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A global meta-analysis of woody plant responses to elevated CO_2: implications on biomass, growth, leaf N content, photosynthesis and water relations

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Abstract

Background: Atmospheric CO_2 may double by the year 2100, thereby altering plant growth, photosynthesis, leaf nutrient contents and water relations. Specifically, atmospheric CO_2 is currently 50% higher than pre-industrial levels and is projected to rise as high as 936 µmol mol^{-1} under worst-case scenario in 2100. The objective of the study was to investigate the effects of elevated CO_2 on woody plant growth, production, photosynthetic characteristics, leaf N and water relations.

Methods: A meta-analysis of 611 observations from 100 peer-reviewed articles published from 1985 to 2021 was conducted. We selected articles in which elevated CO_2 and ambient CO_2 range from 600–1000 and 300–400 µmol mol^{-1}, respectively. Elevated CO_2 was categorized into < 700, 700 and > 700 µmol mol^{-1} concentrations.

Results: Total biomass increased similarly across the three elevated CO_2 concentrations, with leguminous trees (LTs) investing more biomass to shoot, whereas non-leguminous trees (NLTs) invested to root production. Leaf area index, shoot height, and light-saturated photosynthesis (A_{max}) were unresponsive at < 700 µmol mol^{-1}, but increased significantly at 700 and > 700 µmol mol^{-1}. However, shoot biomass and A_{max} acclimatized as the duration of woody plants exposure to elevated CO_2 increased. Maximum rate of photosynthetic Rubisco carboxylation (V_{cmax}) and apparent maximum rate of photosynthetic electron transport (J_{max}) were downregulated. Elevated CO_2 reduced stomatal conductance (g_s) by 32% on average and increased water use efficiency by 34, 43 and 63% for < 700, 700 and > 700 µmol mol^{-1}, respectively. Leaf N content decreased two times more in NLTs than LTs growing at elevated CO_2 than ambient CO_2.

Conclusions: Our results suggest that woody plants will benefit from elevated CO_2 through increased photosynthetic rate, productivity and improved water status, but the responses will vary by woody plant traits and length of exposure to elevated CO_2.

Keywords: Atmospheric CO_2, Biomass production, Leaf nitrogen content, Meta-analysis, Photosynthetic rate, Stomatal conductance, Water use efficiency, Woody plants

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Introduction

Atmospheric CO_2 ($atCO_2$) have increased globally since the industrial revolution, owing to fossil fuel combustion and land cover changes due to increasing human population and the need for rapid economic growth (Jayawardena et al. 2021). Over the past decade, $atCO_2$ has been increasing at an alarming rate of 2.4 μmol mol^{-1} $year^{-1}$ (Li et al. 2021) and it is currently 50% higher than pre-industrial levels (Ebi et al. 2021). It is predicted that $atCO_2$ may rise as high as 936 μmol mol^{-1} by the year 2100 if greenhouse gas emissions are not mitigated (Hu et al. 2018). The increase in $atCO_2$ has serious impacts on plant physiology, productivity, growth, water relations (Bhargava and Mitra 2021; Zhang et al. 2021) and foliage chemistry (Du et al. 2020; Farkas et al. 2021). $AtCO_2$, through CO_2 fertilization, directly increases growth, canopy density and biomass by enhancing photosynthesis (Baig et al. 2015) and indirectly by reducing transpiration via partial closure of stomata (Gonsamo et al. 2021). Photosynthetic upregulation and a subsequent increase in woody plant biomass result from high carbon assimilation, owing to high investment of ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) to carboxylation relative to oxygenation (Wang and Wang 2021a; Raubenheimer and Ripley 2022). Indeed, many short-term studies have reported an increase in C assimilation and a subsequent increase in photosynthesis under saturating light and elevated CO_2 (eCO_2), more so for C_3 species relative to their C_4 counterparts (Zhang et al. 2021; Raubenheimer and Ripley 2022). This is driven mainly by the fact that C_3 photosynthesis does not saturate at current levels of CO_2 (Singer et al. 2020). High CO_2 uptake not only increases shoot growth and biomass, but also root depth and biomass, which further promotes soil nutrient and water uptake, indirectly enhancing photosynthesis (Thompson et al. 2017).

Increased net photosynthetic rate together with reduced transpiration as a result of reduced stomatal conductance (g_s) increase water use efficiency (WUE), thereby counter-acting moisture stress in drought-stricken ecosystems (Zhang et al. 2018; Garhum et al. 2021; Farkas et al. 2021; Mathias and Thomas 2021). At a landscape scale, increased WUE could increase soil moisture, in turn extending the length of the growing season (Li et al. 2019). Thus, CO_2 fertilization and increased WUE may drive landscape-scale vegetation transitions from open to dense woody cover stature (Gonsamo et al. 2021; Raubenheimer and Ripley 2022). However, eCO_2 reduces foliage/browse quality via a phenomenon referred to as dilution effect (Du et al. 2020). This phenomenon is the depletion of leaf N content as a result of higher accumulation of non-structural carbohydrates (NSCs) and biomass (Li et al. 2019). Because a considerable proportion of leaf N is derived from Rubisco, a reduction in Rubisco content at eCO_2 also reduces leaf N (Singer et al. 2020; Kitao et al. 2021; Wang and Wang 2021b). Dilution effect and reduced Rubisco content at eCO_2 reduce herbivore diet quality, as the decline in leaf N and increased C:N ratio reduce foliage digestibility (Du et al. 2020).

Woody plant responses to eCO_2 are very important, yet poorly understood (Bellasio et al. 2018). Understanding how these plants respond to eCO_2 may guide scientists and decision-makers in deriving climate-smart mitigation strategies (Hu et al. 2018). Amongst other disciplines, forestry plays a pivotal role in climate change mitigation by increasing C sinks through afforestation/reforestation (Lefebvre et al. 2021). For this reason, woody plant responses to eCO_2 require a special scientific assessment (Wang and Wang 2021a).

Knowledge of how trees, particularly of different functional traits, will respond to temporal changes in $atCO_2$ is crucial (Wang and Wang 2021b). Some short-term studies hypothesize that photosynthesis will rise linearly with $atCO_2$, whereas others suggest that it may saturate at a certain eCO_2 concentration (Poorter et al. 2021). Testing these two hypotheses may be difficult, particularly the latter, as different tree species exhibit differential C assimilation capacities. Inter and intraspecific variation among woody plants is due to differences in phenology, leaf types, nitrogen fixation capacity and photosynthetic pathways (Mathias and Thomas 2021; Wang and Wang 2021a, b). For instance, leguminous plants are highly likely to respond more positive due to their relationship with rhizobia which facilitates nodulation in legumes, thereby increasing C sink (Singer et al. 2020). Moreover, legumes tend to establish a symbiotic relationship with arbuscular mycorrhizal fungi which in turn increases nutrient uptake, e.g. phosphorous, thereby increasing photosynthesis and biomass (Singer et al. 2020). However, photosynthetic responses to eCO_2 depend not only on plant phylogeny, but also on duration of exposure to eCO_2 (Wang and Wang 2021a). CO_2-induced photosynthetic downregulation as a result of age-dependent changes in plant physiology has been noticed, mainly in long-term experiments (Bellasio et al. 2018; Bhargava and Mishra 2021). Increase in NSCs and reduction in leaf N, rate of photosynthetic Rubisco carboxylation (V_{cmax}) and photosynthetic electron transport rate (J_{max}) over time are implicated as the main drivers of photosynthetic downregulation (Wang and Wang 2021a). The high capacity for ribulose bisphosphate (RuBP) regeneration relative to Rubisco has been reported as a cause of reduction in photosynthetic capacity, leading to eventual downregulation (Bhargava and Mishra 2021; Singer et al. 2020). Ascertaining plant responses to eCO_2 requires thorough assessment of physiological processes inherent in photosynthesis as well as mechanisms underlying these processes across a wide range of CO_2 concentrations and plant traits on long-term basis (Poorter et al.

2021). Amongst others, discerning responses of V_{cmax}, J_{max} and g_s to eCO_2 may provide insights into processes regulating CO_2 diffusion into the leaves and its use for photosynthesis.

A meta-analysis was conducted, firstly, to assess the magnitude and direction of the effects of varying eCO_2 concentrations on woody plant growth, biomass production, photosynthetic characteristics, foliage N content, and water relations. Secondly, to assess the effect of duration of woody plant exposure to eCO_2 on plant biomass, growth, physiology, foliar quality and water relations. Thirdly, to assess how woody plant functional traits modulate responses to eCO_2. We answer the following questions: (1) how does eCO_2 affect below and above-ground productivity, morpho-physiology, foliage nutrient content, and water relations of woody plants? (2) How do woody plants with different phenology, N-fixation ability and leaf characteristics respond to eCO_2?

Materials and methods

Data collection

We compiled a database through extensive online search of peer-reviewed global studies published from 1985 to 2021 that report woody plant responses to eCO_2 (Additional file 1: Fig. S1). The literature search was conducted in Scopus, Science Direct, Google Scholar, BioOne Complete and Web of Science. To qualify for inclusion in this meta-analysis, studies had to meet the following criteria: (1) the experiment conducted paired observations at eCO_2 and aCO_2 treatments; (2) experiment was conducted exclusively on woody plants, preferably, but not limited to, trees used in forestry or grow naturally in forests, woodlands, bushlands and savannas; (3) experimental plants were exposed to eCO_2 and aCO_2 at the same time; (4) growth conditions, e.g. soil physico-chemical composition and hydro-thermal conditions were similar in experimental units (pots/plots) of eCO_2 and aCO_2 treatments and (5) experimental plants were grown as mono-species or monoculture stands, otherwise if grown as mixed stand, we considered the studies where species responses were reported separately.

We obtained a total of 1566 peer-reviewed studies, of which 100 studies with 611 observations (Additional file 1: Fig. S1), reporting on 119 woody species met the selection criteria. The response variables studied included biomass (shoot, root and total; g), shoot height (SH; cm), leaf area index (LAI; m^2 m^{-2}), light-saturated photosynthesis (A_{max}; μmol CO_2 m^{-2} s^{-1}), maximum rate of photosynthetic Rubisco carboxylation (V_{cmax}; μmol m^{-2} s^{-1}), apparent maximum rate of photosynthetic electron transport (J_{max}; μmol m^{-2} s^{-1}), leaf N on an area basis (g m^{-2}), carbon:nitrogen ratio (C:N), stomatal conductance (g_s; mmol H_2O m^{-2} s^{-1}), transpiration rate (Tr; mmol H_2O m^{-2} s^{-1}) and water use efficiency (WUE; μmol CO_2 $mmol^{-1}$ H_2O). The following search keywords were used: "atmospheric CO_2" or "elevated CO_2 or "rising CO_2" or "CO_2 enrichment" in combination with (1) woody plant physiology, (2) photosynthesis, (3) below and above-ground biomass, (4) shoot growth, (5) water loss or transpiration, (6) water use efficiency, (7) stomatal conductance and (8) leaf N contents. When the response variables were reported in units different from those listed in this study, the appropriate conversions were applied.

