

## Meta-Phenomics, Horticulture and the Value of Plant Trait Databases

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**Abbreviations:** DRC: dose-response curve; LDMC: leaf dry matter content; LMF: leaf mass fraction; RDMC: root dry matter content; RMF: root mass fraction; SDMC: stem dry matter content; SLA: specific leaf area; SMF: stem mass fraction

### Abstract

**For a proper understanding of the long-term growth responses of plants to their environment it is indispensable to know the dose-response curves of a wide range of phenotypic traits, for the relevant environmental factors. A database is described that compiles the necessary information on a wide range of growth-related traits, unlocking the information that has accumulated in the literature over the past 50 years. Results for the 12 most important environmental factors are collected. With help of this database it is shown how general dose-response curves can be derived for a range of traits in response to differences in the quantity of light. The information obtained in this way can be used to model the growth of plants and - ultimately - to select for genotypes that are optimally adjusted to a certain combination of environmental factors.**

### THE RESPONSE OF PLANTS TO THEIR ENVIRONMENT

Plants respond to their environment at a wide range of integration levels, from the transcriptional control of DNA at very short time-scales, up to development and reproduction at the very long time-scale. In between these extremes lays a cascade of responses related to the formation and regulation of hormone concentrations and enzyme activities at the cellular level and an array of physiological and morphological adjustments at the organ level. Understanding these responses and the link between the various integration levels is of paramount interest, not in the least for horticulture, as insight into the ways plants react to environmental cues is a prerequisite for the grower to fully exploit the potential that plants offer. It is therefore not surprising that horticultural scientists often have relied on experiments in which a range of phenotypic traits related to plant growth and performance have been studied in relation to the environment. These studies cover such diverse and detailed aspects as the effect of pot size (Liu and Latimer, 1995), pot color (Svenson, 1993), pot form (Keever et al., 1985), type of root substrate used (Di Benedetto et al., 2006), application of exogenous compounds (Hu et al., 2012) and manipulation of flowering time (Runkle and Heins, 2006). However, most attention has been focused on the effect of the 'traditional' a-biotic environmental variables, such as light, CO<sub>2</sub>, nutrients and temperature on plant growth and performance.

Almost all of these environmental factors are continuous, which implies that a plant's response to such a factor can be well described by so-called 'dose-response curves'. Dose response curves (DRCs) generally describe the organismal response of a certain phenotypic trait to a range of levels of a given environmental factor in a continuous way. They have served a long tradition in agriculture in relation to nutrient supply (Mitscherlich, 1909), are frequently used in medical and ecotoxic research (Lacasse et al., 2009), and also found their way in ecophysiological research. Well-known examples are the short-term effects of light and CO<sub>2</sub> on the rate of photosynthesis, which are well described by DRCs and include an underlying model that is rooted in the biochemistry of the photosynthetic light and dark reactions (Von Caemmerer, 2000).

However, DRCs are hardly employed in plant biology when it comes to the analysis of ecophysiological responses at longer time scales, such as the adjustment of biomass allocation, morphology and even growth.

One of the problems that constrains the application of DRCs is the general limited amount of information that can be collected in one experiment. For a proper DRC curve one should measure plant responses over a wider range of levels. To be able to separate linear from saturating responses, or even discern a DRC which shows an optimum, six different levels seem a minimum. When it comes to the example of photosynthesis given above, a full DRC measured at ten different light or CO<sub>2</sub> levels can be easily achieved within hours. However, such short-term responses are not necessarily at all indicative of long-term responses (Van Oosten and Besford, 1995). Hence, if one would like to construct DRCs of photosynthesis-light or photosynthesis-CO<sub>2</sub> relationships, one needs to grow plants for a considerable part of their life cycle (at least weeks, but for woody species likely much longer) at 6 or more light or CO<sub>2</sub> levels. Here resides a problem. Although such a wide range of levels is sometimes considered, also in horticulture (e.g., Funnell et al., 1998), it is certainly not the norm. For reasons of feasibility, most experiments comprise only two or three levels of a given environmental factor. The construction of DRCs is then seriously hampered. Overcoming this problem would definitely improve our insights into the plant's behavior and allow for better modeling of growth and productivity.

### **THE NEED FOR AN ECOPHYSIOLOGICAL DATABASE**

A second point I want to discuss here is the need for a salvage of existing data. Each year, a tremendous number of ecophysiological experiments are carried out, not only within the horticultural domain, but also in forestry, agriculture and ecology. The financial investments made by society in the form of subsidies to research institutes and university groups that carry out these experiments are enormous. A larger fraction of the results is probably reported in the literature. However, these scientific articles are necessarily written in a condensed manner, and only contain a fraction of the collected data. Even the data that are reported may be difficult to retrieve, especially as the questions of interest that raise a posteriori may be different from the questions that the authors had in mind when writing the manuscript.

