Tansley review

A meta-analysis of responses of C_3 plants to atmospheric CO_2: dose–response curves for 85 traits ranging from the molecular to the whole-plant level

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Summary

Generalised dose–response curves are essential to understand how plants acclimate to atmospheric CO_2. We carried out a meta-analysis of 630 experiments in which C_3 plants were experimentally grown at different $[CO_2]$ under relatively benign conditions, and derived dose–response curves for 85 phenotypic traits. These curves were characterised by form, plasticity, consistency and reliability. Considered over a range of 200–1200 μmol mol^{-1} CO_2, some traits more than doubled (e.g. area-based photosynthesis; intrinsic water-use efficiency), whereas others more than halved (area-based transpiration). At current atmospheric $[CO_2]$, 64% of the total stimulation in biomass over the 200–1200 μmol mol^{-1} range has already been realised. We also mapped the trait responses of plants to $[CO_2]$ against those we have quantified before for light intensity. For most traits, CO_2 and light responses were of similar direction. However, some traits (such as reproductive effort) only responded to light, others (such as plant height) only to $[CO_2]$, and some traits (such as area-based transpiration) responded in opposite directions. This synthesis provides a comprehensive picture of plant responses to $[CO_2]$ at different integration levels and offers the quantitative dose–response curves that can be used to improve global change simulation models.

I. Introduction

Plants are the major primary producers on earth. Over time, they have evolved various mechanisms to take up CO_2 from their environment and, using light energy, to reduce this CO_2 to sugars (Lambers & Oliveira, 2019). These photosynthetic reactions fuel a plant's growth and reproduction, but also have important ecological ramifications, as most other organisms in the world directly or indirectly depend on plant productivity. Over geological timescales, plants have even engineered the Earth's system, by removing a substantial fraction of the atmospheric CO_2 while increasing oxygen levels, with all its downstream consequences for the physical environment and the organisms living on this planet (Berner, 2004). However, up to the industrial revolution these changes generally have been so slow that even long-lived organisms such as trees have not experienced substantial changes over their lifetime.

The finding of Keeling *et al.* (1976) that atmospheric [CO_2] is rising because of anthropogenic emissions has sparked much interest among biologists in how individual plants and ecosystems will respond to this continuing increase (Körner, 2000). As a result, many experiments have been carried out in growth chambers, glasshouses and open top chambers (OTCs), often focusing on the effects of a doubling in atmospheric [CO_2]. Various reviews and meta-analyses have synthesised this knowledge. Generally, for species with a C_3 type of photosynthesis a doubling of the [CO_2] results in *c.* 40% higher rates of photosynthesis (Ainsworth *et al.*, 2002), an increase of *c.* 40% in plant biomass (Poorter & Navas, 2003), and *c.* 33% higher yields (Kimball, 1983). Because of concerns about the translation from laboratory-based experiments to more natural conditions (Kimball *et al.*, 1997; Poorter *et al.*, 2016), an important addition in the last decades has been Free Air CO_2 Enrichment (FACE) studies, in which elevated CO_2 concentrations can be applied under realistic field conditions, albeit that – for financial reasons – the experimentally elevated CO_2 levels are generally only *c.* 50% higher than ambient. Data from FACE experiments show increased rates of light-saturated photosynthesis of *c.* 31% and yield increases for various crops around 18% (Ainsworth & Rogers, 2007; Kimball, 2016; Ainsworth & Long, 2021).

Most of the studies so far have focused on two CO_2 levels only, as marginal costs for additional equipment are generally high. An intrinsic problem with such two-level experiments is that plant responses to CO_2 may not necessarily be linear. Therefore, it is difficult to interpolate or extrapolate results obtained from such studies (Körner, 1995; Becklin *et al.*, 2017). A minority of papers have studied plant responses over a wider range of concentrations, and indeed observed saturating responses (Juurola, 2003; Zheng *et al.*, 2019). Others have focused on lower-than-ambient CO_2 levels, in order to understand how plants and vegetation functioned during pre-industrial and glacial times (reviewed by Gerhart & Ward, 2010). It would be worthwhile if the results of this wide variety of controlled experiments could be integrated into a more general perspective that is applicable over a wider range of CO_2 concentrations. One way to achieve this is by constructing dose–response curves from many independent, small experiments by scaling plant responses for each experiment with reference to a common CO_2 level (MetaPhenomics approach; Poorter *et al.*, 2010). In this way, information from a broad diversity of experiments and a wide range of CO_2 concentrations can be combined, and responses of different functional groups can be compared. Such full dose–response curves therefore allow better insight into how plants respond, not only to various future CO_2 levels, but also to conditions from the past.

Another issue is that most experimental studies, for logistical reasons, concentrate on a limited number of plant traits. To better understand plant responses to CO_2, it would be insightful to integrate a wide range of traits that covers both anatomy, morphology, the chemical composition of plants, various physiological aspects of the C, N and H_2O economy as well as growth and reproduction. To be able to compare and rank the plasticity of all these traits requires a common methodology. Dose–response curves are very well suited for such a standardised comparison.

In this review, we first discuss briefly the changes in CO_2 concentrations plants have faced over geological time scales and the variation they currently experience in time and space. Focusing on C_3 plants, we then apply the MetaPhenomics approach and summarise literature data for 630 experiments in which plants were grown at various experimentally manipulated CO_2 levels. We derived dose–response curves for 85 traits, and analysed their shape, consistency and reliability. Based on these curves, we established plasticity indices over the 200–1200 $\mu mol\ mol^{-1}$ CO_2 range, to compare the response of different traits more easily. Finally, as both CO_2 concentration and light intensity stimulate photosynthesis, similarity in responses may be expected for some but not all traits. We therefore analysed for which variables the CO_2 and light responses of plants are of similar magnitude and direction, which ones are affected in independent directions and for which traits the responses are opposite.

II. Variation in [CO_2] in time and space

CO_2 concentrations vary in time and space, with consequences for both plant evolution and acclimation. At early geological time scales atmospheric [CO_2] was very high, with crude estimates of > 8000 $\mu mol\ mol^{-1}$ (from here onwards indicated as ppm) during the Precambrian period (Sheldon, 2006). Partly due to weathering of rocks, partly due to the massive transformation of plant biomass into C-rich deposits, a strong decline in CO_2 occurred over time. Over the last 400 million years, when vascular land plants diversified, estimated CO_2 concentrations varied between 180 and 2000 ppm (Fig. 1a), with particularly low values during the ice-ages, when the solubility of CO_2 in the ocean water was high (Lüthi *et al.*, 2008) and terrestrial decomposition slowed (Ciais *et al.*, 2012). Keeling *et al.* (1976) not only showed that [CO_2] high in the troposphere has been on the rise again since the last century, but also how it oscillates within a year. These oscillations are driven by seasonal variation in CO_2 uptake of the vegetation and its subsequent decomposition and cause relative small deviations from the yearly tropospheric mean, ranging from < 0.1% to 0.5% (Fig. 1b; Keeling *et al.*, 1996). Depending on local wind and turbulence conditions, an atmospheric boundary layer of typically

50–2000 m covers the Earth's surface, which partially decouples the CO_2 concentration right above the vegetation from concentrations higher in the troposphere. Hence, the yearly [CO_2] oscillations at this level are often larger, deviating by *c.* 3–5% from mean tropospheric values (Fig. 1b). Although the seasonal build-up and breakdown of plant biomass is massive on a global scale, the magnitude of this fluctuation in CO_2 concentration is not likely to have a substantial effect on plant functioning.

A stronger source of variation is the diurnal rhythm *within* the vegetation. During the night, when wind speed and turbulence are often low, and mixing with air masses higher in the atmosphere restricted, the respiratory output of plants and soil may cause the [CO_2] of the air around the plants to rise to values > 20% larger than tropospheric levels (Fig. 1c), and occasionally to concentrations > 100% larger (Ney & Graf, 2018). Although substantial in size, these high night values mostly occur when plant photosynthesis and transpiration are low or negligible, and so we presume that their effects on vegetation functioning are small. More consequential may be the drop in [CO_2] that occurs during the day. Relative to tropospheric values, this drop can exceed 10% (Fig. 1c), large enough to affect photosynthesis. All these values are modest compared with the CO_2 concentrations of the air inside the soil, where values 3–30× higher than tropospheric levels have been reported (Fig. 1d). Finally, CO_2 concentrations will also vary inside plants, and can go down to < 150 ppm inside the intercellular spaces of leaves when photosynthesis is active, but may be up to 1000–200 000 ppm in stems and roots (Teskey *et al.*, 2008; Sage & Khoshravesh, 2016).

III. Methodology

1. Data compilation

An extended description of methods is given in Supporting Information Notes S1. In short, we defined 85 plant traits of interest (see Table 1 for definitions and abbreviations) and screened the literature for experiments in which plants were grown experimentally at different levels of CO_2 and without pronounced

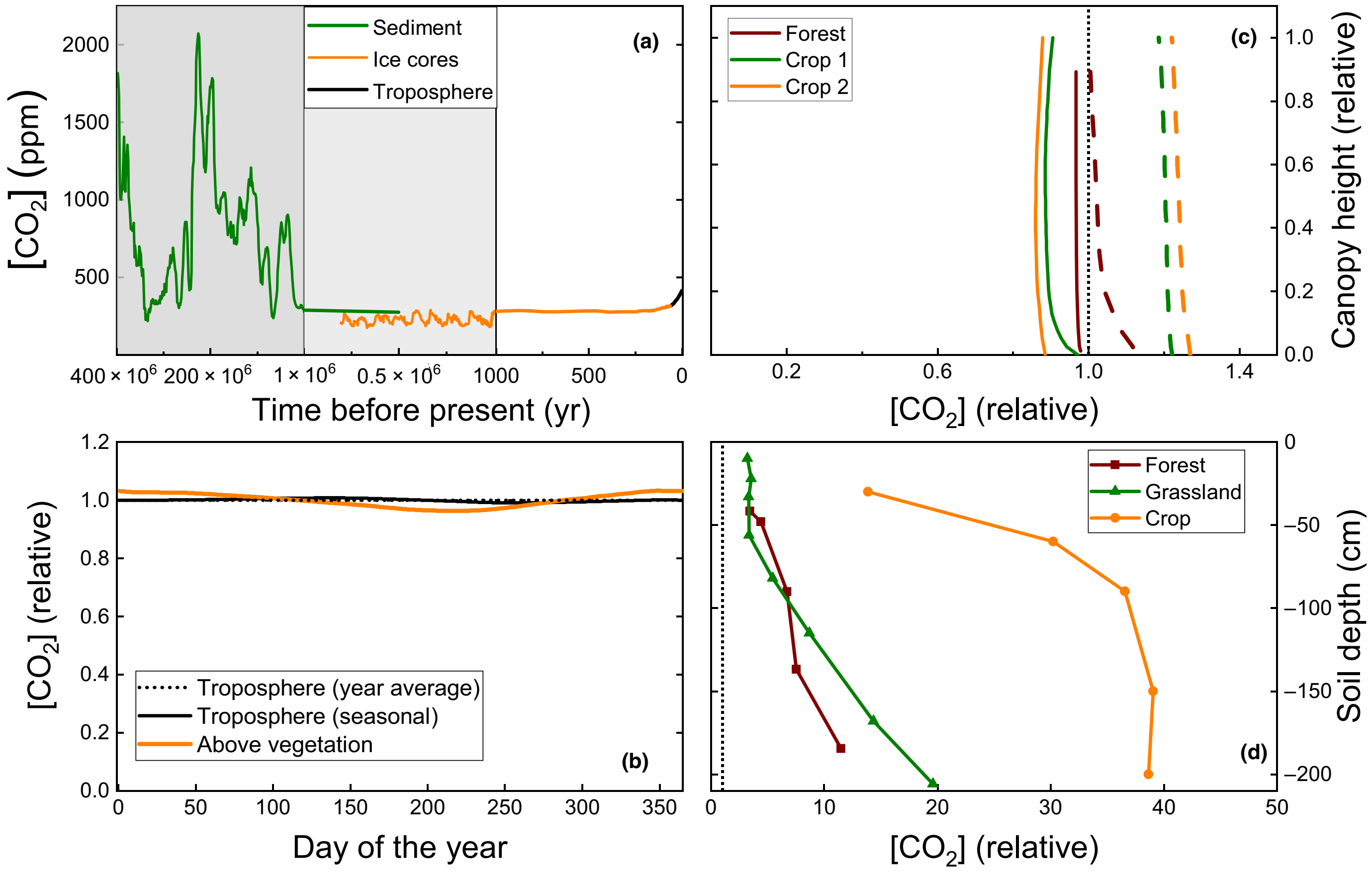

Fig. 1 Variation in [CO_2] in time and space at various scales. (a) Variation over the last 400 million years. (b) Seasonal variation in the northern-hemisphere troposphere (as measured at Mauna Loa) and above the vegetation (as measured for 140 eddy-covariance towers). (c) Vertical profiles through the canopy at the middle of the day (continuous lines) and the middle of the night (broken lines). (d) Vertical profiles in the soil. Values in (b–d) are all given relative to tropospheric values measured in the same year at Mauna Loa (black dashed line). Note that the subpanels in (a) with different shading have different but connecting time scales. All CO_2 axes start at 0 to better judge proportional changes. Data in (a) are from Foster *et al*. (2017; sediment), Bereiter *et al*. (2015; ice cores) and Keeling *et al*. (2001; with continuing data from https://scrippsco2.ucsd.edu/data/atmospheric_co2/primary_mlo_co2_record.html); for (b) from Pastorello *et al*. (2020), filtered for 30°–60°N and daytime, and Thoning *et al*. (2021); for (c) from the datasets underlying Ney & Graf (2018; crop 1, *Hordeum vulgare*; crop 2, *Beta vulgaris*), Heinesch *et al*. (2008) and Aubinet *et al*. (2018; forest), and for (d) from Fierer *et al*. (2005; grassland), Wang *et al*. (2013; crop) and Carmi *et al*. (2013; forest).