The CO_2 treatment was considered elevated when the concentration was $\geq$600–1000 μmol mol^{-1} and ambient when it falls within a range of 300–400 μmol mol^{-1}. The eCO_2 treatment was categorized into three discrete concentrations of < 700, 700 and > 700 μmol mol^{-1}. The 700 μmol mol^{-1} CO_2 was used as a reference scenario based on the IPCC Special Report on Emissions Scenarios (SRES A1B) which predicted that CO_2 will rise to 700 μmol mol^{-1} in 2100, whereas < 700 and > 700 μmol mol^{-1} represent Representative Concentration Pathway scenarios (RCP 4.5 and 8.5), respectively (Meinshausen et al. 2011). RCP 4.5 represents a scenario where CO_2 rises below 700 μmol mol^{-1} (approximately 650 μmol mol^{-1}; Thomson et al. 2011), whilst RCP 8.5 represents a rise above 700 μmol mol^{-1} (approximately 936 μmol mol^{-1}) in 2100 (Hu et al. 2018). These RCPs differ in that RCP 4.5 assumes a scenario where measures are put in place to mitigate gas emissions (Thomson et al. 2011), whereas RCP 8.5 assumes a business-as-usual scenario without reductions in gas emissions (Schwalm et al. 2020).

In each study, we recorded mean ($\overline{X}$), standard deviation, sample size, reference and study duration, ambient and elevated CO_2 treatments. The $\overline{X}s$ were extracted directly from tables and or through digitizing figures using Engauge digitizer V 4.1 software (http://digitizer.sourceforge.net/).

This meta-analysis comprised largely of short-term studies, in which woody plants were exposed to eCO_2 for a median time of less than a year (Additional file 1: Fig. S16 to S20). For short-term studies that conducted repeated measures, we selected $\overline{X}$ of the last sampling date because the time for plant acclimatization to CO_2 chambers was very short (< 2 weeks) in some studies. These generally include studies in which woody plant seedlings were germinated or transplanted outdoors and later transferred to CO_2 chambers. However, for longer-term studies, running over a year, we applied a more conservative approach, in which we averaged the $\overline{X}s$ across repeated measures (Poorter et al. 2021). The duration (length) of tree exposure to eCO_2 was recorded for each observation to study age-related responses. Thereafter, the time of exposure to eCO_2 was categorized into the following five classes: < 0.5 year (< 6 months), 0.5–1 year, > 1–2 years, > 2–3 years and > 3 years.

In factorial experiments, we selected the CO_2 treatment where covariates were set at ambient conditions. Thus, in scenarios where drought was manipulated by reducing water supply, $\overline{X}$ for well-watered scenario was selected, assuming that watering was applied close to field capacity. Moreover, when soil fertility and light were manipulated, we selected treatments where woody plants were grown at or close to optimal rate of nutrient supply under full sunlight. If different woody plant species and or subspecies or varieties of the same species were investigated in one study, the observation for each species or variety was considered as an independent case study. Woody plant species were categorized according to N-fixation ability (leguminous and non-leguminous), leaf type (compound leaves with small leaflets, needle-like leaves, narrow leaves and broadleaves) and phenology (evergreen and deciduous). The leaf classification and description is presented in Table 1.

Meta-analysis

The meta-analysis was executed in MetaXL Microsoft (MS Excel addin) version 5.3 (Barendregt et al. 2013). The log-transformed response ratios (lnRR) between treatment (eCO_2) and control (aCO_2) were computed for each response variable in each study. Thereafter, the overall mean response ratios were calculated using mixed effects models. The positive lnRR indicates increase, negative indicates decrease and zero denotes no change. The lnRR employed in this study was as follows:

$$\ln \mathrm{RR} = \ln \frac{\overline{X}_{\mathrm{eCO_2}}}{\overline{X}_{\mathrm{aCO_2}}}, \quad (1)$$

where $\overline{X}_e$ and $\overline{X}_a$ are mean values for elevated and ambient CO_2, respectively.

Here, the lnRRs were converted to percentage response as follows:

$$\text{Percentage change(PC)} = (\ln\mathrm{RR} - 1) \times 100\%. \quad (2)$$

To assess potential bias of the studies, we analysed Spearman's rank-order correlations between sample sizes and InRRs, with the logic that significant ($p < 0.05$) correlation depicts higher bias. This emanates from work done by Wang et al. (2012) which states that, studies that report large mean differences between treatment and control are highly likely to be published compared to studies reporting marginal differences. For all response variables, no significant ($p > 0.05$) correlations were found between response ratios and sample sizes. Thereafter, bootstrapping of data was conducted to generate the 95% confidence intervals (CIs) using 9999 iterations.

If the 95% CI overlaps with zero, the differences between eCO_2 and aCO_2 were regarded as insignificant. The significant differences between eCO_2 concentrations ($n = 3$), N-fixation status ($n = 2$), leaf phenology ($n = 2$), leaf types ($n = 4$) and duration of exposure to eCO_2 ($n = 5$) were affirmed if the 95% CIs did not overlap each other. The between-study variance (I^2) was calculated to examine if the significance of pooled response ratios occurred by chance or due to study heterogeneity. I^2 was computed as:

$$I^2 = 100\% \times \frac{Q_c - df}{Q_c}, \quad (3)$$

where Q_c is the Cochran's Q heterogeneity statistic and df is the degree of freedom (Higgins et al. 2003).

If I^2 was large (> 50%) and the p-value associated with I^2 was significant ($p < 0.05$), removal of outlier studies was conducted to reduce I^2 below 25% (Patsopoulos et al. 2008). To achieve this, we plotted box plots and density plots of the response ratios and applied a remove-and-replace approach, where outlier studies were removed manually and replaced by another study to maintain adequate sample size (Additional file 1: Fig. S1). For the simplicity, the outlier studies were regarded as the studies with response ratios greater than 75thQ + 1.5IQR and lower than 25thQ − 1.5IQR. Here, Q = quartiles (25 and 75th) and IQR = interquartile range. However, the scarcity of studies for some variables constrained the remove-and-replace approach. Thus, the results for the variables represented by at most five studies should be interpreted cautiously as their large CIs may lead to a type 1 error. The regression of root vs shoot biomass, root biomass vs LAI, A_{max} vs leaf N, A_{max} vs V_{cmax}, A_{max} vs J_{max}, A_{max} vs g_s, WUE vs Tr and WUE vs g_s were conducted to study bivariate relationships. The data for each pair of variables used in each relationship were extracted from the same study.

Results

Effect of varying eCO_2 concentrations

The eCO_2 significantly increased total biomass (T_b) compared to aCO_2 and T_b responses were similar across the three eCO_2 concentrations (Fig. 1a). Shoot (S_b) and root biomass (R_b) were enhanced on average by 33 and 34%, respectively, at eCO_2, but the responses were comparable across the three eCO_2 concentrations (Fig. 1b and c). Leaf area index (LAI) and shoot height (SH) were enhanced by comparable magnitude at 700 and > 700 μmol mol^{-1}, with both LAI and SH increasing twofold more at > 700 than 700 μmol mol^{-1} (Fig. 1d and e). The eCO_2 caused

Table 1 The description and demonstration of leaf types of woody plants. Leaf images were adapted from www.google.com

Type	Description	Demonstration
Compound leaves with small leaflets	This leaf type included pinnately compound leaves with rows of small leaflets around a central stalk (petiole). Leaves exhibit a feathery or fernlike shape and some have thorns at the base. Examples include mostly *Acacias*, *Dichrostachys*, *Prosopis, Leucaena* species, etc	
Needle-like leaves	These are narrow and long leaves with sharp, rigid tips. They are harder with a thick wax layer refered to as cuticle. The species characterized by these leaves produce cones. The examples include conifers (*Picea*, *Tsuga*, *Pinus*, *Taxodium* species, etc.)	
Narrow leaves	These included leaves with long and narrow leaflets which are softer than those of conifers. The examples include *Olea*, *Eucalyptus*, *Ormosia*, *Acacia melanoxylon, Acacia pycnantha*, etc. The term "narrow" was used in relation to broad leaves. So, these leaves were narrower than broad leaves	
Broad leaves	Leaves are wider and have a visible network of veins. These leaves included lobed leaves, toothed and untoothed leaves. Examples include *Quercus*, *Acer*, *Tilia*, *Prunus*, *Populus*, *Fagus*, *Celtis* species, etc	

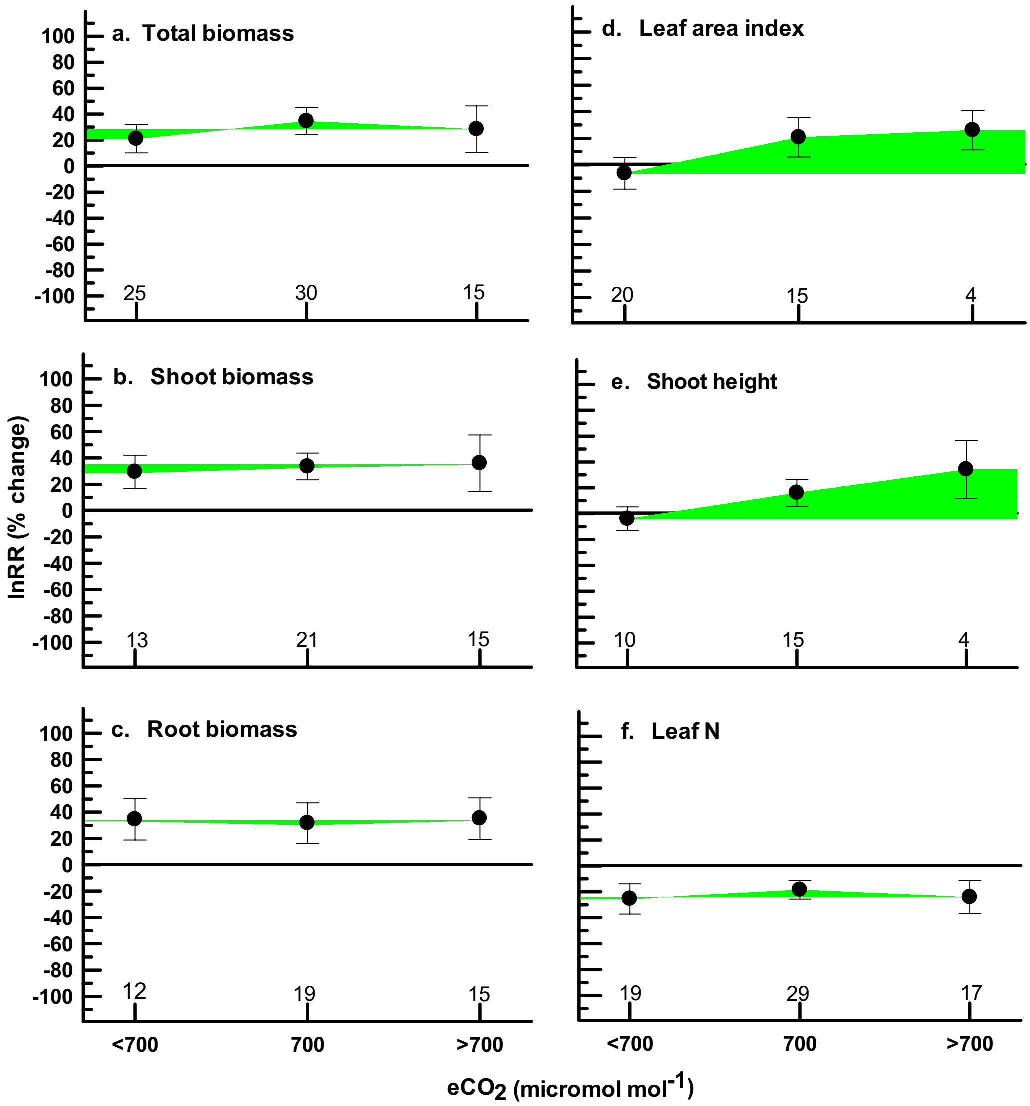

Fig. 1 Percentage change (± 95% CI) in biomass (**a**–**c**), leaf area index (**d**), growth (**e**) and leaf N (**f**) of woody plants grown at eCO_2. The whiskers denote 95% CI and the circles denote mean percentage change (MPC) between aCO_2 and eCO_2. The numbers above the major ticks of the *X*-axis denote number of observations. The area fill (( )) shows the trends and the magnitude of differences between the eCO_2 concentrations. The wider the area the bigger the difference between MPCs

a substantial decrease in leaf N, but the responses were similar across the three eCO_2 concentrations (Fig. 1f).

