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**Contrasting responses of woody and grassland ecosystems
to increased CO₂ as water supply varies**

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1 Experiments show that elevated atmospheric CO₂ (eCO₂) often enhances plant photosynthesis and
2 productivity, yet this effect varies substantially and may be climate-sensitive. Understanding if,
3 where, and how water supply regulates CO₂ enhancement is critical for projecting terrestrial
4 responses to increasing atmospheric CO₂ and climate change. Here, using data from 14 long-term
5 ecosystem-scale CO₂ experiments, we show that the eCO₂ enhancement of annual aboveground
6 net primary productivity (ANPP) is sensitive to annual precipitation and that this sensitivity differs
7 between woody and grassland ecosystems. During wetter years, CO₂ enhancement increases in
8 woody ecosystems but declines in grass-dominated systems. Consistent with this difference,
9 woody ecosystems can increase leaf area index (LAI) in wetter years more effectively under eCO₂
10 than grassland ecosystems. Overall, and across different precipitation regimes, woody systems had
11 markedly stronger CO₂ enhancement (25%) than grasslands (13%). We developed an empirical
12 relationship to quantify ANPP enhancement based on changes in LAI, providing a new approach
13 for evaluating eCO₂ impacts on the productivity of terrestrial ecosystems.

14

15

16 Knowing how elevated atmospheric carbon dioxide (eCO₂) affects the capacity of terrestrial
17 ecosystems to fix and store carbon is critical to understanding the future of the global carbon (C)
18 cycle, including terrestrial productivity and C-cycle feedbacks on the climate system. Evidence
19 from observations and modeling indicates that eCO₂ typically increases net primary production
20 (NPP) of terrestrial ecosystems, but the extent of the response among biomes remains uncertain
21 and can be sensitive to climate and nutrient constraints¹⁻⁴. Two primary physiological mechanisms
22 seem particularly important for understanding the CO₂ fertilization effect: increased leaf-level
23 photosynthesis and decreased stomatal conductance⁵. Consequences of these mechanisms under

24 eCO₂ include increased water use efficiency (WUE)⁶⁻⁹ and reduced water-stress in drier
25 ecosystems⁶.

26 Carbon-flux research in temperate and boreal forests of the Northern Hemisphere has
27 revealed significant increases in WUE over the past two decades, most consistent with the
28 hypothesis of a strong CO₂ fertilization effect attributable to elevated atmospheric CO₂¹⁰.
29 Meanwhile, studies combining remote sensing and modeling report increases in foliage cover and
30 NPP in drier regions of the world, suggesting that CO₂ fertilization has made the land surface
31 “greener”¹¹⁻¹³. Fatichi *et al.*² used a mechanistic model and experimental data to partition the
32 effects of eCO₂ on NPP into the direct effects associated with C assimilation and indirect effects
33 associated with changes in water condition and leaf area index (LAI). They concluded that the
34 indirect effects of eCO₂ account for 28% of the total enhanced plant productivity, with a tendency
35 for greater relative enhancements in arid ecosystems.

36 Free-air CO₂ enrichment (FACE) experiments and open-top chamber (OTC) systems have
37 been used for many years to investigate *in situ* responses of intact plant communities to eCO₂ at
38 ecosystem scales^{9,14,15}. Published results indicate that, for a ~50% increase in CO₂ concentration to
39 ~560 ppm¹⁵⁻¹⁷, aboveground net primary productivity (ANPP) and total NPP in forests increase on
40 average by ≈25%¹⁷. In contrast, results from grassland experiments show that growth responses to
41 eCO₂ (~650 ppm) are somewhat less than in forests, with increases in ANPP ranging from 11% to
42 17%¹⁷. Across all forest and grassland experiments, stomatal conductance consistently decreased
43 and instantaneous WUE increased by 4% to 44%^{18,19}. However, leaf-level changes did not always
44 lead to ecosystem-scale reductions in total water use or increases in soil moisture because of
45 additional transpiration from increased leaf areas^{7,18,19}.

46 Although CO₂ fertilization might be expected to have a greater effect in xeric ecosystems
47 and in drier conditions where and when the benefits of increased WUE are potentially stronger⁶,
48 evidence from enrichment studies is conflicting, with some studies supporting this hypothesis^{9,20}
49 but others not^{16,21}. Inconsistencies in eCO₂ responses of plants to water availability may reflect
50 variation in other factors, such as soil nutrient availability²²⁻²⁴, light limitation⁵, or indirect effects
51 of eCO₂ on LAI via changes of carbon allocation and soil water^{2,19}. Leaf and root structures and
52 mechanisms for acquiring CO₂, water, light, and nutrients vary for different plant life-forms,
53 which may also contribute to differences in eCO₂ responses to water availability.

54 To investigate mechanisms underpinning such inconsistencies, we analyzed data from 14
55 multi-year, ecosystem-scale CO₂ enrichment experiments, covering xeric to wet climates, in
56 ecosystems dominated by grasses, shrubs, or trees (Table S1, S2). These sites are located in
57 temperate and subtropical zones between latitudes of 48°N and 43°S in the northern or southern
58 hemisphere. The criteria for selected sites were based on availability of ANPP data or ANPP
59 enhancement ratios and a minimum eCO₂ treatment duration of 4 years. We explored the
60 responses of ecosystem types to interactions of eCO₂ and water supply. The enhancement ratio of
61 ANPP under eCO₂ to ANPP under ambient CO₂ (EAPP) was used as a measure of the **relative**
62 response of ecosystem productivity to eCO₂. We examined two types of relationships between
63 EAPP and precipitation for woody and grassland ecosystems: (1) annual EAPP (EAPP) and
64 annual precipitation (iPPT) (i.e. an annual sum of monthly precipitation) at a given site over
65 multiple experimental years; and (2) mean ecosystem EAPP (EAPP_{AV}) and mean annual
66 precipitation (MAP) across multiple sites of the same ecosystem type. We evaluated the following
67 three hypotheses: (H1) at a given site and over years, EAPP is greater in drier years; (H2) across
68 multiple sites of the same ecosystem type, EAPP_{AV} is greater in drier locations; and (H3) relative

69 enhancements (both EAPP and EAPP_{AV}) in response to water supply are equivalent for
70 ecosystems dominated by grasses or by woody taxa.

71 To test H1, we focused on the interactive effect of eCO₂ and temporal variations of iPPT
72 on EAPP. To test H2, we examined the interactive effect of eCO₂ and spatial variations of MAP
73 on EAPP_{AV}. The mechanisms underlying these two interactions likely differ. Finally, we tested H3
74 by comparing separate ecosystem types with distinct plant growth forms (i.e., woody and
75 grassland ecosystems) to assess the consistency of the eCO₂ responses in magnitude and trend—
76 given differences in their functional and structural traits, including height, leaf area and
77 orientation, and biomass allocation, which can affect light and nutrient acquisition and may
78 mediate eCO₂ and precipitation interactions.

79

80 **Relationships between EAPP and iPPT within individual ecosystems**

81 Annual precipitation varied widely across years and sites and affected both ANPP and the
82 responses of ANPP to eCO₂. Across all ecosystems, eCO₂ enhanced growth in most years (EAPP
83 >1; Fig. 1a,1b), but responses differed remarkably for woody and grassland ecosystems. Within
84 woody-dominated ecosystems, EAPP was positively related to iPPT and greater in wetter years at
85 a given site (Fig. 1a). In contrast, EAPP within a given grassland ecosystem declined in wetter
86 years (Fig. 1b).

87 The individual site response patterns appear to depend on the dominant life-form, although
88 a linear relationship between EAPP and iPPT was not statistically significant at every individual
89 site (Fig. 1a, 1b, Table S3a). This is particularly true for grassland ecosystems and those located
90 near transition zones such as from semi-arid to moist zones, where growth responses were
91 sometimes confounded with changing species composition under eCO₂^{20,24}. Different

92 carboxylation pathways of C₃ and C₄ grasses could also complicate EAPP responses to iPPT in
93 grassland sites with both physiological types. For instance, C₃ grasses were more responsive to
94 eCO₂ in drier years, whereas C₄ grasses showed little relationship with moisture conditions,
95 despite responding well over typically average precipitation years (Fig. S1; see Supplementary
96 Information about C₃ and C₄ plants).

97 For comparing diverse ecosystems, iPPT is a relatively simple proxy for water supply
98 because of its independence from other site factors. We recognized that growing season
99 precipitation could be a better predictor for plant productivity and sensitivity to eCO₂ at a given
100 site²². The length of a growing season varies annually dependent on local temperature and
101 vegetation types. Lacking growing season data from most sites, we used months from spring to
102 early autumn as a growing season to relate EAPP to growing season precipitation (mPPT).
103 Surprisingly, almost all the relationships weakened compared to those using annual precipitation
104 (Table S3b, Fig.S2). The results suggest that non-growing season precipitation contributes to
105 hydrological conditions in many sites. In temperate sites, soil water recharged by winter
106 precipitation (e.g., snow) might benefit early spring growth, while in evergreen and subtropical
107 sites year-round precipitation has an impact on growth.