A recent meta-analysis we carried out may serve as an example. We aimed to see whether we could recommend scientists a certain minimum pot size for the plants they are using in their experiments (Poorter et al., 2012b). The first thing we wanted to know was the effect of pot size on plant growth. The horticultural community has made a large effort in investigating this problem, and it is relatively easy to derive biomass data at the end of the experiment from the relevant publications (e.g., Liu and Latimer, 1995; Van Iersel, 1997). However, after having shown the strong impact of pot size – for each doubling in pot size the plant mass increased by 43% – we then wanted to analyse at what plant mass per unit pot volume the first signs of growth retardation set in. This requires detailed knowledge about the biomass at early stages of growth. These data are only seldom collected, and if reported – for example in the form of a graph with the progression of dry mass over time – the scale of the y-axis generally does not allow a proper evaluation of differences in dry masses of the young plants (e.g., Carlson and Endean, 1976). In such a case, only additional information from the authors may help to analyse this problem. However, it turns out that data retrieval is not always easy, especially for experiments carried out more than 10 years ago. Authors may be retired, computer files are stored in file formats that are difficult to convert or on media that at present cannot be easily accessed anymore. In quite some cases, data that would have been extremely useful to answer a question that is beyond the original scope of the experiment turn out to be lost forever.

The issue of lost data is not only relevant to those experiments that are not fully described in scientific publications. They do to a certain extent pertain to data of past experiments altogether. The last 50 years has seen a wealth of publications that are highly

relevant to answer very important and basic ecophysiological questions. How do plants respond exactly to a given environmental factor? Is that in a linear way, does it saturate, or is there maybe an optimum? Are these responses general for all plant species, or do species with certain attributes (e.g., C<sub>4</sub>-photosynthesis, N<sub>2</sub>-fixing capabilities, monocots) respond differently from others? And what are the interactions with other environmental factors? The knowledge we have on these topics is often anecdotal, based on a limited number of experiments that we carried out ourselves and additional ones from the vast amount of literature. The responses we have framed in our mind are not always well-defined and neither are they made quantitative. When we have in mind that photosynthesis was decreased due to a given treatment, was that a decrease in the light-saturated rate of photosynthesis, or was it measured as the actual rate of photosynthesis under growth conditions? Has this been measured on a specific leaf, or just a few cm<sup>2</sup> of that leaf, or for the whole plant? Was it measured shortly after the treatment started, later during the vegetative development when new leaves have been formed that were completely acclimated, or maybe in the generative phase where developing fruits shift the source:sink balance of the plants? And does this all differ between species A and species B, or between species groups? If this is not mind-boggling enough, another challenge is that various authors use various units, which adds another dimension to the problem of generalization. This is especially true if different ratios are used. If one study on biomass allocation reports that the shoot:root ratio goes up with decreasing light, and the other that the root mass fraction clearly decreases with increasing light levels, it is already a challenge to keep hold of the main picture.

It is clear that quantitative questions are not easily answered by anecdotal information gathered from a number of publications. More advanced and structured ways to tap this enormous reservoir of knowledge are necessary. One way to do so is by carrying out a meta-analysis, where the biological trait of interest is analysed in response to a given environmental factor. Good examples of such analyses are found in the field of elevated CO<sub>2</sub>, where consistent quantitative analysis of a wider range of literature data can shed light to a specific research question (Kerstiens and Hawes, 1994). A logical but challenging following step is to unlock the data of past experiments by building a structured database that includes not only a wide range of plant traits, but also all important environmental factors. The next section describes an initiative to do this in the field of phenotyping, providing at the same time a way to derive general dose-response curves from a wide range of fragmentary data.

## **META-PHENOMICS**

Recently, an initiative was made to set up a database on plant responses to the environment, called meta-phenomics, with the intention to comprise a wide range of phenotypic plant traits or phenes. All phenes together should constitute the phenome of the plant, in a similar way as the genes together constitute the genome of the plant. In principle, phenotypic data constitute a very wide range of attributes at different integration levels. The ultimate aim of the meta-phenomics database is to integrate as many of the phenotypic data as possible into one structured database. To be able to generate useful information right from the start, data are added on a trait-for-trait basis. The structure of the database follows the design as described by Kattge et al. (2011) and consists currently of ~800 experiments compiled for a total of ~900 plant species. These species includes herbaceous species ranging from *Arabidopsis thaliana* to *Zea mays*, and woody species ranging from shrubs like *Betula nana* to trees like *Eucalyptus regnans* that potentially could become 100 m tall. Among the 900 species there is also a variety of species used in horticulture. Twelve of the main environmental factors that shape plant performance are included (Table 1). Prerequisite for inclusion in the database is that in a given experiment the environment was manipulated in such a way that plants experienced several levels of that factor, while all other environmental factors were kept constant, or manipulated in an orthogonal design.