The A_{max} increased significantly at 700 and >700 µmol mol^{-1} by comparable magnitudes of 21 and 29%, respectively (Fig. 2a). On the other hand, there was no noticeable effect of eCO_2 of <700 and 700 µmol mol^{-1} on V_{cmax} and J_{max}, but rather, both parameters decreased significantly at >700 µmol mol^{-1} (Fig. 2b and c). The g_s decreased significantly on average by 32% at eCO_2 relative to aCO_2 (Fig. 2d). However, Tr declined only at >700 µmol mol^{-1} (Fig. 2e). WUE increased significantly by 35 to 63% from <700 to >700 µmol mol^{-1} (Fig. 2f).

The A_{max} was significantly related to leaf N ($r^2 = 0.30$, $p = 0.024$), J_{max} ($r^2 = 0.83$, $p = 0.002$) and g_s ($r^2 = 0.31$, $p = 0.002$), but not with V_{cmax} ($p > 0.05$; Fig. 3a–d). WUE was negatively related to g_s ($r^2 = 0.12$, $p = 0.046$) and Tr ($r^2 = 0.46$, $p = 0.001$) and positively related to A_{max} ($r^2 = 0.57$, $p < 0.001$; Fig. 3e–g).

Effect of duration of woody plant exposure to eCO_2

Total biomass decreased with increase in duration of exposure to eCO_2, with T_b increasing twofold higher when trees were exposed to eCO_2 for <0.5 year than >3 years (Fig. 4a). Initially, shoot biomass increased by

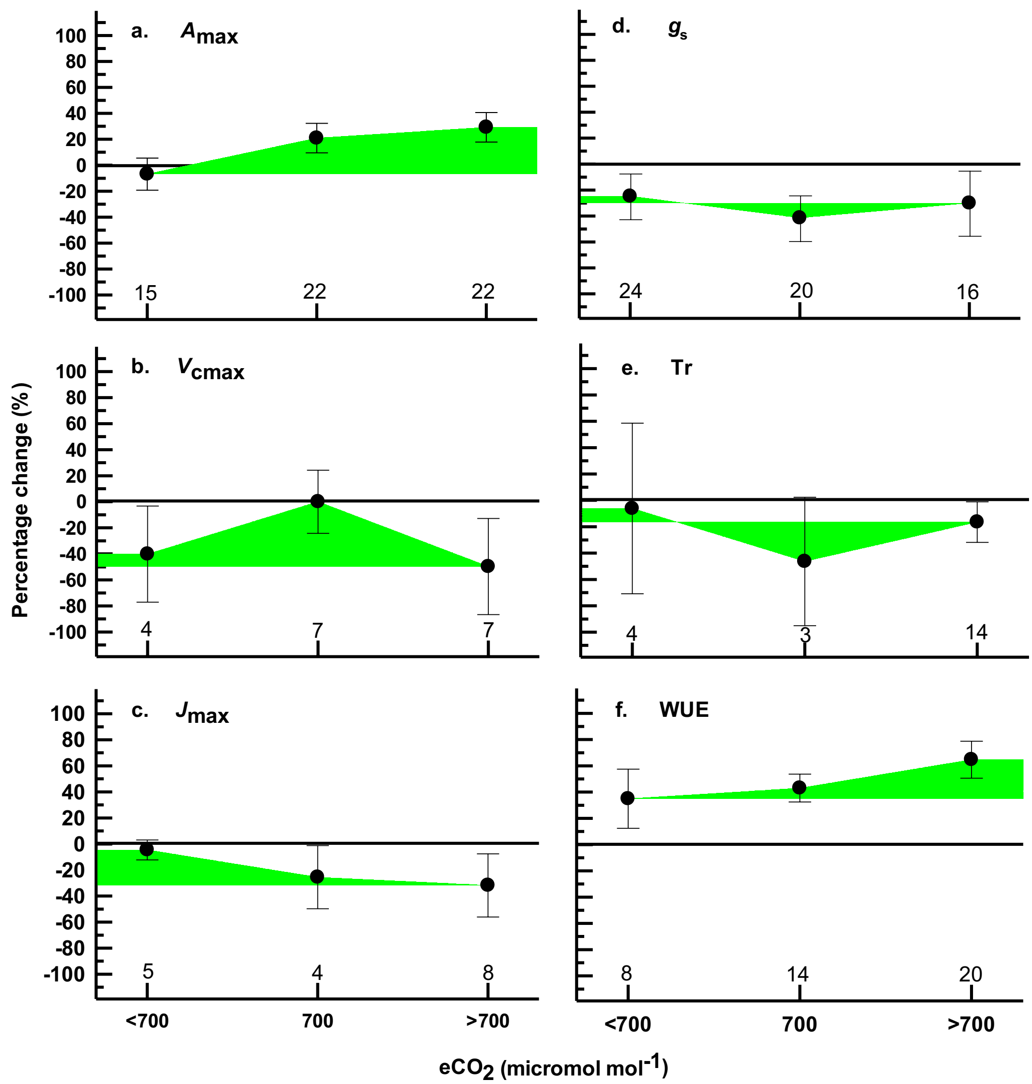

Fig. 2 Percentage change (± 95% CI) in photosynthetic characteristics (**a**–**c**) and water relations (**d**–**f**) of woody plants grown at eCO_2. The whiskers denote 95% CI and the circles denote mean percentage change (MPC) between aCO_2 and eCO_2. The numbers above the major ticks of the *X*-axis denote number of observations. The area fill (( )) shows the trends and the magnitude of differences between the eCO_2 concentrations. The wider the area the bigger the difference between MPCs

13% from < 0.5 to > 1–2 years, after which it declined to aCO_2 levels for trees exposed for > 3 years (Fig. 4b). Root biomass showed similar trends, both increasing by great magnitude for trees exposed to eCO_2 for < 0.5 year than when exposed for longer (Fig. 4c). Leaf N varied widely over different duration of exposure to eCO_2, but differences between eCO_2 and aCO_2 disappeared when plants were exposed for > 1 year to eCO_2 (Fig. 4d).

A_{max} varied over duration of exposure to eCO_2, with significant increase observed when trees were exposed for < 0.5 year (Fig. 5a). Generally, eCO_2 increased A_{max} by 30% for trees exposed for > 2–3 years, whereas it increased by 10% for trees exposed for > 3 years (Fig. 5a). V_{cmax} and J_{max} depicted similar response patterns, being low for trees exposed to eCO_2 for < 0.5 year than when exposed for longer (Fig. 5b and c). Stomatal conductance declined significantly at eCO_2, but the duration of exposure to eCO_2 had no effect on g_s (Fig. 5d). Similarly, transpiration did not differ across duration of exposure to eCO_2 (Fig. 5e). However, WUE increased significantly by 65% for the trees exposed for < 0.5 year compared to trees exposed for > 1–2 years (27%). There were no differences observed for trees exposed for < 0.5 year and other duration of exposure (Fig. 5f).

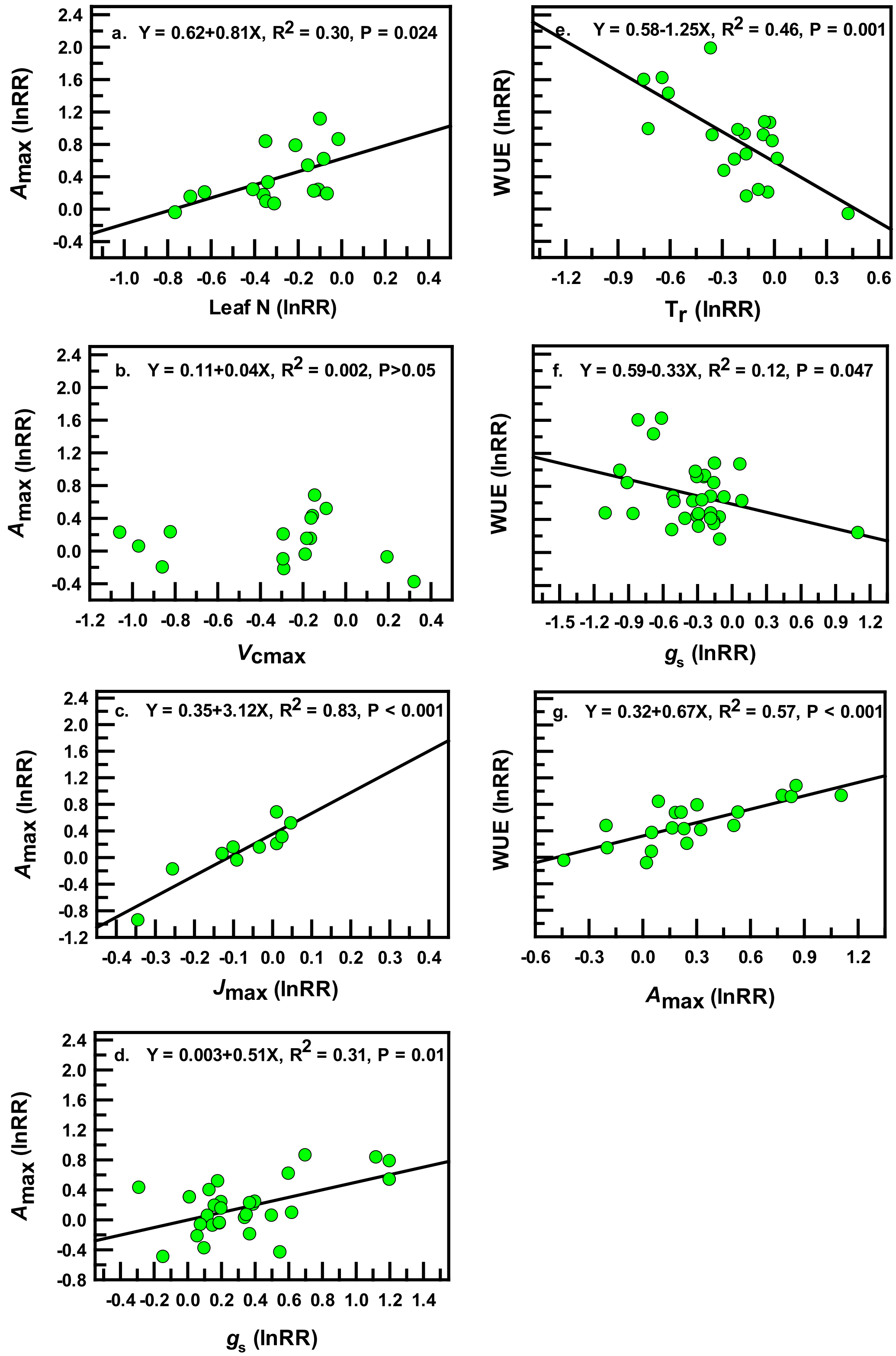

Fig. 3 The relationships between photosynthesis (A_{max}) and leaf N, photosynthetic Rubisco carboxylation (V_{cmax}) and photosynthetic electron transport rate (J_{max}) from **a** to **d** and water use efficiency (WUE) and transpiration (Tr), stomatal conductance (g_s) and A_{max} from **e** to **g**