108 Acknowledging statistical uncertainties in linear regressions of individual sites, we
109 standardized the site data and developed Z-scores to pool annual data of different sites to examine
110 patterns of EAPP-iPPT in woody and grassland ecosystems. The Z-scores eliminate scale
111 differences and facilitate comparisons among sites (see Methods for approaches). The fixed effect
112 regressions confirm the patterns we observed from individual sites: the relative CO₂ enhancement
113 of growth for woody ecosystems increased in wet years ($p < 0.0001$) while the enhancement
114 decreased with annual precipitation for grassland ecosystems ($p < 0.0001$) (Fig.1c, 1d).

115 Although the eCO₂ effect on plants is more directly related to water availability because it
116 changes stomatal conductance, WUE, and plant-water dynamics, temperature can also influence
117 the process through interactions with water. We therefore analyzed the impacts of annual mean
118 temperature (iTEM) on EAPP (using Z-scores), interactive effects, and covariances with other
119 variables, and found no statistically significant relationships ($p= 0.33, 0.71$ and $p= 0.77, 0.57$ for
120 woody and grassland ecosystems, respectively) (Table 1).

121

122 **Relationships between EAPP_{AV} and MAP across sites**

123 Across ecosystems from drier to moister sites, EAPP_{AV} responses to MAP appear to decline with
124 greater MAP for both woody and grassland ecosystems (Fig.2). Thus, in grasslands, the
125 enhancement responses to precipitation were consistent within and across sites: greater for both
126 drier years within a site and drier sites along the precipitation gradient. In contrast, the relative
127 enhancement in woody systems was greater in wetter years within a site but lower for wetter sites
128 across the precipitation gradient (Figs. 1, 2). The inter-site MAP gradient shows that the relative
129 CO₂ fertilization effect on ANPP was greater in drier climates, independent of responses to annual
130 variation in precipitation (Fig. 2), which likely reflects in part the importance of higher WUE in
131 drier regions for maximizing carboxylation while minimizing water cost²⁵. The EAPP_{AV} trends of
132 woody and grassland ecosystems are roughly parallel along the MAP gradient, although the
133 woody ecosystem trend is not statistically significant ($p = 0.18$) due to the low ANPP response in
134 the mature *Eucalyptus* woodland²⁶. Some grassland sites, such as Colorado shortgrass steppe and
135 Swiss meadows, achieve EAPP_{AV} as great as woody ecosystems under similar precipitation
136 conditions (Fig. 2).

137 The sensitivity of EAPP to iPPT within an ecosystem approaches zero (i.e., the slopes of
138 linear functions in Figure 1a, 1b) in wetter ecosystems for both woody and grassland habitats (Fig.
139 S3). Whereas the sensitivity (i.e. the absolute CO₂-induced enhancement per iPPT) declines with
140 annual precipitation, it appears to approach zero at higher MAP for woody systems (ca. 1200 mm)
141 than grasslands (ca. 800 mm) and remains notable even for the wettest woody ecosystems in our
142 dataset. This suggests that some eCO₂ enhancement may be sustained for ecosystems with more
143 abundant precipitation such as tropical rainforests. We observed that considerable eCO₂
144 enhancement of ANPP (~5-15%) is still realized experimentally in relatively mesic ecosystems
145 (Fig. 2) because of the direct eCO₂ fertilization effect and possibly periodic enhancements of WUE
146 due to recurring (short-term) drought in sites even with high MAP^{1,10}. Wetter terrestrial systems
147 often experience some seasonal water stress²⁷; for instance, seasonal water deficits for the loblolly
148 pine in the Duke FACE site frequently led to stomatal closure during part of the growing seasons
149 in drier years²⁸. Elevated CO₂ could alleviate some or all impacts of these dry periods on ANPP.

150

151 **The effect of eCO₂ on LAI mediates the EAPP-iPPT relationship within ecosystems**

152 Our results raise two questions: (1) Why does eCO₂ induce contrasting responses of EAPP to iPPT
153 within woody and grass-dominated ecosystems (Fig 1), despite similar declines of EAPP_{AV} to
154 MAP across sites (Fig 2)?; and (2) Why does EAPP respond differently to annual variations of
155 iPPT than EAPP_{AV} to geographic variations of MAP in woody systems, while the relationships are
156 consistent in grassland ecosystems?

157 Mechanisms that could contribute to the divergent response of the eCO₂ to moisture in
158 woody and grassland ecosystems include: (1) grassland ecosystems allocating additional
159 production belowground in wet years²⁹, potentially limiting ANPP eCO₂ enhancement at these

160 times; (2) differing seasonal sensitivities to moisture limitations, with grass-dominated systems
161 most sensitive early in growing seasons when leaf biomass reaches the maximum^{20,30}, but woody
162 systems affected throughout the growing season³¹; and (3) differences in plant architecture (such
163 as stem height, arrangement of leaves and roots) which influence light interception and limitation
164 aboveground, and access and storage of nutrients belowground. Although these and other potential
165 mechanisms may influence our observations (Fig. 1), no single one is likely to explain all the
166 observed patterns.

167 Because the eCO₂ effects on carbon assimilation efficiency and WUE should be
168 functionally similar in woody vegetation and grasses, we considered indirect eCO₂ effects
169 mediated by enhanced LAI². Such an enhancement may result from increasing carbohydrate and
170 water availability, and relevant changes in plant structures, and could have a compounding
171 impact^{7,32}. Across studies, we found a significant positive relationship ($p < 0.0001$) between EAPP
172 and enhanced LAI (ELAI) over all data from woody and grassland ecosystems, despite mixed
173 spatial and temporal scales (Fig. 3). The contrasting trends of EAPP responses to iPPT (Fig. 1) but
174 similar enhancements of EAPP with greater LAI (ELAI, Fig. 3), lead logically to the conclusion
175 that ELAI responses to iPPT must differ between woody and grassland ecosystems. Therefore, we
176 propose that diverging ELAI responses to iPPT is one possible mechanism causing the contrasting
177 EAPP responses to iPPT within woody and grassland ecosystems.

178 Other evidence from the eCO₂ experimental sites support this LAI-mediated interpretation.
179 FACE experiments in forests indicate that under eCO₂ ANPP and LAI both increase consistently
180 with increasing iPPT, particularly in sites with relatively low LAI^{5,33,34}. LAI increases with eCO₂
181 in most forest and woodland experimental sites, although the magnitude varies with tree species,
182 leaf traits, and stand structure^{19,33}. In the Mojave Desert, a site dominated by shrubs, EAPP only

183 shows great stimulation in wetter years, though EAPP and ELAI indicated enhancements for all
184 treatment years^{34,35}. Leaf-level stomatal conductance in woody ecosystems decreases on average
185 by 21% under eCO₂ at a level of ~550 ppm. However, canopy transpiration does not always
186 decline because increased LAI consumes the water-savings induced by eCO₂³⁶, resulting in similar
187 total soil water use³³. Thus, woody ecosystems effectively support new foliage³⁷ in wetter years,
188 helping to maintain a positive within-site EAPP-iPPT relationship (Fig. S4c) (see Supplementary
189 Information about interactive effects).

190 Grassland ecosystems differ structurally and morphologically from woody systems.
191 Aboveground production (i.e., mostly leaf biomass) and LAI are more closely related in
192 grasslands than in woody ecosystems, as are EAPP and ELAI. The EAPP and ELAI responses in
193 grasslands are very much water-related responses, with water stress reduced by enhanced WUE
194 under eCO₂ in drier years^{9,20}. In wetter years when water is less limiting, the relative eCO₂
195 enhancement for ANPP and LAI is often minimal^{9,30} (Fig. S4d). This result holds for multiple sites
196 including semi-arid shortgrass steppe dominated by C₃ species, mixed grass prairie^{9,38}, and mesic
197 but frequently water-stressed C₄ tallgrass prairie³⁰. In these experimental CO₂ enrichment sites,
198 instead of LAI increasing in wetter years, there was evidence of community shifts to greater
199 abundance of invasive grass species that are usually adapted to moister conditions as well as
200 substantial biomass enhancement of subshrub species^{20,39}.

201 Given the importance of increased LAI for enhancing ANPP, any site complexity affecting
202 LAI dynamics could up- or down-regulate EAPP and affect observed EAPP-iPPT relationships.
203 For example, the aspen forest in the Aspen-FACE study in Wisconsin¹⁴, had a substantially greater
204 increase in LAI under eCO₂ compared to other forest FACE sites (Fig. 3), likely because of the
205 lower starting LAI in the young and expanding forest stand⁵. Together with a greater daily

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

208

209 **Woody ecosystems have greater ANPP enhancement**

210 Across experimental sites with annual precipitation regimes from ~100 to 1700 mm,
211 average EAPP weighted by all experimental years ($EAPP_{AVE}$) in woody ecosystems was about
212 ~26% (n=44) compared to ~16% (n=62) in grassland ecosystems (i.e. significantly different at $p =$
213 0.044; t-test) (Fig. S5a). Experimental eCO_2 levels used in woody ecosystems were fairly
214 consistent (~550 ppm) except the scrub-oak site (~700 ppm) (Table S1a), while grassland sites had
215 various eCO_2 levels (~550-720 ppm), with 6 of 8 grassland sites exposing plants to higher eCO_2
216 (600-720 ppm) (Table S1b). Using the Farquhar model⁴⁰, we estimated these higher eCO_2
217 treatments induce 2-7% greater impact on photosynthetic rates compared to those for the standard
218 550 ppm site treatment (Fig. S6). Similarly, a published meta-analysis⁴¹ shows that higher eCO_2
219 used in grassland experiments (vs. ~550 ppm) could on average cause 3-7% greater responses of
220 plant growth. Therefore, after adjusting eCO_2 treatment levels to 550 ppm by the Farquhar model,
221 the average ANPP enhancement of all experimental years in woody ecosystems is ~25%, while
222 grassland ecosystems is reduced from 16% to 13%, approximately half that for woody ecosystems
223 (Fig. S5b).