Table 1 Description and abbreviations of plant traits used in this review.

Abbreviation	Variable name	Units	Explanation
1. Anatomy and Morphology			
A_{mes}/A	Area of mesophyll relative to leaf area	$m^2\ m^{-2}$	Includes both observations for total mesophyll area as well as for mesophyll area adjacent to intercellular spaces
$DrMaCo_S$	Stem dry matter content	$g\ g^{-1}$	Stem dry mass/fresh mass
$DrMaCo_R$	Root dry matter content	$g\ g^{-1}$	Root dry mass/fresh mass
InLeAr	Individual leaf area	cm^2	Can be either for a specific leaf, or averaged over all leaves
IntLen	Internode length	cm	Length between two nodes
LeaDen	Leaf density	$g\ ml^{-1}$	Leaf dry mass/leaf volume or leaf dry matter content
LMA	Leaf mass per area	$g\ m^{-2}$	Inverse of SLA, scales positively with leaf thickness and density
LeaThi	Leaf thickness	µm	
PlaHei	Plant height	cm	Height from ground level to the shoot apex or highest leaf tip
SleInd	Slenderness index	$m\ m^{-1}$	Stem length/stem diameter of the main stem
SteDia	Stem diameter	mm	Diameter of the stem or root collar
StoDen	Stomatal density	No. mm^{-2}	Based on both leaf sides, or on the abaxial side if adaxial data are not provided
SpStLe	Specific stem length	$m\ g^{-1}$	Stem length/stem mass
SRL	Specific root length	$m\ g^{-1}$	Root length/root mass
VoFrMe	Fraction of leaf volume in mesophyll	$ml\ ml^{-1}$	Mesophyll volume/total leaf volume
VoFrPa	Fraction of palisade cell volume in total mesophyll volume	$ml\ ml^{-1}$	Palisade mesophyll volume/total mesophyll volume
#PaCeLa	Number of palisade cell layers	Numeric	If no data are provided taken from single cross sections per treatment in published papers
#BraTil	Number of branches or tillers	Numeric	Number of tillers (grasses) or 1st-order side branches (dicots), plus the main tiller/axis
2. Chemical composition			
$[C]_L$, $[C]_S$, $[C]_R$	[C] leaf, stem, root	$mg\ g^{-1}$	C concentration in dry matter
C/N_L, C/N_S, C/N_R	C : N ratio leaf, stem, root	$g\ g^{-1}$	
Chl/*A*	Chlorophyll content/area	$\mu mol\ m^{-2}$	No SPAD measurements
Chl*a*/*b*	Chlorophyll *a* : *b*	$mol\ mol^{-1}$	
Chl/N	Chlorophyll to N ratio	$mol\ Chl\ mol^{-1}\ N$	
$[Mine]_L$	[Minerals] leaf	$mg\ g^{-1}$	Minerals (including NO_3^-) or ash
$[NO_3]_L$	[Nitrate] leaf	$mg\ g^{-1}$	
$[Norg]_L$	[organic N] leaf	$mg\ g^{-1}$	Total N, excluding NO_3^--N
Ntot/*A*	Leaf total N content/area	$g\ m^{-2}$	Total N, including NO_3^--N
$[Ntot]_L$	[total N] leaf	$mg\ g^{-1}$	Total N, including NO_3^--N
$[N]_S$, $[N]_R$	[N] stem, root	$mg\ g^{-1}$	Total N or organic N
$[P]_L$, $[P]_S$, [P]R	[P total] leaf, stem, root	$mg\ g^{-1}$	
N/P_L	N : P ratio leaf	$g\ g^{-1}$	
$[SolPhe]_L$	[Soluble phenolics] leaf	$mg\ g^{-1}$	
$SolSug/TNC_L$	Soluble sugar fraction in TNC for leaves	$g\ g^{-1}$	
$SolSug/TNC_R$	Soluble sugar fraction in TNC for roots	$g\ g^{-1}$	
$[TNC]_L$	[Nonstructural carbohydrates] leaf	$mg\ g^{-1}$	
$[TNC]_R$	[Nonstructural carbohydrates] root	$mg\ g^{-1}$	
$[TNC]_S$	[Nonstructural carbohydrates] stem	$mg\ g^{-1}$	
Xant/Chl	Xanthophylls/Chlorophylls	$mmol\ mol^{-1}$	Violaxanthin + Antheraxanthin + Zeaxanthin
3. Physiology			
Abso	Absorptance leaf		% of incident photons (400–700 nm) absorbed by a leaf
ApQuYi	Apparent quantum yield	$mol\ CO_2\ mol^{-1}$ photons	CO_2 fixed per unit photon flux at the leaf, at low PPFD
c_i/c_a	Intercellular $[CO_2]$ relative to outside the leaf	$mol\ mol^{-1}$	Measured at growth light conditions and ambient $[CO_2]$
F_v/F_m-d	Variable fluorescence/maximal fluorescence		Measured during the diurnal period
F_v/F_m-n	Variable fluorescence/maximal fluorescence		Measured during the nocturnal period (pre-dawn)
iWUE	Intrinsic water-use efficiency	$\mu mol\ CO_2\ mol^{-1}\ H_2O$	CO_2 fixed divided by stomatal conductance, measured at ambient light and CO_2 levels
J_{max}/V_{cmax}	Electron transport capacity/ carboxylation capacity	mol and $mol^{-1}\ CO_2$	Measured at saturating light and CO_2 levels
$Phot/A^{GL}$	Photosynthesis at growth light/leaf area	$\mu mol\ CO_2\ m^{-2}\ s^{-1}$	Measured at growth light and CO_2
$Phot/A^{SL}$	Photosynthesis at saturating light/leaf area	$\mu mol\ CO_2\ m^{-2}\ s^{-1}$	Measured at saturating light and growth CO_2
$Phot/Chl^{SL}$	Photosynthesis at saturating light/chlorophyll	$mmol\ CO_2\ mol^{-1}\ s^{-1}$	Measured at saturating light and growth CO_2
$Phot/M^{GL}$	Photosynthesis at growth light/leaf mass	$nmol\ CO_2\ g^{-1}\ s^{-1}$	Measured at growth light and CO_2

Table 1 (Continued)

Abbreviation	Variable name	Units	Explanation
Phot/M^{SL}	Photosynthesis at saturating light/leaf mass	nmol CO$_2$ g^{-1} s^{-1}	Measured at saturating light and growth CO$_2$
Phot/N^{GL}	Photosynthesis at growth light/leaf N	μmol CO$_2$ mol^{-1} N s^{-1}	Measured at growth light and CO$_2$
Refl	Reflectance leaf		% of incident photons (400–700 nm) reflected
ReWaCo$_L$	Relative water content of leaves		
Resp/A_L	Leaf respiration/unit area	μmol m^{-2} s^{-1}	Can be both on an O$_2$ or CO$_2$ basis; generally single leaf
Resp/M_L	Leaf respiration/unit mass	nmol g^{-1} s^{-1}	Can be both on an O$_2$ or CO$_2$ basis; generally single leaf
Resp/M_{L+S}	Shoot respiration/unit shoot mass	nmol g^{-1} s^{-1}	Can be both on an O$_2$ or CO$_2$ basis; whole shoots
Resp/M_R	Root respiration/unit root mass	nmol g^{-1} s^{-1}	Can be both on O$_2$ or CO$_2$ basis
Rubi/A	Rubisco enzyme/area	Numeric	Only for leaves, estimates of both content and activity
StoCon	Stomatal conductance	mmol H$_2$O m^{-2} s^{-1}	Measured at growth light and [CO$_2$] for a single leaf in a leaf cuvette
Trsm	Transmittance leaf		% of incident photons (400–700 nm) transmitted by a leaf
Trsp/A	Transpiration/unit area	mmol H$_2$O m^{-2} s^{-1}	Measured for whole plants, no leaf cuvette measurements
V_{cmax}/A	Carboxylation capacity/unit leaf area	μmol CO$_2$ m^{-2} s^{-1}	
|WatPot-d|	Water potential	MPa	Measured during the diurnal period, absolute values
|WatPot-n|	Water potential	MPa	Measured during the nocturnal period (pre-dawn), absolute values
WUE$_g$	Water-use efficiency for growth	mg biomass g^{-1} H$_2$O lost	Biomass increase per unit water lost
Δ^{13}C	^{13}C discrimination	‰	
4. Growth and reproduction			
ConCos$_L$	Construction costs leaf	g glucose g^{-1}	Glucose mass required to build 1 g of leaf
GenBio	Generative biomass	g plant^{-1}	Seed mass or total reproductive mass
InSeMa	Individual seed mass	mg	Seed mass (or fruit mass if seed mass is not given)
LAR	Leaf area ratio	m^2 kg^{-1}	Leaf area/total vegetative plant mass
LMF	Leaf mass fraction	g g^{-1}	Leaf mass/total vegetative plant mass
PlaInd	Plastochron index	Numeric	Also: total number of leaves on the main stem
RepEff	Reproductive effort	g g^{-1}	Reproductive mass (or seed mass)/total plant mass (or aboveground mass if total mass is not reported)
RGR	Relative growth rate	mg g^{-1} d^{-1}	Rate of increase in biomass/total vegetative plant mass
RMF	Root mass fraction	g g^{-1}	Root mass/total vegetative plant mass
#SeeFru	Number of seeds or fruits per plant	Numeric	Excluded are complicated cases in which species have fruits with many seeds (such as tomato). Included are some observations on number of flowers
SLA	Specific leaf area	m^2 kg^{-1}	Leaf area/leaf mass
SMF	Stem mass fraction	g g^{-1}	Stem mass/total vegetative plant mass
TiToFl	Time to flower	d	From germination to first flower, or to 50% of flowers opened
ULR	Unit leaf rate	g m^{-2} d^{-1}	Rate of increase in biomass/leaf area
VegBio	Vegetative biomass of the plant	g	Reproductive structures excluded
5. Other abbreviations			
CI	Consistency index	%	The number of species × experiment combinations in which, for a given trait, trait values were higher for the highest [CO$_2$] than for the lowest. Values close to 0 or 100 indicate a highly consistent response
DLI	Daily light integral	mol m^{-2} d^{-1}	The flux of photons (400–700 nm) integrated over the day. Values are averaged over the period of active growth of the plants
PI	Plasticity index	–	Ratio in a given trait for the highest and lowest trait values at two levels of an environmental factor. Multiplied by −1 when the relationship is negative
RI	Reliability index	–	Value on a scale from 1 to 10, indicating the reliability of a dose–response curve as a general description of a plant response

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

limitation by other environmental factors. Following the classification of Körner (2006), we therefore restricted the analysis to 'uncoupled systems', experiments with individual plants or monostands sown or planted under relatively benign conditions. We noted the type of growth facility used, and which pot size and other environmental conditions were applied. In case of factorial experiments, we chose the combination of conditions at CO$_2$ control levels in which plants were growing fastest. We only included experiments in which plants had been given enough time to acclimate to the different [CO_2], which we defined as being at those concentrations for at least 2 wk and preferably achieving > 80% of their biomass at that condition. In case of repeated measurements, the time window for data selection depended on the trait of interest: for size variables such as height and biomass as well as generative traits we considered the last harvest, for anatomical, chemical and physiological traits that are expressed per unit area or mass we considered data over a wider trajectory in which plants had had some time to acclimate and were in the vegetative growth or flowering stage. Repeated measurement data were averaged such that for each CO_2 treatment level we obtained one average value per trait per plant species (or genotype) per experiment.

In total, we compiled 2860 records (Experiment × Species × [CO_2] combinations) for a total of 460 species from 95 families. These were studied in 630 experiments, which have been published over the last 65 y. The large majority of the records (78%) were for experiments with two CO_2 levels only. Overall, *c.* 45% of the observations were for plants grown in growth chambers, 35% in glasshouses, 15% from OTCs and 5% from FACE sites. The median duration of the CO_2 exposure was 50 d for herbaceous species, and 122 d for woody ones, and most of the data compiled (82%) were for plants exposed to CO_2 concentrations within the 330–780 ppm range (Fig. S2). References to all papers used are listed in Appendix A1.

2. Data processing

For each species or genotype in each experiment, we calculated by means of interpolation what the value for a given trait would be at a reference CO_2 concentration of 450 ppm. We then scaled all observed means for that species and experiment accordingly by dividing them by this value (Poorter *et al.*, 2010; Fig. S1). All data presented are therefore relative values. After the scaling, we derived dose–response curves in two ways. In the first approach, which is basically assumption free, we aligned all scaled observations (y) by CO_2 concentration (x) and then divided them in 10 equally numbered classes. For each class, we calculated the median x and y value, as well as the 10th, 25th, 75th and 90th percentile of the scaled trait. This allows for a good estimate of normal ranges observed across the literature data. In the second approach, we fitted four classes of dose–response curves through all points: no response ($y = a$), a straight line ($y = a + bx$), a saturating curve based on a monomolecular function ($y = a \cdot [1 - b \cdot e^{(-c \cdot x)}]$), and finally a quadratic relationship to allow for relationships that increase or decrease exponentially or show a local minimum or optimum. We did so by means of the quantile regression package QUANTREG (Koenker *et al.*, 2021) in R (v.4.1.0; R Core Team, 2020), focusing on median values. In this way, we minimised the effect of outlying observations and avoided assumptions about the distribution of the data. Based on the Akaike information criterion (AIC), we then decided which type of curve fitted the data best.