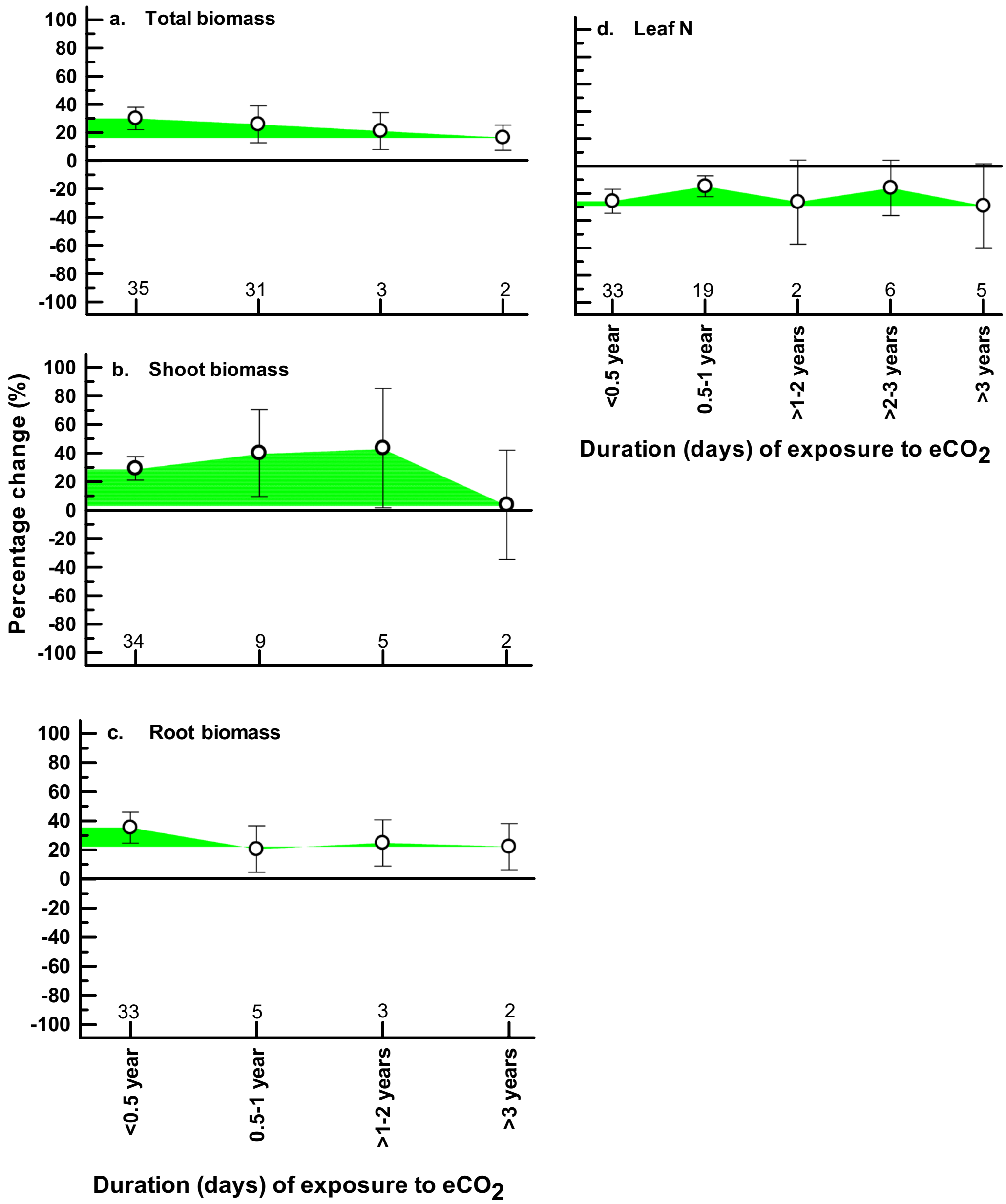

Fig. 4 Percentage change (± 95% CI) in biomass (**a**–**c**) and leaf N (**d**) of woody plants over different duration (years) of exposure to eCO_2. The whiskers denote 95% CI and the circles denote mean percentage change (MPC) between aCO_2 and eCO_2. The numbers above the major ticks of the *X*-axis denote number of observations. The area fill (( )) shows the trends and the magnitude of differences between the different duration of exposure to eCO_2. The wider the area the bigger the difference between MPCs. Key to duration of exposure: 0.5 years denotes half of a year (6 months). There were no observations reported for a period > 2–3 years except for leaf N

Effect of woody plant traits

N-fixation ability had a significant effect on T_b, with leguminous trees exhibiting an increase of 38% compared to non-leguminous trees (27%) at eCO_2 (Fig. 6a). Although N-fixation ability did not affect S_b and R_b, leguminous trees invested more on S_b, whereas non-leguminous trees invested on R_b at eCO_2 (Fig. 6d and g). The leaf phenology had a significant effect on SH, with deciduous trees exhibiting eightfold increase in SH than evergreen trees at eCO_2 (Fig. 7b). Leaf N decreased significantly twofold in non-leguminous trees than legumes (Fig. 7g) and evergreen than deciduous trees (Fig. 7h). Needle-like leaves attained two- to fourfold higher decrease in leaf N than other leaf types (Fig. 7i).

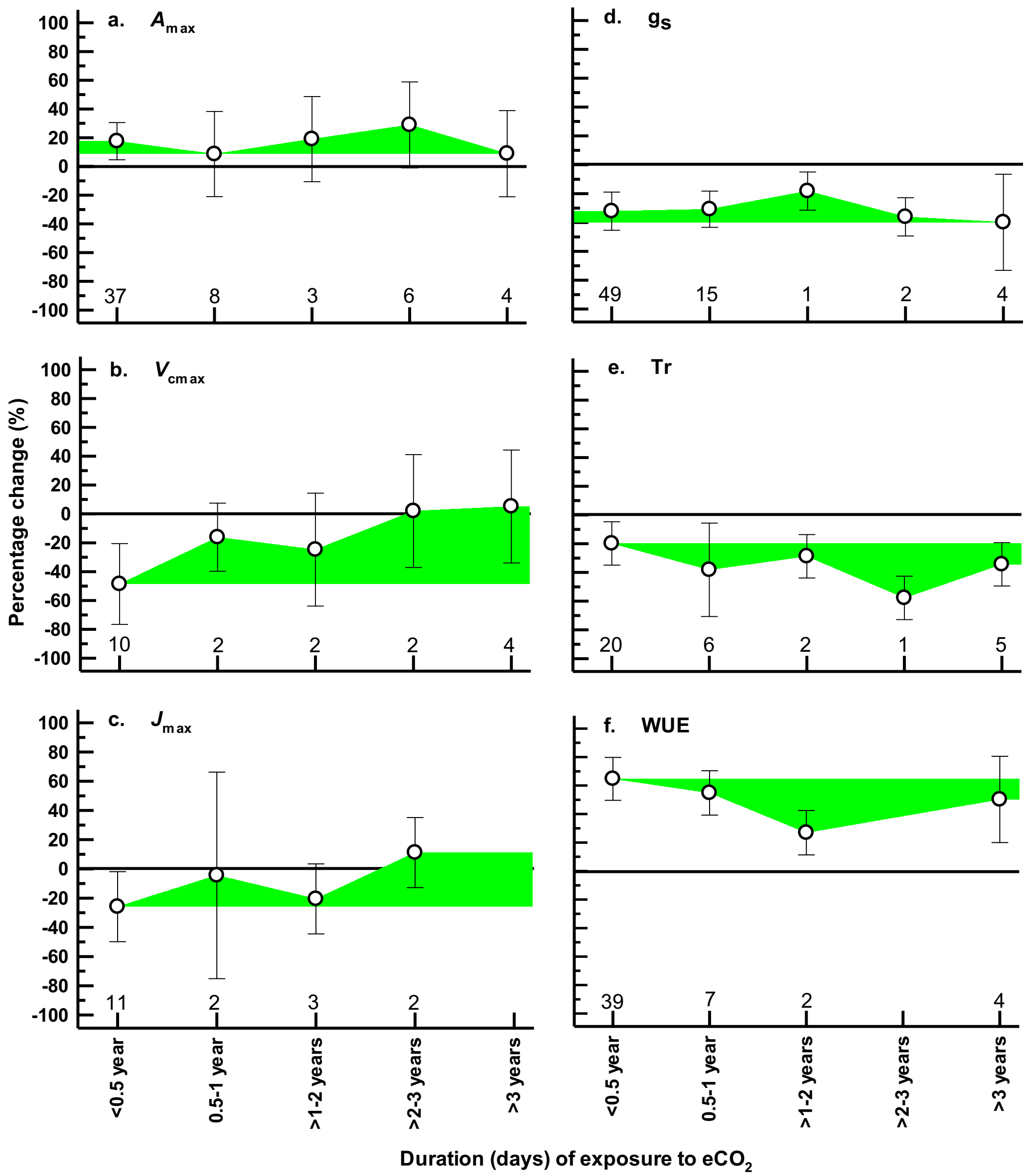

Fig. 5 Percentage change (± 95% CI) in photosynthetic characteristics (**a**–**c**), stomatal conductance (**d**) and water relations (**e**–**f**) of woody plants over different duration (years) of exposure to eCO_2. The whiskers denote 95% CI and the circles denote mean percentage change (MPC) between aCO_2 and eCO_2. The numbers above the major ticks of the *x*-axis denote number of observations. The area fill (( )) shows the trends and the magnitude of differences between duration of exposure to eCO_2. The wider the area the bigger the difference between MPCs. Key to duration of exposure: 0.5 years denotes half of a year (6 months)

Numerically, leguminous trees attained twofold higher increase in A_{max} than non-leguminous trees at eCO_2 (Fig. 8a). The A_{max} was not enhanced by eCO_2 for deciduous trees, whereas it increased by 21% for evergreen trees (Fig. 8b). Compound leaves with small leaflets (27%) and broad leaves (16%) attained more increase in A_{max}, whereas needle-like and narrow leaves were unresponsive to eCO_2 (Fig. 8c). The N-fixation ability significantly affected the responses of V_{cmax} to eCO_2, with non-leguminous trees exhibiting threefold decrease than leguminous trees (Fig. 8d). The V_{cmax} decreased significantly for evergreen trees at eCO_2, but there was no marked difference between evergreen (− 28%) and deciduous trees (− 26%; Fig. 8e). The compound leaves with small leaflets exhibited a decrease in V_{cmax}, whereas other leaf types were unresponsive to eCO_2 (Fig. 8f). Leguminous trees showed greater decrease in J_{max} and neither