To generate general DRCs based on individual plant data requires a form of

scaling. We did so by normalizing all data in one experiment relative to the phenotypic value obtained at a given reference level. Normalised data from a range of experiments were then used to generate the overall DRCs. Top-down contrasts between groups of species can subsequently be made by fitting DRCs to separate subgroups. For more information, the reader is referred to Poorter et al. (2010) or to [www.metaphenomics.org](http://www.metaphenomics.org).

## EXAMPLES FOR THE FACTOR LIGHT

To illustrate the approach described above we will show DRCs of some selected traits for the factor light intensity. Contrary to outdoor agriculture, light is a factor that can be manipulated in the glasshouse, both by reducing light in summer, by additional lamps in winter and/or by timing of seeding throughout the yearly light cycle. Consequently, there has been continuous interest in horticulture on the effect of the dosage and duration light (Marcelis et al., 2006). One of the relevant issues at this moment, for example, is whether plants can be grown with additional light provided during periods at night when the price of electricity from green sources such as windmill parks is low (Kjaer and Ottosen, 2011).

The database includes data that are carried out in growth rooms as well as glasshouses or experimental gardens. To be able to use all information on the same scale, all light data were integrated over the full day. For growth and morphology, this integrated value is a much better descriptor of light than the momentary light level at a given moment in time (Chabot et al., 1979; Poorter and Van der Werf, 1998). Data on the daily photosynthetic photon flux density (DPI) is provided by some authors, but not by all. In that case we estimated those data from the time of the year the experiment was carried out and the average weather data, as compiled by New et al. (1999) for different locations in the world on a month by month basis, and the light transmission as reported by the authors, or using an average transmission level of 0.62 (cf. Heuvelink, 1995; Von Elsner et al., 2000; Max et al., 2012). The reference level we choose was  $8 \text{ mol m}^{-2} \text{ day}^{-1}$ . This value is chosen to encompass most experiments used with different light levels, but does in principle not affect the outcome of the analyses. Values of the trait of interest were then all divided by the value the trait had at the reference level. This implies that the DRCs that are constructed from all these scaled values will have a level of 1.0 at the reference level of that environmental factor.

As a proof of principle, we show responses for three phenotypic traits that have long been known to respond differently to light intensity. The SLA is generally known to decrease with light, the total chlorophyll content per unit leaf area remains roughly constant over a wide range of light levels, and the chlorophyll a:b ratio often increases with light intensity (Björkman, 1981). The actual data that are currently in the database are summarized in Figure 1. SLA strongly decreases and varies 3-fold over the full range of light levels considered. A more extensive discussion is given in Poorter et al. (2009). The median curve is very smooth, probably reflected by the large amount of data present in the database for this trait ( $n=1400$ ). Based on the broken lines, which indicate the 10<sup>th</sup> and the 90<sup>th</sup> percentile of the distribution over the various ranges considered, the total chlorophyll content per unit leaf area sometimes increases, sometimes decreases, but overall there is hardly a response. The intervals are much narrower for the chlorophyll a:b ratio, which probably saturates at higher light levels (Fig. 1C). However, the number of observations is still low ( $n=200$ ), which may explain why the median value seem to fluctuate to some extent. In general, the curves nicely confirm in a quantitative way what the expert knowledge already summarized in a qualitative way.

It is recommended to characterize the biomass allocation in vegetative plants not by the use of shoot:root ratios, but by the characterization of the fraction of biomass invested in leaves, stems and roots (Poorter et al., 2012). When considering the DRCs for these three traits, it is clear that both the fraction to leaves and stems decreases with increasing light levels, whereas the root mass fraction shows a consistent increase in most of the experiments analysed (Fig. 2A-C). However, circa half of this response is due to high-light plants being larger, and larger plants generally allocating relatively less

biomass to leaves (Poorter et al., 2012). Nonetheless, the response has a functional meaning as it allows plants grown at higher light intensities to obtain more resources such as nutrients and water.