Next, we characterised the strength, consistency and reliability of the observed relationships by means of three indices:

(**1**) *Plasticity index (PI)*: Based on the selected dose–response curve for each trait, a PI was derived by calculating the trait values at 200 and 1200 ppm CO_2 and subsequently taking the ratio between the highest and lowest value. We added a minus sign to the PI in case of negative responses to increasing CO_2.

(**2**) *Consistency index (CI)*: For every trait, we evaluated the consistency of the response by calculating the percentage of experimental cases in which the trait value at the highest [CO_2] applied was higher than at the lowest [CO_2]. The overall response is highly consistent across experiments when CI values are close to 0% or 100%, but highly variable and inconsistent when close to 50%.

(**3**) *Reliability index (RI)*: We tried to capture the trustworthiness and generality of the dose–response curve by a reliability index. This index ranges on a relative scale from 1 to 10 and depends positively on the total number of observations on which the curve is based, the number of species for which observations were present and the range of CO_2 concentrations for which data were available, and negatively on the variability of the data.

Further details on the indices and other calculations, as well as the various reasons why we did not split the data for the various growth environments used, are provided in Notes S1.

IV. Dose–response curves for 85 traits

Characteristics of all the calculated dose–response curves are included in Table 2, summary graphs are shown in Figs 3–6, S3, S4. Detailed figures for every trait with additional data are shown in Figs S7–S93. To provide a better overview, we grouped the traits into four sections: Anatomy and morphology of various organs, Chemical composition, Physiology, and Growth and reproduction.

1. Anatomy and morphology

Leaf anatomical plasticity can be informatively studied relative to the changes in leaf mass per area (LMA). LMA shows an increasing and saturating response to CO_2, with a PI of 1.5 (Fig. 2a; Table 2a). LMA is the mathematical product of leaf thickness and leaf density, which both increase in a highly consistent manner and to a similar extent in response to elevated CO_2. There was a small increase in the volumetric fraction of mesophyll relative to the total leaf volume, but the proportion of palisade parenchyma relative to total mesophyll was not affected by CO_2. This is also likely to be the case for the number of palisade cell layers, a presumption we based partly on the few data present, and partly on the fact that this trait is hardly discussed in the CO_2 literature on leaf anatomy. With increased leaf thickness, this would imply that the size of the palisade parenchyma cells increases, and this is what has been observed (Masle, 2000; Uprety *et al.*, 2001). Subcellular analyses have shown that the numbers of chloroplasts and mitochondria per cell are stimulated by CO_2 (Sharma *et al.*, 2014). An important link between anatomy and physiology is the relative amount of mesophyll area aligned to intercellular air spaces (A_{mes}/A; Terashima *et al.*, 2011), for which we only found three reports, with variable results.

Another relevant link between morphology and physiology is through the density of stomata in the epidermis (Fig. 2f). The higher the CO_2 concentration gradient across the leaves, the easier diffusion through the stomata takes place, which could potentially allow plants grown at higher [CO_2] to reduce the number of stomata per unit leaf area. There are indeed a variety of publications that observed a significant negative relationship between stomatal density and [CO_2] during growth. Given that stomates are sometimes well preserved in fossils, this negative acclimatory relationship has been used as one of the proxies to reconstruct paleoclimates. However, there is large variation in the response across species (Apel, 1989), and even among genotypes of a given species (Lake & Woodward, 2008). This led several authors to question the observed relationship (Malone *et al.*, 1993; Ainsworth & Rogers, 2007). Considered over a large body of published data, we found a significantly negative trend with CO_2 (Table 2a). However, the overall PI is very small (−1.1), and the consistency index is low (37%), in line with conclusions by Royer (2001).

The size of various organs is positively affected by CO_2: plant height is larger (Fig. 2g), and so is stem diameter. Both are increased

Table 2 Summary of the dose–response curve analysis for 85 plant traits as dependent on the ambient [CO_2] during growth.

(a)

Trait	CO_2 range (ppm)	No. of observations	No. of species	Fit	Pseudo r^2	Plasticity (PI)	Consistency (CI)	Reliability (RI)	*a*	*b*	*c*
1. Anatomy and morphology											
LMA	100–3300	**1340**	315	S***	0.52	**1.5**	**90**	9	1.201	0.6174	3.06e−3
LeaThi	255–1600	**220**	75	S***	0.54	1.3	**92**	7	1.106	0.4092	3.49e−3
VoFrMe	290–910	70	25	L***	0.15	1.1	77	5	0.9795	4.48e−5	
VoFrPa	290–3200	80	25	–	0.00	1.0	60	5	0.9903	2.30e−5	
#PaCeLa	290–910	20	10	L	0.00	1.0	60	3	1.000	4.92e−19	
StoDen	150–3200	**400**	120	L*	0.01	−1.1	37	8	1.029	−6.48e−5	
LeaDen	160–3200	**240**	80	S***	0.36	1.3	**85**	7	1.095	0.4976	4.22e−3
DrMaCo$_S$	320–1500	30	10	L	0.21	1.0	46	4	0.9836	3.65e−5	
DrMaCo$_R$	160–1500	**100**	40	L	0.00	−1.0	32	5	1.016	−3.62e−5	
InLeAr	160–3300	**240**	65	L*	0.39	1.4	79	6	0.8431	3.47e−4	
PlaHei	100–5000	**500**	125	S***	0.44	**1.5**	**87**	8	1.114	0.9046	5.27e−3
SteDia	160–2000	**180**	55	S***	0.60	**1.5**	**97**	7	1.172	0.6309	3.44e−3
SleInd	160–2000	**170**	50	S	0.05	1.1	49	6	1.001	13.68	2.67e−2
SpStLe	255–1000	50	15	L***	0.65	−1.4	**5**	4	1.150	−3.32e−4	
IntLen	200–2200	50	15	L*	0.56	1.3	**91**	4	0.8624	3.11e−4	
#BraTil	160–3300	**180**	50	S***	0.53	**1.6**	**90**	7	1.221	0.7963	3.50e−3
SRL	180–1000	80	35	L***	0.14	**−1.5**	24	5	1.166	−3.68e−4	
2. Chemical composition											
Ntot/*A*	160–2050	**300**	85	L*	0.01	−1.1	39	7	1.037	−8.33e−5	
[Ntot]$_L$	160–5000	**620**	175	S***	0.56	**−1.5**	**8**	8	0.8233	−1.286	4.27e−3
[Norg]$_L$	200–3000	**170**	55	S***	0.42	−1.4	**11**	6	0.7692	−0.6745	1.88e−3
[NO_3]$_L$	330–5000	70	30	L***	0.36	**−1.8**	21	4	1.223	−4.97e−4	
[Mine]$_L$	330–5000	60	30	L***	0.59	**−1.8**	**4**	4	1.230	−5.12e−4	
[N]$_S$	170–3000	**170**	55	–	0.00	−1.1	17	6	1.040	−8.00e−5	
[N]$_R$	190–3000	**210**	75	L***	0.06	−1.1	31	6	1.052	−1.10e−4	
[C]$_L$	160–3000	**380**	115	–	0.00	−1.0	55	9	1.002	−5.29e−6	
[C]$_S$	170–3000	**120**	45	L	0.00	1.0	73	6	0.9959	8.99e−6	
[C]$_R$	200–3000	**130**	50	L	0.28	1.1	58	6	0.9779	4.93e−5	
C/N$_L$	160–3000	**370**	125	S***	0.57	**1.6**	**94**	8	1.226	0.7515	3.29e−3
C/N$_S$	170–3000	90	35	L	0.00	1.1	81	5	0.9717	4.87e−5	
C/N$_R$	190–3000	**100**	45	S*	0.09	1.2	74	6	1.042	0.4730	5.82e−3
[P]$_L$	180–5000	**160**	55	S***	0.40	−1.4	**12**	6	0.807	−0.766	2.63e−3
[P]$_S$	200–1200	40	15	–	0.00	−1.0	43	3	1.006	−8.68e−6	
[P]$_R$	200–1200	40	20	L	0.05	−1.1	37	3	1.031	−6.75e−5	
N/P$_L$	180–5000	**160**	55	L	0.00	−1.2	32	6	1.066	−1.43e−4	
[TNC]$_L$	180–5000	**360**	100	S***	0.44	**2.0**	**92**	7	1.652	0.774	1.54e−3
[TNC]$_S$	180–1600	80	25	S	0.23	1.4	56	4	1.075	1.190	7.00e−3
[TNC]$_R$	180–1600	**100**	40	L	0.12	1.3	72	4	0.8794	2.57e−4	
SolSug/TNC$_L$	195–5000	**260**	70	L**	0.16	−1.3	28	6	1.101	−2.24e−4	
SolSug/TNC$_R$	280–1600	30	15	–	0.00	1.0	42	3	0.988	3.82e−5	
Chl/*A*	150–3000	**240**	65	L***	0.13	−1.1	39	7	1.052	−1.23e−4	
Chla/*b*	290–1450	**120**	45	L	0.02	−1.0	50	6	1.005	−1.14e−5	
Chl/N	150–2050	**100**	30	L	0.29	−1.2	42	6	1.058	−1.41e−5	
Xant/Chl	280–800	20	10	–	0.00	1.0	62	2	0.998	5.08e−6	
[SolPhe]$_L$	205–1500	60	30	L	0.37	1.4	70	4	0.832	3.60e−4	

Table 2 (Continued)

(b)

Trait	CO_2 range (ppm)	No. of observations	No. of species	Fit	Pseudo r^2	Plasticity (PI)	Consistency (CI)	Reliability (RI)	*a*	*b*	*c*
3. Physiology											
Abso	255–1000	40	15	–	0.00	1.0	46	4	0.998	5.42e−6	
Refl	255–1000	40	10	–	0.00	1.1	64	3	0.955	9.57e−5	
Trsm	255–1000	30	10	L	0.00	−1.4	40	3	1.128	−2.89e−4	
Rubi/*A*	150–2050	**120**	30	L***	0.26	−1.2	28	6	1.092	−2.04e−4	
V_{cmax}/A	150–2000	**330**	105	L***	0.09	−1.2	33	8	1.088	−1.97e−4	
J_{max}/V_{cmax}	150–2000	**270**	85	L***	0.11	1.1	66	7	0.941	1.32e−4	
ApQuYi	200–1000	90	40	L***	0.68	**2.0**	**100**	4	0.636	8.08e−4	
F_v/F_m-n	200–1000	60	25	–	0.00	−1.0	45	6	1.001	−1.68e−6	
F_V/F_m-d	195–3000	**100**	40	–	0.00	−1.0	43	6	1.004	−9.32e−6	
Phot/A^{SL}	150–5000	**650**	185	S***	0.61	**2.6**	**93**	8	1.500	1.086	2.73e−3
Phot/M^{SL}	185–2000	80	25	L***	0.44	**1.8**	75	5	0.689	6.42e−4	
Phot/Chl^{SL}	185–1100	80	30	S***	0.80	**2.5**	**92**	5	1.321	1.358	4.10e−3
Phot/A^{GL}	150–3300	**570**	160	S***	0.65	**2.2**	**93**	8	1.401	1.021	2.94e−3
Phot/M^{GL}	150–2050	**160**	50	L	0.37	**1.5**	78	6	0.819	4.03e−4	
Phot/N^{GL}	150–800	70	30	S***	0.75	**1.9**	**96**	4	1.199	1.150	4.31e−3
Trsp/*A*	160–3200	80	25	S***	0.69	**−2.2**	**3**	5	0.451	−2.749	1.87e−3
StoCon	160–5000	**500**	135	S***	0.50	**−2.4**	**10**	7	0.437	−3.129	2.01e−3
c_i/c_a	150–2000	**200**	65	S	0.08	−1.0	42	7	1.000	−4.252	2.56e−2
$\Delta^{13}C$	155–1900	**120**	45	L***	0.40	1.1	71	7	0.946	1.19e−4	
iWUE	160–5000	**330**	105	L***	0.82	**6.1**	**97**	7	−0.0103	2.22e−3	
WUEg	210–5000	90	35	S***	0.89	**3.4**	**100**	5	2.011	1.042	1.67e−3
|WatPot-n|	180–1000	60	20	–	0.00	−1.1	50	5	1.041	−8.88e−5	
|WatPot-d|	200–2000	**100**	35	L***	0.13	−1.3	26	5	1.102	−2.31e−4	
$ReWaCo_L$	200–2000	20	10	L	0.39	1.0	75	4	0.988	2.47e−5	
Resp/A_L	195–3300	**120**	40	S	0.10	1.1	58	5	1.087	0.2123	2.09e−3
Resp/M_L	160–1750	90	25	–	0.00	1.1	56	5	0.972	−6.42e−5	
Resp/M_{L+S}	320–3300	20	10	–	0.00	−1.2	38	2	1.065	−1.45e−4	
Resp/M_R	290–1000	30	15	–	0.00	1.1	43	2	0.974	−7.86e−5	
4. Growth and reproduction											
RGR	150–5000	**540**	155	S***	0.46	1.3	**86**	8	1.058	0.7846	6.51e−3
ULR	150–5000	**370**	115	S***	0.70	**1.8**	**97**	8	1.350	0.7415	2.45e−3
LAR	150–5000	**740**	205	S***	0.54	**−1.5**	**9**	8	0.876	−1.729	6.12e−3
SLA	100–3300	**1330**	310	S***	0.52	−1.4	**10**	9	0.856	−1.035	4.35e−3
LMF	150–3200	**990**	260	S	0.17	−1.0	43	9	1.000	−2.99e6	0.104
SMF	150–3200	**880**	230	–	0.00	1.0	51	8	1.000	5.12e−19	
RMF	150–3300	**1200**	295	L	0.02	1.0	55	9	0.983	3.69e−5	
$ConCos_L$	330–720	60	25	L***	0.32	−1.1	19	4	1.025	−5.65e−5	
VegBio	150–5000	**1400**	315	S***	0.63	**2.8**	**95**	8	1.466	1.223	3.16e−3
PlaInd	170–3300	70	25	L***	0.21	1.1	78	5	0.964	8.07e−5	
TiToFl	160–5000	**130**	40	L***	0.03	−1.0	38	6	1.005	−1.18e−5	
#SeeFru	160–3000	**200**	50	S***	0.47	**2.0**	**86**	6	1.239	1.218	4.39e−3
InSeMa	160–1050	**160**	40	S**	0.14	1.1	67	6	1.025	0.598	7.91e−3
GenBio	160–5000	**200**	40	S***	0.45	**2.3**	**87**	6	1.277	1.355	4.31e−3
RepEff	150–5000	**220**	30	L	0.00	1.0	49	6	0.999	1.60e−6	

