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# Contrasting responses of woody and grassland ecosystems to increased $CO_2$ as water supply varies

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**Experiments show that elevated atmospheric $CO_2$ ($eCO_2$) often enhances plant photosynthesis and productivity, yet this effect varies substantially and may be climate sensitive. Understanding if, where and how water supply regulates $CO_2$ enhancement is critical for projecting terrestrial responses to increasing atmospheric $CO_2$ and climate change. Here, using data from 14 long-term ecosystem-scale $CO_2$ experiments, we show that the $eCO_2$ enhancement of annual aboveground net primary productivity is sensitive to annual precipitation and that this sensitivity differs between woody and grassland ecosystems. During wetter years, $CO_2$ enhancement increases in woody ecosystems but declines in grass-dominated systems. Consistent with this difference, woody ecosystems can increase leaf area index in wetter years more effectively under $eCO_2$ than can grassland ecosystems. Overall, and across different precipitation regimes, woody systems had markedly stronger $CO_2$ enhancement (24%) than grasslands (13%). We developed an empirical relationship to quantify aboveground net primary productivity enhancement on the basis of changes in leaf area index, providing a new approach for evaluating $eCO_2$ impacts on the productivity of terrestrial ecosystems.**

Knowing how elevated atmospheric carbon dioxide ($eCO_2$) affects the capacity of terrestrial ecosystems to fix and store carbon is critical to understanding the future of the global carbon (C) cycle, including terrestrial productivity and C-cycle feedbacks on the climate system. Evidence from observations and modelling indicates that $eCO_2$ typically increases net primary production (NPP) of terrestrial ecosystems, but the extent of the response among biomes remains uncertain and can be sensitive to climate and nutrient constraints[1–4]. Two primary physiological mechanisms seem particularly important for understanding the $CO_2$ fertilization effect: increased leaf-level photosynthesis and decreased stomatal conductance[5]. Consequences of these mechanisms under $eCO_2$ include increased water use efficiency (WUE)[6–9] and reduced water stress in drier ecosystems[6].

Carbon-flux research in temperate and boreal forests of the Northern Hemisphere has revealed considerable increases in WUE over the past two decades, most consistent with the hypothesis of a strong $CO_2$ fertilization effect attributable to elevated atmospheric $CO_2$[10]. Meanwhile, studies combining remote sensing and modelling report increases in foliage cover and NPP in drier regions of the world, suggesting that $CO_2$ fertilization has made the land surface 'greener'[11–13]. Fatichi et al.[2] used a mechanistic model and experimental data to partition the effects of $eCO_2$ on NPP into the direct effects associated with C assimilation and indirect effects associated with changes in water condition and leaf area index (LAI). They concluded that the indirect effects of $eCO_2$ account for 28% of the total enhanced plant productivity, with a tendency for greater relative enhancements in arid ecosystems.

Free-air $CO_2$ enrichment (FACE) experiments and open-top chamber (OTC) systems have been used for many years to investigate in situ responses of intact plant communities to $eCO_2$ at ecosystem scales[9,14,15]. Published results indicate that, for an ~50% increase in $CO_2$ concentration to ~560 ppm[15–17], aboveground NPP (ANPP) and total NPP in forests increase on average by ~25% (ref. [17]). By contrast, results from grassland experiments show that growth responses to $eCO_2$ (~650 ppm) are somewhat less than in forests, with increases in ANPP ranging from 11% to 17% (ref. [17]). Across all forest and grassland experiments, stomatal conductance consistently decreased and instantaneous WUE increased by 4% to 44% (refs. [18,19]). However, leaf-level changes did not always lead to ecosystem-scale reductions in total water use or increases in soil moisture because of additional transpiration from increased leaf areas[7,18,19].

Although $CO_2$ fertilization might be expected to have a greater effect in xeric ecosystems and in drier conditions where and when the benefits of increased WUE are potentially stronger[6], evidence from enrichment studies is conflicting, with some studies supporting this hypothesis[9,20] but others not[16,21]. Inconsistencies in $eCO_2$

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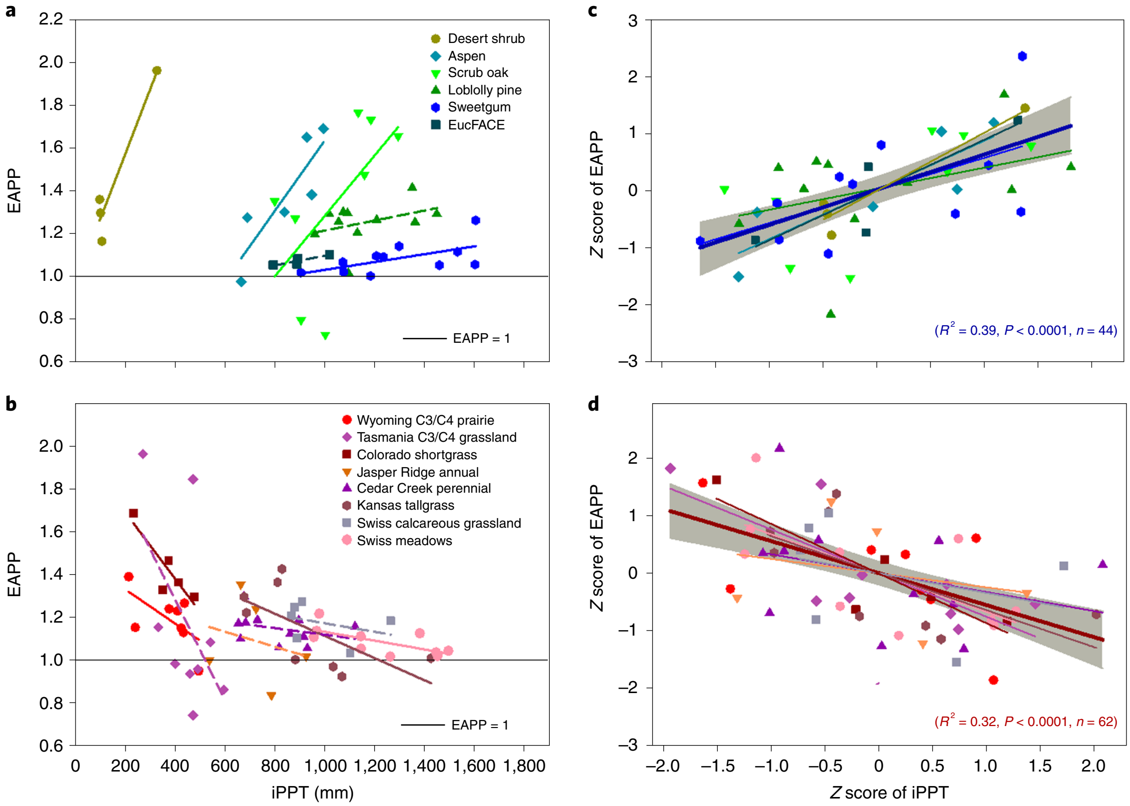

**Fig. 1 | Relationships between $eCO_2$ enhancement of ANPP and iPPT.** EAPP is an enhancement ratio of ANPPe and ANPPa under $eCO_2$ and ambient $CO_2$ treatments. **a**,**b**, EAPP responses to iPPT over multiple experimental years within woody ecosystems (**a**) and within grassland ecosystems (**b**); at $P = 0.1$, solid lines represent the regression statistically significant, dashed lines not significant (Supplementary Table 5); the horizontal line EAPP = 1 denotes no enhancement, while above or below it is enhancement or reduction under $eCO_2$. **c**,**d**, The fixed-effect regressions between *Z* scores of EAPP and iPPT (thick solid lines with confidence intervals of grey areas) for woody (**c**) and grassland (**d**) ecosystems; the thin lines are linear regressions of *Z* scores of individual sites.

responses of plants to water availability may reflect variation in other factors, such as soil nutrient availability[22–24], light limitation[5] or indirect effects of $eCO_2$ on LAI via changes of carbon allocation and soil water[2,19]. Leaf and root structures and mechanisms for acquiring $CO_2$, water, light and nutrients vary for different plant life forms, which may also contribute to differences in $eCO_2$ responses to water availability.

To investigate mechanisms underpinning such inconsistencies, we analysed data from 14 multi-year, ecosystem-scale $CO_2$ enrichment experiments, covering xeric to wet climates, in ecosystems dominated by grasses, shrubs or trees (Supplementary Tables 1–4). These sites are located in temperate and subtropical zones between latitudes 48° N and 43° S in the Northern or Southern Hemisphere. The criteria for selected sites were based on availability of ANPP data or ANPP enhancement ratios and a minimum $eCO_2$ treatment duration of four years. We explored the responses of ecosystem types to interactions of $eCO_2$ and water supply. The enhancement ratio of ANPP under $eCO_2$ ($ANPP_e$) to ANPP under ambient $CO_2$ ($ANPP_a$) (EAPP) was used as a measure of the relative response of ecosystem productivity to $eCO_2$. We examined two types of relationships between EAPP and precipitation for woody and grassland ecosystems: (1) annual EAPP (EAPP) and annual precipitation (iPPT) (an annual sum of monthly precipitation) at a given site over multiple experimental years and (2) mean ecosystem EAPP ($EAPP_{AV}$) and mean annual precipitation (MAP) across multiple sites of the same ecosystem type. We evaluated the following three hypotheses: (H1) at a given site and over years, EAPP is greater in drier years; (H2) across multiple sites of the same ecosystem type, $EAPP_{AV}$ is greater in drier locations; and (H3) relative enhancements (both EAPP and $EAPP_{AV}$) in response to water supply are equivalent for ecosystems dominated by grasses or by woody taxa.