224 Forest sites used in this study are mostly young forests in relatively early developmental
225 stages. One exception is a mature forest of *Eucalyptus* (EucFACE). EucFACE shows little eCO_2
226 enhancement in tree ANPP after 3 years' eCO_2 treatments despite a persistent 19% increase in leaf
227 photosynthesis²⁶. The slight enhancement in ANPP (~5%) presented in this study (Fig. 1, 2) is
228 attributable to abundant understory aboveground vegetation in this open dry woodland⁴². Another

229 mature forest study (WEB-FACE) in the fully-stocked European Beech-oak forest shows that tree-
230 ring increments were small under eCO₂ (Fig. S7)⁴³, on average (4%) lower than the average ANPP
231 enhancement (EAPP_{AV}) in the full-canopy sweetgum site in Oak Ridge (8%). Interestingly,
232 several eCO₂ enrichment studies in mature forests reported remarkable eCO₂ enhancements in
233 photosynthetic capacity or gross primary productivity, but not in carbon pools such as stem wood
234 or woody necromass^{42,44}, which may suggest that mature forests may also respond via increased
235 carbon losses or by transferring photosynthates to unmeasured carbon pools including those
236 belowground.

237 We note that our analysis focusses on enhancement of ANPP rather than NPP because data
238 relating belowground production (BP, i.e. fine root) responses to eCO₂ are sparse and typically
239 less certain. This gap may constrain full understanding of eCO₂ impacts on plant productivity
240 because C allocation to above- and belowground organs differ between woody and grassland
241 ecosystems, and likely shift with changes in carbon and water resources^{45,46}. It is also notable that
242 the forest FACE sites (except Oak Ridge) have much lower fine root allocation ratios than the
243 median value (0.26) of many FluxNet sites⁴⁷. From limited data (Table S5), we found that BP was
244 higher in drier grasslands and moister forests, and BP enhancement was greater in moister sites for
245 both ecosystem types and could be 2-3 times BP under ambient CO₂. Allocation of enhanced
246 production to ANPP and BP was dynamic, which could be affected by seasonal variations of
247 precipitation⁴⁸ (see Supplementary Information regarding belowground production).

248

249 **Remarks and perspectives on terrestrial ecosystems under eCO₂**

250 Returning to our hypotheses, we conclude: H1 (EAPP being greater in drier years) is
251 supported for grassland but not for woody ecosystems; H2 (EAPP_{AV} being greater in drier

252 ecosystems) holds across all ecosystems; and H3 (EAPP responses to water supply being
253 equivalent for woody- and grass-dominated ecosystems) is unlikely.

254 Collectively, the eCO₂ experiments suggest that greater eCO₂ enhancement in productivity
255 will occur in drier years within grass-dominated ecosystems, whereas within woody ecosystems,
256 eCO₂ enhancement is expected greater in wetter years despite the fact that woody ecosystems with
257 drier baseline climates have greater average eCO₂ enhancement of ANPP. The CO₂-induced
258 increase in plant productivity is likely achieved through direct enhancement of photosynthetic
259 efficiency and indirect enhancement by increased WUE, and further augmented by a greater
260 photosynthetic surface (LAI) resulting from more available carbohydrate and water^{2,32}. Our study
261 showed that woody ecosystems can effectively increase production under eCO₂, likely by using all
262 of these mechanisms and particularly by enhancing LAI in years when water is abundant. In
263 contrast, grassland ecosystems, due perhaps to differences in plant architecture and growth form,
264 are less able to increase LAI in wetter years. The relatively more restricted LAI responses in
265 grasslands would reduce the indirect effect enhancing carbon assimilation through enhanced LAI.
266 Instead, excessive soil water in some grassland sites may increase N leaching losses and N
267 limitation^{22,30}, and in others may trigger changes in species composition^{20,39}.

268 Given that woody ecosystems have a markedly stronger ANPP enhancement than
269 grasslands (25% vs.13%, for eCO₂ level at ~550 ppm), occupy ~30% of the Earth's land, and
270 generally have a greater ANPP, our results suggest that eCO₂-enhanced terrestrial ANPP is likely
271 to become increasingly dominated by woody plants under rising atmospheric CO₂, independent of
272 other disturbance- and climate-related effects. However, we caution that as most forest FACE
273 experiments to date have treated relatively young trees, with ecosystem LAI less than six⁵, mature
274 forests are generally underrepresented in our analysis. Our analyses also only focused on ANPP

275 rather than NPP because of limited data regarding the impacts of eCO₂ on BP. Available data
276 show that responses of BP to eCO₂ are complex. Additional belowground research is needed to
277 understand terrestrial responses to eCO₂ and mechanisms controlling carbon allocation.

278 Our finding that LAI plays a pivotal role in plant eCO₂ enhancement is consistent with a
279 number of other recent observations, including: (i) forests with sparse canopies, such as relatively
280 young systems or boreal forests⁴⁹, have a greater potential for eCO₂ enhancement; (ii) drier
281 ecosystems appear to be subject to greater greening, and a greater relative increase in LAI¹¹⁻¹³; and
282 (iii) plants with greater flexibility for increasing LAI, such as lianas in tropical forests⁵⁰, climbing
283 vines in some temperate forests⁵¹, and invasive species capable of strongly competing for
284 photosynthetic space⁵², preferentially benefit from eCO₂. Together, these results, along with the
285 effects of local disturbances, provide mechanistic support for elevated atmospheric CO₂ being a
286 potentially key driver in facilitating increased woody encroachment in arid grasslands and
287 savannas in recent decades⁵³.

288 The eCO₂ experiments in our study ranged from arid to moist ecosystems but only covered
289 temperate to subtropical regions. There remains a lack of eCO₂ experiments in boreal and tropical
290 zones with ecosystems which are particularly vulnerable to climate change. For forest biomes,
291 other studies have reported widespread growth enhancements, likely due to globally elevated
292 atmospheric CO₂^{54,55}. For grassland ecosystems, C₃ grasses appear to enhance productivity
293 through altered WUE with eCO₂. Although C₄ grasses are less sensitive to water supply than C₃
294 grasses, we have limited knowledge about how eCO₂ affects the productivity of C₄ plants, the
295 main component of tropical savannas covering ~20% of Earth's surface. The manipulated CO₂
296 concentrations from the experimental sites used in our analysis vary between 540 to 730 ppm.
297 These values represent the mid-range that would be attained by the end of the century under the

298 IPCC RCP 4.5 and 6.0 scenarios⁵⁶. Atmospheric CO₂ concentration at these levels would cause
299 global temperatures to rise and make the climate system less stable. Our future climate will be
300 partly determined by plant responses to eCO₂, which will modulate ecosystem feedbacks on the
301 climate system. The insights into CO₂ responses from the ecosystem experiments analyzed here
302 can help constrain and validate Earth System Model representations of terrestrial ecosystem
303 responses and their feedbacks to atmospheric CO₂, including critical sensitivity to and interactions
304 with the climate system.

305 Overall, our findings provide new understanding of ecosystem responses to eCO₂ and
306 water availability. The observation that ANPP enhancement is mediated via increased LAI
307 suggests that long-term and inter-annual changes in foliage cover can be used as key indicators of
308 eCO₂ impacts on terrestrial ecosystems. In particular, the empirical, general equation linking
309 increased LAI with enhanced ANPP across different terrestrial ecosystems will be useful for
310 detecting eCO₂ fertilization effects and quantifying large-area changes in terrestrial productivity
311 through satellite-observed changes in LAI. The relationships uncovered among ecosystem types,
312 eCO₂ and water supply can help validate Dynamic Global Vegetation Models and assist with
313 better projecting the future impacts of elevated atmospheric CO₂ and climate change on terrestrial
314 ecosystems.

315

316 **Methods**

317 *Study sites, experimental designs and data*

318 To study the interactive response of productivity to elevated CO₂ and precipitation
319 variability in different ecosystem types, data from eCO₂ experiments of 14 ecosystems were
320 collated from published studies (Table S1a, S1b) or project websites

321 (<http://www.lter.umn.edu/research/data/dataset?ple141>,
322 <http://www.ars.usda.gov/Main/docs.htm?docid=11120>) and the Oak-Ridge National Laboratory
323 websites (<http://cdiac.ornl.gov/ftp/FACE/ndffdata/>, <http://facedata.ornl.gov/npp-cdiac.html>,
324 http://facedata.ornl.gov/ndff/ndff_data_co2weather.html) (Table S1). Studies included six woody
325 ecosystem and eight grassland ecosystem sites. The sites are located in temperate and subtropical
326 zones between latitudes of 48°N and 43°S in the northern or southern hemisphere. The criteria for
327 selected sites were based on availability of ANPP data or ANPP enhancement ratios (EAPP)
328 (either from publications or websites) and having eCO₂ treatments longer than four years at a site.
329 Although we separated the experimental sites into woody and grassland groups based on their
330 lifeforms, both groups have diverse floras. This is particularly true for woody ecosystems which
331 are a mixture of different types including desert shrubs, scrub-oaks, coniferous, and deciduous
332 forests.