Data are for C_3 species only. Columns 2 and 3 indicate the range of $[CO_2]$ for which records are present in the database and the total number of observations (= number of averaged values per species and $[CO_2]$ over all experiments; rounded to the nearest 10). Column 4 shows the number of species for which we have observations for the various traits. The fit refers to the form of the dose–response curve. Fitted equations were either no relationship (–; $Y = a$ where Y is the scaled value of the phenotypic trait of interest and a is the overall average of Y values); linear (L; $Y = a + bX$ where X is the $[CO_2]$), or saturating (S; $Y = a\,(1 - b{\cdot}e\,(-cX))$). The relative weight w_i of the model selected by the AICc test is given by: *, $0.70 < w_i < 0.90$; **, $0.90 < w_i < 0.98$; ***, $w_i > 0.98$, but only indicated in case the CI is <40% or >60%. AICc, Akaike information criterion with a correction for small sample sizes. The pseudo r^2 refers to the approximate fit of the selected equation. The plasticity index (PI) as used here is the highest fitted value in the $[CO_2]$-range 200–1200 divided by the lowest fitted value, with positive values indicating positive trends with $[CO_2]$ and negative values decreasing trends; bold numbers indicate a |PI| 1.45. The consistency index (CI) refers to the percentage of all cases (species × experiment combinations) in which the phenotypic value at the highest $[CO_2]$ was larger than at the lowest $[CO_2]$, indicating the consistency of the response. Values close to 0 or 100 indicate highly consistent positive or negative responses. The next column shows the reliability index, based on the number of records in the database for that trait, the number of different species, the range of $[CO_2]$ levels at which it is measured and the average deviation from the median response, with a relative scale from 1 (low) to 10 (high reliability level). The last three columns give the values for parameters *a*, *b* and – if relevant – *c* for the equations mentioned above.

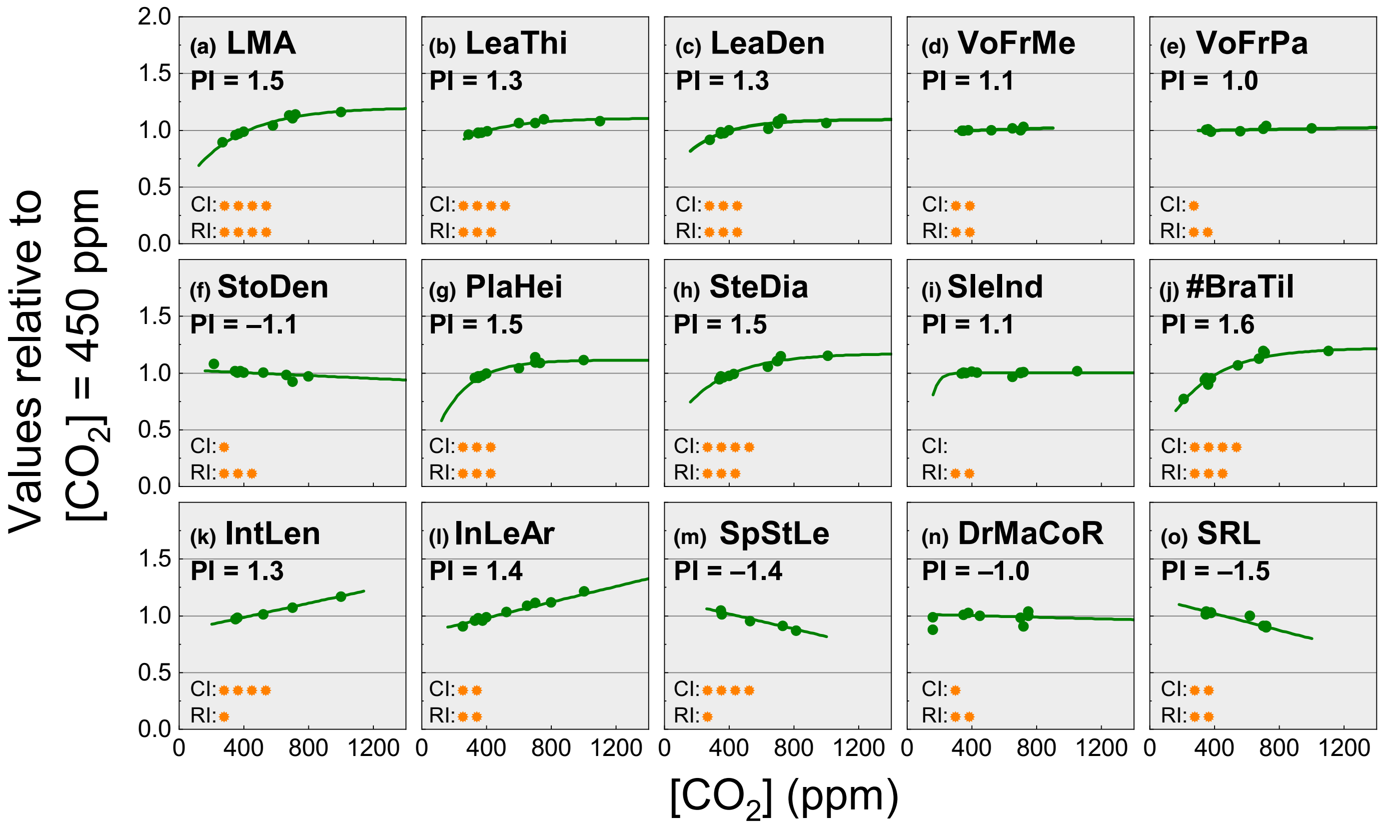

Fig. 2 Dose–response curves of 15 anatomical and morphological traits in relation to atmospheric [CO$_2$] as well as the plasticity index (PI) over the 200–1200 ppm range, the consistency index (CI) and the reliability index (RI). The traits given are (a) LMA, leaf dry mass per area; (b) LeaThi, leaf thickness; (c) LeaDen, leaf density; (d) VoFrMe, volumetric fraction of the leaf taken by mesophyll; (e) VoFrPa, volumetric fraction of the mesophyll taken by palisade parenchyma; (f) StoDen, stomatal density; (g) PlaHei, plant height; (h) SteDia, stem diameter; (i) SleInd, slenderness index; (j) #BraTil, number of branches or tillers; (k) IntLen, internode length; (l) InLeAr, individual leaf area; (m) SpStLe, specific stem length; (n) DrMaCo$_R$, dry matter content of the roots; (o) SRL, specific root length. Data pertain to C$_3$ species only. All scaled values for a given trait were grouped into deciles based on the [CO$_2$] during growth, and median values for each decile group are indicated as green dots in the panels. The closer the points are in the *x*-direction, the denser the information in that range of CO$_2$ concentrations. The line is the curve fitted through all data points present in the 100–2000 ppm range, and given over the CO$_2$ range for which observations were present in the database. The strength of the CI is indicated by the number of orange symbols: none: % increases in the trait value with increasing [CO$_2$] 40–60%; ✹: 30–40% or 60–70%; ✹✹: 20–30% or 70–80%; ✹✹✹: 10–20% or 80–90%; ✹✹✹✹: 0–10% or 90–100%. The strength of the RI: none: RI = 1–2; ✹: 3–4; ✹✹: 5–6; ✹✹✹: 7–8; ✹✹✹✹: 9–10. Graphs are shown up to a [CO$_2$] of 1400 ppm. More detailed information for each variable can be found in Supporting Information Figs S7–S23; Table 2(a).

with high consistency and to a similar extent, and therefore the slenderness index, which is the height : diameter ratio, is hardly affected. High-CO$_2$ plants have more branches or tillers – with the highest PI value in this group of traits – as well as an increased internode length, and individual leaves are larger in size. Most likely, this range of morphological changes is triggered by a higher supply of photosynthates. Specific stem length, the length per unit stem biomass is lower, which accords with the higher stem diameter observed. However, for most of these variables we only found relatively few observations, and their reliability index (RI) is still relatively low.

Whereas leaf density increases with CO$_2$ in a highly consistent manner, densities of stems and roots are unaffected, as judged from their dry matter content (Table 2a; Fig. 2n). An important root trait is specific root length, which decreases with a PI of −1.5, albeit with relatively few observations. The lower SRL is in part due to thicker roots (Nie *et al*., 2013). More effects on plant morphology have been reviewed by Pritchard *et al.* (1999) and Sharma *et al.* (2014).

2. Chemical composition

Whereas leaf biomass per unit leaf area (LMA) increases substantially, there was a (small) decrease in the nitrogen content per unit leaf area (Fig. 3a; Table 2a). This must imply that leaf nitrogen concentration is strongly negatively affected, and this is indeed a highly consistent finding in our analysis, with decreases occurring in 92% of the cases studied. The decrease is stronger for leaf total [N] than for the concentration of organic-N compounds, which fits with the substantial decrease in leaf nitrate concentration (PI = −1.8). The decrease in nitrate, also found in the meta-analysis of Dong *et al.* (2018), is in line with a similar negative response of leaf minerals in total. There was also a decrease in the leaf phosphorus concentration, of slightly smaller magnitude than that for leaf