To test H1, we focused on the interactive effect of $eCO_2$ and temporal variations of iPPT on EAPP. To test H2, we examined the interactive effect of $eCO_2$ and spatial variations of MAP on $EAPP_{AV}$. The mechanisms underlying these two interactions probably differ. Finally, we tested H3 by comparing separate ecosystem types with distinct plant growth forms (woody and grassland ecosystems) to assess the consistency of the $eCO_2$ responses in magnitude and trend—given differences in their functional and structural traits, including height, leaf area and orientation, and biomass allocation, which can affect light and nutrient acquisition and may mediate $eCO_2$ and precipitation interactions.

## Results and discussion

**Relationships between EAPP and iPPT within sites.** The iPPT varied widely across years and sites and affected both ANPP and the responses of ANPP to $eCO_2$. Across all ecosystems, $eCO_2$ enhanced growth in most years (EAPP > 1; Fig. 1a,b), but responses differed remarkably for woody and grassland ecosystems. Within woody-dominated ecosystems, EAPP was positively related to iPPT and greater in wetter years at a given site (Fig. 1a). By contrast, EAPP within a given grassland ecosystem declined in wetter years (Fig. 1b).

The individual site response patterns appear to depend on the dominant life form, although a linear relationship between EAPP and iPPT was not statistically significant at every individual site

**Table 1 | ANOVA of fixed-effect multi-variable regression and covariance of variables**

| **Woody ecosystem** | **d.f.** | **SE** | **MS** | ***F*** | ***P* value** | $R^2$ |
|---|---|---|---|---|---|---|
| Model | 43 | 0.7559 | 5.0554 | 8.8458 | 0.0001 | 0.3988 |
| $EAPP_Z$[a] | $\beta$ | SE | *Z* test | *P* value | $CV_{(Pz,Tz)}$[b] | $CV_{EAPPz}$[c] |
| Intercept | −0.0456 | 0.1296 | −0.3526 | 0.7263 | | |
| $P_Z$ | 0.6633 | 0.1394 | 4.7601 | <0.0001 | 0.8529 | 0.5345 |
| $T_Z$ | 0.0949 | 0.1356 | 0.6995 | 0.4883 | 0.7137 | 0.0329 |
| $P_Z \times T_Z$ | −0.0697 | 0.1498 | −0.4652 | 0.6443 | −0.0596 | 0.1862 |
| Grassland ecosystem | d.f. | SE | MS | *F* | *P* value | $R^2$ |
| Model | 61 | 0.7964 | 5.6536 | 8.9138 | <0.0001 | 0.3158 |
| $EAPP_Z$[a] | $\beta$ | SE | *Z* test | *P* value | $CV_{(Pz,Tz)}$ | $CV_{EAPPz}$ |
| Intercept | 0.0006 | 0.1017 | 0.0059 | 0.9952 | | |
| $P_Z$ | −0.5566 | 0.1087 | −5.1211 | <0.0001 | 0.8709 | −0.4855 |
| $T_Z$ | 0.0318 | 0.1079 | 0.2945 | 0.7694 | 0.9090 | 0.0623 |
| $P_Z \times T_Z$ | 0.0507 | 0.1078 | 0.4702 | 0.6399 | −0.0744 | 0.0234 |

iPPT, iTEM and EAPP of woody and grassland ecosystems were standardized as *Z* scores ($P_Z$, $T_Z$ and $EAPP_Z$), respectively (Methods). SE, standard error; MS, mean square. [a]Dependent variable. [b]Covariances of independent variables $P_Z$ and $T_Z$. [c]Covariances of predictive variables and dependent variable $EAPP_Z$.

(Fig. 1a,b and Supplementary Table 5). This is particularly true for grassland ecosystems and those located near transition zones such as from semi-arid to moist zones, where growth responses were sometimes confounded with changing species composition under $eCO_2$[20,24]. Different carboxylation pathways of $C_3$ and $C_4$ grasses could also complicate EAPP responses to iPPT in grassland sites with both physiological types. For example, $C_3$ grasses were more responsive to $eCO_2$ in drier years, whereas $C_4$ grasses showed little relationship with moisture conditions, despite responding well around typically average precipitation years (Extended Data Fig. 1; see Supplementary Discussion about $C_3$ and $C_4$ plants).

For comparing diverse ecosystems, iPPT is a relatively simple proxy for water supply because of its independence from other site factors. We recognized that growing-season precipitation (mPPT) could be a better predictor for plant productivity and sensitivity to $eCO_2$ at a given site[22]. The length of a growing season varies annually depending on local temperature and vegetation types. Lacking growing-season data from most sites, we used months from spring to early autumn as a growing season to relate EAPP to growing season precipitation (mPPT). Surprisingly, almost all the relationships weakened compared with those using iPPT except the meadow site in Switzerland (Supplementary Table 6 and Supplementary Fig. 1). The results suggest that non-growing-season precipitation contributes to hydrological conditions in many sites. In temperate sites, soil water recharged by winter precipitation (for example, snow) might benefit early spring growth, while in evergreen and subtropical sites, year-round precipitation has an impact on growth.

Acknowledging statistical uncertainties in linear regressions of individual sites, we standardized the site data and developed *Z* scores to pool annual data of different sites to examine patterns of EAPP–iPPT in woody and grassland ecosystems. The *Z* scores eliminate scale differences and facilitate comparisons among sites (see Methods for approaches). The fixed-effect regressions confirm the patterns we observed from individual sites: the relative $CO_2$ enhancement of growth for woody ecosystems increased in wet years ($P < 0.0001$) while the enhancement decreased with annual precipitation for grassland ecosystems ($P < 0.0001$) (Fig. 1c,d).

Although the $eCO_2$ effect on plants is more directly related to water availability because it changes stomatal conductance, WUE and plant–water dynamics, temperature can also influence the process through interactions with water. We therefore analysed the impacts of annual mean temperature (iTEM) on EAPP (using *Z* scores), interactive effects and covariances with other variables and found no statistically significant relationships ($P = 0.4883$, 0.6443 and $P = 0.7694$, 0.6399 for woody and grassland ecosystems, respectively) (Table 1).

**Relationships between $EAPP_{AV}$ and MAP across sites.** Across ecosystems from drier to moister sites, $EAPP_{AV}$ responses to MAP appear to decline with greater MAP for both woody and grassland ecosystems (Fig. 2). Thus, in grasslands, the enhancement responses to precipitation were consistent within and across sites: greater for both drier years within a site and drier sites along the precipitation gradient. By contrast, the relative enhancement in woody systems was greater in wetter years within a site but lower for wetter sites across the precipitation gradient (Figs. 1 and 2). The inter-site MAP gradient shows that the relative $CO_2$ fertilization effect on ANPP was greater in drier climates, independent of responses to annual variation in precipitation (Fig. 1), which likely reflects in part the importance of higher WUE in drier regions for maximizing carboxylation while minimizing water cost[25]. The $EAPP_{AV}$ trends of woody and grassland ecosystems are roughly parallel along the MAP gradient, although the woody ecosystem trend is not statistically significant ($P = 0.15$) due to the low ANPP response in the mature *Eucalyptus* woodland[26]. Some grassland sites, such as Colorado shortgrass steppe, achieve $EAPP_{AV}$ as great as woody ecosystems under similar precipitation conditions (Fig. 2).

