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Review

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Pampered inside, pestered outside? Differences and similarities between plants growing in controlled conditions and in the field

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Summary

Plant biologists often grow plants in growth chambers or glasshouses with the ultimate aim to understand or improve plant performance in the field. What is often overlooked is how results from controlled conditions translate back to field situations. A meta-analysis showed that lab-grown plants had faster growth rates, higher nitrogen concentrations and different morphology. They remained smaller, however, because the lab plants had grown for a much shorter time. We compared glasshouse and growth chamber conditions with those in the field and found that the ratio between the daily amount of light and daily temperature (photothermal ratio) was consistently lower under controlled conditions. This may strongly affect a plant's source : sink ratio and hence its overall morphology and physiology. Plants in the field also grow at higher plant densities. A second meta-analysis showed that a doubling in density leads on average to 34% smaller plants with strong negative effects on tiller or side-shoot formation but little effect on plant height. We found the r^2 between lab and field phenotypic data to be rather modest (0.26). Based on these insights, we discuss various alternatives to facilitate the translation from lab results to the field, including several options to apply growth regimes closer to field conditions.

I. Introduction

Plant performance is strongly affected by environmental conditions. Therefore, short- and mid-term changeability in weather and soil conditions are important contributors to the considerable year-to-year variability in plant growth and reproductive output in the field (Annicchiarico, 2002). This random variability often impedes a clear interpretation of observational and experimental data in disciplines such as plant biology, agronomy, forestry and ecology, and has led many plant biologists to carry out their experiments in glasshouses or growth chambers where they can at least partly control environmental conditions. Growth chambers especially offer strong control over the abiotic environment, facilitating the repetition of experiments on a year-round basis. Typically, seedlings of crops, wild herbs, or trees in such experiments are grown in pots under some form of (additional) light, in an uniform substrate of potting soil or sand, with regular additions of nutrients and water. By growing plants individually and well spaced, plant-to-plant interaction is minimized, which can lead to the additional advantage of reduced plant-to-plant variability (Weiner & Thomas, 1986). Another benefit of an indoor one-plant-one-pot approach is that plants can be treated and manipulated easily, including the handling of large numbers of replicates by means of automated systems, which facilitates phenotyping at a high-throughput level (Fiorani & Schurr, 2013).

The indoor one-plant-one-pot approach is part of a continuum, ranging from plants grown individually in hydroponics or solid media in growth chambers, glasshouses or open-top chambers, to those grown with intra- or interspecific competition in soil in mesocosms, experimental gardens, agricultural fields or (semi)natural habitats. Across this continuum there is large variation in the control of biotic and abiotic conditions. For most of this review, we will compare plants grown in growth chambers and glasshouses – which for ease of reference we will refer to as 'controlled conditions' or 'lab experiments' – with those grown in 'field conditions' – which includes all plants grown outside in soil without any physical barrier towards the environment. Our review is intended for scientists who use controlled facilities but try in the broadest sense to translate the obtained insights to understand plant performance in the field. Sensible extrapolation will depend critically on the environmental conditions plants experience outside, which are somewhat predictable over the seasons but largely beyond human control, and on the conditions used inside, which can be manipulated with increasing precision today.

A wide range of abiotic environmental variables is pertinent to plant growth and development, of which 13 are listed in Table 1. Even if an experimental biologist who plans a growth chamber experiment would have only three levels to choose from for each variable (low, intermediate or high), the number of possible environmental combinations would already amount to a daunting 1.6 million. For scientists who study a subcellular compound or a molecular mechanism unrelated to stress responses, growth conditions will probably not be too critical. For those who want to study a given plant species under 'optimal' growth conditions, a simple preliminary experiment exploring various light, temperature and nutrient conditions will often provide proper environmental conditions for further experimentation. If, however, the aim of the controlled environment study is to compare different genotypes or species and rank them for performance in the field or to understand how plants are affected by a specific biotic or abiotic stress or combinations thereof, the choice of appropriate growth conditions requires more careful attention.

Currently, large communities of plant biologists work either in the lab or the field, each based on a long research tradition. An undesirable consequence might be that this leads to a cultural 'glass wall' between lab and field scientists (Kohler, 2002), with each community developing its own concepts, protocols and terminology for growing plants and evaluating genotypic or environmental effects (Blum, 2014). When these concepts and protocols are not regularly cross-checked and revised, the risk of separately developing islands of knowledge is substantial. Indeed, the extent to which plants from growth chambers and glasshouses contrast or accord with those growing in agricultural or natural field conditions has received only very limited attention (Garnier & Freijsen, 1994; Kaur *et al.*, 2012; Limpens *et al.*, 2012).

It is the aim of this review to quantify some of the differences and similarities between plants grown in controlled and field conditions, and to consider possible steps to facilitate the translation of results from lab to field. First, we consider the available evidence of how and to what extent plants grown under controlled conditions differ from those in the field. Secondly, we evaluate the main differences in (abiotic) environmental conditions experienced by plants in various growth chamber experiments and in the field, both above- and belowground. Thirdly, we analyse the effect of plant density on individual plant traits because plants are often relatively well-spaced in growth chambers or glasshouses but under strong intra- or interspecific competition in the field. Fourthly, we evaluate to what extent a group of genotypes or species that differ in the lab show a similar ranking in the field. Finally, we discuss various options to facilitate the transfer of knowledge from lab to field, including the extended technical capabilities that state-of-the-art growth chambers and glasshouses offer.

II. Phenotypic differences between lab- and field-grown plants

Many scientists share the perception that lab- and field-grown plants often differ, with lab-grown plants having 'softer' leaves and more slender stems. However, there are only a few published experiments that have specifically investigated these differences. Table 2 lists five experiments where plants from the same seed batch were grown under both controlled and field conditions, and two examples where a range of species were grown under controlled conditions and compared with randomly selected field-grown individuals of the same species. Some of these papers reported genetic differences in response to an environmental cue that could be observed in plants in the field but not under controlled conditions, although subsequent adjustments in the growth protocol could eventually reproduce the response under controlled conditions as well. A common result in these studies is a higher specific leaf area (leaf area : leaf mass; SLA) for lab-grown plants. However, we do not know whether these few published papers are

Table 1 Qualitative differences in abiotic conditions between growth chambers, glasshouses, and agricultural or natural fields

Variable	Growth chamber	Glasshouse	Field	Remarks	Reference
(a) Shoot environment					
Light quantity	Low – intermediate ◊	Low – high, depending on season, latitude and shading ♦♦♦	Low – high, depending on season and latitude ♦♦♦	High light intensities in growth rooms may go with a high heat load	
R : FR	≫1.2, depending on lamps used ◊	*c.* 1.2, low at dawn and dusk ♦	*c.* 1.2, low at dawn and dusk ♦	Lower below other plants	Cummings *et al.* (2007)
Spectrum of Photosynthetic active light	Artificial light, often with very narrow wave bands, strongly deviating from sunlight ◊	Sunlight, often shielded in summer and supplemented with lamps in winter ♦	Sunlight ♦	Lamps differ widely in spectrum. LED lamps which get close to the sunlight spectrum are now coming on the market	Schuerger *et al.* (1997), Hogewoning *et al.* (2010)
UV-B	Absent, unless specific UV-lamps are used ◊	Absent, unless specific UV-transmittent glass is used ◊	Variable, depending on solar irradiance, latitude and altitude ♦♦♦	Effects of UV-B on plants partly depend on the intensity of photosynthetic active radiation. Leaves of various species may not develop well without some UV light	Lang & Tibbitts (1983), Caldwell & Flint (1994), Max *et al.* (2012)
Temperature	Moderate ◊ – ♦	Moderate ♦♦	Variable with season ♦♦♦	Although the temperature in growth chambers often varies little, heat shock regimes can be applied relatively easily.	
CO_2	Higher for growth chambers in buildings, lower when many plants are present ♦	*c.* 400 μmol mol^{-1} ◊	*c.* 400 μmol mol^{-1} ◊	High peaks when humans respire in GC	
Ozone	?	?	In summer ♦♦♦	Depending on distance from large cities	
Air humidity (VPD)	Often constant ♦	Variable ♦♦	Highly variable ♦♦♦	Be sure to regulate air humidity by VPD, not % air humidity	
Wind speed and air turbulence	Absent or low, depending on air inlets and vaporizers ◊	Passive due to opening of roof or active when fans are installed ◊	Highly variable ♦♦♦	Locally generated wind in controlled conditions is often variable in space, causing large variability in plant height, mass and allocation	Cordero (1999)
(b) Root Environment					
Temperature	Intermediate ◊	Low – high ♦♦	Highly variable with season ♦	Temperature variation in soil depends on depth	
Nutrient supply	Often high, but strong depletion may occur over time for large plants in small pots ◊	Often high, but strong depletion may occur over time for large plants in small pots ◊	Highly variable, high in agricultural settings, relatively constant over time ◊	Recirculating hydroponics or mixed soil substrates in pots in the lab make for a far more homogenous nutrient distribution than field soils with different horizons	
Water supply	Often high, but strong depletion may occur over time for large plants in small pots ◊	Often high, but strong depletion may occur over time for large plants in small pots ◊	Highly variable, also in time ◊	Watering pots from above or below may have a different impact, as have different drought stress scenarios	Poorter *et al.* (2012b)
Soil Compaction	Generally low, especially in pots with potting soil ◊	Generally low, especially in pots with potting soil ◊	Frequent problem in agricultural soils due to intense tillage and use of heavy farm equipment ♦	Strongly depends on soil type and soil water content	

(a) Environmental variables pertaining to the shoot and (b) the root, respectively. Values are indications of general prevailing conditions in temperate regions but may be different for a specific location. An overall indication of diurnal variability is given as ◊ (absent), ♦ (low), ♦♦ (intermediate), ♦♦♦ (high). R : FR, red to far-red ratio; UV, ultraviolet radiation; VPD, vapour pressure deficit.