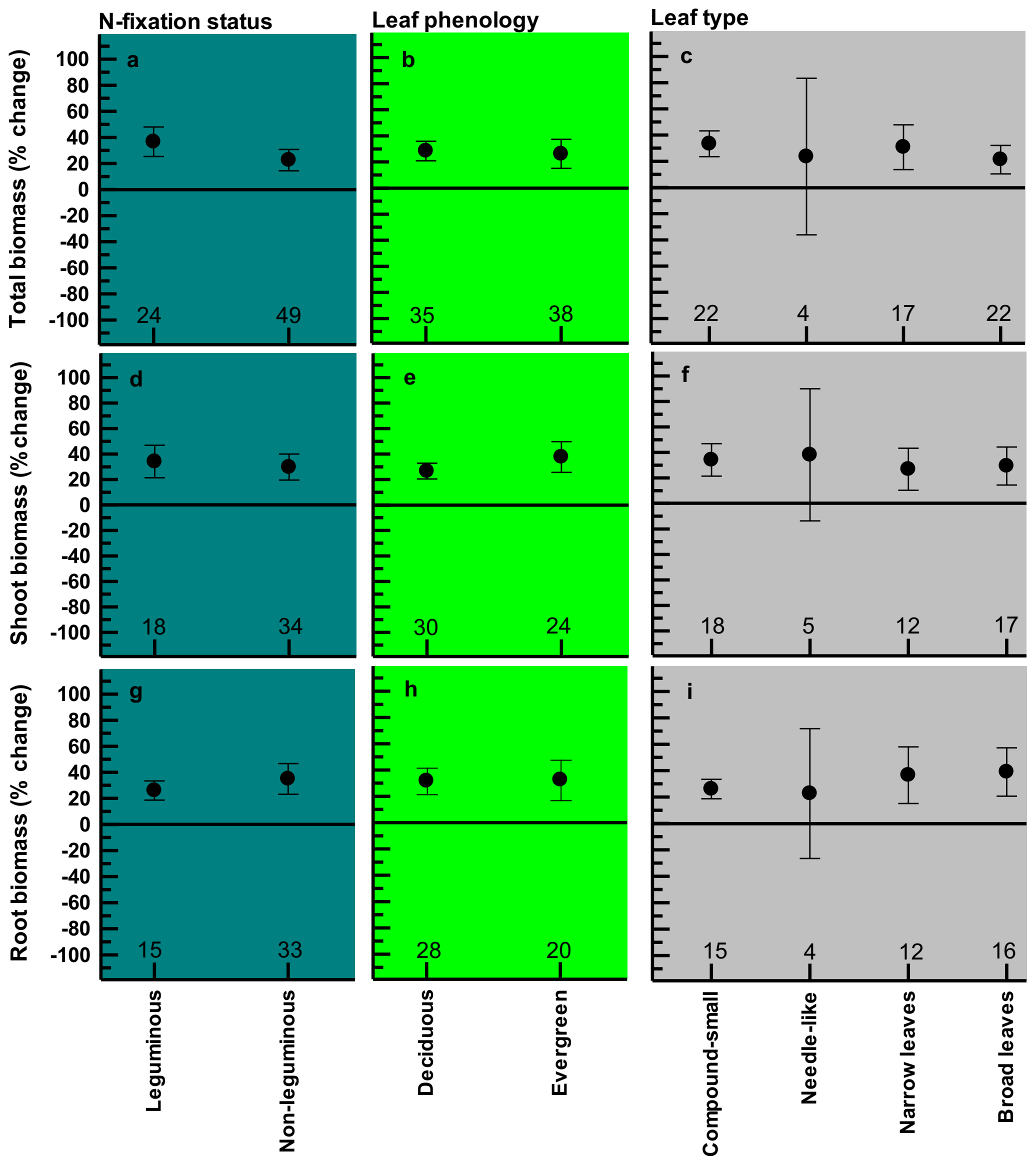

Fig. 6 Percentage change (± 95% CI) in biomass of woody plants with different N-fixation ability (**a**, **d** and **g**), leaf phenology (**b**, **e** and **h**) and leaf types (**c**, **f** and **i**) grown at eCO_2. The whiskers denote 95% CI and the circles denote mean percentage change. The numbers above the major ticks of the *X*-axis denote number of observations. Key to leaf types: Compound-small = compound leaves with small leaflets and Needle-like = needle-like leaves

leaf phenology nor leaf type had a significant effect on J_{max} at eCO_2 (Fig. 8g).

The g_s decreased significantly at eCO_2, more so for leguminous (− 47%) than non-leguminous trees (− 27%; Fig. 9a). The responses of deciduous and evergreen trees on g_s were comparable (Fig. 9b). The decrease in g_s at eCO_2 was significant for broad leaves and compound leaves with small leaflets (Fig. 9c). Transpiration rate was unresponsive to eCO_2 for leguminous and deciduous trees, particularly those bearing compound leaves with small leaflets (Fig. 9d–f). WUE was higher for non-leguminous (69%) than leguminous trees (46%), evergreen (69%) than deciduous trees (52%; Fig. 9g and h) and broad leaves than other leaf types (Fig. 9i).

Discussion

Woody plant responses to varying eCO_2 concentrations

This study indicated that eCO_2 enhances both shoot and root biomass production of trees growing at eCO_2 and this phenomenon has also been reported elsewhere

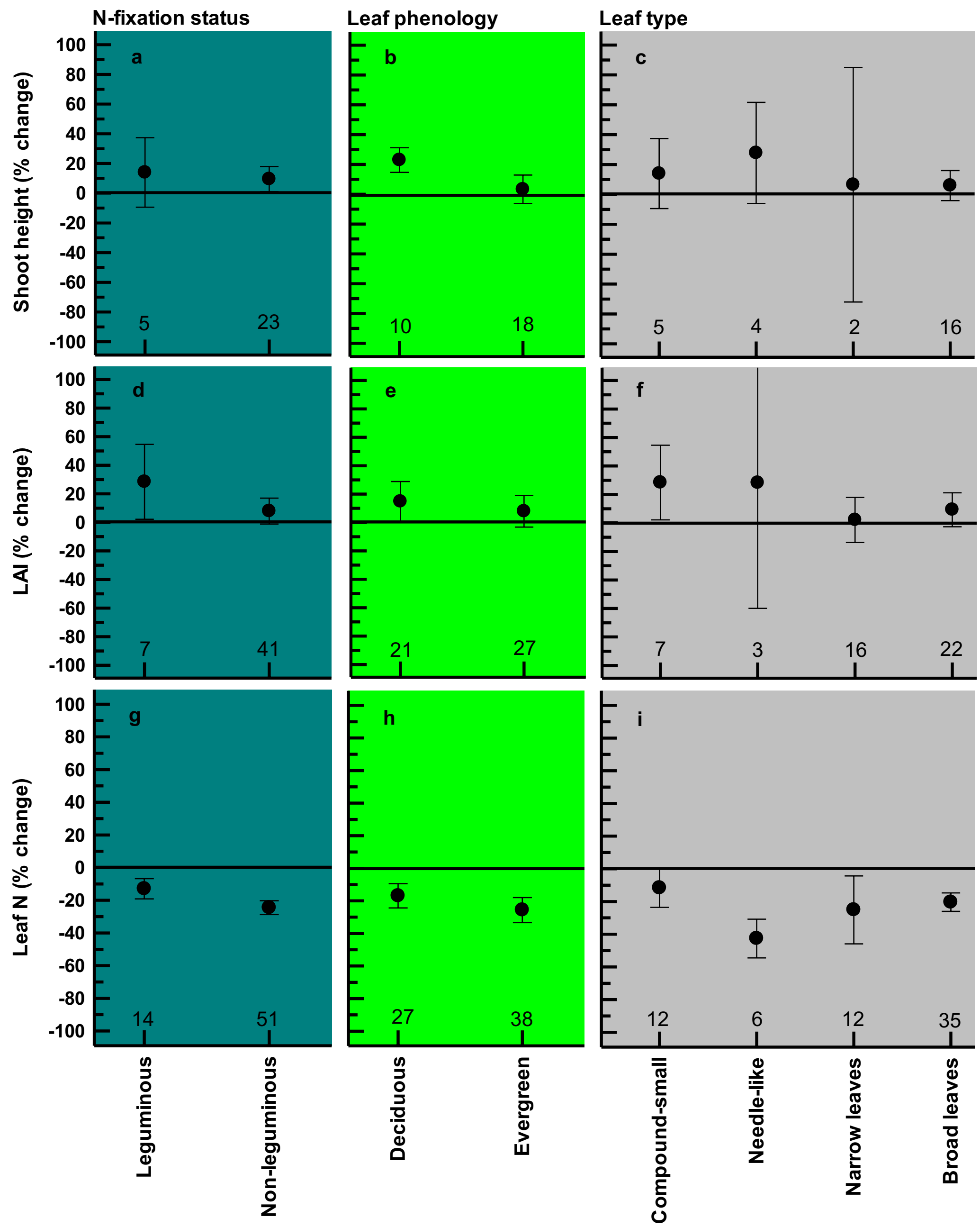

Fig. 7 Percentage change (± 95% CI) in shoot height, LAI and leaf N of woody plants with different N-fixation ability (**a**, **d** and **g**), leaf phenology (**b**, **e** and **h**) and leaf types (**c**, **f** and **i**) grown at eCO_2. The whiskers denote 95% CI and the circles denote mean percentage change. The numbers above the major ticks of the *x*-axis denote number of observations. Key to leaf types: Compound-small = compound leaves with small leaflets and Needle-like = needle-like leaves

(Ainsworth and Long 2005; de Graff et al. 2006; Wang et al. 2012). These responses are more prevalent in juvenile trees because young trees are more responsive to CO_2 and exhibit exponential growth than older trees (Pinkard et al. 2010; Wang et al. 2012). In more than 90% of studies in this meta-analysis, trees were exposed as seedlings to eCO_2, which substantiates higher biomass responses to eCO_2. Otherwise, older trees would respond differently, as their photosynthesis declines with age, since they are no longer exhibiting active vigorous growth (Walker et al. 2020). As woody plants mature, more C is invested in non-photosynthetic