The sensitivity of EAPP to iPPT within an ecosystem approaches zero (the slopes of linear functions in Fig. 1a,b) in wetter ecosystems for both woody and grassland habitats (Extended Data Fig. 2). Whereas the sensitivity (the absolute $CO_2$-induced enhancement per iPPT) declines with annual precipitation, it appears to approach zero at higher MAP for woody systems (~1,200 mm) than for grasslands (~800 mm) and remains notable even for the wettest woody ecosystems in our dataset. This suggests that some $eCO_2$ enhancement may be sustained for ecosystems with more abundant precipitation such as tropical rainforests. We observed that considerable $eCO_2$ enhancement of ANPP (~5–15%) is still realized experimentally in relatively mesic ecosystems (Fig. 2) because of the direct $eCO_2$ fertilization effect and possibly periodic enhancements of WUE due to recurring (short-term) drought in sites even with high MAP[1,10]. Wetter terrestrial systems often experience some seasonal water stress[27]; for example, seasonal water deficits for the loblolly pine in the Duke FACE site frequently led to stomatal closure

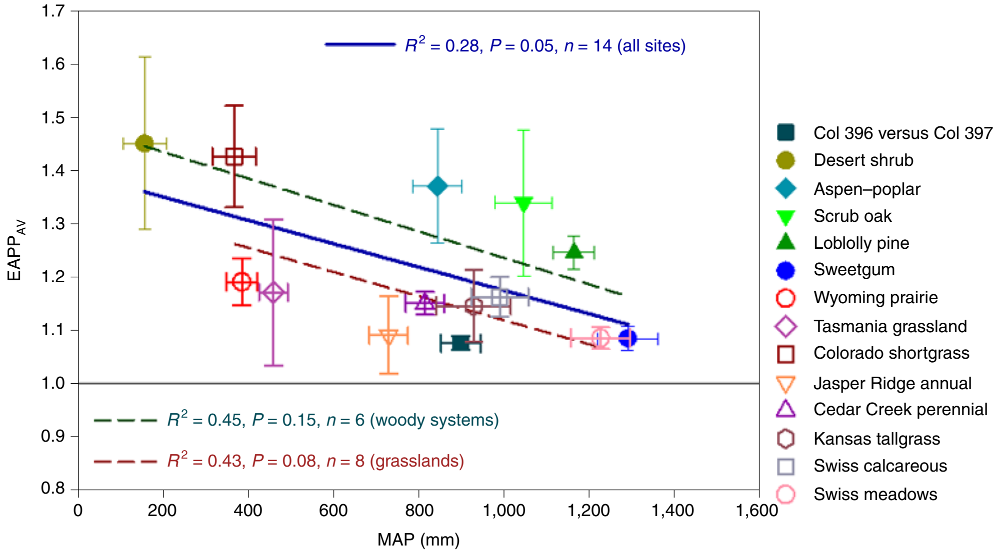

**Fig. 2 | Mean responses of $EAPP_{AV}$ to MAP across multiple ecosystems.** The solid line represents the regression for all sites; the dashed lines are those for woody and grassland ecosystems. The regression for woody ecosystems is not statistically significant due largely to a low $EAPP_{AV}$ at the EucFACE site. Solid symbols are for woody ecosystems and open symbols for grassland ecosystems. Error bars represent the standard error at each site.

during part of the growing seasons in drier years[28]. Elevated $CO_2$ could alleviate some or all impacts of these dry periods on ANPP.

**The effect of $eCO_2$ on LAI mediates EAPP responses to iPPT.** Our results raise two questions. (1) Why does $eCO_2$ induce contrasting responses of EAPP to iPPT within woody and grass-dominated ecosystems (Fig. 1), despite similar declines of $EAPP_{AV}$ to MAP across sites (Fig. 2)? (2) Why does EAPP respond differently to annual variations of iPPT than $EAPP_{AV}$ to geographic variations of MAP in woody systems, while the relationships are consistent in grassland ecosystems?

Mechanisms that could contribute to the divergent responses of the $eCO_2$ to moisture in woody and grassland ecosystems include (1) grassland ecosystems allocating additional production belowground in wet years[29], potentially limiting ANPP $eCO_2$ enhancement at these times; (2) differing seasonal sensitivities to moisture limitations, with grass-dominated systems most sensitive early in growing seasons when leaf biomass reaches the maximum[20,30] but woody systems affected throughout the growing season[31]; and (3) differences in plant architecture (such as stem height, arrangement of leaves and roots), which influence light interception and limitation aboveground and access and storage of nutrients belowground. Although these and other potential mechanisms may influence our observations (Fig. 1), no single one is likely to explain all the observed patterns.

Because the $eCO_2$ effects on carbon assimilation efficiency and WUE should be functionally similar in woody vegetation and grasses, we considered indirect $eCO_2$ effects mediated by enhanced LAI[2]. Such an enhancement may result from increasing carbohydrate and water availability, and relevant changes in plant structures, and could have a compounding impact[7,32]. Across studies, we found a significant positive relationship ($P < 0.0001$) between EAPP and enhanced LAI (ELAI) over all data from woody and grassland ecosystems, despite mixed spatial and temporal scales (Fig. 3). The contrasting trends of EAPP responses to iPPT (Fig. 1) but similar enhancements of EAPP with greater LAI (ELAI, Fig. 3) lead logically to the conclusion that ELAI responses to iPPT must differ between woody and grassland ecosystems. Therefore, we propose that diverging ELAI responses to iPPT is one possible mechanism causing the contrasting EAPP responses to iPPT within woody and grassland ecosystems.

Other evidence from the $eCO_2$ experimental sites support this LAI-mediated interpretation. FACE experiments in forests indicate that under $eCO_2$, ANPP and LAI both increase consistently with increasing iPPT, particularly in sites with relatively low LAI[5,33,34]. LAI increases with $eCO_2$ in most forest and woodland experimental sites, although the magnitude varies with tree species, leaf traits and stand structure[19,33]. In the Mojave Desert, a site dominated by shrubs, EAPP shows great stimulation only in wetter years, although EAPP and ELAI indicated enhancements for all treatment years[34,35]. Leaf-level stomatal conductance in woody ecosystems decreases on average by 21% under $eCO_2$ at a level of ~550 ppm. However, canopy transpiration does not always decline because increased LAI consumes the water savings induced by $eCO_2$[36], resulting in similar total soil water use[33]. Thus, woody ecosystems effectively support new foliage[37] in wetter years, helping to maintain a positive within-site EAPP–iPPT relationship (Supplementary Fig. 2) (see Supplementary Discussion about interactive effects).

Grassland ecosystems differ structurally and morphologically from woody systems. Aboveground production (mostly leaf biomass) and LAI are more closely related in grasslands than in woody ecosystems, as are EAPP and ELAI. The EAPP and ELAI responses in grasslands are very much water-related responses, with water stress reduced by enhanced WUE under $eCO_2$ in drier years[9,20]. In wetter years, when water is less limiting, the relative $eCO_2$ enhancement for ANPP and LAI is often minimal[9,30] (Extended Data Fig. 1). This result holds for multiple sites, including semi-arid shortgrass steppe dominated by $C_3$ species, mixed grass prairie[9,38] and mesic but frequently water-stressed $C_4$ tallgrass prairie[30]. In these experimental $CO_2$ enrichment sites, instead of LAI increasing in wetter years, there was evidence of community shifts to greater abundance of invasive grass species that are usually adapted to moister conditions as well as substantial biomass enhancement of subshrub species[20,39].

Given the importance of increased LAI for enhancing ANPP, any site complexity affecting LAI dynamics could up- or down-regulate EAPP and affect observed EAPP–iPPT relationships. For example, the aspen forest in the Aspen-FACE study in Wisconsin[14] had a substantially greater increase in LAI under $eCO_2$ compared with other forest FACE sites (Fig. 3), probably because of the lower starting LAI in the young and expanding forest stand[5]. Together with a greater

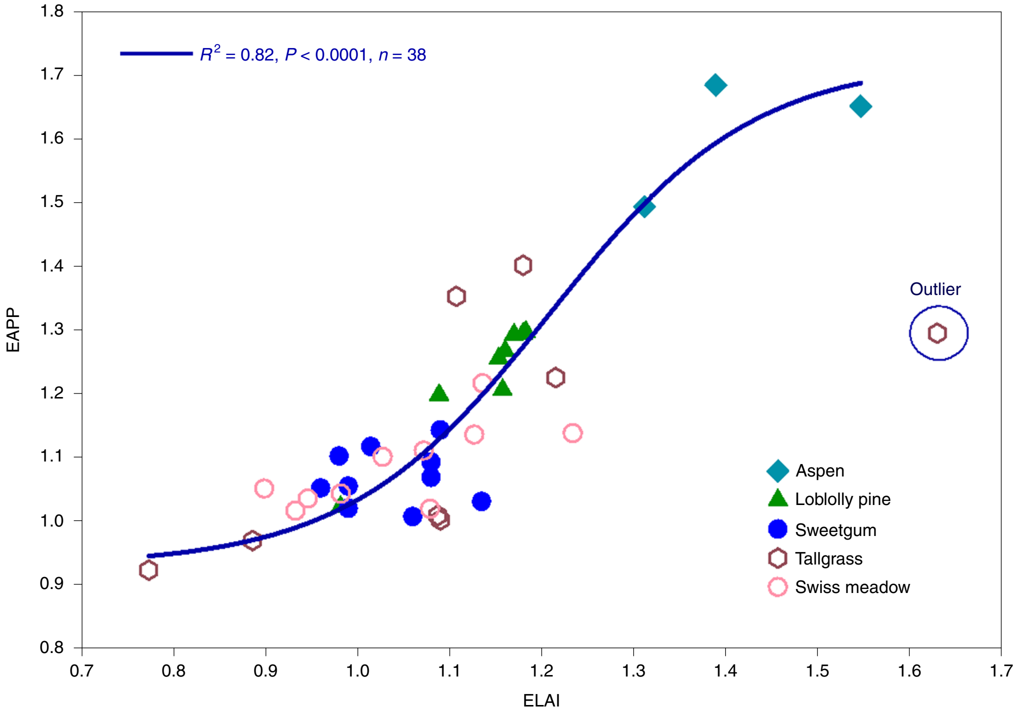

**Fig. 3 | The relationship between EAPP and ELAI.** EAPP and ELAI are, respectively, the enhancement ratios of ANPP and LAI under $eCO_2$ versus ambient treatments. Solid symbols are woody ecosystems; open symbols are grassland ecosystems. A logistic function was used for data fitting (Supplementary Table 7). The excluded outlier was from the $C_4$ tallgrass prairies, which occurred in the driest year of the site with abnormal low LAI at the ambient $CO_2$ plots, causing exceptionally high relative LAI enhancement.

daily interception of light during the growing season, enhanced LAI resulted in a much greater EAPP at this site compared with the other forests (Fig. 2).