Table 2 Comparison of plants of the same genotype or species grown under controlled and field conditions

Reference	Species	Trait	Values in plants from growth chambers or glasshouses relative to field plants
(a) *Same seed lot*			
Patterson *et al.* (1977)	*Gossypium hirsutum*	Photosynthetic activity/area	35% lower
		SLA	55% higher
		Chlorophyll/area	40% lower
Baldwin (1988)	*Nicotiana sylvestris*	Alkaloid concentration in leaves	> 400% increase after defoliation of field-grown plants, no change in the GH. (Modest increase in GH-plants when bigger pots were used)
Külheim *et al.* (2002)	*Arabidopsis thaliana*	Seed production per plant	*npq*-mutant had 3% lower value than WT in the GC, 29% lower in the field. (Field difference could be mimicked in the GC by applying fluctuating light
Han *et al.* (2008)	Six grass species brought from field in monoliths and then grown in the lab	SLA	65% higher
Kaur *et al.* (2012)	*Nicotiana attenuata*	Stem stability	Lignin mutant buckled in the GH, but not in the field. Stability in the field was lost after shielding from wind and UV-B, and gained in the GH after using bigger pots and exposing plants to wind and UV-B
(b) *Random individuals*			
Poorter & De Jong (1999)	22 herbaceous species	SLA	60% higher
Cornelissen *et al.* (2003)	*c.* 100 woody species; young plants from the lab, adult plants in the field	SLA	125% higher
		Leaf Nitrogen concentration	15% higher

(a) Plants from the same seed batch grown for comparison under different conditions. (b) Random plants grown under controlled conditions compared with random plants observed in the field. GC, growth chamber; GH, glasshouse; npq, nonphotochemical quenching; SLA, specific leaf area; UV, ultraviolet radiation; WT, wild-type.

representative of a more general phenomenon or exceptions to a norm simply because corresponding results were considered uninteresting to publish.

In order to reach more general conclusions, we compiled a large dataset for plants grown under controlled and field conditions (> 19 800 records on mean values; see the Appendix for more details). For seven growth-related traits we calculated the median value for each species as observed for plants grown under controlled conditions and in the field in otherwise unrelated experiments. The across-species distribution of the ratio of the median values of lab and field plants is shown in Fig. 1, taken over all species as numbers, and for herbaceous crop, wild herbaceous and woody species separately as box plots. The results follow, at least partly, our expectations: plants grown in the lab generally have a higher SLA and a somewhat higher leaf nitrogen concentration, in line with the conclusions of Garnier & Freijsen (1994). They also have lower rates of light-saturated photosynthesis but faster relative growth rates (rate of growth per unit biomass present; RGR). At the final harvest of the experiment, however, lab-grown plants are shorter and lower in mass, despite their higher RGR. The reason for this is the much shorter duration of lab experiments (Table 3). Although the observed differences varied in strength across the three groups of species we looked at, the trends are mostly consistent. The physiological and morphological differences could partly be the result of covariation with size or age, especially for woody species (Coleman *et al.*, 1994). A plant's RGR, for example, is known to decrease with size, and thus the longer lifespan of plants in the field may partly explain their lower growth rate (Fig. 1). However, environmental differences are likely to play an important role as well.

III. The shoot environment

The environmental conditions in the average experiment vary substantially among growth chambers, glasshouses, and fields. A summary of qualitative generalizations is given in Table 1. We now analyse in a more quantitative way how and to what extent the two aerial factors that are most important for plant growth – light and temperature – vary.

1. Light quantity

In order to quantify what conditions are usually applied in growth chambers, we screened the scientific literature, characterizing light availability by the amount of photons in the photosynthetic range integrated over the day (DLI, daily light integral). We use this variable because there is often a good correlation between DLI and RGR (Poorter & Van der Werf, 1998) and a strong correlation between total intercepted photons during the growing season and crop productivity (Monteith, 1977). Most species in growth chamber experiments are grown with DLI values ranging between 10 and 30 mol m^{-2} d^{-1} (Fig. 2a), with slightly lower values for species that normally occur in arctic or boreal habitats than those normally found in temperate and (sub)tropical regions. *Arabidopsis thaliana* was a clear exception – it is often grown at much lower DLI values (*c.* 6 moles m^{-2} d^{-1}, Fig. 2a). Because we wanted to know

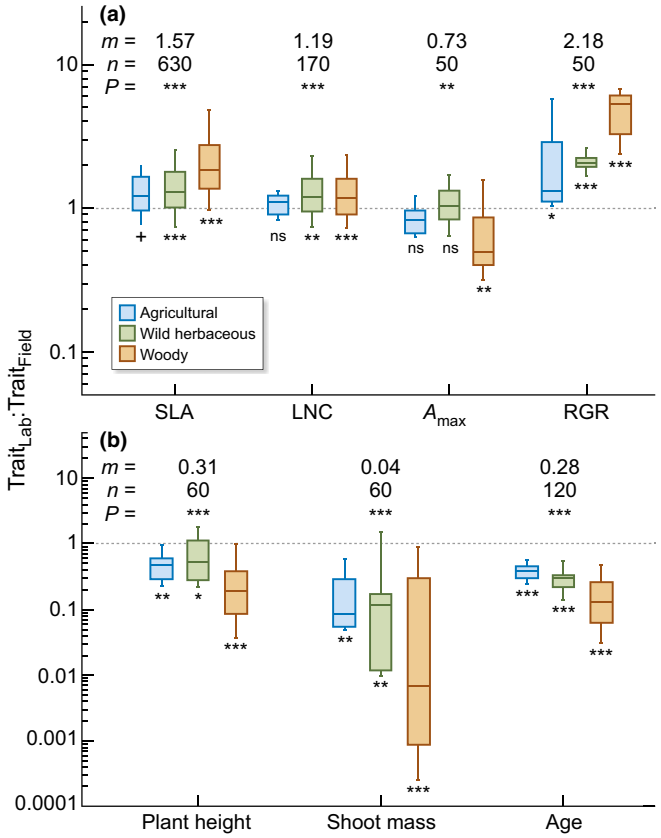

Fig. 1 The ratio of various phenotypic variables as observed for plants grown under controlled conditions relative to those observed for the same species in the field. Data are from the Glopnet (Wright *et al.*, 2004), LEDA (Kleyer *et al.*, 2008) and MetaPhenomics (Poorter *et al.*, 2010) databases, supplemented with additional observations from Poorter *et al.* (2009) and the literature (see Supporting Information Table S1). First, the median value of the observed data was calculated per species and per growth environment, and subsequently the ratio between lab and field was determined from those median values. (a) SLA, specific leaf area ($m^2\ kg^{-1}$); LNC, leaf nitrogen concentration ($mg\ g^{-1}$); A_{max}, photosynthetic capacity ($\mu mol\ m^{-2}\ s^{-1}$); RGR, relative growth rate ($mg\ g^{-1}\ d^{-1}$); (b) Plant height, total plant height (cm); Shoot mass, shoot dry mass (g); Age, age of the plants at the last measurement/harvest of the experiment (d). The box plots characterize the distribution of these ratios across species for three functional groups; boxes indicate the 25th and 75th percentile, and the whiskers the 10th and 90th percentile. Data above the box plots indicate the median response (m), number of species on which the data are based (*n*) and significance (*P*) for all species together. For each trait, we tested deviation from unity with a *t*-test and indicated this in the graph as: ns, nonsignificant; +, $0.05 < P < 0.10$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Table 3 Median lifespan of plants in experiments carried out in growth chambers, glasshouses or in the field

	Median lifespan (d)	*n*
Growth chamber	39	3110
Glasshouse	95	3500
Field	550	700

For *n*, the number of observations on which the median is based, different species included in one experiment were considered and counted separately.