333 Free-air CO₂ enrichment (FACE) and open-top chamber (OTC) CO₂ enrichment systems
334 are manipulative ecosystem-scale experiments. There was also an advanced OTC system
335 established in the site of a Swiss calcareous grassland, which used the Screen-Aided CO₂ Control
336 (SACC) technology. Site locations, conditions, experimental designs, data sources, and the
337 methods of measurements and estimations for the variables used in this study are outlined and
338 described in Table S1 and Table S2. The designs of FACE and OTC in different experimental sites
339 have been widely reported in different publications (see Table S1). Overall, fewer CO₂ enrichment
340 experiments have been established for woody ecosystems than grassland ecosystems. Most woody
341 eCO₂ experiments are based on FACE technology (without the chamber effect) except the scrub-
342 oak ecosystem which used OTCs⁵⁷ (Table S1a, S2a). Grassland experiments were established with
343 either FACE, OTC, or SACC technologies (Table S1b, S2b). In most woody ecosystem

344 experiments, the levels of eCO₂ varied between ~540 and 580 ppm with a mean of 555±15 ppm.
345 An exception is the scrub-oak ecosystem using the OTCs, which applied higher eCO₂ levels
346 (~700-730 ppm) in the treatments. The levels of elevated CO₂ concentration were generally higher
347 in grassland experiments, varying between ~550 and 720 ppm with a mean of 623±62 ppm.

348 At several of the FACE and OTC sites, multiple factors in addition to elevated CO₂ were
349 manipulated, including nitrogen fertilization, water supply, and temperature. For these sites, only
350 the results from the eCO₂ experiments and CO₂ control sites were used. The one exception is for
351 the experiment in Eschikon, Switzerland, where the FACE sites were all treated with low or high
352 levels of N fertilization. Here, we used the average values for the low and high levels of N from
353 the eCO₂ and controlled CO₂ sites. For the OTC and SACC studies, if the experiments included
354 both ambient CO₂ and chamber (OTC) without eCO₂, only the results from the chamber
355 experiments without eCO₂ were used as the control conditions for more suitable comparisons with
356 consideration of chamber effects (Table S2b). Multiple year data were used from each site. The
357 longest experiments were run for more than a decade, but most experiments ran for fewer years,
358 which limits the statistical power for individual sites (Table S3a).

359

360 *Data analyses and statistical modeling*

361 The ANPP enhancement ratio (EAPP) is defined as ANPPE/ANPPa, i.e., aboveground
362 annual net productivity (ANPP) under eCO₂ (ANPPE) divided by ANPP under ambient CO₂
363 concentration (ANPPa). ANPPE and ANPPa were respectively the averages of replicates (plots or
364 subplots) for a given year at a given site (Table S1, S2). EAPP represents the relative enhancement
365 in ANPP by eCO₂, and there is no enhancement if EAPP equals 1. Note that EAPP is distinct

366 from a percentage, although their values are interchangeable. For instance, $EAPP = 1.2$ is
367 equivalent to 20% enhancement in ANPP; and $EAPP = 2.0$ means 100% enhancement.

368 EAPP of each site all passed the Shapiro–Wilk normality test except for the Tasmania site.
369 For each experimental site, a linear regression was fit to the data points representing EAPP against
370 annual precipitation (iPPT) across different years (Fig. 1a, 1b, Table S3a). The slopes of these
371 linear functions, which represent precipitation sensitivity of ANPP enhancement ratios, were
372 extracted for examination (Fig. S3). The site average of EAPP ($EAPP_{AV}$) and the average of iPPT
373 (MAP) of multiple experimental years were estimated for each of the experimental sites. Linear
374 regressions were used to fit $EAPP_{AV}$ and MAP across all ecosystems, and multiple woody and
375 grass dominated ecosystems (Fig. 2. Table S4).

376 In addition, we estimated LAI enhancement ratios ($ELAI = LAI_e/LAI_a$), which is LAI
377 under eCO_2 (LAI_e) divided by LAI under an ambient CO_2 concentration (LAI_a), using data from
378 the few available sites (Table S2). Among 14 sites in this study, only five have LAI data available,
379 including three forests and two grasslands. A logistic equation for the EAPP-ELAI relationship
380 was developed using all available data points (across vegetation types, spatial and temporal scales)
381 by a non-linear regression (Fig. 3, Table S4). SigmaPlot11 was used for statistics and curve fitting.
382

383 *Z-score analysis and statistics*

384 For each experimental site, a linear regression was fit to data representing EAPP against
385 inter-annual precipitation (iPPT) over experimental years (Fig. 1a, 1b, Table S3a). Although
386 EAPP response patterns obviously differed between woody and grassland ecosystems (Fig. 1a,
387 1b), some regressions for individual sites were not statistically significant due to small sample
388 sizes of experimental years. To examine the response patterns, we standardized site data to

389 generate Z-scores based on the mean value and standard deviations of the data at each site, and
 390 then pooled together all site data for analysis:

$$391 \quad Z_{ik} = \frac{X_{ik} - \mu_k}{\sigma_k} \quad (\text{Eq. 1})$$

392 Here, $i = 1, 2 \dots n$ for the sample size of site k , while $k = 1, 2 \dots 6$ for woody ecosystems and $k = 1,$
 393 $2 \dots 8$ for grassland systems. The Z-scores eliminate scale differences in data from different sites
 394 and make them comparable, while retaining statistical properties. The variations in Z-scores
 395 represent interactions between eCO₂ enhancement ratios (EAPP) and annual precipitation (iPPT).
 396 Z-scores of EAPP and iPPT are, respectively:

$$397 \quad EAPP_{Z_{ik}} = \frac{EAPP_{ik} - \mu[EAPP_{ik}]}{\sigma[EAPP_{ik}]} \quad (\text{Eq. 2})$$

$$398 \quad PZ_{ik} = \frac{iPPT_{ik} - \mu[iPPT_{ik}]}{\sigma[iPPT_{ik}]} \quad (\text{Eq. 3})$$

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

401 To assess the impact of mean annual temperature (iTEM) on EAPP and the interactive
 402 effects between iPPT and iTEM, we also generated Z-scores of mean annual temperature:

$$403 \quad TZ_{ik} = \frac{iTEM_{ik} - \mu[iTEM_{ik}]}{\sigma[iTEM_{ik}]} \quad (\text{Eq. 4})$$

404 Because our interest lies in identifying response patterns of EAPP to iPPT rather than to model
 405 parameters, we examined combined data using general regression analysis. Our approach is
 406 analogous to the one-stage IPD (individual participant data) fixed effects meta-regression model.
 407 The one-stage IPD meta-regression approach allows analysis of all individual data values from
 408 across studies simultaneously and has been suggested to have several advantages over traditional
 409 AD (aggregated data) meta-analysis⁵⁸. The meta-regression model is expressed as:

$$410 \quad EAPP_{Z_{ik}} = \beta_0 + \beta_1 PZ_{ik} + \epsilon_{ik} + \zeta_k \quad (\text{Eq. 5})$$

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

412 The variable EAPP is an enhancement ratio of aboveground NPP (EAPP=APPe/APPa)
 413 under ambient CO₂ and eCO₂ treatments. Because CO₂ treatments under ambient CO₂ and eCO₂
 414 were independent experimental units, each EAPP value can be considered as a random sample
 415 from year to year because within-pair differences in measurements are random⁵⁸. In addition, the
 416 data from different sites are also independent among them because the experiments were
 417 independently conducted in different years and under different plot designs (Table S2). These
 418 conditions ensure that EAPP and Z-scores of EAPP from all sites were independent data entries in
 419 the model. In Eq. 5, two terms, ϵ_{ik} and ζ_k denote two types of independent errors for the subgroup
 420 k : the first one, ϵ_{ik} , represents sampling error for sample i , whereas ζ_k denotes between-study
 421 heterogeneity. However, ζ_k can be ignored in the equation for our analysis because we applied a
 422 fixed effect model with z-scores (as the mean Z-score of each site all equals zero and the effect
 423 sizes between-studies are not the concern in the analysis). The heterogeneity variance between-
 424 sites is encapsulated in the intercept of the regression model. Therefore, the one-step IPD fixed
 425 effect meta-regression analysis can be carried out virtually as a regular linear model applied to
 426 pooled data from all sites⁶⁰.

$$427 \quad \widehat{EAPP}_{Z_{ik}} = \hat{\beta}_0 + \hat{\beta}_1 P_{Z_{ik}} \quad (\text{Eq. 6})$$

428 The sampling error ϵ_{ik} (Eq. 5) was estimated by the root mean square error (MSE) and used to
 429 estimate 95% confidence intervals of the model (Fig. 1c, 1d).

430 The statistical analyses were performed with SPSS v.28.0 (SPSS Inc, Chicago, IL)
 431 supplemented with the plug-in macros MetaReg.sps. Using Z-scores, we were able to unify the
 432 data from different sites for analyses. The results show that fitted linear curves are statistically
 433 significant for both ecosystem types ($p < 0.0001$), which confirm the patterns we observed from

434 individual sites. To further investigate the impact of annual mean temperature on eCO₂
435 enhancement ratios of ANPP and interactions with annual precipitation, we added Z-scores of
436 iTEM as an additive predictor and an interaction term to Eq. 5 and reported the ANOVA in Table
437 1. The multi-variable regression results verify that annual precipitation has opposite impacts on
438 EAPP in woody and grassland ecosystems, and annual mean temperature has no significant effect
439 on EAPP.