**Woody ecosystems have greater ANPP enhancement.** Across experimental sites with annual precipitation ranging from ~100 to 1,700 mm, average EAPP weighted by all experimental years ($EAPP_{AVE}$) in woody ecosystems was ~25% ($n$ = 44) compared with ~16% ($n$ = 62) in grassland ecosystems (Extended Data Fig. 3a). Experimental $eCO_2$ levels used in woody ecosystems were fairly consistent (~550 ppm) except in the scrub-oak site (~700 ppm) (Supplementary Table 1), while grassland sites had various $eCO_2$ levels (~550–720 ppm), with six of eight grassland sites exposing plants to higher $eCO_2$ (600–720 ppm) (Supplementary Table 2). Using the Farquhar model[40], we estimated these higher $eCO_2$ treatments induce 3–8% greater impact on photosynthetic rates compared with those for the standard 550 ppm site treatment (Extended Data Fig. 4). Similarly, a published meta-analysis[41] shows that higher $eCO_2$ used in grassland experiments (versus ~550 ppm) could on average cause 3–7% greater responses of plant growth. Therefore, after adjusting $eCO_2$ treatment levels to 550 ppm by the Farquhar model, the average ANPP enhancement of all experimental years in woody ecosystems is ~24%, while in grassland ecosystems it is reduced from 16% to 13%, approximately 11% less enhancement than woody ecosystems (significantly different at $P$ = 0.011; $t$ test) (Extended Data Fig. 3b).

Forest sites used in this study are mostly young forests in relatively early developmental stages. One exception is a mature forest of *Eucalyptus* (EucFACE). EucFACE shows little $eCO_2$ enhancement in tree ANPP after three years' $eCO_2$ treatments despite a persistent 19% increase in leaf photosynthesis[26]. The small enhancement in ANPP (~7%) presented in this study (Figs. 1 and 2) is mainly attributable to abundant understory aboveground vegetation in this open dry woodland[42]. Another mature forest study (WEB-FACE) in the fully stocked European Beech-oak forest shows that tree-ring increments were small under $eCO_2$ (Supplementary Fig. 3)[43], on average (4%) lower than the $EAPP_{AV}$ in the full-canopy sweetgum site in Oak Ridge (~8%). Interestingly, several $eCO_2$ enrichment studies in mature forests reported remarkable $eCO_2$ enhancements in photosynthetic capacity or gross primary productivity, but not in carbon pools such as stem wood or woody necromass[42,44], which may suggest that mature forests may also respond via increased carbon losses or by transferring photosynthates to unmeasured carbon pools, including those belowground.

We note that our analysis focuses on enhancement of ANPP rather than NPP because data relating belowground production (BP, fine root) responses to $eCO_2$ are sparse and typically less certain. This gap may constrain full understanding of $eCO_2$ impacts on plant productivity because C allocations to above- and belowground organs differ between woody and grassland ecosystems and probably shift with changes in carbon and water resources[45,46]. It is also notable that the forest FACE sites (except Oak Ridge) have much lower fine-root allocation ratios than the median value (0.26) of many FluxNet sites[47]. From limited data (Supplementary Table 8), we found that BP was higher in drier grasslands and moister forests, and BP enhancement was greater in moister sites for both ecosystem types and could be two to three times BP under ambient $CO_2$. Allocation of enhanced production to ANPP and BP was dynamic, which could be affected by seasonal variations of precipitation[48] (see Supplementary Discussion regarding BP).

**Remarks on terrestrial ecosystems under $eCO_2$.** Returning to our hypotheses, we conclude that H1 (EAPP being greater in drier years) is supported for grassland but not for woody ecosystems, H2 ($EAPP_{AV}$ being greater in drier ecosystems) holds across all ecosystems and H3 (EAPP responses to water supply being equivalent for woody- and grass-dominated ecosystems) is unlikely.

Collectively, the $eCO_2$ experiments suggest that greater $eCO_2$ enhancement in productivity will occur in drier years within grass-dominated ecosystems, whereas within woody ecosystems, $eCO_2$ enhancement is expected to be greater in wetter years despite woody ecosystems with drier baseline climates having greater average $eCO_2$ enhancement of ANPP. The $CO_2$-induced increase in plant productivity is probably achieved through direct enhancement of photosynthetic efficiency and indirect enhancement by increased WUE, and further augmented by a greater photosynthetic surface (LAI) resulting from more available carbohydrate and water[2,32]. Our study showed that woody ecosystems can effectively increase production under $eCO_2$, probably by using all of these mechanisms and particularly by enhancing LAI in years when water is abundant. By contrast, grassland ecosystems, due perhaps to differences in plant architecture and growth form, are less able to increase LAI in wetter years. The relatively more restricted LAI responses in grasslands would reduce the indirect effect enhancing carbon assimilation through enhanced LAI. Instead, excessive soil water in some grassland sites may increase N leaching losses and N limitation[22,30] and in others may trigger changes in species composition[20,39].

Given that woody ecosystems have a markedly stronger ANPP enhancement than grasslands (24% versus 13% for $eCO_2$ level at ~550 ppm), occupy ~50% of Earth's land (including forests, shrublands and woody savannas) and generally have a greater ANPP, our results suggest that $eCO_2$-enhanced terrestrial ANPP is likely to become increasingly dominated by woody plants under rising atmospheric $CO_2$, independent of other disturbance- and climate-related effects. However, we caution that as most forest FACE experiments to date have treated relatively young trees, with ecosystem LAI less than six (ref. [5]), mature forests are generally underrepresented in our analysis. Our analyses also focused only on ANPP rather than NPP because of limited data regarding the impacts of $eCO_2$ on BP. Available data show that responses of BP to $eCO_2$ are complex. Additional belowground research is needed to understand terrestrial responses to $eCO_2$ and mechanisms controlling carbon allocation.

Our finding that LAI plays a pivotal role in plant $eCO_2$ enhancement is consistent with a number of other recent observations, including that (1) forests with sparse canopies, such as relatively young systems or boreal forests[49], have a greater potential for $eCO_2$ enhancement; (2) drier ecosystems appear to be subject to greater greening and a greater relative increase in LAI[11–13]; and (3) plants with greater flexibility for increasing LAI, such as lianas in tropical forests[50], climbing vines in some temperate forests[51] and invasive species capable of strongly competing for photosynthetic space[52], preferentially benefit from $eCO_2$. Together, these results, along with the effects of local disturbances, provide mechanistic support for elevated atmospheric $CO_2$ being a potentially key driver in facilitating increased woody encroachment in arid grasslands and savannahs in recent decades[53].

The $eCO_2$ experiments in our study ranged from arid to moist ecosystems but covered only temperate to subtropical regions. There remains a lack of $eCO_2$ experiments in boreal and tropical zones with ecosystems that are particularly vulnerable to climate change. For forest biomes, other studies have reported widespread growth enhancements, probably due to globally elevated atmospheric $CO_2$[54,55]. For grassland ecosystems, $C_3$ grasses appear to enhance productivity through altered WUE with $eCO_2$. Although $C_4$ grasses are less sensitive to water supply than $C_3$ grasses, we have limited knowledge about how $eCO_2$ affects productivity of $C_4$ plants, the main component of tropical savannahs covering ~20% of Earth's surface. The manipulated $CO_2$ concentrations from the experimental sites used in our analysis vary between 540 and 720 ppm. These values represent the mid-range that would be attained by the end of the century under the Intergovernmental Panel on Climate Change Representative Concentration Pathway 4.5 and 6.0 scenarios[56]. Atmospheric $CO_2$ concentration at these levels would cause global temperatures to rise and make the climate system less stable. Our future climate will be determined partly by terrestrial responses to $eCO_2$, which will modulate ecosystem feedbacks on the climate system. The insights into $CO_2$ responses from the ecosystem experiments analysed here can help constrain Earth System Model representations of terrestrial ecosystem responses and their feedbacks to atmospheric $CO_2$, including critical sensitivity to and interactions with the climate system.