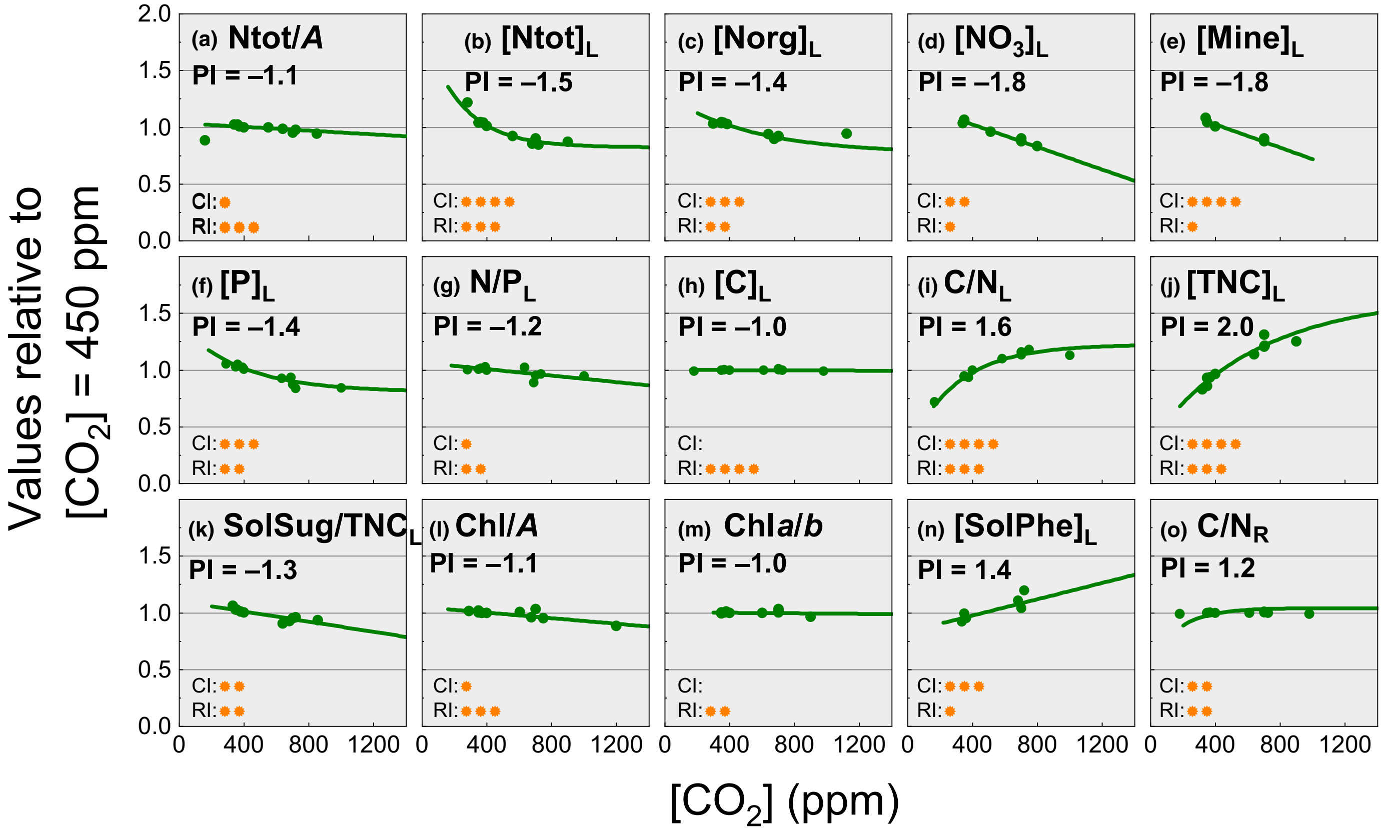

Fig. 3 Dose–response curves of 15 chemical traits in relation to atmospheric $[CO_2]$ as well as the plasticity index (PI) over the 200–1200 ppm range, the consistency index (CI) and the reliability index (RI). The traits shown are (a) Ntot/*A*, nitrogen content per unit leaf area; (b) $[Ntot]_L$, total nitrogen concentration of the leaves; (c) $[Norg]_L$, organic nitrogen concentration of the leaves; (d) $[NO_3]_L$, nitrate concentration of the leaves; (e) $[Mine]_L$, mineral concentration of the leaves; (f) $[P]_L$, total P concentration of the leaves; (g) N/P_L, nitrogen : phosphorus ratio of leaves; (h) $[C]_L$, carbon concentration of the leaves; (i) C/N_L, carbon : nitrogen ratio of the leaves; (j) $[TNC]_L$, total nonstructural carbohydrate concentration of the leaves; (k) $SolSug/TNC_L$, fraction of the total nonstructural carbohydrate concentration of the leaves taken by soluble sugars; (l) Chl/*A*, chlorophyll content per unit leaf area; (m) Chl*a*/*b*, chlorophyll *a* : *b* ratio; (n) $[SolPhe]_L$, soluble phenolic concentration of the leaves; (o) C/N_R, carbon : nitrogen ratio of the roots. Data pertain to C_3 species only. All scaled values for a given trait were grouped into deciles based on the $[CO_2]$ during growth, and median values for each decile group are indicated as green dots in the panels. The closer the points are in the *x*-direction, the denser the information in that range of CO_2 concentrations. The line is the fitted curve fitted through all data points present in the 100–2000 ppm range, and given over the CO_2 range for which observations were present in the database. The strength of the CI is indicated by the number of orange symbols: none: % increases in the trait value with increasing $[CO_2]$ 40–60%; ✱: 30–40% or 60–70%; ✱✱: 20–30% or 70–80%; ✱✱✱: 10–20% or 80–90%; ✱✱✱✱: 0–10% or 90–100%. The strength of the RI: none: RI = 1–2; ✱: 3–4; ✱✱: 5–6; ✱✱✱: 7–8; ✱✱✱✱: 9–10. Graphs are shown up to a $[CO_2]$ of 1400 ppm. More detailed information for each variable can be found in Supporting Information Figs S24–S50; Table 2(a).

nitrogen. Consequently, the leaf N : P ratio declined to some extent (PI = −1.2; Table 2a), in line with the conclusions of Du *et al.* (2019). Leaf carbon concentration was unaffected by CO_2, and so the C : N ratio of the leaves increased solely due to the decreasing [N].

Total nonstructural carbohydrates (TNC) of leaves clearly increased with increasing CO_2 (Fig. 2j), indicating that the source : sink balance, the ratio between sugar supply by the leaves and sugar consumption by respiration and the growing tissues of the plant is shifted more towards a sink limitation (Burnett *et al.*, 2016). Most of these changes are due to additional accumulation of both starch and sugars, although a small but significant shift towards a lower proportion of soluble sugars occurs at elevated CO_2. There was a marginal decrease in the chlorophyll content per unit leaf area, with low consistency, and no effect on the chlorophyll *a* : *b* ratio. In those cases in which both chlorophyll and N have been measured, a small decrease in the Chl/N ratio was found (Table 2a), but the change is too small to infer substantial rearrangement in the investment of N in the light and dark reactions of the photosynthetic apparatus. Xanthophyll cycle pigments, expressed per unit chlorophyll, are unaffected, which indicates that there is no systematic effect on photoprotection either. Increased sugar availability may have stimulated the production of secondary compounds such as soluble phenolics. The increase is substantial (PI = 1.4), but with a low RI. The observed increase is in line with the meta-analysis of Dong *et al.* (2018), and could have important ramifications for plant–animal interactions.

Observations on the chemical composition of stems and roots are less common. Decreases in N concentrations have been observed, but they are of much smaller magnitude (PIs = −1.1; Table 2a) than in leaves, and this is reflected by small increases in the C : N ratios of these organs (Fig. 3o; Nie *et al.*, 2013). TNC concentrations did increase, however, more consistently in roots than in stems.

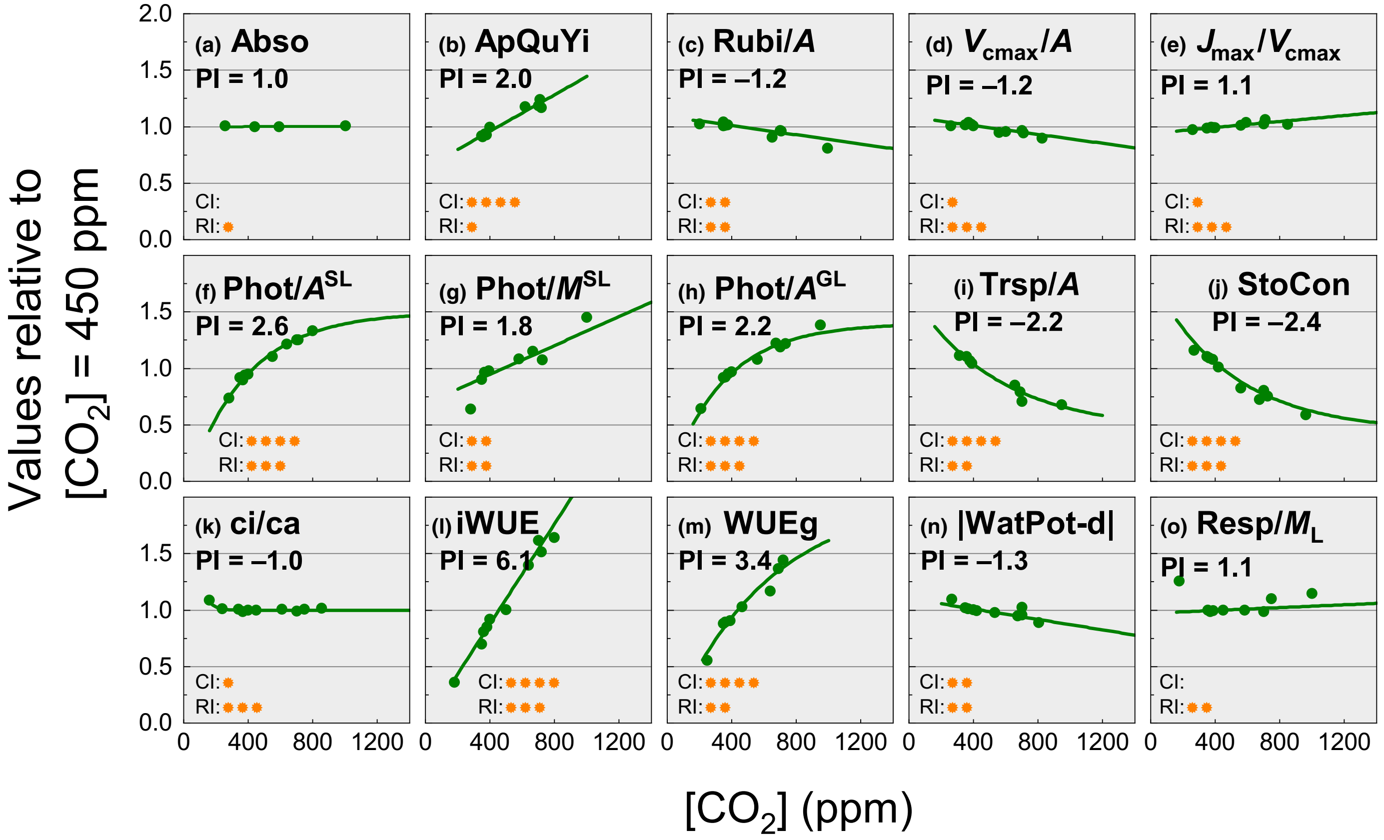

Fig. 4 Dose–response curves of 15 physiological traits in relation to atmospheric $[CO_2]$ as well as the plasticity index (PI) over the 200–1200 ppm range, the consistency index (CI) and the reliability index (RI). The traits shown are (a) Abso, absorptance; (b) ApQuYi, apparent quantum yield; (c) Rubi/A, Rubisco content per unit leaf area; (d) V_{cmax}/A, maximum rate of carboxylation per unit leaf area; (e) J_{max}/V_{cmax}, ratio between maximum rate of electron transport and maximum rate of carboxylation; (f) Phot/A^{SL}, rate of photosynthesis per unit leaf area at saturating light and growth $[CO_2]$; (g) Phot/M^{SL}, rate of photosynthesis per unit leaf mass at saturating light and growth $[CO_2]$; (h) Phot/A^{GL}, rate of photosynthesis per unit leaf area at growth light and $[CO_2]$ conditions; (i) Trsp/A, whole-plant transpiration rate per unit leaf area; (j) StoCon, stomatal conductance; (k) c_i/c_a, ratio of intercellular to ambient $[CO_2]$; (l) iWUE, intrinsic water-use efficiency of the photosynthetic process; (m) WUE_g, water-use efficiency based on growth; (n) |WatPot-d|, water potential during the diurnal period in absolute numbers; (o) Resp/M_L, leaf respiration rate per unit leaf mass. Data pertain to C_3 species only. All scaled values for a given trait were grouped into deciles based on the $[CO_2]$ during growth, and median values for each decile group are indicated as green dots in the panels. The closer the points are in the x-direction, the denser the information in that range of CO_2 concentrations. The line is the fitted curve fitted through all data points present in the 100–2000 ppm range, and given over the CO_2 range for which observations were present in the database. The strength of the CI is indicated by the number of orange symbols: none: % increases in the trait value with increasing $[CO_2]$ 40–60%; ✱: 30–40% or 60–70%; ✱✱: 20–30% or 70–80%; ✱✱✱: 10–20% or 80–90%; ✱✱✱✱: 0–10% or 90–100%. The strength of the RI: none: RI = 1–2; ✱: 3–4; ✱✱: 5–6; ✱✱✱: 7–8; ✱✱✱✱: 9–10. Graphs are shown up to a $[CO_2]$ of 1400 ppm. More detailed information for each variable can be found in Supporting Information Figs S51–S78; Table 2(b).

3. Physiology

Light absorptance was not affected by the $[CO_2]$ during growth (Fig. 4a), but there might be a small decrease in leaf transmittance (Table 2b). As for nitrogen content per area, small decreases were found in the Rubisco content per area. This accords with a decrease in V_{cmax} as derived from short-term CO_2 response curves of photosynthesis. Although J_{max} and V_{cmax} are generally strongly coordinated (Wullschleger, 1993), on average a small increase in the J_{max}/V_{cmax} ratio is found, with low consistency. Medlyn *et al.* (1999) reported that J_{max} and V_{cmax} were affected to the same extent, but this was over a two-fold range in $[CO_2]$ only, whereas a six-fold range is considered here. Light-saturated photosynthesis was limited by carboxylation capacity at low $[CO_2]$ and by electron transport and RuBP regeneration at high $[CO_2]$ (Sage, 1994). The observed increase in J_{max}/V_{cmax} with $[CO_2]$ therefore leads to a more efficient utilisation of the photosynthetic apparatus. Increased atmospheric $[CO_2]$ also causes a higher intercellular CO_2 concentration. Consequently, elevated CO_2 levels at the site of Rubisco suppress photorespiration, thereby enhancing the apparent quantum yield, the number of photons used to reduce one molecule of CO_2. The positive effect on apparent quantum yield is highly consistent, also when plants are grown at elevated CO_2 for longer periods. Another gauge for the functioning of the photosynthetic apparatus is the variable fluorescence. There are no indications that F_v/F_m is negatively affected, neither when measured during the night, nor during the day (Table 2b).