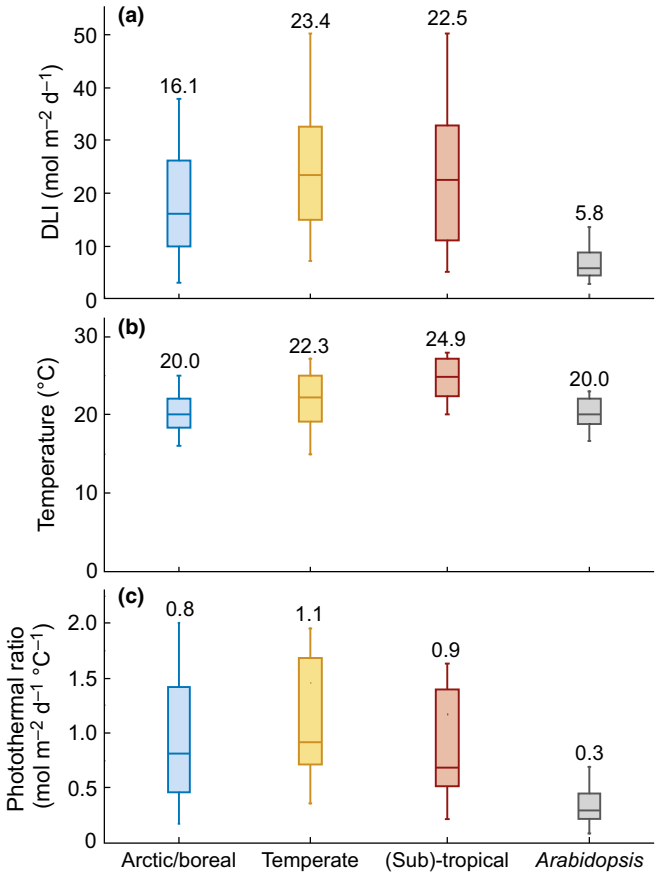

Fig. 2 (a) The daily amount of light (daily light integral (DLI), number of quanta in the 400–700 m range m^{-2} integrated over 24 h); (b) mean temperature (over 24 h); and (c) the photothermal ratio (DLI divided by the daily mean temperature) as used in growth chamber experiments with species from arctic/boreal origin, from temperate and from (sub)tropical regions. Data for *Arabidopsis* were considered separately and are from 100 publications from the scientific literature; data for species from the various ecological zones are taken from the MetaPhenomics database (Poorter *et al.*, 2010) and consists of 260 herbaceous and 110 woody species, in 320 and 100 different experiments, respectively. The distribution of the data is characterized by box plots, where boxes indicate the 25th and 75th percentile, and the whiskers the 10th and 90th percentile. The numbers next to the boxes indicate the median value.

how light intensities in growth chambers compared with those in the field, we used a detailed climatic database spanning 30 yr of observations (New *et al.*, 1999) to analyse monthly-averaged DLI levels for the five main ecological zones in the world, as discerned by the FAO (FAO, 2012). We chose 20 different locations from each zone (see Supporting Information Table S2), concentrating for ease of analysis on low-altitude locations in the Northern Hemisphere. In arctic, boreal and temperate climates, the seasons differ strongly (Fig. 3a). In these ecological zones, spring is characterized by relatively bright conditions, as compared with autumn. DLI values in the months of the year with lowest irradiance logically decrease strongly and linearly with latitude, but this is far less so for the months with highest DLI. On average, highest DLI values are found in summer in temperate and subtropical regions (*c.* 40–45 mol $m^{-2}\ d^{-1}$), with only slightly lower values in the tropical and boreal regions. For a comparison of field conditions and growth chambers, we discriminate between the first phase of the growing season ('spring'), when plants are often young and vegetative, and a

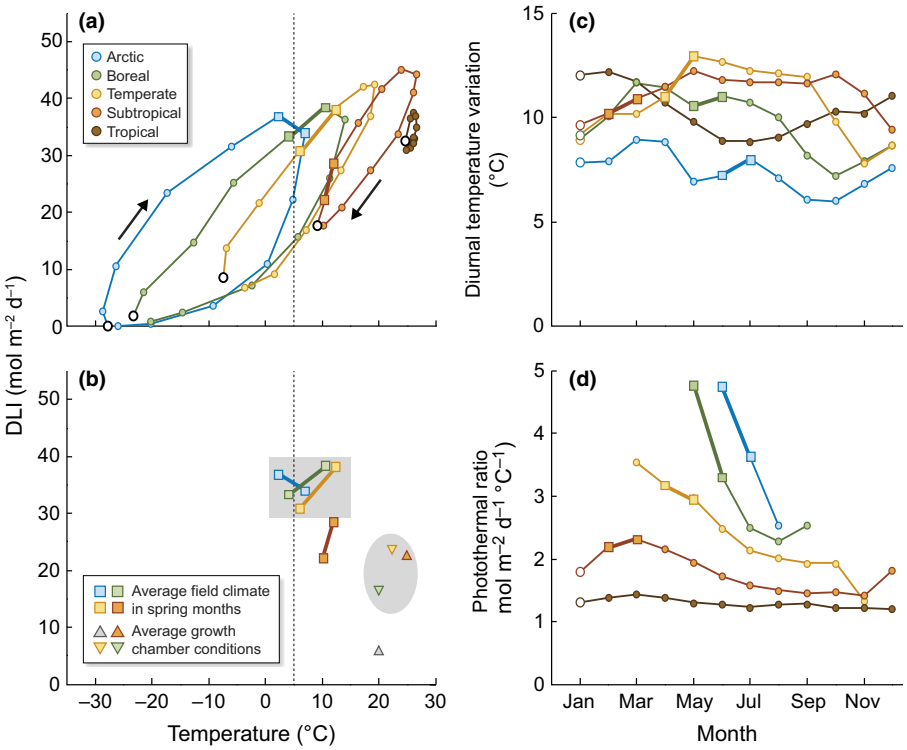

Fig. 3 (a) Progression over the year of monthly averaged values of daily light integral (DLI) and daily mean temperature in the world's five ecological zones. (b) Progression of DLI and temperature when considered for that part of the growing season where most plant species germinate or resprout after winter. The median values for plants from those zones while grown in growth chambers is also given. (c) Diurnal variation in air temperature ($T_{max} - T_{min}$) over the various months of the year, and (d) the photothermal ratio for the world's five ecological zones plotted as the time-course over the part of the year with supra-zero temperature values. All data are average values per month of the year and based on 20 lowland locations per climate zone. See the Appendix for more information. For simplicity of presentation and interpretation, locations were restricted to lowland sites in the Northern hemisphere. Large open circles indicate values for January, closed squares the period where most germinated plants in that climate zone show active vegetative growth, arrows the course of time over the year. In (b) the grey rectangle indicates the DLI and temperature range in common during active growth from the arctic to temperate zones. The triangles show the median value for growth chamber experiments with *Arabidopsis thaliana* (black), species from arctic and boreal zones (green), temperate zones (yellow), and (sub)tropical regions (orange; based on Fig. 2). The grey ellipse indicates the light and temperature range in common in most growth chamber experiments. The dotted line indicates 5°C, for many species the lower temperature limit for leaf elongation.

second phase ('summer'), when plants are older and often generative. In ecological zones with frost (i.e. arctic, boreal and temperate), seed germination or resprouting of overwintering plants generally begins in early spring. DLI levels of the two months with most active vegetation growth are shown in Fig. 3(b). Interestingly, in all three zones this period has very similar light intensities, indicated by a grey rectangle. The median DLIs applied in growth chambers for species from the various ecological zones are indicated by a grey oval. Clearly, in many experiments, young plants in the growth chamber experience light intensities that are > 30–50% below what plants of the same species experience in the field. The discrepancy becomes even larger during the summer period.

An evaluation of average DLI values in glasshouse experiments is less straightforward. In scientific reports, specifications of the light climate are usually marginal and – if present at all – often limited to the minimum light intensity provided by additional lighting or peak light intensity. Measured at noon on a sunny day, glasshouses may transmit 60–80% of outside visible light intensities (Von Elsner *et al.*, 2000). However, when integrated over the whole day transmission values as low as 30% have been reported (Cabrera-Bosquet *et al.*, 2016). Light transmission also decreases when shade nets or liming are used to reduce radiation load in summer. As long as DLI is not measured directly, the light environment in glasshouses remains poorly described, but – as for growth rooms – is likely to be considerably lower than what young plants experience in the peak of the vegetative growth season in the field.

In addition to seasonal progression, there is substantial diurnal variation in light quantity depending on cloud cover and the angle of the sun. By intercepting direct sunlight, clouds may decrease actual light intensity by > 85% in just seconds. Moreover, a significant part of the daily light within canopies and in understorey plants comes through sunflecks (Pearcy, 1990). By contrast, most growth chambers supply a fixed light spectrum programmed to have no variation in light quantity during the day. Although plants can often cope well with the absence or presence of light fluctuations, a negative effect of temporary high light peaks on growth at a given DLI is reported regularly (Wayne & Bazzaz, 1993; Poorter & Van der Werf, 1998; Alter *et al.*, 2012).

2. Temperature

We also determined the daily 24-h averaged temperatures for a wide range of growth-room experiments and compared them with values

observed in the field over the various months of the year. Many species are grown between 18 and 28°C, with higher temperatures used for species from (sub)tropical areas (Fig. 2b). Most growth-chamber experiments with *Arabidopsis* apply air temperatures in a relatively narrow range of *c.* 20°C. Considering that most growth chamber experiments focus on young plants, all of these values are considerably higher than the average air temperatures prevalent in spring in the field. In the three ecological zones with subzero winters, seeds are germinating or overwintering plants start to resprout when temperature during at least part of the day exceeds 3–5°C (Porter & Gawith, 1999; Körner, 2008). During most of the vegetative growth stage, the average 24-h temperature in these zones ranges between 5 and 15°C (Fig. 3b). This difference between lab and field is profound, given that many processes over the 5–25°C range, including enzymatic transformations, cell division (Tardieu *et al.*, 2000) and cell cycle time (Rymen *et al.*, 2007), respond strongly to temperature.

The air temperature in the field showed a substantial diurnal variation, with daily maximum and minimum temperature differing on average by 7–12°C, and a larger divergence during summer for temperate and subtropical regions (Fig. 3c). These temperatures are routinely measured at *c.* 1.5 m above the soil. Shorter plants growing in open vegetation may experience considerably greater diurnal air temperature variations (Stoutjesdijk & Barkman, 2014). Large thermal variation contrasts strongly with the temperature regime in most growth chamber experiments. In our survey, > 25% of these experiments applied no day–night temperature difference, and 50% applied a variation of less than 6°C (Fig. 4). Therefore, the diurnal variation in air temperature commonly applied in growth chamber experiments is modest.