Overall, our findings provide new understanding of ecosystem responses to $eCO_2$ and water availability. The observation that ANPP enhancement is mediated via increased LAI suggests that long-term and interannual changes in foliage cover can be used as key indicators of $eCO_2$ impacts on terrestrial ecosystems. In particular, the empirical, general equation linking increased LAI with enhanced ANPP across different terrestrial ecosystems will be useful for detecting $eCO_2$ fertilization effects and quantifying large-area changes in terrestrial productivity through satellite-observed changes in LAI. The relationships uncovered among ecosystem types, $eCO_2$ and water supply can be used to validate Dynamic Global Vegetation Models and assist with better projecting the future impacts of elevated atmospheric $CO_2$ and climate change on terrestrial ecosystems.

## Methods

**Study sites, experimental designs and data.** To study the interactive response of productivity to elevated $CO_2$ and precipitation variability in different ecosystem types, data from $eCO_2$ experiments of 14 ecosystems were collated from published studies (Supplementary Tables 1–4) or project websites[57] and the Oak Ridge National Laboratory websites[58] (Supplementary Tables 1–4). Studies included six woody ecosystem and eight grassland ecosystem sites. The sites are located in temperate and subtropical zones between latitudes 48° N and 43° S in the Northern or Southern Hemisphere. The criteria for selected sites were based on availability of ANPP data or EAPP (from either publications or websites) and having $eCO_2$ treatments longer than four years at a site. Although we separated the experimental sites into woody and grassland groups on the basis of their life forms, both groups have diverse floras. This is particularly true for woody ecosystems, which are a mixture of different types, including desert shrubs, scrub oaks, coniferous and deciduous forests.

FACE and OTC $CO_2$ enrichment systems are manipulative ecosystem-scale experiments. There was also an advanced OTC system established in the site of a Swiss calcareous grassland, which used screen-aided $CO_2$ control (SACC) technology. Site locations, conditions, experimental designs, data sources and the methods of measurements and estimations for the variables used in this study are outlined and described in Supplementary Tables 1–4. The designs of FACE and OTC in different experimental sites have been widely reported in different publications (Supplementary Tables 1 and 2). Overall, fewer $CO_2$ enrichment experiments have been established for woody ecosystems than for grassland ecosystems. Most woody $eCO_2$ experiments are based on FACE technology (without the chamber effect) except the scrub-oak ecosystem, which used OTCs[59] (Supplementary Tables 1 and 3). Grassland experiments were established with FACE, OTC or SACC technology (Supplementary Tables 2 and 4). In most woody ecosystem experiments, the levels of $eCO_2$ varied between ~540 and 580 ppm with a mean of 555 ± 15 ppm. An exception is the scrub-oak ecosystem using the OTCs, which applied higher $eCO_2$ levels (~700 ppm) in the treatments. The levels of elevated $CO_2$ concentration were generally higher in grassland experiments, varying between ~550 and 720 ppm, with a mean of 623 ± 62 ppm.

At several of the FACE and OTC sites, multiple factors in addition to elevated $CO_2$ were manipulated, including nitrogen fertilization, water supply and temperature. For these sites, only the results from the $eCO_2$ experiments and $CO_2$ control sites were used. The one exception is for the experiment in Eschikon, Switzerland, where the FACE sites were all treated with low or high levels of N fertilization. Here, we used the average values for the low and high levels of N from the $eCO_2$ and controlled $CO_2$ sites. For the OTC and SACC studies, if the experiments included both ambient $CO_2$ and chamber (OTC) without $eCO_2$, only the results from the chamber experiments without $eCO_2$ were used as the control conditions for more suitable comparisons with consideration of chamber effects (Supplementary Table 4). Multiple-year data were used from each site. The longest experiments were run for more than a decade, but most experiments ran for fewer years, which limits the statistical power for individual sites (Supplementary Table 5).

**Data analyses and statistical modelling.** EAPP is defined as ANPPe/ANPPa: aboveground ANPP under $eCO_2$ divided by ANPP under ambient $CO_2$ concentration. ANPPe and ANPPa were, respectively, the averages of replicates (plots or subplots) for a given year at a given site (Supplementary Tables 1–4). EAPP represents the relative enhancement in ANPP by $eCO_2$, and there is no enhancement if EAPP equals 1. Note that EAPP is distinct from a percentage, although their values are interchangeable. For example, EAPP = 1.2 is equivalent to 20% enhancement in ANPP, and EAPP = 2.0 means 100% enhancement.

EAPP of each site, except for the Tasmania site, passed the Shapiro–Wilk normality test. For each experimental site, a linear regression was fit to the data points representing EAPP against iPPT across different years (Fig. 1a,b and Supplementary Table 5). The slopes of these linear functions, which represent precipitation sensitivity of ANPP enhancement ratios, were extracted for examination (Extended Data Fig. 2). The site $\mathrm{EAPP}_{\mathrm{AV}}$ and the MAP of multiple experimental years were estimated for each of the experimental sites. Linear regressions were used to fit $\mathrm{EAPP}_{\mathrm{AV}}$ and MAP across all ecosystems, and multiple woody and grass-dominated ecosystems (Fig. 2 and Supplementary Table 7).

In addition, we estimated ELAI, which is LAI under $eCO_2$ (LAIe) divided by LAI under an ambient $CO_2$ concentration (LAIa), using data from the few available sites. Among 14 sites in this study, only five have LAI data available, including three forests and two grasslands. A logistic curve for the EAPP–ELAI relationship was used for fitting available data points (across vegetation types and spatial and temporal scales) (Fig. 3 and Supplementary Table 7). SigmaPlot11 was used for statistics and curve fitting.

***Z*-score analysis and statistics.** For each experimental site, a linear regression was fit to data representing EAPP against iPPT over experimental years (Fig. 1a,b and Supplementary Table 5). Although EAPP response patterns obviously differed between woody and grassland ecosystems (Fig. 1a,b), some regressions for individual sites were not statistically significant due to small sample sizes of experimental years. To examine the response patterns, we standardized site data to generate *Z* scores based on the mean value and standard deviations of the data at each site and then pooled together all site data for analysis:

$$Z_{ik} = \frac{X_{ik-\mu_k}}{\sigma_k} \tag{1}$$

Here, $i = 1, 2 \ldots n$ for the sample size of site $k$, while $k = 1, 2 \ldots 6$ for woody ecosystems and $k = 1, 2 \ldots 8$ for grassland systems. The *Z* scores eliminate scale differences in data from different sites and make them comparable while retaining statistical properties. The variations in *Z* scores represent interactions between EAPP and iPPT. The *Z* scores of EAPP and iPPT are, respectively:

$$\mathrm{EAPP}_{z_{ik}} = \frac{\mathrm{EAPP}_{ik} - \mu\,[\mathrm{EAPP}_{ik}]}{\sigma\,[\mathrm{EAPP}_{ik}]} \tag{2}$$

$$P_{zik} = \frac{\mathrm{iPPT}_{ik} - \mu\,[\mathrm{iPPT}_{ik}]}{\sigma\,[\mathrm{iPPT}_{ik}]} \tag{3}$$

The *Z* scores vary below or above zero, showing annual variations of EAPP and indicating relatively drier or wetter years in the sites (Fig. 1c,d).

To assess the impact of iTEM on EAPP and the interactive effects between iPPT and iTEM, we also generated *Z* scores of iTEM:

$$T_{z_{ik}} = \frac{\mathrm{iTEM}_{ik} - \mu\,[\mathrm{iTEM}_{ik}]}{\sigma\,[\mathrm{iTEM}_{ik}]} \tag{4}$$

Because our interest lies in identifying response patterns of EAPP to iPPT rather than to model parameters, we examined combined data using general regression analysis. Our approach is analogous to the one-stage individual participant data (IPD) fixed-effects meta-regression model. The one-stage IPD meta-regression approach allows analysis of all individual data values from across studies simultaneously and has been suggested to have several advantages over traditional aggregated data meta-analysis[60] The meta-regression model is expressed as:

$$\mathrm{EAPP}_{z_{ik}} = \beta_0 + \beta_1 P_{z_{ik}} + \epsilon_{ik} + \zeta_k \tag{5}$$

Here, $i$ = 1, 2,…$n_k$, and $n_k$ is the sum of sample sizes of all sites.