Given these considerations, it can be anticipated that photosynthesis measured under saturating light (Phot/A^{SL}) and the prevailing CO_2 conditions during growth is strongly positively affected by

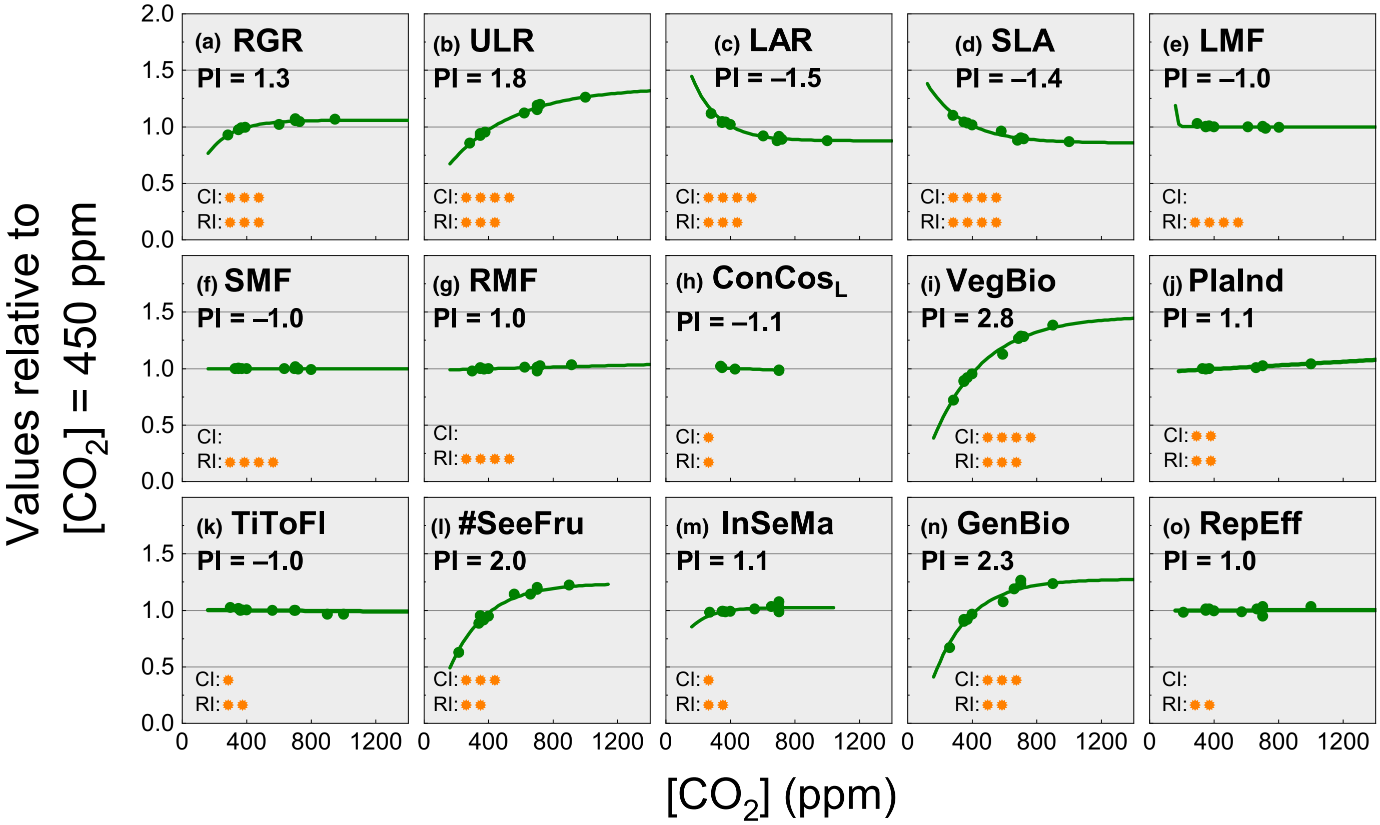

Fig. 5 Dose–response curves of 15 growth and reproduction-related traits in relation to atmospheric [CO$_2$] as well as the plasticity index (PI) over the 200–1200 ppm range, the consistency index (CI) and the reliability index (RI). The traits shown are (a) RGR, relative growth rate; (b) ULR, unit leaf rate; (c) LAR, leaf area ratio; (d) SLA, specific leaf area; (e) LMF, leaf mass fraction; (f) SMF, stem mass fraction; (g) RMF, root mass fraction; (h) ConCos$_L$, construction costs of the leaves; (i) VegBio, vegetative biomass per plant; (j) PlaInd, plastochron index; (k) TiToFl, time to flower; (l) #SeeFru, number of seeds or fruits per plant; (m) InSeMa, individual seed mass; (n) GenBio, generative biomass per plant; (o) RepEff, reproductive effort. Data pertain to C$_3$ species only. All scaled values for a given trait were grouped into deciles based on the [CO$_2$] during growth, and median values for each decile group are indicated as green dots in the panels. The closer the points are in the *x*-direction, the denser the information in that range of CO$_2$ concentrations. The line is the fitted curve fitted through all data points present in the 100–2000 ppm range, and given over the CO$_2$ range for which observations were present in the database. The strength of the CI is indicated by the number of orange symbols: none: % increases in the trait value with increasing [CO$_2$] 40–60%; ✸: 30–40% or 60–70%; ✸✸: 20–30% or 70–80%; ✸✸✸: 10–20% or 80–90%; ✸✸✸✸: 0–10% or 90–100%. The strength of the RI: none: RI = 1–2; ✸: 3–4; ✸✸: 5–6; ✸✸✸: 7–8; ✸✸✸✸: 9–10. Graphs are shown up to a [CO$_2$] of 1400 ppm. More detailed information for each variable can be found in Supporting Information Figs S79–S93; Table 2(b).

[CO$_2$]. Indeed, with a PI of 2.6 the response is strong, particularly in the low-CO$_2$ range (Fig. 4f). The response of Phot/A^{SL} looks similar to the usual CO$_2$-response curve of photosynthesis, as determined at a given day for a specific leaf. However, it is not identical as V_{cmax} and J_{max} (to a lesser extent) typically decrease at high growth [CO$_2$], whereas they are constant in short-term measurements. Similar to that expected from short-term measurements, the curve saturates above 1000 ppm, as under these conditions Phot/A^{SL} is limited by J_{max} and most of the photorespiration is suppressed. Responses of similar magnitude as Phot/A^{SL} are achieved when the area-based rate of photosynthesis measured under growth light conditions is considered. Mass-based rates are less stimulated than area-based values, due to higher LMA at high [CO$_2$].

Whereas photosynthetic rates more than doubled over the 200–1200 ppm range, area-based transpiration and stomatal conductance more than halved (Fig. 4i,j). With stomatal density hardly affected (Fig. 2f), the implication is that the decreased transpiration rate is mainly due to stomatal closure (Ainsworth & Rogers, 2007). An improved photosynthesis at decreased transpiration rates implied strong increases in intrinsic water-use efficiency (iWUE), the rate of photosynthesis divided by stomatal conductance under growth conditions. The observed plasticity index (PI = 6.1) is the largest among all traits considered here. WUE at the whole-plant level, measured as biomass increase per unit water transpired, also increased strongly. With a consistency index (CI) of 100, it is one of the rare variables reported to increase with CO$_2$ in all the studies compiled. The reduced transpiration rate is not reflected in a substantial change in the pre-dawn water potential, but water potential during the light period was less negative, as can be derived from the lower normalised values of absolute water potentials at high CO$_2$ (Fig. 4n).

Most leaf respiration rates are measured in leaf cuvettes with portable infrared gas analysers (IRGAs), which face problems with CO$_2$ diffusion across the gaskets (Flexas *et al.*, 2007). It has been shown that this can lead to the erroneous conclusion of a reduction in respiration with CO$_2$ enrichment (Davey *et al.*, 2004). We therefore compiled only those respiration measurements in which the problem of large concentration differences across the cuvette was explicitly dealt with. Overall, we found little effect of growth [CO$_2$] on mass-based leaf, shoot or root respiration, which contrasts with the meta-analysis of Wang & Curtis (2002). They reported overall depressed respiration rates at high [CO_2], most likely because they included some earlier measurements in which no precautions for CO_2 diffusion across the leaf cuvette gasket were taken.

4. Growth, development and reproduction

Growth has been well studied, and relative growth rate (RGR) increased with CO_2, with a PI of 1.3 (Fig. 5a; Table 2b). RGR is the product of unit leaf rate (ULR) and leaf area ratio (LAR). ULR (also known as net assimilation rate) is the increase in biomass per unit time and leaf area, and is generally well correlated with the rate of photosynthesis across species or treatments (Poorter & Van der Werf, 1998). This is also true for CO_2, although the PI is somewhat lower (but of the same order of magnitude) as the actual rate of photosynthesis under growth conditions. The higher ULR is counterbalanced by a decrease in LAR, the amount of leaf area per unit total plant mass. The decrease in LAR is primarily caused by a decrease in specific leaf area (SLA; leaf area/leaf mass). The other component that determines LAR is the leaf mass fraction (LMF), which did not change at all over the 200–1200 ppm range, and the same was true for allocation of biomass to stems and roots (SMF and RMF, respectively).

Construction costs of leaves indicated how much glucose was required to drive all the biosynthetic reactions to produce 1 g of leaf (Villar & Merino, 2001). Construction costs are slightly, but consistently, lower at elevated CO_2 (Fig. 5h), which will at least partly be due to a reduced protein content, as we deduce from the decrease in organic N, which are costly to produce, and the increased starch and sugar concentrations, which are compounds with low construction costs. Total vegetative biomass formed (VegBio) is then the integrated result of changes in all the above variables. This has been frequently measured and showed a strong (PI = 2.8) and highly consistent response, with saturation at higher [CO_2].

Notwithstanding the strong increase in biomass, speed of development was only marginally affected, as judged by the plastochron index, which measures the number of leaves or leaf pairs formed on the main stem over a given period of time (Fig. 5j). Overall, the time to flowering was not affected, with low consistency across experiments (CI = 38%; see also Springer & Ward, 2007). There was a strong increase in the number of seeds, fruits or flowers produced per plant (PI = 2.0; see also Jablonski *et al.*, 2002). Individual seed mass was also increased, but to a much smaller extent, as is expected for a variable that generally is not strongly affected by the environment. The curve for total production of generative mass (seeds, fruits) is rather similar to that of the vegetative biomass. Consequently the reproductive effort or harvest index was markedly constant.

V. The overall response of plants to CO_2

1. A whole-plant perspective

As shown in Section IV, CO_2 affected many phenotypic traits. Some of these are primary responses; other traits are indirectly influenced. For a better overview of what happens at the whole-plant level, we have summarised a range of trait responses and interactions in a knowledge graph (Figs 6, see S5 for an animated version). The black and red arrows between traits indicate positive and negative relationships between trait pairs, under the condition that all other variables remain constant. Arrows within a box indicate the PI of the CO_2 response for that particular trait. There are three primary effects of [CO_2] on plants with cascading effects on other traits. First, CO_2 concentration at the site of Rubisco rises, which enhances photosynthesis by increasing substrate concentration around the enzyme. This is noticeable in the dose–response curves for both area-based and mass-based photosynthesis measured at light saturation, but also when determined at growth light conditions. For short-term responses, this is well captured by the Farquhar–Von Caemmerer–Berry model (Farquhar *et al.*, 1980). The same model also encapsulates the second effect, which is reduced photorespiration when the $CO_2 : O_2$ ratio at the site of Rubisco increases. This will increase CO_2 fixation at a given electron transport rate, therefore enhancing apparent quantum yield. Third, increased CO_2 levels inside the leaf negatively affect stomatal conductance and therefore transpiration (Leakey *et al.*, 2012). The exact mechanism is still unknown (Engineer *et al.*, 2016), although the various genes involved are beginning to be identified (Gamage *et al.*, 2018). Both the increased photosynthesis and the decreased stomatal conductance are among the strongest trait responses in this analysis, indicating that they persist even after plants acclimated to the various CO_2 levels.

Assuming optimal stomatal control, Medlyn *et al.* (2011) derived that the ratio between photosynthesis and stomatal conductance, which is termed ‘intrinsic water-use efficiency’, should be linearly related to the ambient CO_2 level. Indeed, we found that the intrinsic WUE was linearly related to growth CO_2 concentration over the full range considered. The decrease in conductance has various downstream consequences. Transpiration rate per unit area decreases, with diminished evaporative cooling and therefore leaf temperature will probably increase (Bernacchi *et al.*, 2007). This partly nullifies the decreased conductance, as a larger vapour pressure difference across the leaf has in itself a stimulating effect on transpiration. The overall decrease in transpirational demand will result in less soil water consumption. In experiments in which water supply is regularly and amply supplied, this will not have further consequences, but in other cases water potential as measured during the day may become less negative. The experimental regime may therefore explain why the observed response in plant water potential is relatively variable. The ratio between intercellular and ambient [CO_2] is markedly similar across CO_2 levels, consistent with theory predicting much weaker control of optimal c_i/c_a by [CO_2] than by, for example air temperature and vapour pressure deficit (Wang *et al.*, 2017).

Although LMA is substantially affected by [CO_2], effects on leaf anatomy are only marginal. There is not much evidence that there are increases in the number of palisade cell layers. Also the relationship between the volumes of palisade and spongy parenchyma (VoFrPa) did not change. Nonetheless, individual leaves probably are larger in all dimensions. There was an increase in leaf density, which is at least partially caused by accumulation of