440

441 *Uncertainty in data application*

442 Synthesizing growth and productivity responses from CO₂ enrichment experiments present
443 challenges about how to properly collate needed data and assemble them from different sites and
444 sources. There are relatively few CO₂ enrichment experiments, and each is unique in terms of
445 vegetation, site conditions, experimental design, and the number of experimental years. Although
446 many forest FACE experiments used a protocol designed to improve experimental consistency,
447 there were still great disparities in plot layouts, sampling, and data processing methods (Table
448 S2a). The experiments of grassland ecosystems were even more diverse. Different grassland sites
449 applied different CO₂ enrichment technologies and equipment (FACE, OTC, or SACC), different
450 enriched CO₂ levels, different plot sizes and sampling repetitions, and different harvest methods
451 and turnover (Table S2b). All those internally inherited variations affect statistical results when
452 drawing conclusions with across-site comparisons.

453 Here we chose to compare ANPP enhancement ratios (EAPP) against the single variable
454 annual precipitation (iPPT), a key reason being to simplify comparisons among sites and reduce
455 inconsistency. Annual precipitation is a variable independent from temperature and other site
456 factors and reflects site water conditions experienced by plants *in situ*. It is suitable for comparing

457 the effect of eCO₂ on ANPP across different sites. In addition, we found growing season
458 precipitation (mPPT) does not relate better to EAPP than annual precipitation (iPPT) (Fig. S2,
459 Table S3b). Even when using a simple variable such as iPPT, i.e., the sum of monthly
460 precipitation over one year, the actual value of iPPT varies depending on whether the operator
461 chooses to use hydrological year, calendar year, different first month in northern and southern
462 hemisphere, and whether to include snow or only rainfall, etc. Wherever possible, we used iPPT
463 data provided by site researchers (Table S1) because we assume that they know best how to
464 represent iPPT. Although temperature is also an important variable affecting plant growth and
465 hydrological dynamics, our analyses show that it has little effect on eCO₂ enhancement.

466 For ANPP data used in this study, we found uncertainty could result from different
467 analyses, which might result in different values even when starting from the same raw data (e.g.,
468 this study vs. Hovenden⁴⁸). Various factors could contribute to different conclusions. For instance,
469 vegetation in grassland ecosystems may have C₃ and C₄ grasses and forbs, and whether one
470 includes forbs (as we did) in the data processes impacts results. Some grassland OTC experiments
471 set up control plots with or without chambers; using chambered or un-chambered ambient plots as
472 reference could result in different ANPP enhancement ratios.

473 Grassland experiments also need to deal with biomass harvest and some experiments may
474 alter harvest protocols over experimental years, for instance changing from two harvests in early
475 and late summers to one in mid-summer. Changes in harvest protocols may affect estimated eCO₂
476 effects on ANPP in grassland ecosystems because growth responses to eCO₂ during earlier and
477 later growing seasons are often different.

478 Finally, researchers at some experimental sites may adjust their site data based on their
479 knowledge of the sites, requiring sound judgement and understanding to do appropriately. All

480 these issues increase the uncertainty associated with data-processing in addition to sampling and
481 measurement uncertainties.

482

483 **Data availability**

484 All data needed to reach conclusions in the paper are presented in the paper and/or the
485 Supplementary Materials with figures or tables. Additional data related to this paper may be
486 requested from the authors.

487

488 **References**

489

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622

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635

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637 D.Y.H., O.L.P., and R.N. provided concepts and substantial editing of the manuscript; R.J.N.,
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641

642 **Figure Legends**

643 Figure 1. Relationships between eCO₂ enhancement of ANPP and annual precipitation. EAPP is
644 an enhancement ratio of ANPP under eCO₂ (ANPPe) and ambient CO₂ (ANPPa) treatments. (a)
645 EAPP responses to annual precipitation (iPPT) over multiple experimental years within woody
646 ecosystems, and (b) within grassland ecosystems; at * $p=0.1$, solid lines represent the regression
647 statistically significant, dashed lines not significant (Table S3a); the horizontal line EAPP = 1
648 denotes no enhancement, while above or below it enhancement or reduction under eCO₂. The
649 fixed effect regressions between Z-scores of EAPP and iPPT (thick solid lines with confidence
650 intervals of gray areas) in (c) woody and (d) grassland ecosystems; the thin lines are linear
651 regressions of Z-scores of individual sites.

652

653 Figure 2. Mean responses of eCO₂ enhancement (EAPP_{AV}) to mean annual precipitation (MAP)
654 across multiple ecosystems. EAPP_{AV} is the mean EAPP of experimental years, while MAP the
655 mean annual precipitation (iPPT) of experimental years at a given site. The solid line represents
656 the regression for all sites; the dashed lines are those for woody and grassland ecosystems. The
657 regression for woody ecosystems is not statistically significant at * $p=0.1$, largely due to a low

658 EAPP_{AV} at the EucFACE site. Solid symbols are for woody ecosystems and open symbols for
659 grassland ecosystems. Error bars represent the standard errors (SEs) at each site.

660

661 Figure 3. The relationship between EAPP and ELAI. EAPP and ELAI are respectively the
662 enhancement ratios of ANPP and LAI under eCO₂ vs. ambient treatments. Solid symbols are
663 woody ecosystems, open symbols grassland ecosystems. A logistic function was used for data
664 fitting (Table S4). The excluded outlier was from the C₄ tallgrass prairies, which occurred in the
665 driest year of the site with abnormal low LAI at the ambient CO₂ plots, causing exceptionally high
666 relative LAI enhancement.

667

668

Table 1. ANOVA of fixed effect multi-variable regression and covariance of variables. Annual precipitation (iPPT), annual mean temperature (iTEM), and ANPP enhancement ratios (EAPP) of woody and grassland ecosystems, were standardized as z-scores (P_z , T_z and $EAPP_z$), respectively (see Methods).

Woody ecosystem	<i>df</i>	<i>SE</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	R^2
<i>Model</i>	43	0.7527	5.0657	8.9409	0.0001	0.4014
EAPP _z ^{&}	<i>B</i>	<i>SE</i>	<i>z-test</i>	<i>P-value</i>	$CV_{(P_z, T_z)}$ [*]	CV_{EAPP_z} [†]
Intercept	0.0106	0.1144	0.0926	0.9268		
P_z	0.6372	0.1233	5.1679	< 0.0001	0.8636	0.5343
T_z	0.1209	0.1235	0.9789	0.3336	0.8133	0.0317
$P_z \times T_z$	0.0473	0.1243	0.3805	0.7053	-0.1186	0.0244
Grassland ecosystem	<i>df</i>	<i>SE</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	R^2
<i>Model</i>	61	0.8151	8.2825	8.2825	0.0001	0.3073
EAPP _z ^{&}	<i>B</i>	<i>SE</i>	<i>z-test</i>	<i>P-value</i>	$CV_{(P_z, T_z)}$	CV_{EAPP_z}
Intercept	0.0027	0.1064	0.0254	0.9800		
P_z	-0.6053	0.1217	-4.9737	< 0.0001	0.8684	-0.4549
T_z	-0.0319	0.1107	-0.2882	0.7743	0.9090	0.0318
$P_z \times T_z$	0.0686	0.1215	0.5646	0.5743	-0.0964	0.0126