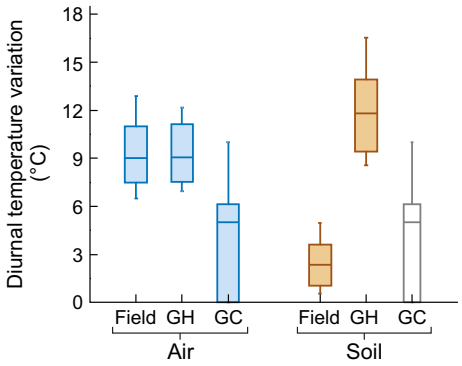

Fig. 4 Diurnal variation in air and soil temperature as observed in different growth environments. Observations in the field are overall values taken from diurnal air temperature variation, given in Fig. 3(c) and soil temperature variation at 20 cm depth, as given in Fig. 6(c). Data for the glasshouse (GH) are derived from a preliminary experiment in summer 2014 in the glasshouse of Research Centre Jülich. Data from the growth chambers (GC) are derived from the difference in day and night air temperature in *c.* 400 experiments from the MetaPhenomics database (Poorter *et al.*, 2010). The data for the root environment are an indication and based on the assumption that the temperature of the soil in pots in growth chambers will closely follow the air temperature. The distribution of the data is characterized by box plots, where boxes indicate the 25th and 75th percentile, and the whiskers the 10th and 90th percentile. Note that more than 25% of the growth chamber experiments apply no temperature difference between day and night.

A morphological variable, such as internode length, amongst others, is known to respond positively to a temperature difference between day and night (Myster & Moe, 1995) and diurnal temperature changes may partly regulate the clock genes (Hsu & Harmer, 2014). For various species, including important crop species such as *Oryza* and *Malus*, flowering, fruiting and yield may also depend strongly on the occurrence of relatively cool nights during fruit setting. For *Oryza*, a 1°C *increase* in the minimum night temperature during the growing season has been linked to a 10% *reduction* in grain yield (Peng *et al.*, 2004). The effect of a 1°C lower night temperature on overall vegetative plant growth seems less pronounced, with decreases reported in the range of 0–2% (Frantz *et al.*, 2004; Kanno *et al.*, 2009).

3. Consequences for plant growth

Most plants in growth chambers are kept at air temperatures close-to-optimal for growth, and low-to-intermediate light levels (*c.* 21°C, *c.* 20 mol m^{-2} d^{-1} for plants from boreal and temperate zones). These conditions are quite different from what young, actively growing plants experience in the field. (*c.* 10°C, *c.* 35 mol m^{-2} d^{-1}; Fig. 3b). What effects does this have on the growth of plants? Both light and temperature have a strong impact on accumulated plant biomass, as judged from dose-response curves for growth that summarize a wide range of different experiments (Poorter *et al.*, 2010). In the average experiment, the effect of increasing DLI from 20 to 35 mol m^{-2} d^{-1} results in a 60% increase in biomass (Fig. 5a), which is relatively moderate. The change in temperature from 10 to 21°C results in a much greater increase (*c.* 600%; Fig. 5b). Plants outside may experience higher temperatures when exposed to direct sunlight or lower light intensities when shaded by neighbours. Nevertheless, it is likely that environmental differences of this magnitude may affect the general physiology of a plant. Under average growth chamber conditions, processes that depend mainly on temperature, such as cell division, may operate relatively faster than in the field, whereas processes that depend strongly on light, such as photosynthesis, tend to be impaired. Consequently, many plant species in these chambers will likely perform under carbon limitation, making them 'source-limited'. In field conditions, however, plants have high rates of photosynthesis but relatively slow cellular division and growth. Hence, young field plants are more likely to be 'sink-limited' (Poorter *et al.*, 2013; Körner, 2015). The source : sink relationship is an important concept that is pertinent to understanding the growth of all plant species and has received much attention in both horticulture and agriculture (Marcelis, 1996; Li *et al.*, 2015). Unfortunately, we cannot easily measure it, and proper interpretation requires good insight into the physiology of an individual species. The photothermal ratio (PTR) is an interesting and easily measured alternative that has been proposed to gain insight into the balance between the supply of sugars by photosynthesis and the rate of cell division (Fischer, 1985; Liu & Heins, 1997). Researchers have used this concept for various horticultural and crop species to optimize vegetative growth (Liu & Heins, 2002) and seed production (Islam & Morison, 1992) using a temperature baseline depending on species. Because we aim to compare environments,

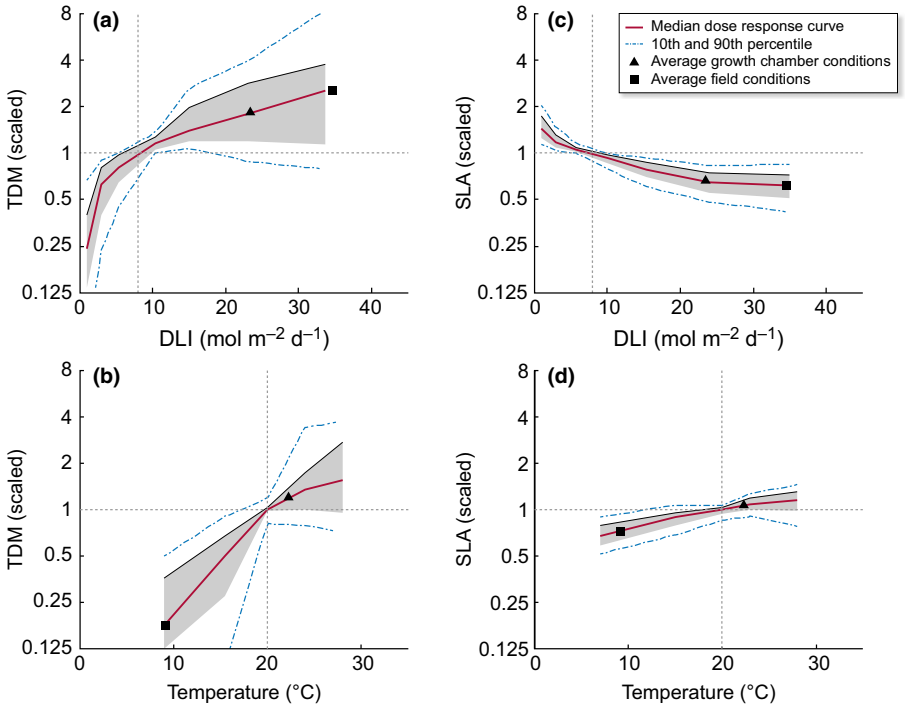

Fig. 5 (a, b) Dose–response curves of total dry mass (TDM); and (c, d) specific leaf area (SLA) as dependent on: (a, c) daily light integral (DLI); and (b, d) mean daily temperature. Red line, median; grey shaded area, interquartile range (25th–75th percentile); blue dashed lines, 10th and 90th percentile. These curves are based on the MetaPhenomics database (Poorter *et al.*, 2010), and show relative values scaled to 1 at a DLI of 8 mol m^{-2} d^{-1} (a, c) or a temperature of 20°C (b, d). Average light and temperature conditions during spring in the field in the temperate zone and in the average growth chamber experiment with temperate species (Fig. 3b) are indicated by a black square and triangle, respectively.

we apply this concept more broadly as the ratio between the daily amount of light and the mean daily temperature above 0°C. For the various ecological zones, we calculated PTR values during the growing season. The ratio is relatively high at the beginning of the growing season (Fig. 3d), especially in arctic regions. (Sub)tropical regions have a much lower PTR and hardly show any fluctuation throughout the year. PTR values in growth chambers are clearly lower than what plants will experience in any but the most shaded conditions (Figs 2c, 3b), and this was true for glasshouses as well (< 1.0 throughout the year; data not shown). The implication for the present review is that by choosing conditions in controlled environments that traditionally are close to room temperature and relatively low light intensities, we study (young) plants that are physiologically in a very different state than plants growing in the field.