The variable EAPP is an enhancement ratio of aboveground NPP (EAPP = APPe/APPa) under ambient $CO_2$ and $eCO_2$ treatments. Because $CO_2$ treatments under ambient $CO_2$ and $eCO_2$ were independent experimental units, each EAPP value can be considered a random sample from year to year because within-pair differences in measurements are random[61]. In addition, the data from different sites are independent among them because the experiments were independently conducted in different years and under different plot designs (Supplementary Tables 3 and 4). These conditions ensure that EAPP and *Z* scores of EAPP from all sites were independent data entries in the model. In equation (5), two terms, $\epsilon_{ik}$ and $\zeta_k$, denote two types of independent errors for the subgroup $k$: the first one, $\epsilon_{ik}$, represents sampling error for sample $i$, whereas $\zeta_k$ denotes between-study heterogeneity. However, $\zeta_k$ can be ignored in the equation for our analysis because we applied a fixed-effect model with *Z* scores (as the mean *Z* score of each site equals zero and the effect sizes between studies are not the concern in the analysis). The heterogeneity variance between sites is encapsulated in the intercept of the regression model. Therefore, the one-step IPD fixed-effect meta-regression analysis can be carried out virtually as a regular linear model applied to pooled data from all sites[62].

$$\widehat{\mathrm{EAPP}}_{zik} = \hat{\beta}_0 + \hat{\beta}_1 P_{z_{ik}} \tag{6}$$

The sampling error $\epsilon_{ik}$ (equation (5)) was estimated by the root mean square error and used to estimate 95% confidence intervals of the model (Fig. 1c,d).

The statistical analyses were performed with SPSS v.28.0 (SPSS Inc.) supplemented with the plug-in macros MetaReg.sps. Using *Z* scores, we were able to unify the data from different sites for analyses. The results show that fitted linear curves are statistically significant for both ecosystem types ($P < 0.0001$), which confirms the patterns we observed from individual sites. To further investigate the impact of iTEM on $eCO_2$ enhancement ratios of ANPP and interactions with iPPT, we added *Z* scores of iTEM as an additive predictor and an interaction term to equation (5) and reported the ANOVA in Table 1. The multi-variable regression results verify that iPPT has opposite impacts on EAPP in woody and grassland ecosystems, and iTEM has no significant effect on EAPP.

**Uncertainty in data application.** Synthesizing growth and productivity responses from $CO_2$ enrichment experiments presents challenges about how to properly collate needed data and assemble them from different sites and sources. There are relatively few $CO_2$ enrichment experiments, and each is unique in terms of vegetation, site conditions, experimental design and the number of experimental years. Although many forest FACE experiments used a protocol designed to improve experimental consistency, there were still great disparities in plot layouts, sampling and data processing methods (Supplementary Tables 1 and 3). The experiments of grassland ecosystems were even more diverse. Different grassland sites applied different $CO_2$ enrichment technologies and equipment (FACE, OTC or SACC), different enriched $CO_2$ levels, different plot sizes and sampling repetitions and different harvest methods and turnover (Supplementary Tables 2 and 4). All those internally inherited variations affect statistical results when drawing conclusions with across-site comparisons.

Here we chose to compare EAPP against the single variable iPPT, a key reason being to simplify comparisons among sites and reduce inconsistency. iPPT is a variable independent from temperature and other site factors and reflects site water conditions experienced by plants in situ. It is suitable for comparing the effect of $eCO_2$ on ANPP across different sites. In addition, we found growing-season precipitation (mPPT) does not relate better to EAPP than does iPPT (Supplementary Fig. 1 and Supplementary Table 6). Even when using a simple variable such as iPPT, that is, the sum of monthly precipitation over one year, the actual value of iPPT varies depending on whether the operator chooses to use hydrological year, calendar year, different first month in Northern and Southern Hemispheres, whether to include snow or only rainfall and so on. Wherever possible, we used iPPT data provided by site researchers because we assume that they know best how to represent iPPT. Although temperature is also an important variable affecting plant growth and hydrological dynamics, our analyses show that it has little effect on $eCO_2$ enhancement.

For ANPP data used in this study, we found uncertainty could result from different analyses, which might result in different values even when starting from the same raw data (for example, this study versus Hovenden[48]). Various factors could contribute to different conclusions. For example, vegetation in grassland ecosystems may have $C_3$ and $C_4$ grasses and forbs, and whether one includes forbs (as we did) in the data processes impacts results. Some grassland OTC experiments set up control plots with or without chambers; using chambered or unchambered ambient plots as reference could result in different ANPP enhancement ratios.

Grassland experiments also need to deal with biomass harvest, and some experiments may alter harvest protocols over experimental years, for example, changing from two harvests in early and late summers to one in mid-summer. Changes in harvest protocols may affect estimated $eCO_2$ effects on ANPP in grassland ecosystems because growth responses to $eCO_2$ during earlier and later growing seasons are often different.

Finally, researchers at some experimental sites may adjust their site data based on their knowledge of the sites, requiring sound judgement and understanding to do appropriately. All these issues increase the uncertainty associated with data processing in addition to sampling and measurement uncertainties.

**Reporting Summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this article.

## Data availability

Data collated and used for analyses, figures and tables of this study are available for access (https://doi.org/10.2737/RDS-2021-0093). The processed data underlying Figs. 1–3 and Extended Data Figs. 1–4 are available in the Source Data files. Full description of the original datasets is provided in Supplementary Tables 1–4. Source data are provided with this paper.

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## Author contributions

Y.P. assembled and analysed the data and wrote the manuscript; R.B.J., D.Y.H., O.L.P. and R.S.N. provided concepts and substantial editing of the manuscript; R.J.N., R.O., P.B.R., A.L., K.E.M. and C.O. were the major investigators for the e$CO_2$ experiments, providing the data, insightful comments and editing; R.B., J.H. and Y.L. edited and provided comments on the manuscript.

## Competing interests

The authors declare no competing interest.