[&]Dependent variable

^{*}Covariances of independent variables P_z and T_z

[†]Covariances of predictive variables and dependent variable $EAPP_z$

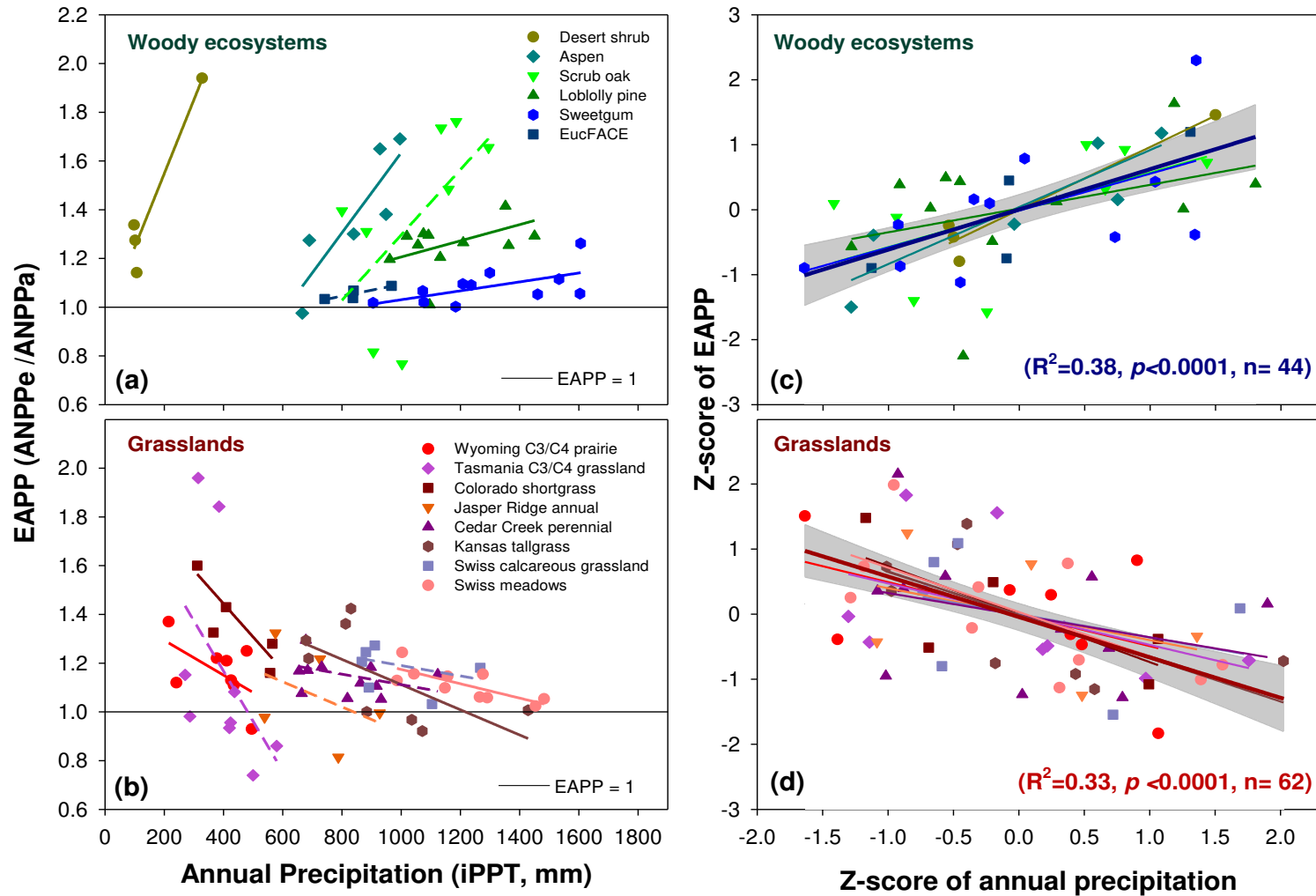


Figure 1. Relationships between $e\text{CO}_2$ enhancement of ANPP and annual precipitation. EAPP is an enhancement ratio of ANPP under $e\text{CO}_2$ (ANPPE) and ambient CO_2 (ANPPa) treatments. (a) EAPP responses to annual precipitation (iPPT) over multiple experimental years within woody ecosystems, and (b) within grassland ecosystems; at $*p=0.1$, solid lines represent the regression statistically significant, dashed lines not significant (Table S3a); the horizontal line EAPP = 1 denotes no enhancement, while above or below it enhancement or reduction under $e\text{CO}_2$. The fixed effect regressions between Z-scores of EAPP and iPPT (thick solid lines with confidence intervals of gray areas) in (c) woody and (d) grassland ecosystems; the thin lines are linear regressions of Z-scores of individual sites.

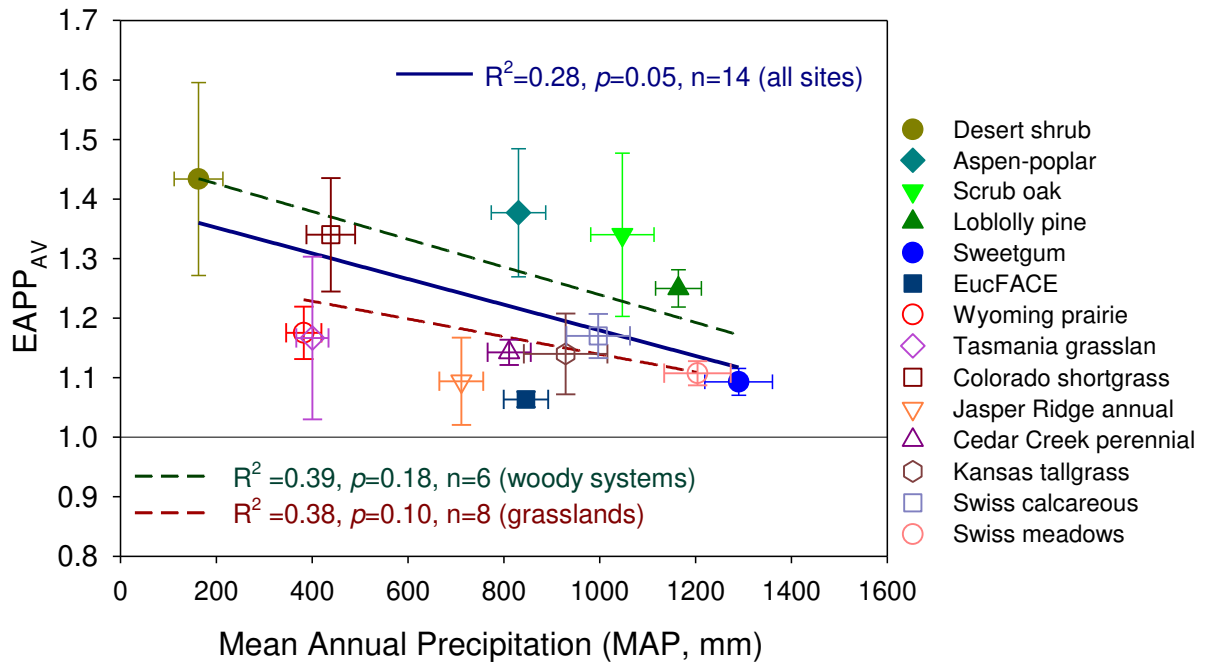


Figure 2. Mean responses of eCO₂ enhancement (EAPP_{AV}) to mean annual precipitation (MAP) across multiple ecosystems. EAPP_{AV} is the mean EAPP of experimental years, while MAP the mean annual precipitation (iPPT) of experimental years at a given site. The solid line represents the regression for all sites, the dashed lines those for woody and grassland ecosystems. The regression for woody ecosystems is not statistically significant at $*p=0.1$, largely due to a low EAPP_{AV} at the EucFACE site. Solid symbols are for woody ecosystems and open symbols grassland ecosystems. Error bars represent the standard errors (SEs) at each site.

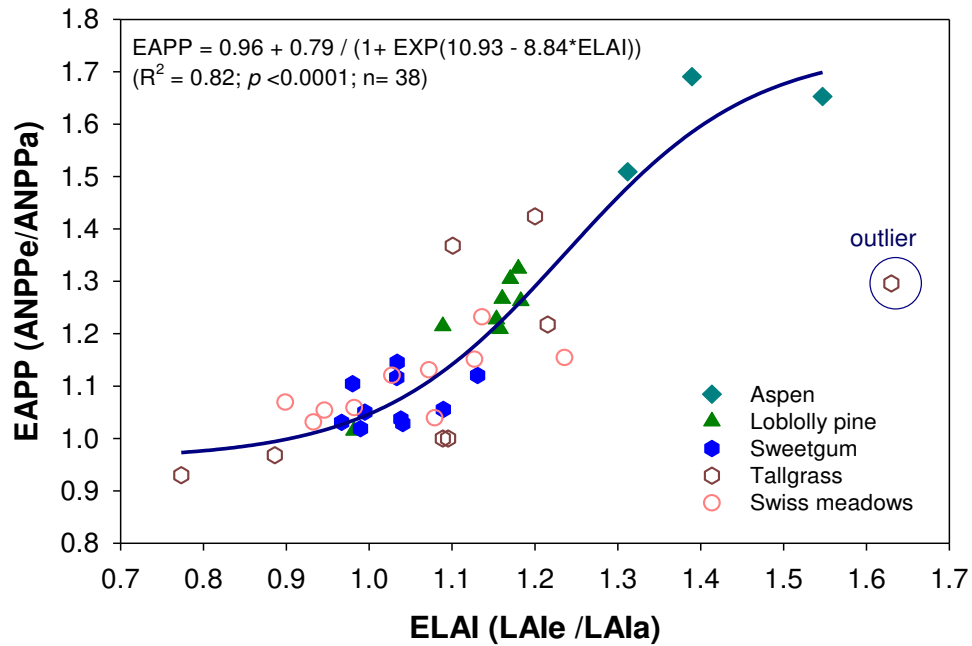


Figure 3. The relationship between EAPP and ELAI. EAPP and ELAI are respectively the enhancement ratios of ANPP and LAI under eCO₂ vs. ambient treatments. Solid symbols are woody ecosystems, while open symbols are grassland ecosystems. A logistic function was used for data fitting (Table S4). The excluded outlier was from the C₄ tallgrass prairies, which occurred in the driest year of the site with abnormal low LAI at the ambient CO₂ plots, causing exceptionally high relative LAI enhancement.

Supplementary Information

Supplementary Text

Table S1-S5

Figure S1-S6

Supplementary Text

Different EAPP responses to iPPT by C₃ and C₄ plants

C₃ and C₄ plants have different carboxylation pathways¹. C₃ plants use the rubisco (ribulose biphosphate carboxylase/oxygenase) enzyme to produce a 3-carbon molecule in the first step of carbon fixation, which is also known as the Calvin Cycle. The oxygenase activity of rubisco causes ~25% of fixed carbon to be lost in a process of photorespiration. C₄ plants use an alternate enzyme, PEP (phosphoenolpyruvate carboxylase) to produce a 4-carbon intermediate molecule (malate) in the initial step of carbon fixation. As PEP does not have oxygenase activity, it is more efficient for attaching CO₂ than rubisco. The specialized leaf anatomy in C₄ plants includes two types of photosynthetic cells, which are mesophyll cells on the leaf exterior near stomata containing PEP, and bundle sheath cells in the leaf interior away from stomata containing rubisco. The malate is transported to internal bundle sheath cells and releases CO₂ after decarboxylation, which is then fixed by rubisco as part of the Calvin Cycle. As there is very low oxygen content inside bundle sheath cells, rubisco is less likely to react to O₂ and lose carbon.