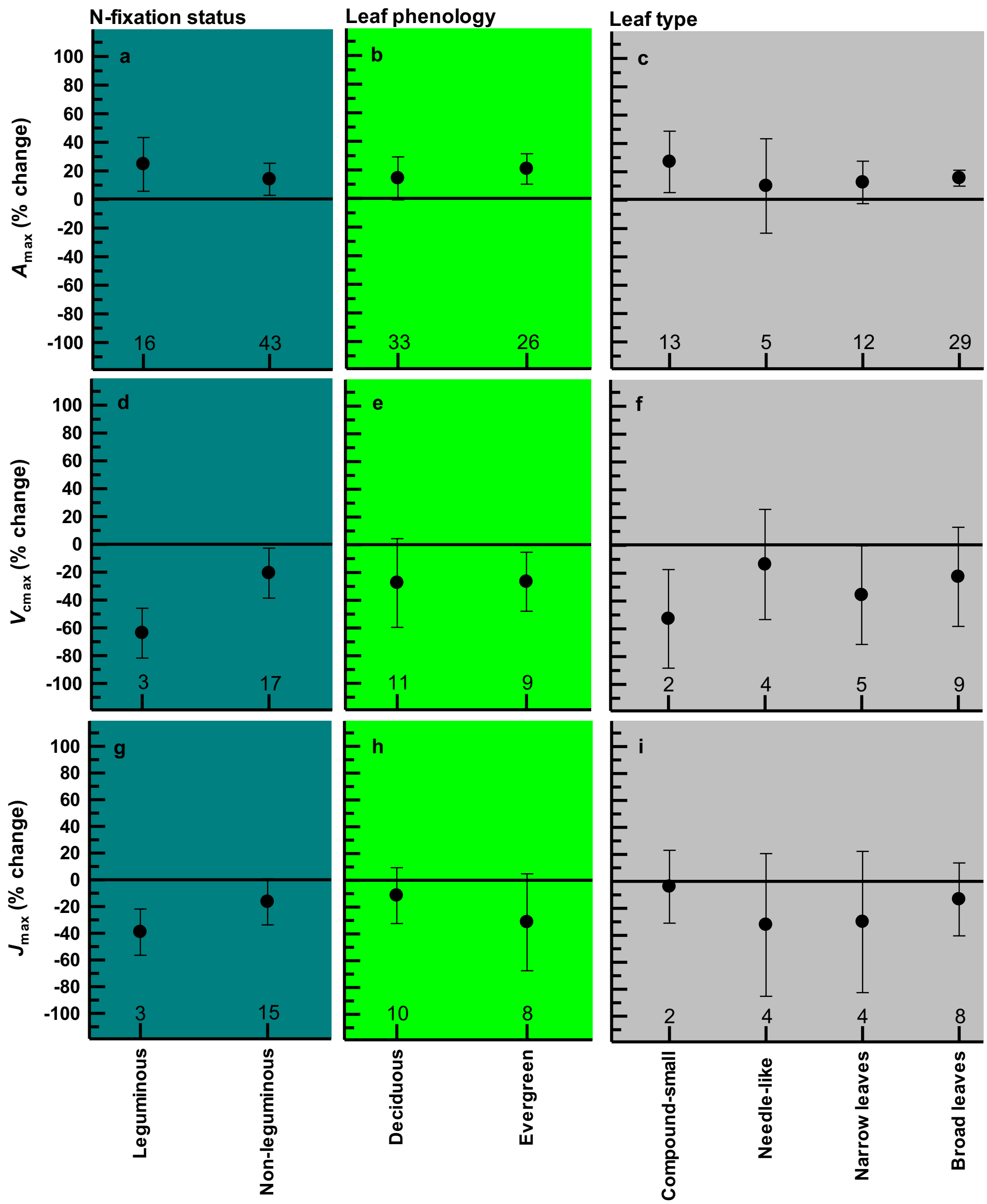

Fig. 8 Percentage change (±95% CI) in photosynthetic characteristics (A_{max}, V_{cmax} and J_{max}) of woody plants with different N-fixation ability (**a**, **d** and **g**), leaf phenology (**b**, **e** and **h**) and leaf types (**c**, **f** and **i**) grown at eCO_2. The whiskers denote 95% CI and the circles denote mean percentage change. The numbers above the major ticks of the *X*-axis denote number of observations. Key to leaf types: Compound-small = compound leaves with small leaflets and Needle-like = needle-like leaves

structures, resulting in reduced photosynthetic capacity which reduces biomass production (Curtis and Wang 1998). The root and shoot biomass were similar across the three eCO_2 concentrations, indicating that above and below-ground biomass increase regardless of the degree of rise in CO_2. The positive relationship between root biomass and shoot biomass, and LAI indicates that C allocation to roots plays a big role in increasing woody canopies (Additional file 1: Fig. S3). The higher root biomass is not only important as a C sink, but also for soil water and nutrient uptake (Thompson et al. 2017; Wang and Wang 2021b). Plants that produce more roots, largely deep-rooted trees have an advantage to access ground water during periods of moisture

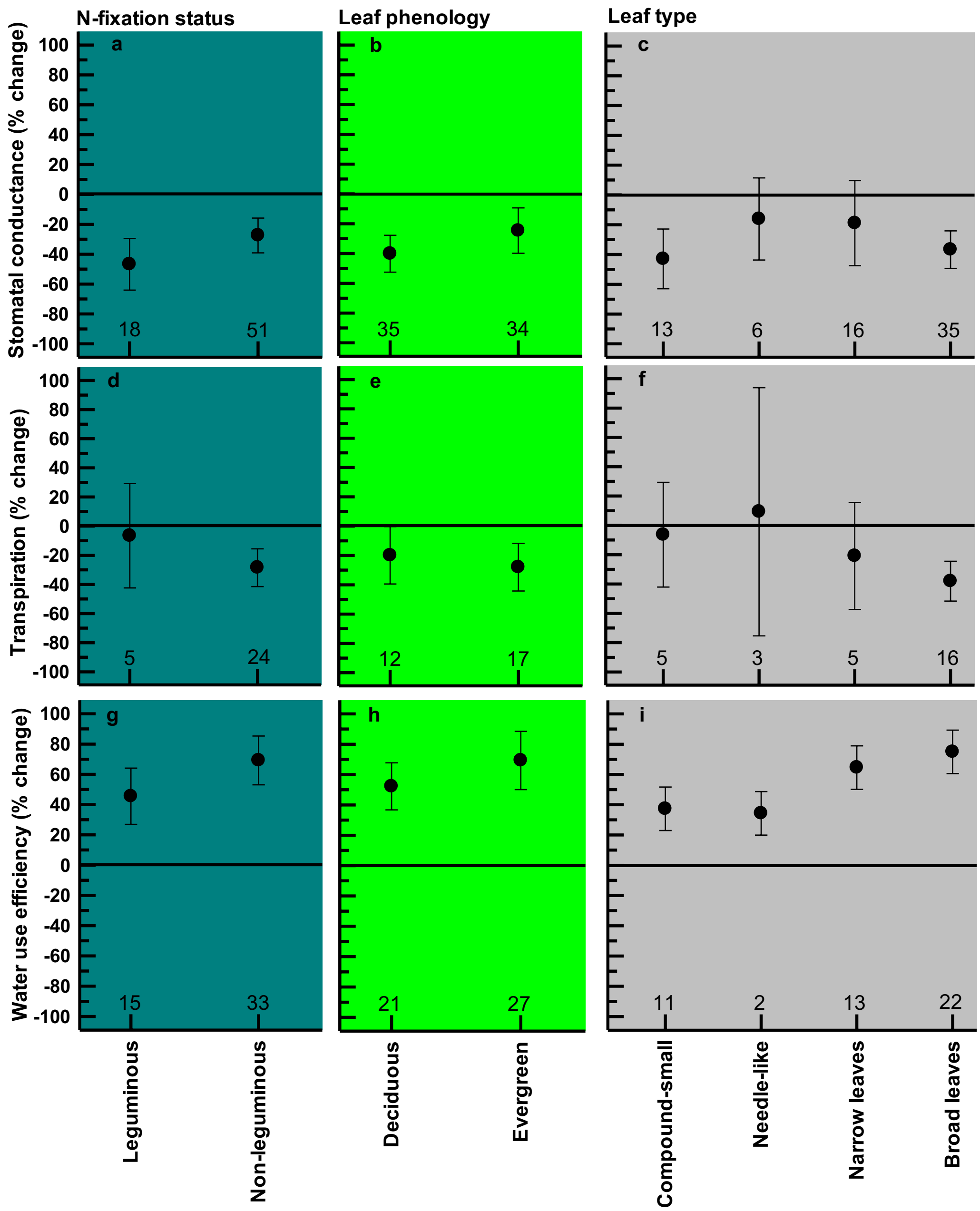

Fig. 9 Percentage change (±95% CI) in stomatal conductance, transpiration rate and water use efficiency of woody plants with different N-fixation ability (**a**, **d** and **g**), leaf phenology (**b**, **e** and **h**) and leaf types (**c**, **f** and **i**) grown at eCO_2. The whiskers denote 95% CI and the circles denote mean percentage change. The numbers above the major ticks of the *X*-axis denote number of observations. Key to leaf types: Compound-small = compound leaves with small leaflets and needle-like = needle-like leaves

stress and drought (Uddin et al. 2018). While higher biomass investment on leaves increases C sequestration, the residence time of C might be shorter relative to roots (Walker et al. 2020). Leaf area index was similar between 700 and >700 μmol mol^{-1} (Fig. 1d), but shoot height was taller at >700 μmol mol^{-1} (Fig. 1e), suggesting that CO_2 might increase stem elongation without significant effects on tree canopy sizes if eCO_2 increases above 700 μmol mol^{-1}. The lack of increase in LAI at >700 μmol mol^{-1} was likely due to the lack of increase in the rate of photosynthesis as depicted by similar A_{max} at 700 and >700 μmol mol^{-1} (Fig. 2a).

The leaf N content decreased markedly across eCO_2 concentrations, which may be ascribed to N dilution by accumulation of secondary compounds, as depicted by increase in the C:N ratio at eCO_2 (Additional file 1: Fig. S4). Our results further indicated that, regardless of the extent of increase in CO_2 in the future, leaf N will decrease by almost the same magnitude. The eCO_2-driven decrease in leaf N (18–25%) in this study is higher than 16 and 12% decrease reported by Curtis and Wang (1998) and Jayawardena et al. (2021), respectively. In this study, the percentage change in leaf N was calculated from mean N content of the last sampling date for short-term studies, of which for most studies, this time was towards the end of the growing season. Thus, the decline in leaf N could be ascribed to senescing leaves, lack of replacement of older leaves by new ones and N translocation to below-ground plant parts (Tom-Dery et al. 2019).

A decline in leaf N implies that herbivores will depend largely on N-deficient foliage (Coley et al. 2002) and this may need a change of feeding habits (Farkas et al. 2021) and increased foliage intake to compensate for N deficiency (Jayawardena et al. 2021). A decline in leaf N content implied that eCO_2 may reduce decomposition rate of the leaf litter as well as N cycling (Norby et al. 1999). These effects have serious implications not only for herbivores, but also for plant nutrition because N deficiency in the soil may hinder plant growth. The increase in leaf C:N ratio is consistent with Du et al. (2020) in their recent meta-analysis of the responses of leaf nutrients to eCO_2.

The V_{cmax} and J_{max} declined at eCO_2 indicating that rise in CO_2 downregulates carboxylation rate of Rubisco and electron transport rate. A depletion in maximum carboxylation rate of Rubisco at eCO_2 has been reported widely by previous meta-analytic studies working not only with trees, but also with crops and grasses (Wang et al. 2012). However, A_{max} was enhanced by a similar degree at 700 and >700 μmol mol^{-1}, indicating that downregulation of V_{cmax} and J_{max} did not completely negate photosynthesis. Positive relationships between A_{max} and J_{max}, leaf N and g_s (Fig. 3) indicated that photosynthesis was, in fact, controlled by biochemical processes and stomatal aperture at eCO_2. The positive relationship between A_{max} and g_s indicates that despite decline in g_s at eCO_2 concentrations, this did not lead to stomatal limitation of photosynthesis. A reduction in conductance may limit C assimilation, more so in needle-like leaves which have dense leaves and thick cell walls of the photosynthetic cells that may limit diffusion of CO_2 into the chloroplast (Guo et al. 2022). A positive relationship between g_s and A_{max} was also reported by Medrano et al. (2002) and Guo et al. (2022). Since CO_2 activates Rubisco, increased CO_2 diffusion into the active site of Rubisco modulated by g_s means increase in V_{cmax} and thus enhanced A_{max}. For example, when V_{cmax} was similar between eCO_2 and aCO_2, A_{max} increased at 700 μmol mol^{-1}, but when V_{cmax} decreased at >700 μmol mol^{-1}, A_{max} did not increase anymore (Fig. 2a and b). The relationship between V_{cmax} and J_{max} (Additional file 1: Fig. S2), as has been reported in other studies, e.g. Gardner et al. (2021) and Byeon et al. (2021), indicated that enhancement of A_{max} at eCO_2 was a function of a coordination between V_{cmax} and J_{max} (Yang et al. 2021). On the other hand, a coupling between leaf N and A_{max} was not surprising (Fig. 3a), given that 15–35% of leaf N is allocated to Rubisco, a key enzyme facilitating photosynthesis (Evans et al. 1989; Luo et al. 2021). In their recent model of N allocation, Bachofen et al. (2022) showed that more leaf N was partitioned to V_{cmax} in the uppermost and to J_{max} in the bottom of the tree canopy. The relationship between leaf N and A_{max} observed in this study suggests that more leaf N was invested in photosynthetic apparatus. Otherwise, a decoupling between leaf N and A_{max} would suggest a reallocation of N to non-photosynthetic machinery, which would lead to acclimation of A_{max}.