## Additional information

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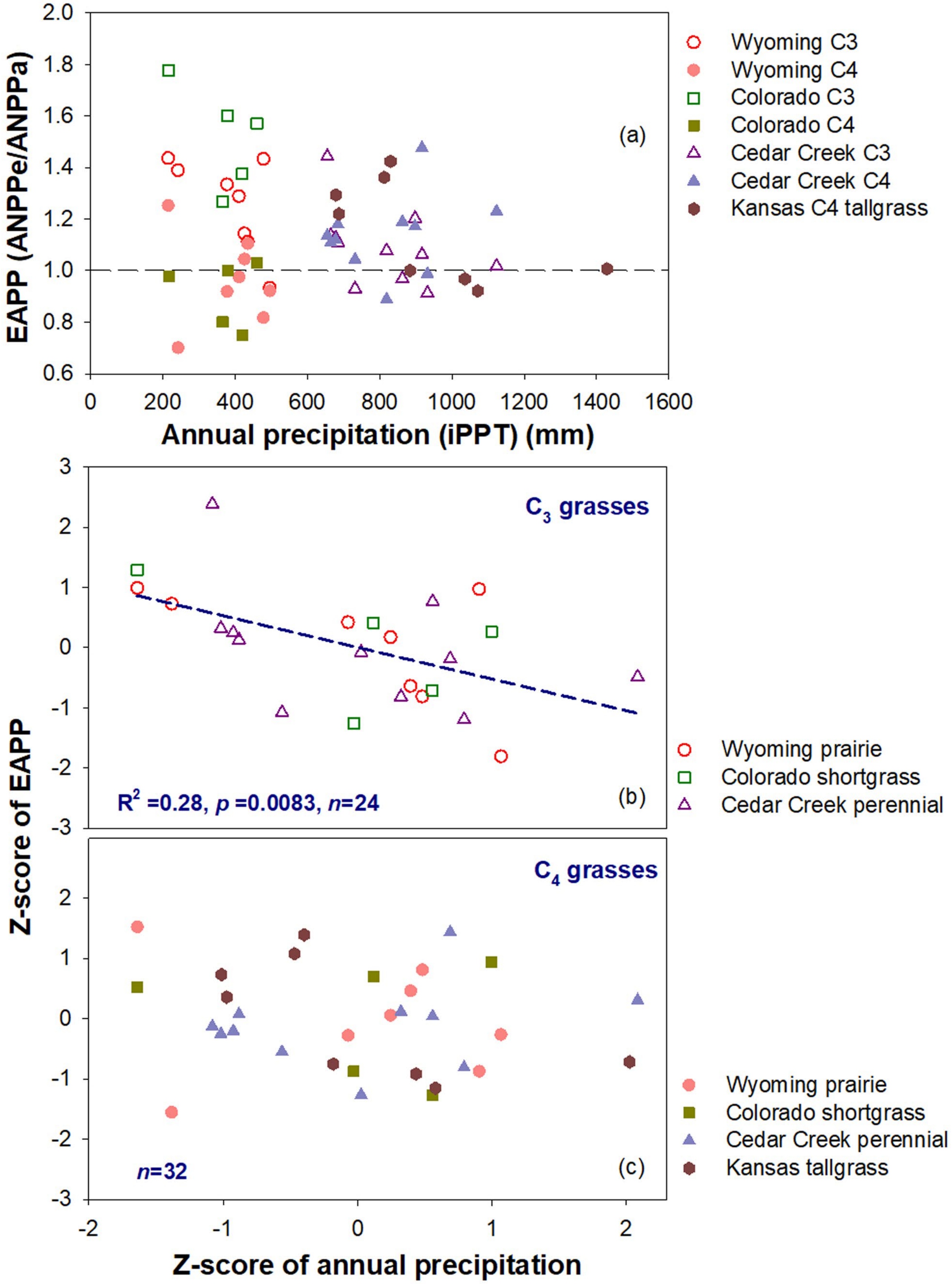
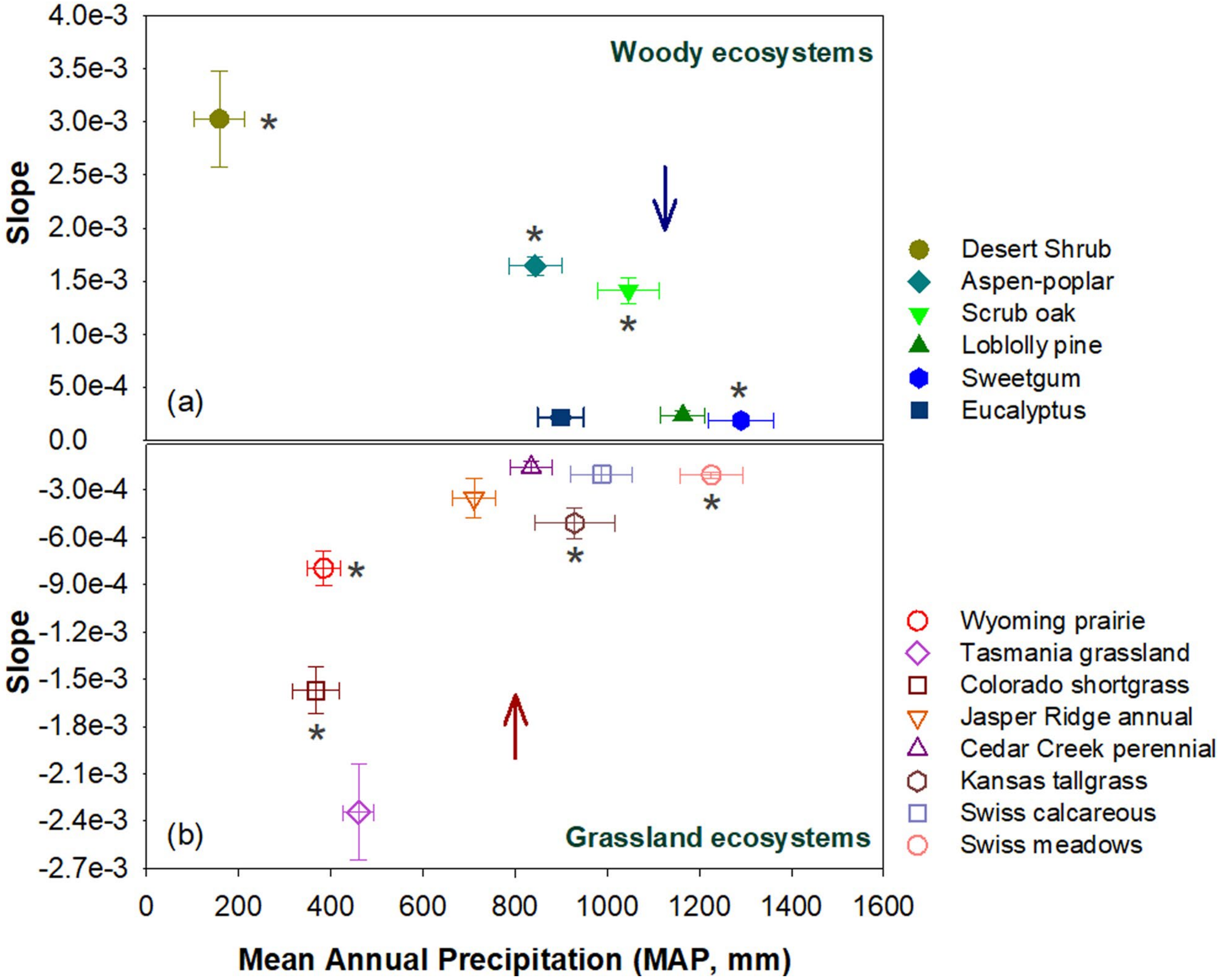
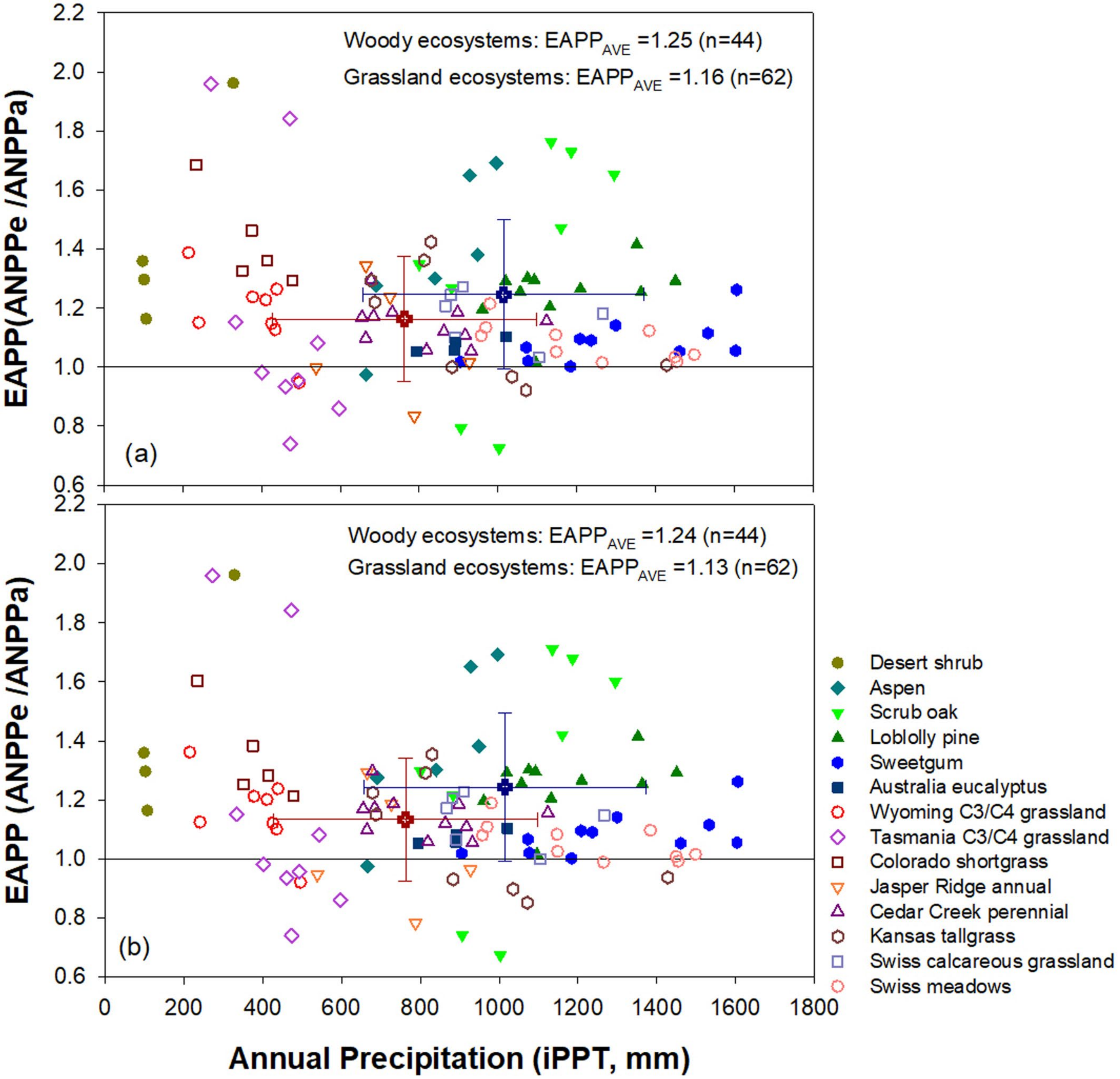