With this photosynthetic advantage, C₄ plants have adapted better than C₃ plants to conditions of drought and hot climate as well as to nitrogen and CO₂ limitation. Therefore, C₃ and C₄ plants are expected to respond differently to eCO₂ treatments and water supply. Among 8 grassland sites of the experiments, tallgrass prairies of the Kansas site are dominated by C₄ grasses. Other sites are more or less dominated by C₃ species mixed with

C₄ grasses. The experiments at Cedar Creek established separate C₃ and C₄ subplots each with one or more grass species. Only 4 sites (including the Kansas site) have available data identifying C₃ and C₄ species (Fig. S1a), which can be used to examine respectively their EAPP responses to iPPT.

With these limited data, the results show that EAPP of C₃ plants are generally consistent in responses, decreasing with increasing iPPT (Fig. S1b). EAPP of C₃ plants is greater in drier sites (e.g. Wyoming PHACE, Colorado steppe) than a moderately moist site (Cedar Creek). The latter site EAPP became less than 1 under higher iPPT, which means lower production under eCO₂ than under ambient treatments. EAPP of C₄ grasses relating to iPPT appears to be diverse: in drier sites (Wyoming, Colorado), it was insensitive with most EAPP <1, indicating negative impacts of eCO₂ on ANPP; at the moister site of Cedar Creek, EAPP >1, indicating generally positive impacts of eCO₂; and in the tallgrass prairies (Kansas), EAPP decreased from positive impacts of eCO₂ to negative impacts from drier to wetter years (Fig. S1a).

The Z-score analyses show that EAPP of C₃ grasses declined with annual precipitation, whereas that of C₄ grasses did not have a clear relationship with annual precipitation (Fig. S1b, 1c). However, ANPP enhancement of C₄ grasses was relatively greater when iPPT was near average (or slightly wetter than average) of annual precipitation at the site (Fig. S1c). From those different responses by C₃ and C₄ plants, it seems that productivity of C₃ plants was more enhanced by increased WUE; in contrast, C₄ plants that adapt well to water limitation could promote productivity at higher CO₂ when experiencing average or slightly wetter conditions. Both C₃ and C₄ grasses show lower ANPP under eCO₂ than ambient treatments during very wet years, which could be

interpreted as relatively more limited nitrogen due to the legacy effect of more consumed soil nitrogen and also possibly more N leaching loss in moister eCO₂ sites due to water-saving². The experiments in the tallgrass prairies dominated by C₄ grasses suggested that the majority of eCO₂ response was due to increased WUE, and that N-limitation was the major constraint with wetter conditions as the N-fertilization experiments at the site enhanced the eCO₂ effect in wetter years³.

Direct relationships of ANPP-iPPT in forests and grasslands

In the main text, we examined the relationship between ANPP enhancement ratio (EAPP) and iPPT (Fig. 1), which show contrasting response patterns between woody and grassland ecosystems. Here, we examine direct relationships between ANPP and iPPT. Among the 14 experimental sites used in this study that have EAPP data, only 12 sites have ANPP data available, 5 from forest and 7 from grassland sites (the other two sites only have EAPP data). The ANPP data from those different sites were standardized to Z-scores for overall analyses. We anticipated that temporal autocorrelation at each site is likely to be minimal because analyses aggregated plots at each site and each ANPP is an average of several measurements from several plots. These plots are located separately and designed to avoid spatial pseudo-replication and a single replicate measurement over time (See Table S2 for experimental designs and sampling methods). Nevertheless, the Durbin-Watson test was performed for testing temporal autocorrelation. It shows there is no temporal autocorrelation in the ANPP data except a few inconclusive cases (Table S6). This also ensures Z-scores of ANPP are independent data entries in the model. The results indicate that ANPP was more enhanced in wetter years with eCO₂ in woody ecosystems,

although ANPP under both eCO₂ and ambient treatments was positively related to iPPT (Fig. S4c). In grassland ecosystems, ANPP was positively related to iPPT only with ambient CO₂ while there was no significant relationship with iPPT under eCO₂, although eCO₂ enhanced ANPP (Fig. S4d). These results further confirm the contrasting patterns of EAPP-iPPT between woody and grassland ecosystems resulted from the previous Z-score analyses (Fig. 1c and 1d).

Interactions affecting EAPP responses to precipitation

Puzzled by the observations (Fig. 1, Fig. 2) that show contrasting responses of EAPP to annual precipitation (iPPT) within woody and grass-dominated ecosystems but similar patterns of EAPP_{AV} responses to MAP across sites, we examined interactive effects of eCO₂ with temporal variations of iPPT on EAPP and with spatial variations of MAP on EAPP_{AV}.

We consider that EAPP responses to iPPT at a given site over multiple years were affected by both enhanced WUE and enhanced LAI. As enhanced WUE under eCO₂ was decreased with higher iPPT, the enhanced LAI could increase with iPPT within woody ecosystems to supplement a diminished WUE effect on ANPP (Fig. S4c). It is likely that the effect of enhanced LAI exceeded that of decreased WUE within woody ecosystems in order to maintain positive EAPP-iPPT relationships. In contrast, within grassland sites, ELAI did not appear to increase in wetter years enough to provide additional contributions to ANPP enhancement (Fig. S4d), and the effect of decreasing WUE likely dominated the EAPP pattern, which declined with iPPT. Greater N limitation in wetter years could also contribute to the decline of EAPP².

For the site average of EAPP ($EAPP_{AV}$), annual variability of EAPP influenced by WUE and LAI was averaged, and $EAPP_{AV}$ declined with increasing MAP, mainly reflecting the effect of decreased WUE from drier to moister locations. The seemingly contrary responses to precipitation within compared to across woody ecosystems, as well as between woody and grassland ecosystems, are different manifestations of the combined effects of enhanced WUE and LAI annually at a given site versus averaged across multiple sites along a precipitation gradient.

Impact of eCO_2 on belowground production

Forest enrichment studies indicated that the contribution of BP to total NPP was normally low, ranging from 3 to 16%, depending on nutrient and soil conditions, plant species, and land-use history^{4,5}. As mentioned earlier, grasslands have high root:shoot ratios with approximately 56 to 96 % of total plant production in natural grassland systems belowground⁶. Thus, eCO_2 enhancement on BP could be different between grassland and forest ecosystems.

Based on limited data (Table S5), we found that BP enhancement ratios ($EBP = BPe/BPa$) generally are more variable than EAPP in response to iPPT. In the forest sites, EBP could range between 2 and 254% (Table S5), although overall this contributed little to total NPP at the aspen and loblolly pine sites (both ~2% of NPP) because BP was low to start with. However, the sweetgum site was quite different. In this experiment, enhanced BP could account for 9% of total NPP because of much higher BP and contributed 59% of total enhanced production (compared to 6% in the aspen forest and 9% in the loblolly pine forest).

In the grassland sites, EBP under eCO₂ was not consistent and ranged from changes of -37% to +137% (Table S5). At the Jasper Ridge annual grassland, BP was mostly not enhanced (EBP < 1), which could reflect a strategy of reducing C allocation to BP in short-lived annual species with improved soil water conditions. On average, BP was generally higher in the drier Wyoming site compared to the Jasper Ridge annual grassland and Kansas tallgrass prairie under eCO₂ (322, 260, 246 g m⁻², respectively), although the relative enhancement ratio (EBP) is higher in the moister Kansas tallgrass site (+26%, -11%, +56%, respectively). The enhanced BP in the Wyoming site contributed more to NPP (37%) and total enhanced production (86%), compared to the moist Kansas tallgrass site for NPP (8%) and total enhanced production (58%).

Higher BP (fine roots) in drier grasslands but moister forests may reflect C allocation strategies for differing resource needs—likely water for drier grasslands but nutrients for moister forests. However, the enhancement ratio, EBP, was higher in moister sites for both forests and grasslands, suggesting similar increased needs for acquiring nutrients with less water stress in both types of ecosystems (Table S5). In addition, the relative enhancement ratios in ANPP and BP in the same year were often opposite (i.e. higher EAPP often accompanied a lower EBP, and vice versa)⁷, indicating dynamic allocation of enhanced C production to ANPP and BP. This suggests that total NPP enhancement under eCO₂ could not only be greater than ANPP enhancement, but also less sensitive to iPPT than ANPP due to this compensating effect of above-and belowground enhancement ratios. However, ANPP and BP data from more experiments clearly are needed to make robust conclusions.