A final set of variables considered here are the dry matter contents of leaves, stems and roots. They are defined as the dry mass relative to the fresh mass of the various organs and form an indication of the chemical composition of the plant. Leaf and stem dry matter content strongly increase with light (Fig. 2D-F), reflecting the shift from large vacuoles with high nitrate concentrations in low-light plants to cells with small vacuoles and more sugars in high-light plants. Interestingly, dry matter content of the roots is not affected by light (Fig. 2F), which could imply that there are probably less changes for this organ at the anatomical and chemical level than for the above-ground organs.

## THE VALUE OF DATABASES IN HORTICULTURE

Currently, biological databases are spreading in the field of plant biology. Most of them are at the level of gene (e.g., Rhee et al., 2003) and gene expression (Zimmermann et al., 2004), some of them focusing on ecological data (e.g., Kattge et al., 2011). There is no doubt that such databases are fostering our insights, by allowing access to a wide array of data that are compiled in a systematic way, which facilitates generalisations made on a wide number of measurements. Although strong developments are going on in the horticultural field at the gene (e.g., Müller et al., 2005) and genotype/cultivar level, databases with ecophysiological information are still relatively underdeveloped. By unlocking the vast array of horticultural experiments that have been carried out in the past with a well-curated database, dose-response curves could be established for a wide range of traits and environmental factors. This may not only improve the models that are used to evaluate different horticultural practices (Marcelis et al., 1998), it may also be used to analyse to what extent different groups of species have different dose-response curves. Given the characterization of the distribution at any point on the curve, the current approach could also be used to find genotypes that have deviating dose-response curves, and therefore may be useful for breeding practices. Databases such as the one described here will therefore undoubtedly going to play an important role in shaping the field of horticulture in the future.

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## **Tables**

Table 1. Environmental factors considered in the meta-phenomics database. Values are based on daily averages during the experiment. Nutrient and water stress cannot be easily measured. The severity of these stresses was therefore expressed on a quantitative scale by dividing the total biomass of the low-resource plants by the biomass of the control plants in the same experiment.

Environmental factor	Range considered	Units
Irradiance	1-50	mol m <sup>-2</sup> day <sup>-1</sup>
R:FR	0.2-1.2	mol mol <sup>-1</sup>
UV-B	1-20	kJ m <sup>-2</sup> day <sup>-1</sup>
CO <sub>2</sub>	200-1200	μmol mol <sup>-1</sup>
O <sub>3</sub>	5-100	nmol mol <sup>-1</sup>
Nutrients	0.02-1	rel. units
Water	0.05-1	rel. units
Waterlogging	absent/present	-
Submergence	absent/present	-
Temperature	5-35	°C
Salinity	0-1	fraction of seawater
Soil compaction	1.0-1.6	g ml <sup>-1</sup>