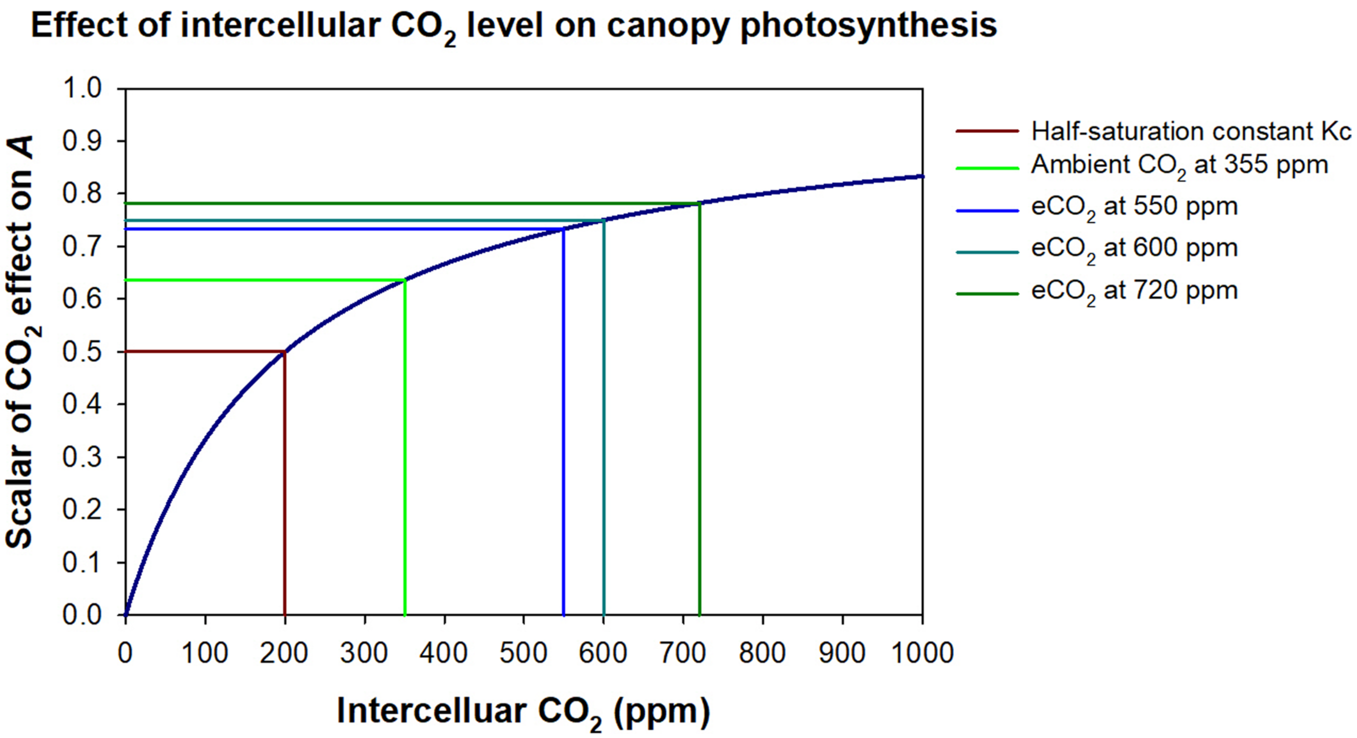
**Extended Data Fig. 1 | Responses of $C_3$ and $C_4$ grasses to $eCO_2$.** (**a**) EAPP responses of $C_3$ and $C_4$ grasses to annual precipitation (iPPT); (**b**) the Z-score analysis for $C_3$ grasses, and a linear regression; and (**c**) the Z-scores analysis for $C_4$ grasses; there is not an obvious relationship between EAPP and iPPT.



**Extended Data Fig. 2 | Sensitivity of ANPP enhancement to annual precipitation (slopes of the linear functions (Supplementary Table 5).** (**a**) Across woody and across (**b**) grassland ecosystems. A positive slope means EAPP increasing with increasing iPPT at a given site; a negative slope EAPP decreasing with increasing iPPT. Error bars are the standard errors (SEs) for slopes and MAP, respectively. The symbol '*' is used for sites with a linear regression at $*p = 0.1$. Arrows show MAP levels when slopes approach zero in woody and grassland ecosystems.



**Extended Data Fig. 3 | Mean ANPP enhancements affected by eCO$_2$ levels.** (**a**) Mean values of EAPP for all sampling years and all sites (EAPP$_{AVE}$) of woody (solid symbols) and grassland (open symbols) ecosystems; EAPP responses to iPPT are not significantly different between woody and grassland ecosystems (t-test: $p = 0.055$); (**b**) EAPP$_{AVE}$ of woody and grassland ecosystems after adjusting higher eCO$_2$ concentrations used in experiments to 550 ppm based on the Farquhar model (Extended Data Fig. 4); EAPP responses to iPPT are significantly different between woody and grassland ecosystems (t-test: $p = 0.011$). Error bars represent standard deviations (SDs).



**Extended Data Fig. 4 | Effects of $CO_2$ levels on canopy photosynthetic rates illustrated by the Farquhar model.** Y-axis shows the impact (scalar) of intercellular $CO_2$ levels on canopy photosynthesis rates, given an assumption of optimal intercellular $CO_2$ level being close to the atmospheric level. Relatively higher $CO_2$ concentrations were used in 6 enrichment experiments (600–720 ppm) compared to the $CO_2$ concentration (~550 ppm) used in forest ecosystems.

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# Reporting Summary

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## Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

| n/a | Confirmed | |
|---|---|---|
| ☐ | ☒ | The exact sample size ($n$) for each experimental group/condition, given as a discrete number and unit of measurement |
| ☐ | ☒ | A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly |
| ☐ | ☒ | The statistical test(s) used AND whether they are one- or two-sided<br>*Only common tests should be described solely by name; describe more complex techniques in the Methods section.* |
| ☐ | ☒ | A description of all covariates tested |
| ☐ | ☒ | A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons |
| ☐ | ☒ | A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals) |
| ☐ | ☒ | For null hypothesis testing, the test statistic (e.g. $F$, $t$, $r$) with confidence intervals, effect sizes, degrees of freedom and $P$ value noted<br>*Give P values as exact values whenever suitable.* |
| ☒ | ☐ | For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings |
| ☒ | ☐ | For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes |
| ☒ | ☐ | Estimates of effect sizes (e.g. Cohen's $d$, Pearson's $r$), indicating how they were calculated |

*Our web collection on statistics for biologists contains articles on many of the points above.*

## Software and code

Policy information about availability of computer code

| | |
|---|---|
| Data collection | All data were collated from the study websites, the Oak Ridge National Lab's FACE study website and publications. The references about data are listed in the Supplementary Tables 1-2. All the data were put together by Excel spreadsheets. |
| Data analysis | The Excel Data Analysis, SigmaPlot 11, SPSS v.28.0 and the plug-in macros MetaReg.sps were used for data analyses. there are computer coded generated for this study. |

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

## Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

Data collated and used for analyses, figures and tables of this study are available for access (https://doi.org/10.2737/RDS-2021-0093). The processed data underlying Figures 1-3 and Extended Data Figures 1-4 are available in the Source Data files. Full description of the original datasets is provided in Supplementary Tables 1-4.

# Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

# Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

| | |
|---|---|
| Study description | This is a synthesis study that uses the data collated from 14 CO2 enrichment experiments. The designs of experiments including equipments, sample plots, replicates, sampling methods, data processing are described in the Supplementary Tables 1-4. The study applied general statistical methods, Z-score analysis, and fixed effect IPD meta-regression for analyzing the data and deriving response patterns between CO2 enhancement in aboveground net primary production and annual precipitation. |
| Research sample | The data were based on measurements of annual aboveground net primary production (ANPP) from control plots with ambient CO2 and plots with higher CO2 treatments in the study sites. |
| Sampling strategy | Woody and grassland ecosystems have different strategies for sampling. In general, woody ecosystems used tree stem and height measurements, litter baskets and biomass conversion methods to estimate ANPP, while grassland ecosystems applied harvest methods to estimate ANPP. |
| Data collection | The scientists in the experimental sites collected raw data and processed them and presented in websites or publications. Yude Pan collated data from different sources including some contributions from co-authors (who are scientists of the experiments). |
| Timing and spatial scale | The experiments were run in different years, ranging as early as 1989 to the latest 2016. All experiments were at ecosystem scales, and the sites are located in temperate and subtropical zones between latitudes of 48oN and 43oS in the northern or southern hemisphere. |
| Data exclusions | We selected the study sites running experiments more than 4 years and having more than 4 years' data of ANPP or enhancement ratios of ANPP because we exploring response patterns of ANPP enhancement in this study. |
| Reproducibility | The manipulative experiments were diverse and expensive, most of the experiments have been ended years ago. In general, these experiments are not the type that could have reproducibility. |
| Randomization | The experimental designs (see Supplementary Tables 3-4) considered randomness in selecting plot locations and sampling methods. However, this study only used data from these experiments, was not directly involved with the issue of randomization. |
| Blinding | Blinding is not relevant to this study. |

Did the study involve field work? ☐ Yes ☒ No

# Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

## Materials & experimental systems

| n/a | Involved in the study | |
|---|---|---|
| ☒ | ☐ | Antibodies |
| ☒ | ☐ | Eukaryotic cell lines |
| ☒ | ☐ | Palaeontology and archaeology |
| ☒ | ☐ | Animals and other organisms |
| ☒ | ☐ | Human research participants |
| ☒ | ☐ | Clinical data |
| ☒ | ☐ | Dual use research of concern |

## Methods

| n/a | Involved in the study | |
|---|---|---|
| ☒ | ☐ | ChIP-seq |
| ☒ | ☐ | Flow cytometry |
| ☒ | ☐ | MRI-based neuroimaging |