IV. The root environment

1. Temperature

Unlike air temperature, soil temperature data are scarce, and we did not find sufficiently detailed data for an in-depth characterisation of all five ecological regions. General principles, however, can be illustrated using an extensive dataset with systematic measurements carried out all over the USA (Bell *et al.*, 2013). We chose 20 sites with very diverse climatic conditions (Table S2) and calculated for each site how mean monthly soil temperature covaried with the mean monthly air temperature. Data for one such site is shown in Fig. 6(a). At subzero air temperatures, the coupling is poor: soil temperatures hardly covary with air temperature under those conditions at any depth, possibly because snow cover acts as a layer of isolation or frost stops convective heat transfer (Groffman *et al.*, 2001). By contrast, roots in the topsoil during the growing season will experience a mean temperature that tracks mean air temperature quite well. We quantified this coupling by calculating the slope of the soil vs air temperature relationship, with a value of zero indicating no coupling and a value of one strict coupling. Taken over all 20 sites, the coupling is strong for the topsoil (Fig. 6b). But even at 1 m depth, the mean monthly soil temperature rises by 0.75°C for every 1°C increase in mean air temperature. As such, this situation is comparable to what plants experience in climate chambers, where root and air temperature are strongly linked as well. There is a contrast when it comes to the diurnal variation in temperature. The deeper roots of field-grown plant get into the soil, the less diurnal temperature fluctuation they experience (Fig. 6c). For the Bell *et al.* (2013) dataset, the median diurnal fluctuation at 0.2 m depth is only 1.2°C, which is far less than the diurnal variation in air temperature of > 10°C. It will also be different from those growth chamber experiments in which day and night temperatures are programmed to vary because pot temperatures will follow air temperature with some delay. The situation in glasshouses may again be distinct; in an exploratory experiment we carried out in summer, we found the diurnal variation in air temperature to be similar to that in the field (median values of 9.0°C in both cases; Fig. 4). Soil temperature inside the pots followed air temperature with some delay but increased quickly when direct solar radiation hit the pot wall. In these cases, containers heated up locally to > 20°C above air temperature, reaching values over 50°C in summer. As with soil, there is variation in temperature among roots of different depths, but plants in pots have a different profile, with stronger and faster changes than plant roots experience in the field. The implications of soil temperature gradients and temperature variation on plant growth are not clear (Füllner *et al.*, 2012). Thermophilic species will probably not be

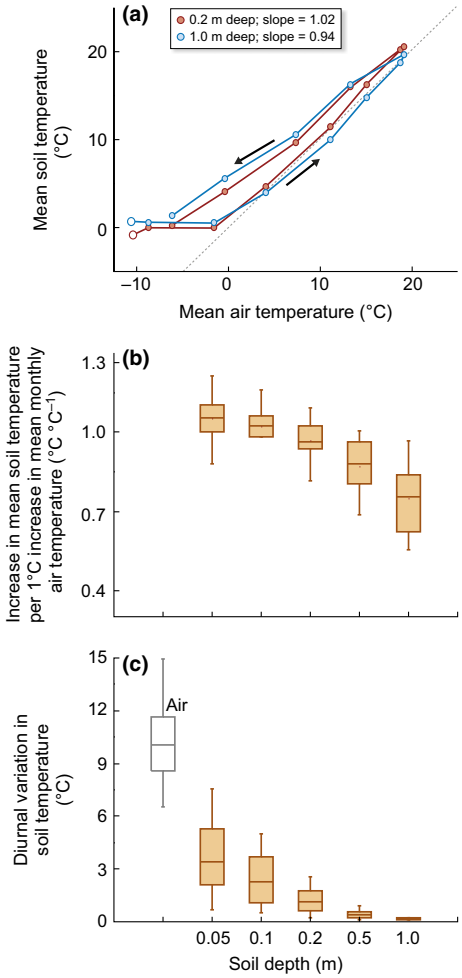

Fig. 6 (a) Relationships between the mean monthly air and soil temperature measured at depths of 0.2 m (red) and 1.0 m (blue) in Maine, USA. The slope of the line at both depths, fitted through all data with supra-zero air temperatures, is indicated as well. (b) The absolute increase in the mean monthly soil temperature with a 1° increase in the mean monthly air temperature. (c) Diurnal variation in soil temperature as dependent on soil depth and calculated over a full year of measurements. All data are from Bell *et al.* (2013) and pertain for (b) and (c) to 20 locations in 20 states all over the United States of America (for locations see Supporting Information Table S3). Most of these sites are covered by herbaceous vegetation. The arrows in (a) indicate the direction of the yearly time course, the dotted line the 1:1 relationship. Box plots are described in the legend of Fig. 1.

greatly affected by high pot temperatures, but they could be well above the optimum for psychrophilic species. Precautions to prevent overheating may therefore be useful.

2. Nutrients, water and pots

Many controlled-environment experiments use containers filled with potting soil, sand or sieved field topsoil. Clay is not often used, mainly because the aggregates are easily destroyed during handling, which leads to poorly structured, low oxygen soil and because of difficulties in harvesting the roots. Potting soil is widely applied because it is lightweight, has a large water-holding capacity and a low impedance for root growth. By combining potting soil with ample supply of water and nutrients, which is often the case in controlled environments, one can obtain plants with high growth rates. Another advantage of containers is that they are generally small and therefore easy to handle.

It should be realized, however, that this way of growing plants provides an unusual root environment. First, most pots will contain plants in a much smaller rooting volume than what they would occupy in the field. In 2 months, even the roots of a small species such as Arabidopsis can reach a depth of 50 cm (Barboza-Barquero *et al.*, 2015). Small containers are known to have a negative impact on root functioning, root distribution and plant growth (Poorter *et al.*, 2012a). A second drawback of pots that are small relative to plant size is that water and nutrients can be quickly depleted if care is not taken. Third, most solid substrates in pots are well-mixed and therefore lack the strong vertical gradients of natural field soils. In the field, nitrate may leach to deeper soil levels with precipitation (Cassman *et al.*, 2002; Chen *et al.*, 2010), whereas less mobile nutrients, such as phosphorus and potassium, may accumulate in topsoil where organic matter or fertilizer is present. Soil pH also may decrease with depth, with consequences for the solubility and availability of various macro- and micronutrients (Lynch & Wojciechowski, 2015). Additionally, in many agricultural systems, we find a retracting water table at the end of the growing season. In such environments, rooting depth is positively related to soil exploration and plant performance (Manschadi *et al.*, 2006; Wasson *et al.*, 2012). This is not easily mimicked in pots although gradients in pots probably exist due to method of watering (from top or bottom), unequal root distribution and fertigation. Another problem of well-watered small pots can be that the water potential in the root zone becomes close to zero. Consequently oxygen availability is much lower than in the field because most air spaces are filled with water (Passioura, 2006).

3. Plant–soil feedbacks

One gram of field soil contains as many as 5000–10 000 taxa of soil microbes and multicellular organisms (Torsvik & Øvreås, 2002), including enemies, mutualistic symbionts such as mycorrhizal fungi and nitrogen-fixing microbes, and decomposer organisms. Many aspects of plant performance are influenced by 'plant–soil feedbacks', the mutual interaction between plants and these soil-related organisms (Bever *et al.*, 1997). Plant–soil feedbacks also may affect the abiotic status of the soil, and can have both positive and negative effects on the growth of individual plants (Wardle, 2002). Its importance may be exemplified by the role it is supposed to play in biodiversity–productivity relationships; negative plant–soil feedback often gets stronger with decreasing plant diversity, explaining the typical low biomass production in monocultures or low-diversity mixtures (Maron *et al.*, 2011; Schnitzer *et al.*, 2011). This phenomenon, which is well known from agriculture, may easily decrease individual plant biomass by > 20% and is a strong motivation for crop rotation (Kirkegaard *et al.*, 2008). However, plant–soil feedback also can be neutral or positive, usually in the case of plant species from later successional stages (Kardol *et al.*, 2006). One of the underlying mechanisms by which the microbial community around the roots, the microbiome, exerts its influence

is the way infections affect root morphology and physiology. For instance, roots may be much shorter branched and lack root hairs in soil where individuals of the same species have grown previously than in sterilized soil or soil precultured by other plant species (Van der Putten *et al.*, 1990). Constrained root development, in turn, may hamper a plant's uptake of water and nutrients. For example, introduction of resistance or tolerance against soil-borne pathogens has been the best factor for improving drought resistance of wheat crops in Mediterranean environments, simply because healthy roots will proliferate stronger and function better (R. Richards, pers. comm.).

The root substrates mostly used under controlled conditions are very different from soil in the field. Hydroponic systems and sieved sand are practically devoid of most functional groups of soil organisms. But also potting soil lacks a well-developed soil food web, as it often has been sterilized by steaming in order to reduce disease risk. During most of the usually brief experimental periods in lab experiments, the microbial community will be dominated by bacteria and geared towards the decomposition of easily degradable substances. Therefore, many of the biotic interactions that roots have with their environment in the field will be lacking under controlled conditions.

In conclusion, the root environment has a profound effect on plant growth, both directly and indirectly through soil physics, chemistry, the soil microbiome and the soil fauna. Unfortunately, quantification of the root environment is challenging, not least because soil characteristics can be highly variable in space (both horizontally and vertically) and time (Ettema & Wardle, 2002; Walter *et al.*, 2009). Nonetheless, in both controlled and field experiments, it is highly informative to characterize at least relatively easily measured variables, such as soil temperature, compaction, pH and maximum water content. Although the translation from lab to field is notoriously difficult, especially when nutrient or water limitations are of interest and soils are highly diverse in structure and microbial composition (Blum, 2014), it has been shown that with sufficient knowledge about both physiological processes and environmental conditions it is feasible (Tardieu, 2003).

V. Effects of plant density

Controlled experiments in growth chambers or glasshouses are often performed with individuals rather than groups of plants. If the experimental design includes intermediate harvests, the one-plant-per-pot approach often allows for incremental spacing, minimizing physical plant–plant interference and mutual shading even for large plants. However, many researchers have limited space available, and plants often will be grown at such a density that some form of light competition occurs, especially when plants becomes larger. A possible density effect, therefore, depends on plant size, developmental stage and architecture, or growth habit. Young *Arabidopsis* plants are easily grown at a density of 300 plants m^{-2}, whereas for larger *Helianthus annuus* a density of 1 plant m^{-2} may still imply mutual shading. Nonetheless, the densities used under controlled conditions will not easily reach the levels that are normal in the field. For example, under agricultural conditions, a density of 250–320 plants m^{-2} is normal for a species like *Hordeum vulgare*, whereas plants of the same size grown in controlled growth facilities are often held at a density of 20–50 plants m^{-2}. The presence of neighbours reduces not only the light intensity but also wind speed and soil temperature (Pimentel *et al.*, 1962), whereas humidity will increase. Next to changes in physical factors, plants also are able to sense the presence of neighbours by, for example, the altered red : far red ratio of the light, touch, and increased concentrations of ethylene or other gaseous compounds, and they respond to these cues by altering their physiology and morphology (Baluska & Ninkovic, 2010; De Wit *et al.*, 2012). Both in a natural and agricultural setting, these indirect responses may be as relevant for the plant as the direct response to changes in abiotic factors.