## Figures

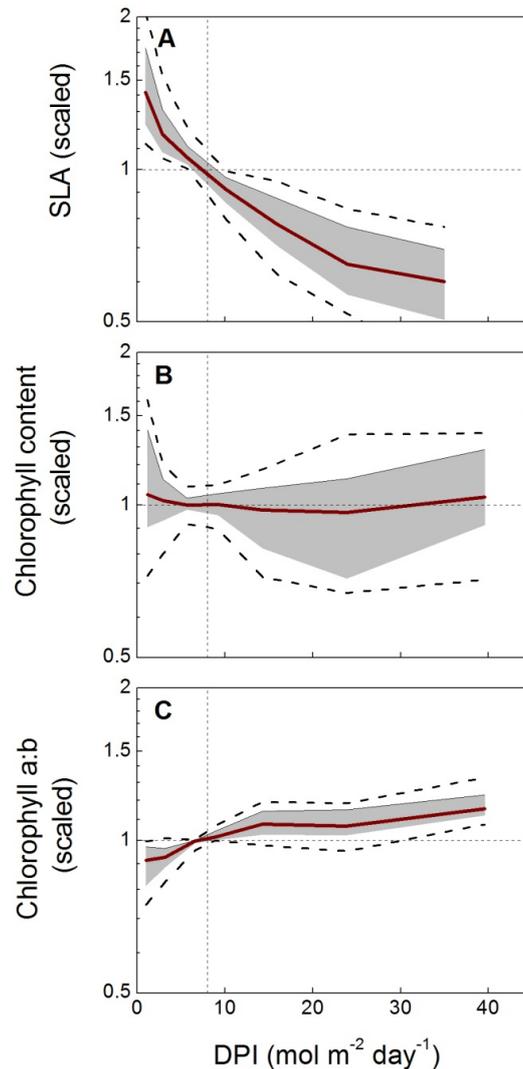


Fig. 1. Dose-response curves of A) SLA (specific leaf area; normalized values derived from original values expressed in  $\text{m}^2 \text{kg}^{-1}$ ), B) Chlorophyll content per unit leaf area (originally in  $\mu\text{mol m}^{-2}$ ) and C) Chlorophyll a:b ratio (originally in  $\text{mol mol}^{-1}$ ) as dependent on the light levels (DPI, daily photosynthetic photon irradiance) during growth. Data are a compilation of results from circa 200 different experiments where plants were grown in growth chambers, glasshouses or experimental gardens with different levels of light (listed in Poorter et al., 2009, 2012a). Data were binned in 7 ranges of DPI, and for each of those bins the distribution was characterized by the 10<sup>th</sup> and 90<sup>th</sup> percentile (broken lines), the 25<sup>th</sup> and 75<sup>th</sup> percentile which together show the interquartile range (shaded area) and the median value as indicated by the bold red line. The vertical line indicates the reference level of light ( $8 \text{ mol m}^{-2} \text{ day}^{-1}$ ), the horizontal line indicates no change in the phenotypic trait relative to the value at the reference level. Data are based on 1400, 280 and 200 mean observations, respectively for the three traits.

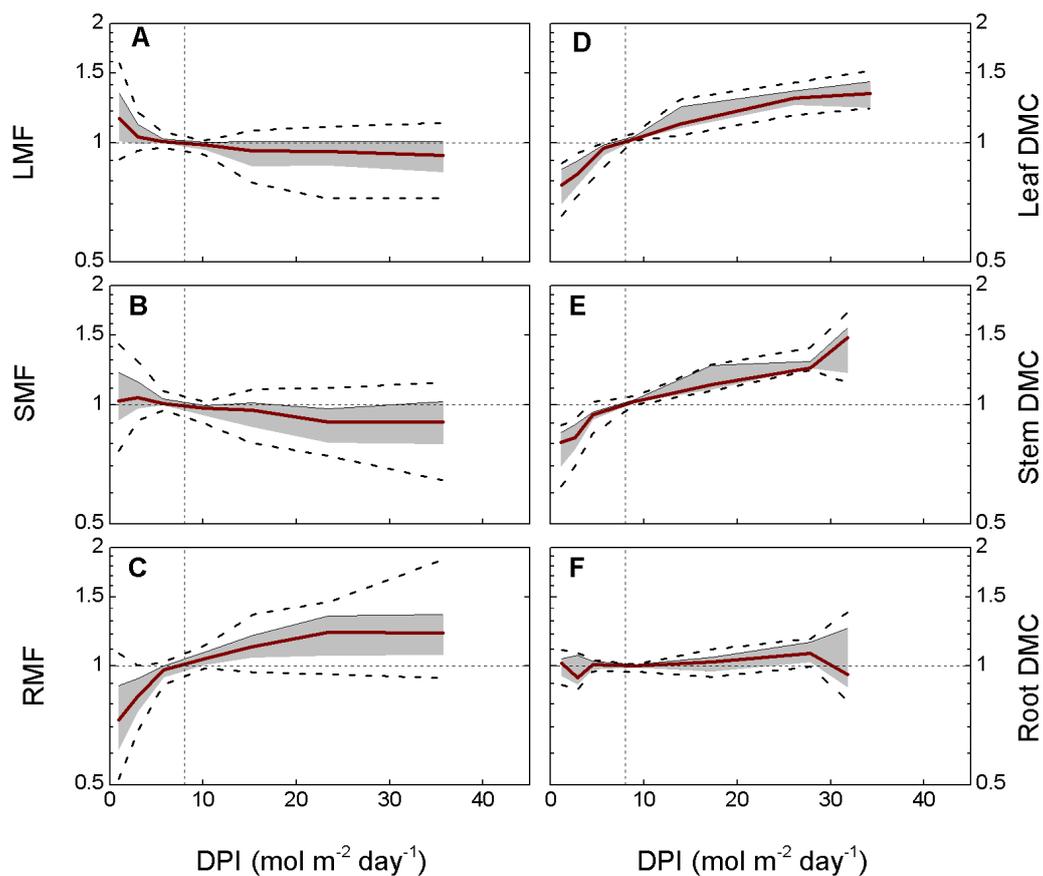


Fig. 2. Dose-response curves of A) LMF (leaf mass fraction; normalized values derived from original values expresses in  $\text{g g}^{-1}$ ), B) SMF (stem mass fraction) and C) RMF (root mass fraction) D) LDMC (leaf dry matter content; original in dry mass/fresh mass  $\times 100$ ), E) SDMC (stem dry matter content) and F) RDMC (root dry matter content) as dependent on the light levels (DPI, daily photosynthetic photon irradiance) during growth. For more information see the legend of Figure 1FC.