In our meta-analysis, the similarity in A_{max} between 700 and >700 μmol mol^{-1} suggests that eCO_2 may stimulate photosynthesis up to 700 μmol mol^{-1}, above which the rate of stimulation declines in woody plants. This leads to a speculation that, given the linear increase in atmospheric CO_2 with time, photosynthesis may acclimatize to CO_2 above 700 μmol mol^{-1}. This is supported by the trends of LAI which increased by similar magnitude at 700 and >700 μmol mol^{-1} (Fig. 1d), indicating limited enhancement of leaf production and photosynthesis at eCO_2 above 700 μmol mol^{-1}. This could be ascribed to saturation of Rubisco which normally occurs at eCO_2 of 700–1000 μmol mol^{-1} at which photosynthesis is limited by ribulose-1,5-bisphosphate (RubP) regeneration (Bond and Midgley 2000). Similarly, Runkle (2015) attest that the effect of eCO_2 is negligible at 800–1000 μmol mol^{-1}. However, in their meta-analysis, Poorter et al. (2021) found that photosynthesis was saturated at eCO_2 above 1000 μmol mol^{-1}. Albeit they did not study tree responses, Zheng et al. (2018) found that eCO_2 above 600 μmol mol^{-1} downregulated photosynthesis on plants grown at a wide range of 600–1600 μmol mol^{-1}. Photosynthetic downregulation was ascribed to a concurrent downregulation of V_{cmax} and J_{max} at eCO_2 (Zheng et al. 2018). However, it appears that 700 μmol mol^{-1} as an estimate for future eCO_2 may cause uncertainty for future projections. The uncertainty of 700 μmol mol^{-1} is expected, given unpredictable variation in CO_2 emissions in space and time (Prentice et al. 2001). Variability in future CO_2 emissions caused largely by variability in human population increase and energy demand may lead to deviation of future eCO_2 from 700 μmol mol^{-1}, thereby reducing reliability of this concentration for future projections (Prentice et al. 2001).

Stomatal conductance and transpiration rate were reduced and the WUE was increased by eCO_2. The decline in transpiration at eCO_2 was not surprising, as the eCO_2 reduces stomatal conductance and density (Kerstiens et al. 1995). The decline in g_s and Tr coupled with increase in A_{max} under eCO_2 as observed here facilitated increase in water use efficiency. A reduction in g_s at eCO_2 is reported in many studies (Xu et al. 2016; Baligar et al. 2021; Wang and Wang 2021a, b; Zhang et al. 2021) and this response is reported to be more advantageous in water limited areas. In their meta-analyses, Wang and Wang (2021a) and Walker et al. (2020) reported a decrease in g_s in trees grown at eCO_2. Although the decrease of g_s in the current meta-analysis is lower than that reported by Wang and Wang (2021a) and Walker et al. (2020), all these studies concur on that eCO_2 reduces g_s. The negative relationships between WUE and g_s, and Tr suggest that reduction in g_s and Tr improve water status of woody plants grown at eCO_2. The slope was steeper for transpiration (Fig. 3e), signifying that a reduction in water loss plays a more important role in increasing WUE. This may help delay the onset and reduce the degree of moisture stress (Wang et al. 2012), in turn extending the length of the growing season in forest ecosystems (Souza et al. 2019).

Woody plant responses over different duration of exposure to eCO_2

The apparent increases in woody plant biomass for trees exposed for < 0.5 year agrees with other previous studies. Woody plants, more so young plants are highly sensitive and responsive to CO_2 fertilization (Raubenheimer and Ripley 2022). This was also confirmed by greater increases in photosynthesis of trees exposed for < 0.5 year to eCO_2 (Fig. 5a), of which most were exposed as seedlings (Additional file 1). Moreover, water use and N use efficiency are high during early stages of exposure to eCO_2. These together with CO_2 fertilization promote stem elongation and girth size, leaf production and branching, thereby increasing shoot biomass (Bhargava and Mishra 2021). In this study, root biomass as well as total biomass declined with increase in duration of exposure to eCO_2 (Fig. 4a and c), indicating that responses to eCO_2 are age-dependent, as plants acclimatized to eCO_2 as they mature. Similarly, Idso (1999) showed a gradual decline in biomass of *Quercus* and *Pinus* species over a duration of 35 years, with declines commencing as early as less than 5 years of exposure to eCO_2. Our results suggested that over a long-term exposure to eCO_2, trees may exhibit sink limitations due to age-related ecophysiological changes. For root biomass, declining trends were expected given that our dataset was derived largely from pot experiments in which rooting depth probably was limited by the pot size (Curtis and Wang 1998). However, shoot biomass increased up to > 2–3 years of exposure to CO_2 (Fig. 4b), signifying that shoot biomass does not rely only on its relationship with root biomass. This result agrees with Zhang et al. (2011) who found higher shoot biomass 3 years after tree exposure to eCO_2.

A_{max} was enhanced during short-term exposure (< 0.5 year), beyond which A_{max} stimulation became insignificant, with response trend declining towards the levels of aCO_2 for trees exposed for more than 3 years. This result signifies that photosynthetic stimulation by eCO_2 is transient and that it is strongest on actively growing plants (Dusenge et al. 2019). This was confirmed by weakened effects of eCO_2, characterized by photosynthetic acclimation for woody plants exposed for > 3 years (Fig. 5a), 4 to 5 years specifically (Additional file 1: Fig. S10). However, in this study, trees exposed for > 3 years to eCO_2 were already 3–8 years old during application of CO_2 treatment. Thus, we postulate that the age at exposure to eCO_2 could have played a role in photosynthetic acclimation. Photosynthetic acclimation was noticed as early as less than a year of exposure to eCO_2 (Ainsworth et al. 2002; Hymus et al. 2002), after three growing seasons in *Picea sitchensis* (Centrito and Jarvis 1999) and after 10 years for *Liquidambar styraciflua* elsewhere (Warren et al. (2015). Eamus and Jarvis (2004) showed that photosynthesis may acclimatize as early as few months of exposure to eCO_2. Generally, as plants grow, there is more accumulation of non-structural carbohydrates (NSC) accompanied by a depletion of leaf N, which therefore reduces photosynthetic capacity at eCO_2. In this study, we show that leaf N was consistently reduced by eCO_2 over different durations of exposure, with A_{max} appearing to follow the leaf N trends. The downregulation of A_{max} as duration of exposure to eCO_2 increases is more common in evergreen species, as N in previous year's leaves tends to be depleted relative to current year's leaves (Medlyn et al. 1999). V_{cmax} and J_{max} were tightly coupled, depicting similar trends over duration of exposure to eCO_2. However, the coupling of these photosynthetic traits does not appear to have influenced A_{max} responses, as there were no obvious relationships between A_{max} and these parameters over different duration of exposure.

The g_s remained low and similar across different durations of exposure to eCO_2. We found no stomatal acclimation to eCO_2 over time. As a result, transpiration was reduced by almost similar magnitudes across different durations of exposure to eCO_2. Likewise, Wang and Wang (2021a, b) found no stomatal acclimation to eCO_2 in their recent meta-analysis. However, despite the lack of variation in g_s and Tr over time, WUE was highest for woody plants exposed for < 0.5 year to eCO_2, indicating that greater photosynthesis observed in trees exposed for < 0.5 year increased WUE. The numerically low WUE for trees exposed for longer (> 3 years) could be ascribed to acclimation of A_{max}, which probably reduced sink strength of trees, resulting in decline in shoot photosynthetic responses. Another possibly explanation for low WUE could be reallocation of photosynthates to non-photosynthetic organs, e.g. stem and roots instead of leaves, resulting in reduced photosynthesis. This is supported by abrupt decline in shoot production over 3 years of exposure to eCO_2, whereas root biomass was consistently 20% higher in eCO_2 relative to aCO_2. However, this meta-analysis was derived from short-term studies (< 10 years), hence it is unclear how woody plants exposed more than 10 years would respond to eCO_2. This may cause uncertainty in future projections of woody plant responses to future eCO_2 because plant responses to eCO_2 become weak as plants age (Wang and Wang 2021a). Thus, future research on long-term exposure of woody plants using free-air CO_2 enrichment (FACE) is warranted to unpack age-related physiological responses and provide insights into sink strength of forests over a long-term to derive precise projections for future.

Influence of woody plant functional traits on responses to eCO_2

Consistent with previous studies, the current study indicates that leguminous trees attained more biomass than non-leguminous trees at eCO_2. This was expected, given that leguminous trees use symbiosis to fix N, which gives them advantage over non-leguminous trees, especially in N-limited soils (Chen and Markhan 2021; Kou-Giesbrecht et al. 2021). Similar findings where a leguminous plant attained more biomass than non-leguminous plant grown at eCO_2 were reported by Lee et al. (2003). Moreover, Singer et al. (2020) reported that leguminous species have a close relationship with arbuscular mycorrhizal fungi which promotes efficient uptake of P, in turn increasing biomass of leguminous trees. In addition, increase in nodule mass in legumes which is non-existent in non-leguminous trees could have contributed to the total biomass production of legumes. Interestingly, more biomass was allocated to shoot in leguminous trees, whereas non-leguminous trees invested more on root production. High shoot biomass of leguminous trees could be attributable to high leaf production, as depicted by greater increases in LAI at eCO_2 (Fig. 7d), probably due to a synergy between C fertilization and N-fixation. Our findings agree with Zhang et al. (2011) who reported a substantial increase in shoot biomass and no change in root biomass of a leguminous shrub (*Caragana microphylla*) growing at eCO_2. High root production by non-leguminous trees may facilitate greater C input into the soil via rhizodeposition, more so if root respiration is minimal (de Graaf et al. 2006).

Increased shoot height of deciduous trees at eCO_2 than evergreen trees is not surprising because according to Poorter and Navas (2003), evergreen trees grow more slowly than deciduous trees. Deciduous species capitalize on higher photosynthesis per unit leaf mass (Zhang et al. 2021) and leaf N content which facilitate rapid growth relative to evergreen trees (Givnish 2002). Moreover, the cost of utilizing C for production of secondary compounds at the expense of photosynthesis, common in evergreen trees, suppresses shoot growth (Givnish 2002).

However, it is worth noting that this meta-analysis was derived largely from short-term experiments, hence, we report more on seedlings and or juveniles of different phenology rather than older plants. Thus, for an example, if deciduous and evergreen seedlings were grown at eCO_2 at the beginning of a growing season and shoot measurements taken at the end of the season, deciduous seedlings may gain an advantage due to: (1) greater and rapid photosynthesis they attain before dormancy and (2) evergreen seedlings might be deprived an advantage to grow during winter when deciduous seedlings are dormant. Moreover, the scarcity of studies reporting long-term growth of trees in eCO_2 limits understanding of how leaf N in older plants respond to eCO_2 relative to juveniles. Thus, the present results are inconclusive and cannot be generalized for trees exposed to eCO_2 longer than one growing season, due to age and size-dependent changes in plant physiology (Saxe et al. 1998; Garner et al. 2021).