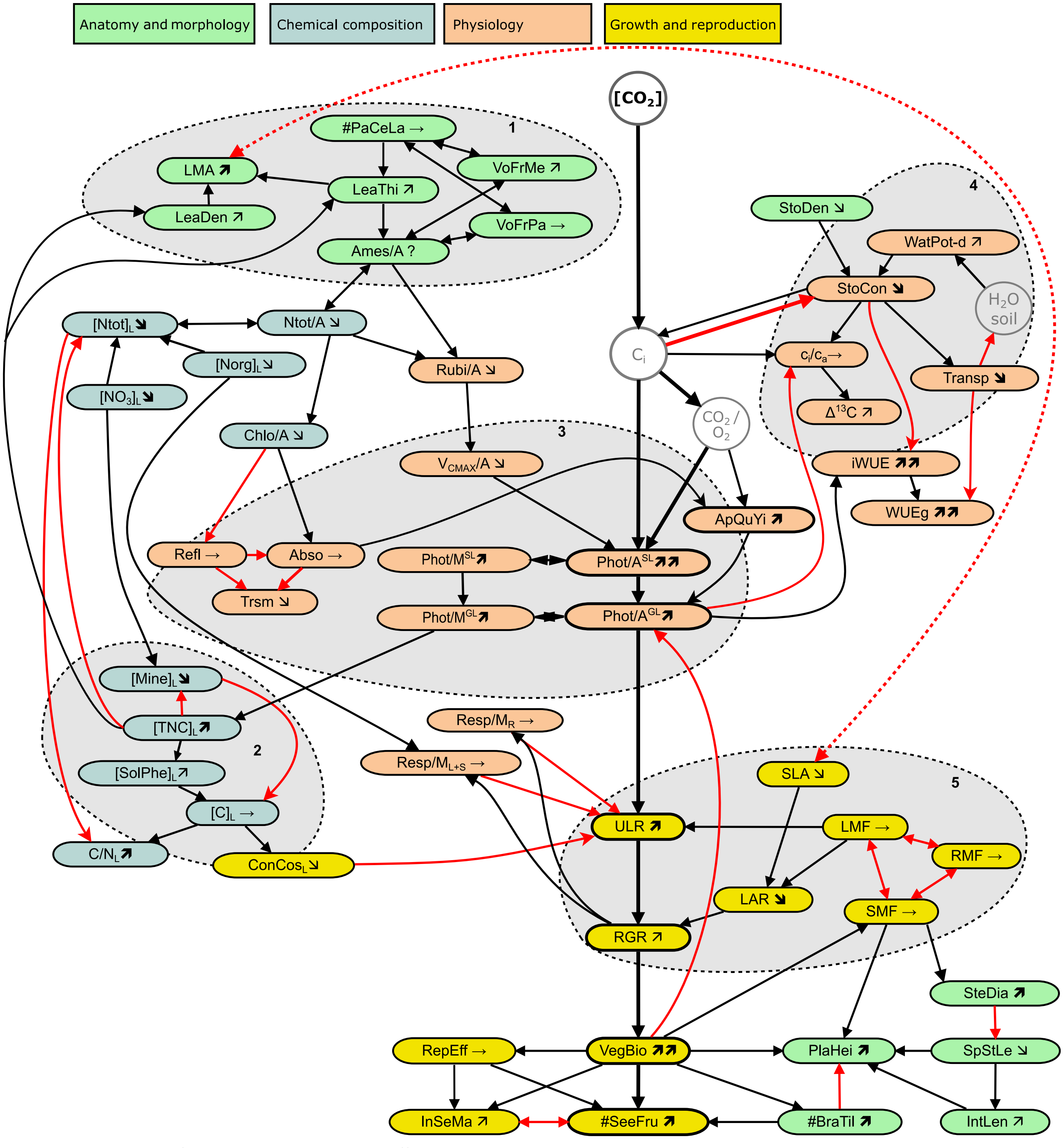

Fig. 6 Knowledge graph of plant traits and how they are affected by atmospheric [CO$_2$]. The lines with arrows between boxes indicate positive (black) or negative (red) relationships between two traits when all other traits would remain constant. Arrows behind each trait indicate whether the effect of [CO$_2$] on that trait is positive (upward arrows), neutral (horizontal arrows) or negative (downward arrows). Bold arrows indicate that the plasticity index (PI) is > 1.45 or < -1.45, respectively, double bold arrows a PI > 2.45. The relationship is considered neutral if the AICc test (where AICc is the Akaike information criterion with a correction for small sample sizes) selected this alternative, or when the consistency index (CI) was between 40% and 60%. The primary chain of C-economy events from [CO$_2$] through vegetative biomass and production of seeds or fruits is given by the bold vertical axis in the middle of the graph. All changes in other traits may modulate the primary chain of events. The grey areas are a visual aid to discriminate between groups of traits from different subfields: (1) Leaf anatomy; (2) Chemistry. (3) C-economy, (4) Water economy, (5) growth-related traits. Groups of traits related to N-economy, stem morphology and reproduction were not separately indicated for clarity reasons. The dotted red line connects leaf dry mass per area (LMA) and specific leaf area (SLA), which represent two different expressions representing the same trait. An animated version of this graph is given in Supporting Information Fig. S5. See Table 1 for list of abbreviations.

starch and sugars ([TNC]$_L$). Increased starch concentrations often go with thicker leaves, but to what extent this is caused simply by increased starch granule volume is unclear. The accumulation of TNC is generally large, in both a relative and an absolute sense and is – next to a decreased N concentration and increased LMA – a hallmark of a plant's response to high CO_2. This can accumulate to such an extent that it dilutes the concentration of other compounds (Poorter *et al.*, 1997). To what extent leaf chemical composition is affected independently of TNC accumulation remains an outstanding issue.

Soluble phenolic concentration increases, even against the diluting effect of increased TNC, whereas mineral concentrations in total, as well as nitrate in particular, decrease. A decrease in [NO_3] may also be caused by the lower transpiration rate at high [CO_2], which results in a decreased mass flow of soil solutes from the soil environment toward the roots (McDonald *et al.*, 2002; Taub & Wang, 2008), or because NO_3 uptake is downregulated (Zheng, 2009). An alternative hypothesis suggested that nitrate reduction in the chloroplasts is reduced due to lower photorespiration (Bloom *et al.*, 2012), but this would probably result in an *increased* nitrate concentration, which is not often observed. All suggested mechanisms in the end have a negative effect on both total and organic leaf [N] and, notwithstanding higher LMA, also a marginally negative effect on total N content per leaf area. However, the total content of N per plant is higher in high-CO_2 plants (Andrews *et al.*, 2019), because the proportional increase in plant mass is larger than the decrease in plant [N]. Leaf phosphorus concentration also diminishes, but not to the same extent as nitrogen, resulting in a reduced N : P ratio of the leaves. This cannot be explained by dilution through TNC accumulation alone, and would fit with the idea that the uptake of mobile ions such as nitrate is relatively strongly impaired by the decreased mass flow, whereas uptake of immobile nutrients such as P is not affected.

There was also a small decrease in chlorophyll/area, which apparently has no consequences for light absorptance, as this is unaffected by [CO_2]. The measured amount and/or activity of Rubisco per unit area declined, without negative consequence for the actual rates of photosynthesis, which remain stimulated due to the higher internal CO_2 levels. Long-term effects on respiration rates have been debated for a long time. Based on high photosynthetic and growth rates one would expect increased mass-based respiration, but due to lower organic-N concentration one would expect respiration to be reduced (Dusenge *et al.*, 2019). Both for leaves, whole shoots and roots, the evidence suggests that neither of the two happens or that the two contrasting effects cancel each other out.

At the level of whole-plant growth, surprisingly little happens in terms of biomass allocation over a wide CO_2 trajectory. In that sense, plants do not seem to follow the functional equilibrium concept of preferential allocation to the organ that limits growth most, which is so well known for light and nutrients (Bloom *et al.*, 1985; Poorter *et al.*, 2012). Perhaps the balance is more complicated, as elevated CO_2 reduces both the need for a higher leaf investment because of increased photosynthesis, and a higher root investment for water uptake because of decreased transpiration. Possibly, the reduced concentration of organic N is a consequence of plants not shifting their allocation pattern towards more roots. The lower SLA (higher LMA) decreases the leaf area : total mass ratio, and this explains why the positive and large effect of increased photosynthesis on ULR, the growth rate per unit leaf area, does not show up in a comparable stimulation of RGR. Nonetheless, the relatively small increase in RGR over the experimental period has strong positive consequences on overall plant size. This stimulation was reflected in a range of variables, not only biomass but also stem and root morphology as well as the number of branches and tillers. Although not all branches or tillers produce seed, increased branching is certainly one of the ways plants increase the number of sinks. Whereas individual seed mass is stimulated in some cases, most of the stimulation in reproduction is due to increased seed numbers. The CO_2-induced increase in seed mass often goes with an increase in the C : N ratio of the seeds, which reduces nutritional value as well as seed vigour (Zhu *et al.*, 2018; Lamichaney & Maity, 2021).

2. The shape of the dose–response curves

The above analyses are based on PI values, comparing the ratio of values at 1200 and 200 ppm CO_2. However, the shape of the dose–response curve is also important. Over the CO_2 range considered, we found no traits with a local maximum or minimum, or with exponential responses. Here, *c.* 45% were linear, and 38% saturating, with the remaining traits unaffected. Some of the traits have not yet been determined over the full 200–1200 ppm range we considered, and may turn out to be saturating when data become available over a wider span. A range of key traits (e.g. LMA, area-based photosynthesis, stomatal conductance, ULR and generative biomass) have saturating curves. For these five traits, 31–70% of the total change over the 200–1200 ppm range will have already been realised at the current [CO_2] of 415 ppm; for vegetative biomass it is 64%. A logical consequence of this saturation is that, over time, the effect of a doubling in [CO_2], which has been kind of standard in CO_2 research, is becoming smaller: over the 350–700 ppm range, often studied 30 y ago, the biomass stimulation is 45%, over the 415–830 range it diminishes to 36%.

Two more points require attention. From a palaeobiological perspective, plant performance at low [CO_2] is a relevant topic in itself (Gerhart & Ward, 2010; Temme *et al.*, 2013). As discussed earlier, our plasticity analysis over the 200–1200 ppm trajectory found that plants do not follow the functional equilibrium concept and do not change biomass allocation to the organ that is supposed to be most limiting at low CO_2, in this case the leaves. However, closer inspection of the data showed that, at very low CO_2 levels (< 200 ppm), plants do allocate a larger fraction of biomass to the leaves, at the expense of stems and roots (Figs S83–S85). Residual analysis showed that SLA also increases more strongly in this range, with additional evidence of a decreased leaf C concentration. Clearly, in the very low CO_2 range, plants respond strongly to the deteriorated C gain. An interesting question in that respect is at what [CO_2] can plants not grow anymore? For C_3 plants, the CO_2 compensation point for photosynthesis strongly depends on temperature, but will often be in the range 35–60 ppm (Bauer & Martha, 1981). Due to respiration of leaves, roots and other plant organs, the CO_2-compensation for the C balance of the whole plant will be higher. Campbell *et al.* (2005) estimated this whole-plant CO_2 compensation point for growth to be well below 100 ppm. To what extent CO_2 derived from root or soil respiration affects this CO_2 compensation point for growth is still unknown, but experiments in which only root zone $[CO_2]$ is manipulated have shown that there can be substantial effects on leaf morphology, photosynthesis and growth (He *et al.*, 2010; Sun *et al.*, 2011). Analogous to what happens at low light, we had expected reproductive growth to be more strongly negatively affected than vegetative biomass, but this did not show up in the data compiled, as reproductive effort remains markedly constant (Fig. 5o).

The second point is whether there is an optimal $[CO_2]$ for plant performance, and at which levels $[CO_2]$ becomes supraoptimal. With a CI of 95% for total biomass, there were only few experiments in which plants at the highest $[CO_2]$ were smaller than those at the lowest level. Variation can be due to differential species responses (Zheng *et al.*, 2018), but might also be simply caused by sampling 'error' (Poorter & Navas, 2003). In horticultural practice, CO_2 enrichment up to 800–1000 ppm is often applied. This may serve as a first approximation for the optimal CO_2 level, albeit those concentrations are also determined by the financial return on the additional costs for the CO_2 supplied. Some reports have shown an optimum growth in the 1000–2000 ppm range, with small decreases in the order of 10% above 2000 ppm (Jolliffe & Ehret, 1985). Others found no indication of supraoptimal growth at levels as high as 30 000 ppm (Imazu *et al.*, 1966; Vaughn *et al.*, 2003). Inspection of all the dose–response curves of individual experiments in our database suggested strong saturation above 1500 ppm, but no supraoptimality. With photosynthesis saturating at these levels, and respiration unaffected, no negative primary effects on C balance would be expected. Although morphological disorders such as leaf rolling, chlorosis and necrosis have been observed (Ehret & Jolliffe, 1985; Wheeler *et al.*, 1993), they could potentially also be due to impurities in the CO_2 source (e.g. ethylene or NO_x). Other species may show leaf-tip chlorosis under high CO_2, because of reduction in transpiration and a concomitant decrease in calcium and boron transport to the youngest leaves (Nederhoff, 1994). Interestingly, there have been reports of much *higher* transpiration rates at extremely high $[CO_2]$, especially at night (Levine *et al.*, 2009). To the extent that disorders show up at elevated $[CO_2]$, they generally do not preclude positive responses in total biomass. Based on the current but scarce evidence, we postulate that the level at which CO_2 becomes supraoptimal for the biomass accumulation of most C_3 plants will lie well above 3000 ppm. However, there are indications that for seed yield, supraoptimal CO_2 levels may be lower (Grotenhuis & Bugbee, 1997).

VI. Comparison between responses to $[CO_2]$ and light

The photosynthetic process in plants is generally co-limited by $[CO_2]$ and light. Consequently, sugar production will go up when either of the two increases. To what extent then does an increase in $[CO_2]$ have the same effect on the various plant traits as an increase in light intensity? Poorter *et al.* (2019) analysed the response of plants to the daily light integral (DLI; mol photons m^{-2} d^{-1}) in a similar way as has been done here for $[CO_2]$. The range in DLI they considered for their plasticity calculation was 50-fold, which is much larger than the six-fold range in $[CO_2]$ we considered here, and therefore the PI values cannot be compared directly. In Fig. S5 we compare the plasticity values for $[CO_2]$ with those for DLI calculated over a six-fold range (4–24 mol m^{-2} d^{-1}). An alternative approach is to use the CI discussed earlier as an indicator of the direction of the response: a value of 0% indicates that a trait decreased consistently across experiments, whereas a value of 100% indicates a consistent increase. We mapped these estimates of consistency for light and $[CO_2]$ in Fig. 7 for 80 traits for which we have information available. For ease of interpretation we subdivided this full area into nine regions, which showed for each of the two environmental factors whether the response is mostly negative (CI < 25%), rather variable (25 < CI < 75%) or predominantly positive (CI > 75%). A range of traits reacted in a rather similar way to increased $[CO_2]$ and light, colour coded with black dots in Fig. 7. For example, in both cases the area-based rate of photosynthesis and the ULR consistently increased at higher $[CO_2]$ and light, and so did the leaf TNC concentration, stem diameter, number of branches and tillers, vegetative biomass and number of seeds or fruits per plant. Conversely, SLA consistently decreased, and so did total leaf [N] and [P] as well as specific stem length. Most of the responses that are in the upper-right or lower-left corner are probably explained by a common increase in sugar availability, and it is likely that signal transduction pathways related to sugar sensing are (co-) involved in the genetic regulation of these acclimatory changes (Lastdrager *et al.*, 2014; Barbier *et al.*, 2015).