The question then arises how density affects plant performance. Many agricultural experiments have considered the effect of density on vegetation structure and total productivity (see review by Papadopoulos & Pararajasingham (1997)). We are specifically interested in how density affects the phenotypic characteristics of individual plants; therefore, we have carried out a meta-analysis of 100 experiments, which is summarized in Fig. 7 and explained in the Appendix. Across all experiments, a doubling in density on average decreased total vegetative plant mass by a median value of 33% and relative growth rate (RGR) by 9%. Biomass allocation differences were small, but stem mass fraction (SMF) had a consistent increase (5%), which is even stronger if an allometric correction for size is made (Poorter *et al.*, 2012c). At the same time, the allocation to leaves (LMF) and roots (RMF) decreased somewhat. Overall, a doubling in density increased specific leaf area (SLA) by 9%, probably because the leaves inside vegetation experience lower light intensities (Poorter & De Jong, 1999). The nitrogen concentration in the leaves is not strongly affected, but photosynthesis per unit leaf area is reduced by 12%, as far as this can be properly measured *in situ*. Height overall is not affected systematically – in some cases, densely grown plants are taller and in other cases shorter than the control plants. Interestingly, Nagashima & Hikosaka (2011) showed that in an artificial vegetation of potted *Chenopodium* plants, individuals that were experimentally manipulated to be lower than the neighbouring plants increased stem elongation, whereas plants that were given a height advantage actually retarded growth until the moment that they were equal in height to the others. High-density stands show a similar kind of homeostasis with plants compensating smaller biomass by a strong increase in specific stem length (stem height/stem dry mass; 39% increase per density doubling), achieving similar heights as plants in more open stands. High-density plants also show a strongly reduced number of tillers or shoots. Reproductive effort (seed mass/shoot or total plant mass) is not affected but total seed mass per plant is dramatically lower, due in part to a decrease in individual seed mass but mainly to a strong reduction in seed number (Fig. 7). Notwithstanding several feedback mechanisms, plant-to-plant variability and the difference between dominants and sub-dominants often increase (Weiner & Thomas, 1986).

Plants show less apical dominance and produce more tillers or side branches when they are grown with relatively wide spacing. When nutrient availability allows, this brings in a positive feedback

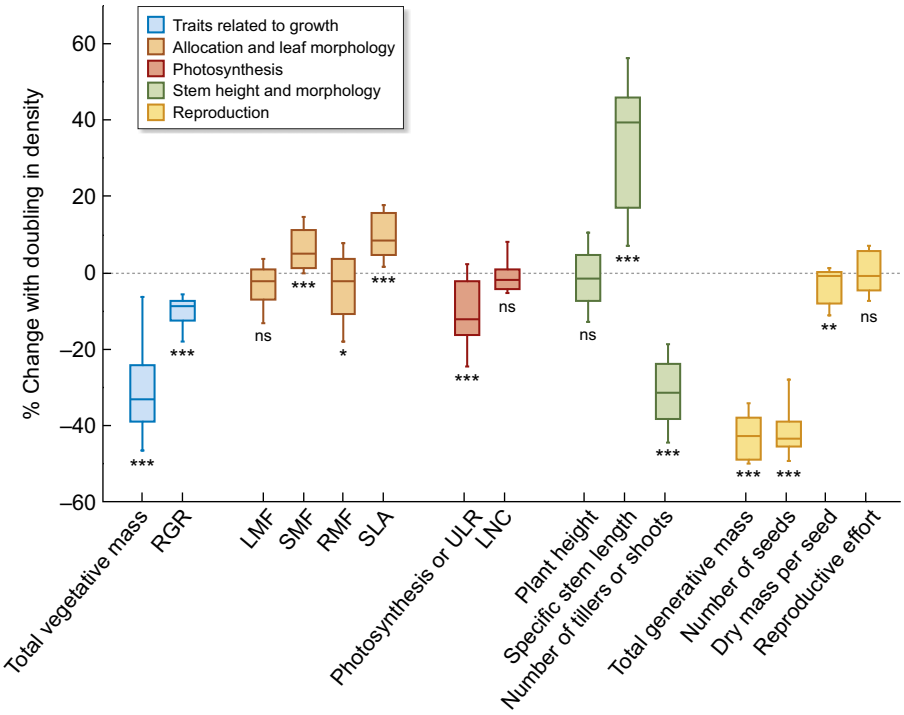

Fig. 7 Meta-analysis of the effect of plant density on phenotypic characteristics of individual plants. For each experiment, we calculated the percentage change in the variables of interest for a doubling in plant density, following the approach described by Poorter *et al.* (2012a). The underlying data come from a total of 100 experiments with varying density, partly carried out in the lab, partly in the field (for references see Supporting Information Table S4). The distribution of the data is characterised by box plots, where boxes indicate the 25th and 75th percentile, and the whiskers the 10th and 90th percentile. Colour of the boxplots indicate their biological class: blue, traits related to growth; orange, allocation and leaf morphology; red, photosynthesis; green, stem height and morphology; yellow, reproduction. For each trait, we tested deviation from zero change with a *t*-test and indicated its significance in the graph as: ns, nonsignificant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. RGR, relative growth rate; LMF, leaf mass fraction; SMF, stem mass fraction; RMF, root mass fraction; SLA, specific leaf area; ULR, unit leaf rate; LNC, leaf nitrogen concentration.

loop: a slight increase in leaf area might bring about more light interception, more photosynthesis, more leaf growth and therefore an even stronger carbon gain. This positive feedback loop does not occur when plants are competing with each other for light (Körner, 2006). As a consequence, plants grown individually respond strongly to elevated CO_2, whereas the same plants growing in competition hardly respond (Lovelock *et al.*, 1998; Winter & Lovelock, 1999). It might, therefore, be argued that plants grown in small groups better reflect the response of plants in vegetation than individually grown plants. Indeed, the growth response to elevated CO_2 in mixed cultures of various plant species, for example, can be much better forecasted by the CO_2-response of those species grown in monocultures than by the CO_2-response of plants grown individually (Poorter & Navas, 2003). In agriculture and forestry, it has been known for a long time that genotypes which show high growth rates as isolated plants do not necessarily produce high crop yields when grown in monoculture (Donald & Hamblin, 1976; Cannell, 1978). Along similar lines, Tollenaar & Wu (1999) concluded that modern cultivars of *Zea mays* had better yields than older cultivars mainly because they perform better under high densities.

It could be argued that the use of growth chambers, which are often characterized by low light intensities, a clear light gradient, high humidity and low wind speed, may partly mimic the environmental situation that plants experience in a canopy. However, the abiotic gradients in vegetation will partly be different, and so is the fact that competition for light, nutrients and water is not within the different parts of one plant but among neighbours. Hence, spacing can be a confounding factor when we compare plants under controlled conditions with those in the field.

VI. Consistency among species or genotypes in ranking between lab and field

Having discussed how plants may differ between lab and field and identifying possible causes thereof, two questions arise. The first is whether or not light, temperature and plant density can quantitatively explain the observed phenotypic differences. To examine this, we focus on SLA because ample data are available for this trait. In one study where the SLA of 22 species in growth chamber and field were compared, lab-grown plants were found to have on average 60% higher values (Poorter & De Jong, 1999). It is known that light and temperature are the most important factors affecting SLA and we used published generalized dose–response curves for SLA (Poorter *et al.*, 2009) to evaluate the extent to which these two factors could explain the observed differences between lab and field plants. Based on the environmental conditions as applied during this particular experiment in the growth chamber ($16\ mol\ m^{-2}\ d^{-1}$; 20°C) and estimates from meteorological observations in the field, the lower light intensities in the growth

chamber were expected to increase SLA by 26% and the higher temperature by 24% (Fig. 5c,d). Thus, both factors are likely to be major contributors to the higher SLA of growth chamber-grown plants. A difference in plant density is likely to be an additional factor, but because the low plant density used in the growth chamber actually *decreases* SLA, it cannot explain the remaining part of the 60% difference. Clearly, other factors, such as the high availability of water or nutrients in the growth chamber or the absence of wind, also will have their influence.

The second important question is whether the direction of response to the environment or the ranking of genotypes or species for a given trait is similar when measured in controlled environments or in the field. In other words, we may find that traits differ in absolute values (Fig. 1), but there still may be a good correlation between lab and field observations that allows a translation from lab to field. Few experiments have focussed on this question and the literature is mixed. For example, on the one hand, ranking of soybean cultivars according to UV-B sensitivity was hardly affected by growing plants in the glasshouse or field (Teramura & Murali, 1986). On the other, the bean cultivar with largest biomass in the field under low P conditions showed lowest values in hydroponics (Beebe *et al.*, 2006). Limpens *et al.* (2012) concluded that basic physiological responses often work in the same direction in lab and field. In a meta-analysis of > 200 experiments on nitrogen effects in *Sphagnum*, for example, physiological responses were found to be similar in lab and field. However, growth responses were often different, and depended strongly on the context of the experiment, in their case the presence or absence of vascular plants. To obtain a more general picture, we analysed 17 experiments where a range of genotypes or species were compared for growth-related traits such as SLA, leaf nitrogen concentration or yield. Overall, there was indeed a concordance between lab and field, although the median r^2 of the correlation between phenotypic data from lab and field was rather modest (0.26; Table 4). Hence, we cannot assume *a priori* that lab experiments always will predict genotypic ranking in the field as well.