The leaf N was higher in leguminous than non-leguminous trees, as a result, C:N was higher for the latter than the former at eCO_2 (Additional file 1: Fig. S6). Similar findings were reported in other previous studies (e.g. Du et al. 2020) and are often ascribed to the dilution effect, as a result of high accumulation of biomass and non-structural carbohydrates (Xia et al. 2021). The higher C:N in non-leguminous trees relative to leguminous trees could be explained largely by low decline in leaf N for the latter compared to the former.

Despite the lack of statistical differences on A_{max} responses to eCO_2 between leguminous and non-leguminous trees, the twofold increase in A_{max} attained by the former compared to the latter need to be considered. The A_{max} increased regardless of higher decrease in V_{cmax} and J_{max} for leguminous trees relative to non-leguminous trees. Similar results were reported in the meta-analysis by Wang and Wang (2021a), where V_{cmax} and J_{max} declined and A_{max} increased under eCO_2. High allocation of biomass to shoot could have enhanced photosynthesis in leguminous trees than in non-leguminous trees which allocate more biomass to roots (Fig. 6d and g).

The positive responses of A_{max} to eCO_2 were substantial for compound leaves with small leaflets, which are mostly legumes, e.g. *Acacias* and *Prosopis* species. This finding further supports higher A_{max} attained by leguminous trees, which is attributable to high leaf N and higher investment on shoot biomass than in non-leguminous trees. A_{max} was also increased in broadleaves (Fig. 8c), owing to thicker palisade mesophyll layers that keep high CO_2 in the leaves, such that even when stomata closes, photosynthesis remains high (Zhang et al. 2021).

Stomatal conductance declined for both leguminous and non-leguminous trees. However, transpiration rate remained similar between eCO_2 and aCO_2 regardless of the decline in g_s for leguminous trees, which consequently translated to low WUE compared to non-leguminous trees (Fig. 9a, d and g). This response is surprising given that stomatal closure limits water loss (Zhang et al. 2021; Li et al. 2021). It is, however, worthy to postulate that higher reduction in g_s exhibited by leguminous trees increased leaf temperature, which probably amplified diffusion out of water in the leaves (Kerstiens et al. 1995). The higher WUE for non-leguminous trees was driven mainly by a decline in Tr (Fig. 9d). As has been reported in other previous studies (e.g. Soh et al. 2019), evergreen trees had higher WUE than deciduous trees. Similarly, Zhang et al. (2021) reported higher WUE for evergreen broadleaved trees than deciduous broadleaved trees elsewhere.

In this study, higher WUE for evergreen trees could be explained by the balance between A_{max} and Tr, whereas deciduous trees exhibited a numerically low A_{max} and higher Tr. The higher photosynthesis normally shown by evergreen trees plays an important role in increasing WUE (Soh et al. 2019). The broadleaved trees attained higher WUE than other leaf types due to reduced g_s and Tr (Fig. 9), suggesting that eCO_2 in broadleaved forests may enhance soil moisture. This could be an important adaptation strategy to the future climate characterized by extreme temperatures and drought. The low enhancement of WUE for compound leaves with small leaflets is attributable to the lack of decline in Tr. On the other hand, the lack of decline in g_s for the needle-like leaves observed in this study was also reported for conifers by Saxe et al. (1998) in their systematic review. Generally, the guard cells of conifers are less sensitive to eCO_2 (Ainsworth and Rogers 2007). As a result, in this study, WUE in needle-like leaves was low, owing to high Tr caused by unresponsive behaviour of g_s to eCO_2.

Conclusions

Overall, this meta-analysis revealed that eCO_2 increases woody plant growth, productivity, photosynthetic rate and water status, but reduces foliage quality via reduced leaf N. It appeared however, that photosynthesis is enhanced to a certain degree, after which the rate of stimulation declines at eCO_2 above 700 μmol mol^{-1}, signifying that photosynthetic acclimation is likely at relatively high CO_2. This response appears to be age-dependent, as the photosynthetic acclimation was more apparent in plants exposed for a longer duration to eCO_2 than those exposed for less than a year. The increase in photosynthesis especially during early exposure to eCO_2 together with reduction in water loss were central in improving water use efficiency of woody plants. Our results further indicated that responses to eCO_2 are dependent on woody plant traits. The high biomass production and low decline in leaf N in leguminous trees at eCO_2 indicated that these woody plants may be more important as a source of forage for herbivores than non-leguminous trees. Broad leaves showed a substantial increase in water use efficiency than other leaf types, underpinning that through this water saving strategy broadleaved forests would be less vulnerable to the future extreme climate.

Abbreviations

A_{max}: Light-saturated photosynthesis; aCO_2: Ambient carbon dioxide; $atCO_2$: Atmospheric carbon dioxide; eCO_2: Elevated carbon dioxide; g_s: Stomatal conductance; J_{max}: Apparent maximum rate of photosynthetic electron transport; LAI: Leaf area index; LTs: Leguminous trees; NLTs: Non-leguminous trees; SLA: Specific leaf area; V_{cmax}: Maximum rate of photosynthetic Rubisco carboxylation; WUE: Water use efficiency; Tr: Transpiration.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-022-00397-7.

Additional file 1: Fig. S1. A flowchart depicting gathering and screening of global studies for the meta-analysis. The plus (+) and minus (−) signs indicate studies that were qualified and disqualified for the meta-analysis, respectively. **Fig. S2.** The relationship between J_{max} and V_{cmax} of woody plants grown at elevated CO_2. **Fig. S3.** The relationships between root biomass and shoot biomass (a), and LAI (b) of the woody plants grown at eCO_2. The relationships were conducted on the actual natural log response ratios. **Fig. S4.** Percentage change (± 95% CI) in carbon:nitrogen ratio (C:N) of woody plants grown at eCO_2. The whiskers denote 95% CI and the circles denote mean percentage change (MPC) between aCO_2 and eCO_2. The numbers above the major ticks of the *X*-axis denote number of observations. The area fill (green color) shows the trends and the magnitude of differences between the eCO_2 concentrations. The wider the area the bigger the difference between MPCs. **Fig. S5.** Percentage change in leaf area index and height of woody plants over different duration (years) of exposure to eCO_2. The whiskers denote 95% CI and the circles denote mean percentage change (MPC) between aCO_2 and eCO_2. The numbers above the major ticks of the *X*-axis denote number of observations. The area fill (green color) shows the trends and the magnitude of differences between the eCO_2 concentrations. The wider the area the bigger the difference between MPCs. Key to period of exposure: 0.5 years denotes half of a year (6 months). There were no observations reported for a period > 2–3 years for these parameters. **Fig.**

S6. Percentage change (±95% CI) in leaf N and C:N of woody plants with different N-fixation ability (a, d and g), leaf phenology (b, e and h) and leaf types (c, f and i) grown at eCO_2. The whiskers denote 95% CI and the circles denote mean percentage change. The numbers above the major ticks of the *X*-axis denote number of observations. Key to leaf types: Compound-small = compound leaves with small leaflets and Needle-like = needle-like leaves. **Fig. *S7*.** Leaf area index (A) and total biomass (B) of woody plants grown at eCO_2. RR = response ratio. The grey dots indicate the data points or observations and the black square is the mean RR. **Fig. S8.** Shoot (A) and root biomass (B) of woody plants grown at eCO_2. RR = response ratio. The grey dots indicate the data points or observations and the black square is the mean RR. **Fig. S9.** Shoot height (A) and specific leaf area (B) of woody plants grown at eCO_2. RR = response ratio. The grey dots indicate the data points or observations and the black square is the mean RR. **Fig. S10.** Light saturated photosynthesis (A_{max}) of woody plants grown at eCO_2. RR = response ratio. The grey dots indicate the data points or observations and the black square is the mean RR. **Fig. S11.** Photosynthetic carboxylation of Rubisco (V_{cmax}; A) and electron transport rate (J_{max}; B) of woody plants grown at eCO_2. RR = response ratio. The grey dots indicate the data points or observations and the black square is the mean RR. **Fig. S12.** Leaf N (A) and C:N ratio (B) of woody plants grown at eCO_2. RR = response ratio. The grey dots indicate the data points or observations and the black square is the mean RR. **Fig. S13.** Stomatal conductance (g_s) of woody plants grown at eCO_2. RR = response ratio. The grey dots indicate the data points or observations and the black square is the mean RR. **Fig. S14:** Transpiration (Tr; A) and water use efficiency (WUE; B) of woody plants grown at eCO_2. RR = response ratio. The grey dots indicate the data points or observations and the black square is the mean RR. **Fig. S15.** Density plots indicating data dispersion of biomass (A), growth (B), photosynthetic (C) and water related parameters of woody plants grown at eCO_2. RR = response ratio. **Fig. S16.** The experimental length (days) of woody plant exposure to eCO_2 for biomass assessment. The violin indiacates the distribution of data. The bold horizontal line denotes a median time and the black square inside the box denotes mean ($\overline{X}$) duration of the exposure to eCO_2. The upper and lower vertical whiskers are 25th and 75th quartiles, respectively. The upper and lower edges of the box denote maximum and minimum duration (days) of woody plant exposure to eCO_2. **Fig. S17.** Length (days) of woody plant exposure to eCO_2 for assessment of leaf area index (LAI), specific leaf area (SLA) and shoot height (SH). The violin indiacates the distribution of data. The bold horizontal line denotes a median duration and the black square inside the box plots denotes mean ($\overline{X}$) duration of the exposure to eCO_2. The upper and lower vertical whiskers are 25th and 75th quartiles, respectively. The upper and lower edges of the box denote maximum and minimum duration (days) of woody plant exposure to eCO_2. **Fig. S18.** Length (days) of woody plant exposure to eCO_2 for assessment of stomatal conductance (g_s), transpiration (Tr) and water use efficiency (WUE). The violin indiacates the distribution of data. The bold horizontal line denotes a median duration and the black square inside the box plots denotes mean ($\overline{X}$) durationof the exposure to eCO_2. The upper and lower vertical whiskers are 25th and 75th quartiles, respectively. The upper and lower edges of the box denote maximum and minimum duration (days) of woody plant exposure to eCO_2. **Fig. S19.** Length (days) of woody plant exposure to eCO_2 for assessment of light saturated photosynthesis (A_{max}), carboxylation of Rubisco (V_{cmax}) and electron transport rate (J_{max}). The violin indiacates the distribution of data. The bold horizontal line denotes a median duration and the black square inside the box plots denotes mean ($\overline{X}$) duration of the exposure to eCO_2. The upper and lower vertical whiskers are 25th and 75th quartiles, respectively. The upper and lower edges of the box denote maximum and minimum duration (days) of woody plant exposure to eCO_2. Dots indicate outlier observations. The few extreme outliers (mostly studies spanning over 5 years) were removed from the graphs. **Fig. S20.** Length (days) of woody plant exposure to eCO_2 for assessment of leaf N and C:N ratio. The violin indiacates the distribution of data. The bold horizontal line denotes a median durationand the black square inside the box plots denotes mean ($\overline{X}$) duration of the exposure to eCO_2. The upper and lower vertical whiskers are 25th and 75th quartiles, respectively. The upper and lower edges of the box denote maximum and minimum duration (days) of woody plant exposure to eCO_2.

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Author contributions
All authors conceived the ideas of study. MMA gathered the data, performed statistical analysis and wrote the manuscript. MMA and MME generated the graphs. MIS, FM, JT, MME, ICM and HTP read and provided valuable corrections in several drafts of this manuscript. All authors read and approved the final manuscript.

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Declarations

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Competing interests
The authors declare that they have no conflict of interest.

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