A second group of traits, also colour coded black, did not respond, or reacted only marginally to both factors: chlorophyll content per unit leaf area, leaf absorptance, mass-based leaf and root respiration rates as well as the nocturnal values of water potential and fluorescence (F_v/F_m). These traits are still following the overall diagonal of similar responses, but the responses are variable in both cases. More interesting is the group of traits that responds to one factor only. A few traits are predominantly affected by $[CO_2]$ (colour coded blue). Apparent quantum yield was increased by CO_2 only, due to a direct reduction in photorespiration by elevated CO_2 (Section IV). Whereas photosynthetic capacity and organic-N concentration, both expressed per unit leaf mass, are little affected by light, they are increasing respectively decreasing at higher $[CO_2]$. This implies that the maximum photosynthetic nitrogen-use efficiency, which is the ratio between photosynthetic capacity and leaf nitrogen concentration, is unaffected by light (Poorter & Evans, 1998), but stimulated by $[CO_2]$ (Zhang *et al.*, 2013). Plant height, individual leaf area as well as internode length are consistently stimulated by CO_2 but not so by light availability. Light affects more traits (colour coded red), as it has much stronger formative effects on leaf and plant development. In general, the number of palisade cell layers increased more at high light, and with it the amount of Rubisco and V_{cmax} per unit leaf area. Also the increased chlorophyll $a:b$ ratio is a typical hallmark of acclimation to high light, and so is (at the other side of the graph) the decrease in chlorophyll/N. We presumed that the range of receptors that sense

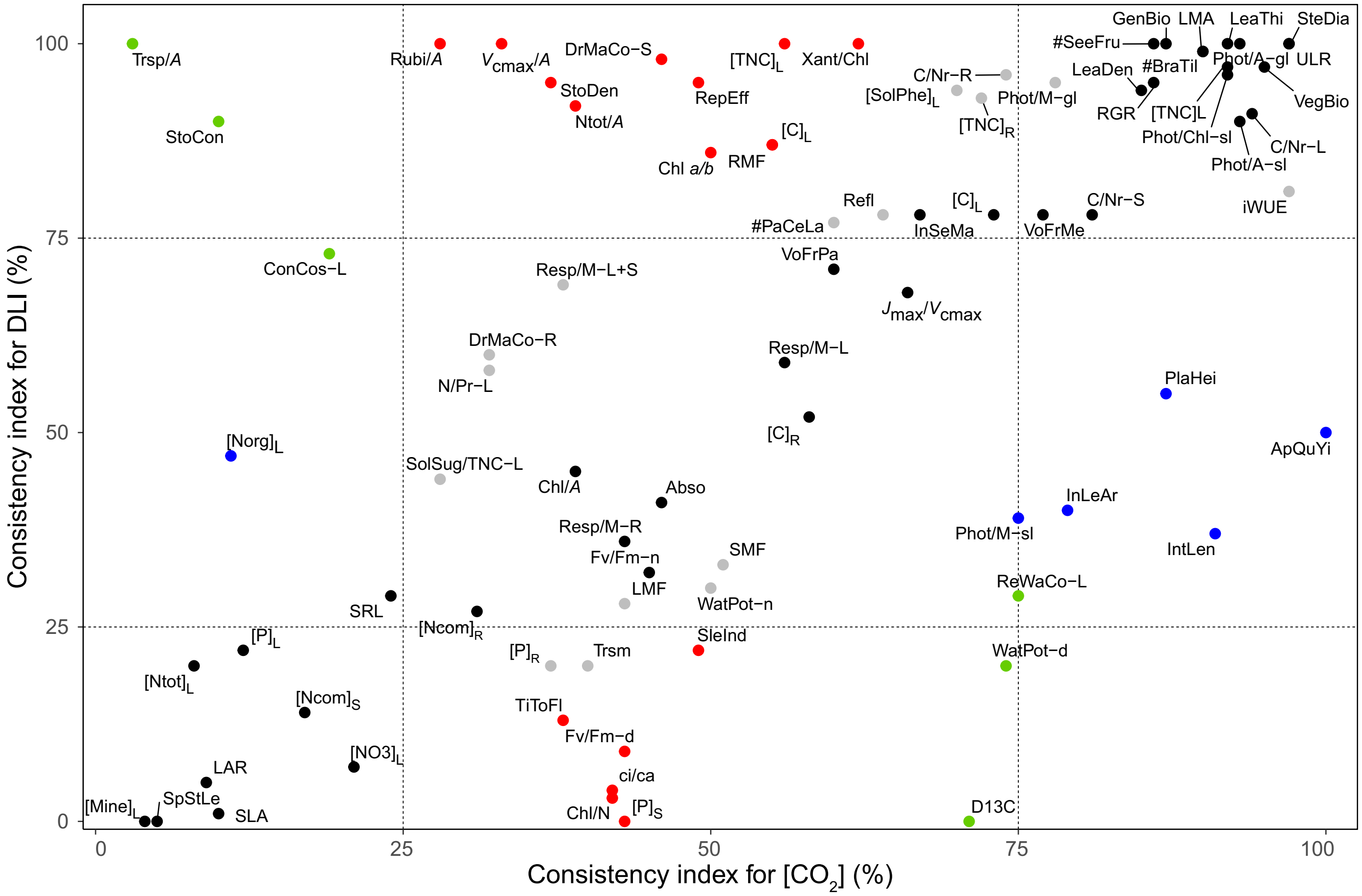

Fig. 7 Comparison of the consistency in response of plants to [CO_2] and daily light integral (DLI; mol m^{-2} d^{-1}) with respect to a wide range of plant traits. Explanation of the trait abbreviations is given in Table 1. The overall consistency index (CI; percentage of the species × experiment combinations in which trait values were higher for the highest level than for the lowest level) as calculated for 500 experiments in which the DLI (data from Poorter *et al*., 2019) was varied, plotted against the same index based on the 630 CO_2 experiments in the current analysis. The dotted lines indicate CI values of 25% and 75% and are a visual support to judge which traits are relatively marginally affected in both cases (middle area), strongly positively or negatively affected by [CO_2] (right and left part of the graph) and/or strongly positively or negatively by DLI (top or bottom part). Colours of the points are a visual aid and show (1) in black: traits similarly affected by DLI and CO_2; (2) in blue: predominantly affected by CO_2; (3) in red: traits predominantly affected by light; (4) in green: traits responding in opposite directions; (5) in grey: all other traits. A comparison based on plasticity index values is shown in Supporting Information Fig. S6.

quantity and/or quality of light (cryptochromes, phytochromes; Ballaré & Pierik, 2017) are playing a more dominant role here than the above-mentioned sugar sensors, as both environmental factors affected starch and sugar levels similarly.

As discussed above, stomatal density is only marginally sensitive to CO_2, but showed a much stronger and more consistent response to increased light. This has relevant ramifications for those efforts in which stomatal density in fossils is used to reconstruct the paleoclimate: if light intensity has varied over geological timescales, for example because of changes in water vapour and cloud cover in the air, or if leaves developed in a more shady habitat, this probably had a stronger effect on stomatal density than the variation in atmospheric CO_2 concentration *per se*. This implied that paleo-climate reconstructions based on acclimatory dose–response curves of stomatal density should be approached with care.

A fourth and very small set of traits showed opposing responses to light and CO_2. Some of those traits, which are colour coded green, are found in the upper left part of the graph, where light is strongly stimulating and [CO_2] is strongly inhibiting. Traits found here are stomatal conductance and area-based transpiration, which generally increase with light, as the higher carboxylation rates of photosynthesis have to be matched with an increased CO_2 conductivity, with higher water loss as a consequence. This problem is less relevant at increased [CO_2], as it creates a far steeper CO_2 diffusion gradient between the atmosphere and the leaf interior, implying that water loss can be restricted with little penalty on C gain. Close to the opposite, lower-right part, we found leaf water potential during the diurnal phase. Data for leaf water potential showed less negative values, so an improved water status at high [CO_2], but more negative values at high light. All these traits depended on stomatal regulation, which is known to be regulated by at least two independent pathways, of which the internal CO_2 sensor(s) discussed earlier is one (Gamage *et al.*, 2018) and a phototropin sensing blue light is another (Inoue & Kinoshita, 2017).

VII. Concluding remarks

1. Outlook

The focus of this review centres around the effects of aerial CO_2 concentration at the organismal level. By establishing generalised dose–response curves for a wide range of traits we tried to contribute to the understanding of how C_3 plants acclimate to one of their vital environmental factors. However, with so much change in ambient $[CO_2]$ ahead and so little past experience or possibilities for large-scale experiments, there is societal pressure to use this knowledge to improve our understanding of future crops, ecosystems and possibly for system Earth (IPCC, 2014; Walker *et al.*, 2021). With the acknowledgement that every integration level has its own feedbacks and peculiarities, we identified four relevant steps to further our understanding and applied the resulting dose–response curves fruitfully.

(**1**) Better define the curves, especially at the outer ends of the CO_2 range. There are few data on plant functioning below 300 and above 1000 ppm, and some of the curves we derived therefore still have low reliability. At low $[CO_2]$, there are indications for strong physiological and morphological responses (Section V.2). What compensatory mechanisms take over under these conditions, in which sugar availability becomes low although light is abundant? What is the CO_2 compensation point of growth, and how is reproduction affected in this range? At the other end, at what level does $[CO_2]$ becomes supraoptimal? Although there are no clear indications for deleterious effects of $[CO_2]$ as high as 5000 ppm on vegetative biomass, it is as yet unclear what happens physiologically and biochemically at these levels.

(**2**) Understanding interspecific variation in the dose–response curves. Here, we focused on the 'average' C_3 species. Which are the traits for which species with a C_4 or CAM type of photosynthesis will show very different dose–response curves, and which are similar? Moreover, how large is the variation in dose–response curves and plasticity among functional types of C_3 species?

(**3**) Understanding trait integration physiologically, also under suboptimal growth conditions. Our compilation is for plants grown under relatively benign conditions, often with one plant per pot rooted in nutrient-rich and well-watered potting soil. How do these dose–response curves change when plant density is high and resources are suboptimal? We know, both from controlled experiments and FACE systems, that plant biomass responses to elevated $[CO_2]$ are stronger in the presence of ozone, relatively unaltered by low water availability, and reduced at low temperatures and low nutrient levels (Poorter & Pérez-Soba, 2001; Ainsworth & Long, 2021). But what happens to the dose–response curves of other traits, and which are, in the end, the key traits that modulate the relative CO_2 response of biomass and reproduction at suboptimal conditions?

(**4**) Integrate these dose–response curves into crop and ecosystem models. Many process-based models run with fixed parameter values for a given species or functional type and do not allow for environmental acclimation in structural or functional variables (Xu & Trugman, 2021). However, acclimation is an essential component in plant performance and fitness. Some routines that rely on optimisation procedures for photosynthesis or sugar allocation, for example, may partly accommodate for plant acclimation, but this is more difficult for structural variables. For example, most ecosystem models use a fixed LMA for different functional types, but adding an empirical relationship that incorporates LMA responses to increasing CO_2 significantly changes the outcome of such models (Kovenock & Swann, 2018). Going forward, vegetation models will increasingly be equipped to predict plant nonstructural carbohydrate pools, and the observed empirical relationships will be valuable for model development. The observed change in soluble phenolics is directly relevant to community models that predict herbivore nutrition, and to models that include litter quality as a control on decomposition. The relationships presented for the number of seeds/fruits and generative dry mass could be directly relevant to models that predict seed dispersal, recruitment, and population dynamics.

(**5**) Finally, to improve our understanding of biological systems and their models, comparison of the dose–response curves derived here with those calculated for different state or rate variables in crop and ecosystem models would be very insightful (Hasegawa *et al.*, 2017; Yin *et al.*, 2021).

2. Conclusions

We established dose–response curves to $[CO_2]$ for 85 ecophysiological traits of C_3 species and ranked them in terms of plasticity from strongly negative to strongly positive. These curves give a comprehensive insight into how plants respond to a wide range of CO_2 concentrations under otherwise close-to-optimal conditions and are very useful for integration in or comparison with trait-based simulation models. By contrasting these responses with those to light intensity, we better understand the various ways by which plants acclimate to their environment.

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Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request, following an embargo.

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Appendix A1

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Supporting Information

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

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

Fig. S2 Distribution of observations for four traits over the $[CO_2]$ range of 0–2000 ppm.

Fig. S3 Dose–response curves of the 14 morphological and chemical traits that were not included in Figs 2 and 3.

Fig. S4 Dose–response curves of the 13 physiological and growth-related traits that were not included in Figs 4 and 5.

Fig. S5 Animated build-up of the knowledge graph presented in Fig. 6.

Fig. S6 Plasticity indices for the response to a six-fold difference in light (daily light integral over the 4–24 $\mathrm{mol\ m^{-2}\ d^{-1}}$ range) vs those for a six-fold difference in $[CO_2]$ (200–1200 ppm).

Fig. S7–S23 Specific figures per trait, for the group of anatomical and morphological variables.

Fig. S24–S50 Specific figures per trait, for the group of chemical variables. For more information see the legend above.

Fig. S51–S78 Specific figures per trait, for the group of physiological variables. For more information see the legend above.

Fig. S79–S93 Specific figures per trait, for the group of growth and reproduction-related variables. For more information see the legend above.

Notes S1 Extended Materials & Methods.