, Schurr U, Finck A, Gibon Y et al (2012b) The art of growing plants for experimental purposes: a practical guide for the plant biologist. Funct Plant Biol 39:821–838. https://doi.org/10.1071/FP12028

Poorter H, Niinemets Ü, Ntagkas N, Siebenkäs A, Mäenpää M, Matsubara S, Pons T (2019) A meta-analysis of plant responses to light intensity for 70 traits ranging from molecules to whole plant performance. New Phytol 223:1073–1105. https://doi.org/10.1111/nph.15754

Poorter H, Knopf O, Wright IJ, Temme A, Hogewoning SW, Graf A et al (2022) A meta-analysis of responses of C_3 plants to atmospheric CO_2: dose-response curves for 85 traits ranging from the molecular to the whole plant level. New Phytol, in press. https://doi.org/10.1111/nph.17802

Portsmuth A, Niinemets Ü, Truus L, Pensa M (2005) Biomass allocation and growth rates in Pinus sylvestris are interactively modified by nitrogen and phosphorus availabilities and by tree size and age. Can J For Res 35:2346–2359. https://doi.org/10.1139/x05-155

Queitsch C, Hong SW, Vierling E, Lindquist S (2000) Heat shock protein 101 plays a crucial role in thermotolerance in Arabidopsis. Plant Cell 12:479–492. https://doi.org/10.1105/tpc.12.4.479

Quentin AG, Pinkard EA, Ryan MG, Tissue DT, Baggett LS, Adams HD et al (2015) Non-structural carbohydrates in woody plants compared among laboratories. Tree Physiol 35:1146–1165. https://doi.org/10.1093/treephys/tpv073

Richter SH, Garner JP, Würbel H (2009) Environmental standardization: cure or cause of poor reproducibility in animal experiments? Nat Meth 6:257–261. https://doi.org/10.1038/nmeth.1312

Rodríguez-López NF, Martins SC, Cavatte PC, Silva PE, Morais LE, Pereira LF et al (2014) Morphological and physiological acclimations of coffee seedlings to growth over a range of fixed or changing light supplies. Env Exp Bot 102:1–10. https://doi.org/10.1016/j.envexpbot.2014.01.008

Røst LM, Brekke Thorfinnsdottir L, Kumar K, Fuchino K, Eide Langørgen I, Bartosova Z et al (2020) Absolute quantification of the central carbon metabolome in eight commonly applied prokaryotic and eukaryotic model systems. Metabolites 10:74. https://doi.org/10.3390/metabo10020074

Sahoo JP, Behera L, Sharma SS, Praveena J, Nayak SK, Samal KC (2020) Omics studies and systems biology perspective towards abiotic stress response in plants. Am J Plant Sci 11:217. https://doi.org/10.4236/ajps.2020.1112152

Scheibe R (2004) Malate valves to balance cellular energy supply. Physiol Plant 120:21–26. https://doi.org/10.1111/j.0031-9317.2004.0222.x

Shameer S, Ratcliffe RG, Sweetlove LJ (2019) Leaf energy balance requires mitochondrial respiration and export of chloroplast NADPH in the light. Plant Physiol 180:1947–1961. https://doi.org/10.1104/pp.19.00624

Sicher RC, Bunce JA (1997) Relationship of photosynthetic acclimation to changes of rubisco activity in field-grown winter wheat and barley during growth in elevated carbon dioxide. Phot Res 52:27–38. https://doi.org/10.1023/A:1005874932233

Sims DA, Pearcy RW (1989) Photosynthetic characteristics of a tropical forest understory herb, *Alocasia macrorrhiza*, and a related crop species, *Colocasia esculenta* grown in contrasting light environments. Oecologia 79:53–59. https://doi.org/10.1007/BF00378239

Tardieu F, Cabrera-Bosquet L, Pridmore T, Bennett M (2017) Plant phenomics, from sensors to knowledge. Curr Biol 27:R770–R783. https://doi.org/10.1016/j.cub.2017.05.055

Terashima I, Araya T, Miyazawa SI, Sone K, Yano S (2005) Construction and maintenance of the optimal photosynthetic systems of the leaf, herbaceous plant and tree: an eco-developmental treatise. Ann Bot 95:507–519. https://doi.org/10.1093/aob/mci049

Valladares F, Niinemets Ü (2008) Shade tolerance, a key plant feature of complex nature and consequences. Ann Rev Ecol Evol Syst 39:237–257. https://doi.org/10.1146/annurev.ecolsys.39.110707.173506

Van der Ploeg RR, Böhm W, Kirkham MB (1999) On the origin of the theory of mineral nutrition of plants and the law of the minimum. Soil Sci Soc Amer J 63:1055–1062. https://doi.org/10.2136/sssaj1999.6351055x

Van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecol Lett 13:235–245. https://doi.org/10.1111/j.1461-0248.2009.01418.x

Walters RG (2005) Towards an understanding of photosynthetic acclimation. J Exp Bot 56:435–447. https://doi.org/10.1093/jxb/eri060

Waring RH, McDonald AJS, Larsson S, Ericsson T, Wiren A, Arwidsson E et al (1985) Differences in chemical composition of plants grown at constant relative growth rates with stable mineral nutrition. Oecologia 66:157–160. https://doi.org/10.1007/BF00379849

Wayne PM, Bazzaz FA (1993) Birch seedling responses to daily time courses of light in experimental forest gaps and shadehouses. Ecology 74:1500–1515. https://doi.org/10.2307/1940078

Yin X, Struik PC (2017) Can increased leaf photosynthesis be converted into higher crop mass production? A simulation study for rice using the crop model GECROS. J Exp Bot 68:2345–2360. https://doi.org/10.1093/jxb/erx085

Zhang Y, Friml J (2020) Auxin guides roots to avoid obstacles during gravitropic growth. New Phytol 225:1049. https://doi.org/10.1111/nph.16203

Poorter H, Lambers H, Evans JR (2014) Trait correlation networks: a whole-plant perspective on the recently criticized leaf economic spectrum. New Phytol 201:378–382. https://doi.org/10.1111/nph.12547