For a full understanding of lab-to-field concordance we also need insight into the phenotypic correlation between two experiments repeated in the lab, and similar correlations for experiments repeated in the field. We only found information on the second comparison. Correlating literature data on the yield of 10 or more genotypes grown in the field with yield data of the same genotypes at the same location in a subsequent year, the median r^2 we obtained was 0.08 (Table 4). Unexpectedly, this is significantly lower than for the lab–field correlation. This could be caused by the fact that our lab-to-field compendium not only included yield data, but also some data on physiological and morphological traits, for which probably fewer genes are involved and a better concordance might be expected (Ghanem *et al.*, 2015). An alternative explanation is that yield in the field is affected by many random fluctuations in climate, which partly can be classified as extreme events of various nature (Sivakumar *et al.*, 2005). Such high and random variability in environmental conditions might cause a large genotype-by-environment interaction when we repeat an experiment twice in the field, larger than when we repeat it twice under (semi-)controlled and therefore less variable conditions. Given that lab-to-field extrapolations only need to deal with random variability in one year, there is the possibility that a well-designed lab experiment has better predicting ability for the ranking of genotypes in the field than field data taken from a random year of field trials.

Table 4 The concordance of phenotypic measurements when genotypes or species are compared under controlled conditions (growth chamber, glasshouse) and the field, or when a range of genotypes is compared for performance from year-to-year in the same field

	Lab to field		Year-to-year in the field		
Percentiles	r (n = 30)	r^2	r (n = 53)	r^2	P
P_{10}	0.09		−0.08		
P_{25}	0.30		0.10		
P_{50}	0.51	0.26	0.29	0.08	*
P_{75}	0.70		0.54		
P_{90}	0.79		0.67		

Data for lab to field are a summary for 17 publications by means of percentiles. Consistency in ranking is measured as the Pearson correlation of the relationship across species or genotypes for a given plant trait, for example individual shoot mass in the lab and total shoot mass or yield per m^2 in the field. More information about the method is given in the Appendix. Data for year-to-year observations in the field are based predominantly on the Pearson correlation of yield data for at least 10 genotypes grown at the same experimental site for two consecutive years, and pertain to 13 different crop species in total. *P*, the significance of the difference in *r* values for lab to field and for year-to-year in the field, based on a two-sided *t*-test ($P < 0.05$). Median r^2 values are given as well. The references to the articles on which this table is based are given in Supporting Information Tables S5 and S6.

VII. Translation of lab results to the field

Clearly, the translation from lab observations to patterns and processes in the field is a challenge not only for a discipline like ecology with its myriad of interactions, but also for agronomy and forestry, where field conditions are somewhat more under human control. The larger the step from lab to field is, the less straightforward the translation will be. Below we discuss some options to better integrate the two levels.

1. Programming growth chambers

Since the efforts of pioneers including Harvey (1922) and Davis & Hoagland (1928), growth chambers have seen strong technical advances, especially in the control of the aerial environment. Some growth chambers can operate with an air temperature as low as 5°C, and others can achieve light intensities over 1000 μmol m^{-2} s^{-1}. LED lamps are now available with a spectrum of photosynthetic active radiation that is very similar to sunlight and with independently regulated UV-A and far-red wavebands. Occasionally, CO_2 and other gases, such as ozone, are also actively regulated and can be manipulated to achieve not only higher but also lower concentrations than current levels. With computer control, we can now set any variable to change at specific moments during the diurnal cycle. Therefore, the most sophisticated growth chambers available today are able to simulate a wide range of environmental conditions and

sometimes even have the capacity to track the temporal variability observed at that time outside (Thiel *et al.*, 1996). Considering these increased capabilities, what environmental regime can be best applied? There are at least five alternatives.

Growing plants under constant conditions Many scientists employ a growth chamber regime with a constant day temperature close to 20°C, a constant light intensity during the day, and a somewhat lower temperature during the night. This strategy successfully produces plants that grow well within a reasonable time frame and have 'close-to-maximum' growth rates (Grime & Hunt, 1975). Constant conditions during the day are likely to minimize the risk of strong diurnal plant rhythms, allowing more freedom in the time of day that plants can be sampled and measured. An additional advantage is that the regime can be described easily and simply copied by others who want to repeat the experiment. Moreover, data are readily comparable to previous work or that of others who employed a simple growth regime. It is furthest away from field conditions, though.

Growing plants under constant conditions but with a higher photothermal ratio This will generally imply a lower day and night temperature than what is currently used and a larger day–night difference. It could also imply higher energy costs by applying longer photoperiods and higher light intensities than often used. However, such a growth protocol would generally come closer to the light and temperature levels as well as the photothermal ratio which plants experience in the field (Fig. 3). Junker *et al.* (2015) reported a doubling in the r^2 between the shoot mass of lab- and field-grown maize plants just by decreasing the air temperature in the glasshouse to levels characteristic for springtime in the field.

Growing plants with light intensities and temperatures that fluctuate through the day Usually, light intensities in the field are highest around noon, whereas air temperature is highest somewhere in the afternoon and lowest at the end of the night. This variation likely has a negative effect on growth (Bertolli & Souza, 2013) but positive consequences for the diurnal rhythm of the plants (Fondy *et al.*, 1989). The same is true for light quality, with (end-of-day) far-red illumination as a clear example of how plant morphology is affected (Cummings *et al.*, 2007). For any study on diurnal rhythms, inclusion of a diurnally fluctuating regime is very important, yet this type of protocol is rarely applied.

Growing plants with conditions that change between days In some experiments, growth chambers are programmed to mimic seasonal changes based on the progression of climate data over the seasons averaged over multiple years (Black-Samuelsson & Eriksson, 2002; Li *et al.*, 2014). These designs can be relevant, especially when plant development shifts are of interest. Alternatively, plants could be subjected to a 'stress test': plants could go through a number of repeatable cycles in which, for example, for a specific period of time plants would be subjected to different temperatures, light intensities and/or water supplies interspersed with intermediate values. The advantage of this regime could be that species or genotypes are not tested with just one specific combination of environmental conditions but are confronted with a range of conditions. Although repeatability across growth facilities is often a challenge, even with simple growth regimes (Massonnet *et al.*, 2010), we could envisage that stress tests could improve the correlation between performance in the field and lab, therefore resulting in more widely applicable results.

Growing plants under exactly the same conditions as outside This is the most extreme option, in which temporal variability could be very high. The question is whether or not such temporal variation is desirable to program because it is difficult to reproduce in any other lab, which precludes independent testing. However, it could be very insightful in a context where one of the environmental factors is compared at two levels, for example ambient temperature and ambient plus some degrees Celsius, with all other factors tracking outside conditions. However, in most cases some form of abstraction and simplification of the target field environment is probably desired.

2. Programming glasshouses

Glasshouse technology also has made strong advances in the last decades in terms of design, materials (Von Elsner *et al.*, 2000; Max *et al.*, 2012) and environmental controls. Techniques now have been developed where plants in the glasshouse could be grown at a constant temperature and/or DLI (Albright *et al.*, 2000). Nevertheless, the challenge for most glasshouses will be to provide plants with sufficient light, especially at higher latitudes in winter. When operating at high temperatures, the photothermal ratio under these conditions may drop to levels lower than 0.5. Applying more lamps is an option in that case, and so may be a decrease in the air temperature.

3. Pots and soil

Although we still lack mechanistic understanding, it is clear that the type and volume of root substrate and its history can all be crucial for plant performance. Using soil or potting substrate inoculated with a range of field-derived or lab-grown microorganisms is one way to incorporate some field conditions (Bai *et al.*, 2015). The challenge will be to make these model microbiomes comparable over successive experiments. Another option would be to repeat experiments that studied plants in potting soil by growing them in the soil in which they normally grow. Finally, pot volume for a given experiment is best chosen so that final plant size per root volume remains larger than 2 g l^{-1} (Poorter *et al.*, 2012a).

4. Scaling up to the field

In experimental field plots, a similar level of control and manipulation of environmental variables is usually not feasible, with the possible exception of nutrients. However, in the last two decades a moderate degree of control over CO_2, ozone, water supply and soil temperature has been achieved in a number of experiments by means of Free Air Carbon Dioxide technology (Kubiske *et al.*, 2015), rain-out shelters (Gherardi & Sala, 2013) or

soil heating (Hanson *et al.*, 2011). These techniques are often applied to crops or existing vegetation, but there is also a range of experiments that have used mesocosms, small-scale, simplified ecosystems that are man-made and replicable (Lawton, 1996; Stewart *et al.*, 2013). All these installations may serve as very useful stepping stones to translate the observations from controlled experiments with individual species to the multispecies complexity of the outer world. One drawback is that they are often specialized, high-cost facilities that are not easy to operate. A simpler, readily available option is to work in growth chambers or glasshouses but with small monocultures rather than isolated plants. Although this will require the use of larger containers and may involve more work when it comes to harvesting, the gain in realism, especially when it comes to the space that individual plants can occupy, could outweigh the increased effort (Hohmann *et al.*, 2016). An intermediate option would be to use single plants grown in narrow but tall containers placed at high density. Experimental gardens are another stepping stone when the focus is more on the comparison of genotypes or species than on treatments.

So far, this review has paid ample attention to the steps that can be taken in laboratories by altering environmental conditions in controlled environments or using hybrid facilities. However, this is not a one-way road. To enable systematic comparisons between lab and field conditions, both lab and field scientists need to provide a standard set of descriptors informing on the above- and belowground environment in their studies. Standard reporting of climate variables such as precipitation or water supply, light and air temperature, as well as soil characteristics and temperature, are necessary. The current development of inexpensive sensors and sensor networks that can track the environment continuously over time will certainly augment our insights into the field environment and the challenges that plants face there.

5. Thinking in dose–response curves

Although experiments with two contrasting levels of an environmental factor are informative about the ways plants acclimate to a given environmental factor, they do have a limitation in that it is difficult to generalize towards other situations where the two levels of that environmental factor are not exactly similar. Establishing dose–response curves allows for much easier generalization and quantitative evaluation (Fig. 5; Mitscherlich, 1909; Poorter *et al.*, 2010). Experiments that allow for the construction of dose–response curves are therefore very useful.

6. Using models to predict treatment effects in the field

The next challenge is to find out how individual dose–response curves should be integrated and whether or not the effects of different environmental factors multiply or add up. We also do not know how these responses change with a plant's source : sink ratio. Simulation models are a good tool to integrate fragmented physiological knowledge and provide estimates of the outcome at higher integration levels. Responses of leaf elongation rate to temperature or drought could be quantified in the lab and then used to predict the actual performance of plants in the field in a model based on integrated thermal time, modelled dose–response curves like Arrhenius plots, or environmental variables, such as vapour pressure deficit (Tardieu & Tuberosa, 2010; Parent & Tardieu, 2012). Carbon-based models could integrate component processes like photosynthesis and respiration to scale up to the responses of entire crops (Hammer *et al.*, 2005), forests, or even ecosystems (Sakschewski *et al.*, 2015). Global circulation models use this approach for the whole planet.

It is important that such high-level models do not merely scale the lab measurements as the application of simple dose–response curves would do. Instead, high-level models should incorporate the essential negative and positive feedback that will affect the responses of plants and the resulting vegetation (Poorter *et al.*, 2013). One such feedback is the acclimation of plants over time, which requires special attention when information from short-term measurements in the laboratory is used to scale plant responses in the field. A classic example is the temperature response of respiration, which can have a Q_{10} well above 2.0 when a plant organ is measured at consecutively different temperatures but closer to 1.0 and inconstant when measured in plants grown for longer periods at different temperatures (Atkin & Tjoelker, 2003). Functional–structural plant models (FSPMs) are the latest advance in the plant modelling community and have the benefit that they more easily incorporate phenotypic data, specific environmental effects on individual plant organs, and even plant anatomy, because they explicitly simulate plant structure and density (Vos *et al.*, 2010). They might be useful in grasping the differences in density between lab- and field-grown plants both above- and belowground (Postma & Lynch, 2012; Song *et al.*, 2013).

VIII. Conclusions

Experiments under controlled conditions play an important role in understanding plant responses to their environment. Although these experiments sometimes challenge plants with severely limiting levels of a given environmental factor, it is true that most plants are grown under relatively benign conditions, especially of temperature, water and nutrients. The translation of knowledge from lab to field is not necessary straightforward, but various avenues could make this translation more successful. One would be to apply abiotic conditions in growth chambers or glasshouses that are overall more similar to those which plants experience in the field, thereby making the translation step smaller. The photothermal ratio could be an interesting concept for choosing relevant conditions. Other options could be to use more natural soils and/or to study plants at appropriate plant densities. Finally, if we have more thorough knowledge about the above- and belowground conditions that plants experience under various conditions, modelling could be another way to bridge the gap between controlled environments and the field.

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Author contributions

U.S., R.P., F.F. and H.P. planned the manuscript; R.P., T.W., F.F. and H.P. carried out the measurements; M.K. provided data; J.P. and H.P. compiled literature data; and W.H.v.d.P., J.P. and H.P. wrote the manuscript with input from all of the other authors.

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Appendix

Materials and Methods

Definitions

Many experiments use plants grown in growth chambers where light and temperature are fully controlled or glasshouses where these conditions can fluctuate. Other experiments take place in agricultural fields or experimental gardens, usually without further interference from investigators, except for some form of fertilization and maybe the application of a treatment factor. Experiments in forestry will even refrain from fertilization, and this is also true for ecological experiments and trait screenings that sample plants growing in nature. For the present paper, the first group is designated as 'lab-grown' plants, the second group as 'field-grown' plants. There is also a range of intermediate experiments, in which plants are grown in shade-houses, open-top chambers, in containers in experimental gardens or in mesocosms. For simplicity, this intermediate group will not be considered in this paper, except in section VII.

Lab–field database

In order to compare the overall values of lab- and field-grown plants, we queried several databases (Wright *et al.*, 2004; Kleyer *et al.*, 2008; Poorter *et al.*, 2009) where many measurements for wild species growing in the field are collated. We combined those with the MetaPhenomics database (Poorter *et al.*, 2010; www.metaphenomics.org), which focuses on the environmental responses of crop, wild herbaceous and woody species grown under experimentally manipulated conditions, and added to that our own compilation of data from lab and field studies. Because species identity is the most important source of variation in this type of

analyses (Kazakou *et al.*, 2014), we analysed each species separately. For each species or genotype and treatment in one experiment, we retained one value: the average value over the season for specific leaf area, leaf nitrogen concentration and photosynthetic capacity (in case various measurements over the season were made, senescing leaves excluded), and the relative growth rates (RGR) of plants in the vegetative phase. For woody species, RGR was calculated for experiments where various harvests were made within one growing season for seedlings 1 or 2 years after seeding or planting. Total plant height and shoot dry mass were taken from the end of the experiment. The age of the plants at last harvest was also recorded and counted as days from germination. In case only sowing dates were given, we assumed a germination period of 7 d for herbaceous species and 14 d for woody species. The database includes > 19 800 records (mean values) based on data from *c.* 1540 publications and *c.* 4680 species. Because many woody and also wild herbaceous species have not been grown under controlled conditions, there are only 550 species for which information is present under both lab and field conditions.

For each species, we characterized the observed values for age and the six growth-related traits across experiments and treatments by means of the median value, analysing plants grown under controlled and field conditions separately. We then calculated for each species the ratio of these median values for lab and field and indicated the distribution across all species for which this ratio could be calculated by box plots. A *t*-test for deviation from unity (H_0, hypothesis of no difference) was performed after log-transforming all data.

Plant density database

In order to characterize the effect of plant density on the traits of individual plants, we carried out a meta-analysis. We included data from 100 publications where monocultures of plants were analysed at different plant densities. They comprised experiments in growth chambers (10%), glasshouses (30%) and the field (60%) for both crops (30%), wild herbaceous (35%) and woody species (35%; see Supporting Information Table S4 for references). Phenotypic data for plants at the various densities were taken for the last day of the experiment on which they were measured. If reported, density was taken as the average density of plants at the beginning and end of the experiment, thus taking partly into account the effect of self-thinning. Because experiments ranged widely in the densities (plants m^{-2}) considered and density effects are also strongly dependent on plant size, we decided to scale the effects within experiments by calculating for each experiment and measured trait the percentage change for each doubling of plant density. This approach considers the slope of the log-transformed values in density and plant traits and is explained in mathematical detail by Poorter *et al.* (2012a).

Because some traits turned out to be reported only in a few papers, we pooled response data on vegetative shoot mass with those of vegetative total plant mass, short-term photosynthesis measurements with observations on unit leaf rate from growth analyses, and responses in reproductive effort calculated as generative biomass relative to whole plant mass with those based on shoot mass only.

Concordance between lab and field data

In order to assess the concordance between lab and field data we screened the literature for experiments or measurements that were carried out both under controlled and field conditions, focusing on the ranking of genotypes or species rather than treatments. Measured variables were partly size-related traits (e.g. shoot dry mass, plant dry mass, yield; 55% of the cases), partly morphological (e.g. specific leaf area (SLA), specific root length; 15%) or physiological and chemical (e.g. photosynthesis, leaf nitrogen concentration; 30%). Because most mass data are expressed per plant in the lab, but per unit ground area in the field we only considered correlations. Experiments were only included in cases where five or more genotypes or species were measured. The distribution of the observed correlations was summarized by percentiles. References to the literature sources are given in Table S5.

Concordance between years in the field

The same procedure as above was followed in the year-to-year comparison of genotypes over two consecutive years at the same location in the field. Because of a wider availability of data, we restricted ourselves to cases where 10 or more genotypes were measured. Over 95% of the observations pertained to yield per m^2, for a total of 13 crop species. References to the literature sources are given in Table S6.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Table S1 Data references used for the meta-analysis of differences in plant trait values between lab- and field-grown plants (Fig. 1)

Table S2 Locations used to establish the progression in light and temperature over the seasons among the five ecological zones in the world (Fig. 3)

Table S3 Locations used to establish the progression of soil temperatures over the seasons and their relation to air temperature (Fig. 6)

Table S4 References used for the data pertaining to the meta-analysis of density effects (Fig. 7)

Table S5 References used for the data pertaining to the meta-analysis of lab–field correlations (Table 4)

Table S6 References used for the data pertaining to the meta-analysis of field–field correlations over two consecutive years (Table 4)

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