Table S1a. CO₂ enrichment sites of woody ecosystems, data sources, and key references

Woody Ecosystem	Location	Long-term climate*	Experiment design**	Data source		Additional References
				ANPP	Annual PPT of sites	
Nevada desert shrub	Mojave Desert, NV, USA (36° 46' 30", 115° 57' 45" & 36° 45' 20", 115° 59' 15")	MAP: 130 mm MAT: 16.9 °C	FACE, ~550 ppm CO ₂ ; 1998-2002	Nowak <i>et al.</i> ⁸ (Fig. 7); http://cdiac.ornl.gov/ftp/FACE/ndffdata/	Housman <i>et al.</i> ⁹ (Table 1); http://facedata.ornl.gov/ndff/ndff_data_co2weather.html	Naumburg <i>et al.</i> ¹⁰ Evans <i>et al.</i> ¹¹
Wisconsin aspen-poplar forest	Rhineland, WI, USA (45.6°N, 89.5°W)	MAP: 800 mm MAT: 5.3 °C	FACE, ~560 ppm CO ₂ ; 1998-2003	Nowak <i>et al.</i> ⁸ (Fig. 7); Isbrands <i>et al.</i> ¹² (Table 4); http://facedata.ornl.gov/npp-cdiac.html	NCDC Rhineland (477113)***	Percy <i>et al.</i> ¹³ Norby <i>et al.</i> ⁴ Karnosky <i>et al.</i> ¹⁴ Norby & Zak ¹⁵
Florida scrub oak	Merritt Island, FL, USA (28°38'N, 80°42'W)	MAP: 1310 mm MAT: 22.4 °C	OTC ~700 ppm CO ₂ ; 1996-2007	Seiler <i>et al.</i> ¹⁶ (Fig. 1c, Fig. 2)	Seiler <i>et al.</i> ¹⁶ (Fig. 2); NCDC Merritt island (0000FMER); NCDC Titusville (00088942)	Hymus <i>et al.</i> ¹⁷ Day <i>et al.</i> ¹⁸ Dijkstra <i>et al.</i> ¹⁹
Duke loblolly pines	Duke Forest Chapel Hill, NC, USA (35° 58' N, 79° 05' W)	MAP: 1203 mm MAT: 15.0 °C	FACE I & FACE II ~550 ppm CO ₂ ; 1994-2004	Oren <i>et al.</i> ²⁰ (Fig. 1); McCarthy <i>et al.</i> ²¹ (Table 2, Fig. 5); http://facedata.ornl.gov/npp-cdiac.html	NCDC Chapel Hill (311677) http://facedata.ornl.gov/ndff/ndff_data_co2weather.html	Oren <i>et al.</i> ²² Delucia <i>et al.</i> ^{23,24} Finzi <i>et al.</i> ²⁵ McCarthy <i>et al.</i> ^{26,27} Norby & Zak ¹⁴
Oak Ridge sweetgum plantation	Oak Ridge National Laboratory, Oak Ridge, TN, USA (35°54'N, 84°20'W)	MAP: 1410 mm MAT: 14.7 °C	FACE ~537 ppm CO ₂ ; 1998-2008	Norby <i>et al.</i> ²⁸ (Table 1); http://facedata.ornl.gov/npp-cdiac.html ;	NCDC Oak Ridge (406750) http://facedata.ornl.gov/ndff/ndff_data_co2weather.html	Norby <i>et al.</i> ^{4,29,30} Norby & Zak ¹⁵
EucFACE Mature evergreen <i>Eucalyptus</i> woodland	Western Sydney, Australia (33°36'S, 150°44'E)	MAP: 809 mm MAT: 17.5°C	FACE ~550 ppm CO ₂ ; 2013-	Jiang <i>et al.</i> ³¹ https://researchdata.edu.au/aboveground-net-primary-2013-2015/754374	Jiang <i>et al.</i> ³¹ Australia BM Richmond - UWS Hawkesbury (67021)	Ellsworth <i>et al.</i> ³²

*MAP: Long-term annual precipitation; MAT: long-term mean annual average temperature. The long-term MAP may not be same as the MAP of experimental years in an experimental site, which mostly lasted less than a decade.

** The designed eCO₂ levels are described in the table, and the control CO₂ was the ambient CO₂ for those experimental years.

***For precipitation data, station names and numbers from the U.S. NOAA National Climate Data Center (NCDC) are given when off-site climate data were used.

Table S1b. CO₂ enrichment sites of grassland ecosystems, data sources, and key references

Grass Ecosystem	Location	Long-term climate	Experiment design	Data source		Other References
				ANPP	Annual PPT of sites	
Wyoming mixed grass prairie (C ₃ /C ₄)	PHACE, High Plains Grasslands Research Station, Cheyenne, WY, USA (41°11'N, 104°54'W)	MAP: 397 mm MAT: 7.2 °C	FACE ~600 ppm CO ₂ ; 2006-2013	Kevin Mueller (personal communication)	Kevin Mueller (personal communication)	Morgan <i>et al.</i> ³³ Muller <i>et al.</i> ⁷
Tasmania mixed native grassland (C ₃ /C ₄)	TasFACE Experiment, the Southeastern Tasmania, Australia (42°42'S, 147°16'E)	MAP: 560 mm MAT: 11.6 °C	FACE ~550 ppm CO ₂ ; 2002-2010 (data in this work)	Hovenden <i>et al.</i> ^{2,34} (Fig. 1a).	Hovenden <i>et al.</i> ³⁴ (Fig. 1c). Australia BM Melton Mowbray (94201)	Hovenden <i>et al.</i> ^{35,36}
Colorado shortgrass steppe (C ₃ /C ₄)	Center Plains Exp. Range, Nunn, CO, USA (40°50'N, 104°43'W)	MAP: 320 mm MAT: 9.0 °C	OTC ~720 ppm CO ₂ ; 1997-2001	Morgan <i>et al.</i> ³⁷ (Fig. 3).	Site data http://www.ars.usda.gov/Main/docs.htm?docid=11120	Morgan <i>et al.</i> ^{38,39}
Jasper Ridge annual grassland	Jasper Ridge Biological Preserve, CA, USA (37°40'N, 122°23'W)	MAP: 582 mm MAT: 15 °C	FACE ~655 ppm CO ₂ ; 1999-2003	Dukes <i>et al.</i> ⁴⁰ (Fig. 4)	Site data (requested from R Jackson) NCDC Woodside (00049792)	Shaw <i>et al.</i> ⁴¹
Cedar Creek perennial prairie (C ₃ /C ₄)	BioCON Experiment, Cedar, MN, USA (45°24'N, 93°12'W)	MAP: 679 mm MAT: 6.4 °C	FACE ~560 ppm CO ₂ ; 1998-2008	Study site: http://www.lter.umn.edu/research/data/dataset?ple141	Site data http://www.lter.umn.edu/research/data/ NCDC Cedar (211390)	Reich <i>et al.</i> ⁴²
Kansas tallgrass prairie (C ₄)	North of Manhattan, KS, USA (39.12°N, 96.35°W)	MAP: 840 mm MAT: 12.7 °C	OTC ~700 ppm CO ₂ ; 1989-1996	Owensby <i>et al.</i> ⁴³ (Fig. 3)	NCDC Manhattan (144972)	Owensby <i>et al.</i> ³ Knapp <i>et al.</i> ⁴⁴ Jastrow <i>et al.</i> ⁴⁵
Swiss calcareous grassland*	Nenzlingen, Switzerland (47°33'N, 7°34'E)	MAP: 883 mm MAT: 9.2 °C	SACC ~600 ppm CO ₂ ; 1994-1999	Niklaus & Körner ⁴⁶ (Fig. 1)	Niklaus & Körner ⁴⁶ (Table 1)	Körner <i>et al.</i> ⁴⁷
Swiss meadows**	ETH station, Eschikon, Switzerland (47°27'N, 8°41'E)	MAP: 1108 mm MAT: 8.6 °C	FACE ~600 ppm CO ₂ ; 1993-2002	Hebeisen <i>et al.</i> ⁴⁸ (Fig. 1b); Däpp <i>et al.</i> ⁴⁹ (Fig. 1b); Schneider <i>et al.</i> ⁵⁰ (Fig. 1b)	Hebeisen <i>et al.</i> ⁴⁸ (Table 1); NCDC Zurich (SZ000003700)	Lüscher <i>et al.</i> ^{51, 52} Soussana & Lüscher ⁵³ Schneider <i>et al.</i> ⁵⁴

* The site used Screen-Aided CO₂ Control (SACC) technology for eCO₂ exposure system, which is a middle ground between FACE and traditional OTC.

** Response of *Lolium perenne* using the average data of low and high N fertilization under ambient and elevated CO₂.

Table S2a. Descriptions of experimental sites of woody ecosystems, experimental designs, data collections and estimation methods

Site	Plot designs, data, and methods estimating ANPP and annual precipitation
Nevada desert shrubs	Three plots set for both ambient and eCO ₂ treatments. Each plot is 25 m in diameter. Growth of shoots (diameter & length) was converted to biomass growth via regressions derived from harvested shoot data. ANPP was estimated as annual biomass growth for eCO ₂ and ambient plots. Precipitation was measured at the study site based on precipitation events. Annual PPT (iPPT) was the sum of hydro-year from October to September.
Wisconsin aspen-poplar forest	Three replicates for each control and elevated CO ₂ block in treatment rings. Tree stem (D & H) and litterfall were measured. Empirical equations converted stem volume growth to biomass growth. ANPP was stem biomass growth plus leaf biomass and averaged for eCO ₂ and ambient plots, which are only available for 2001-2003. For 1998-2000, biomass growth was estimated from volume growth and indices of wood density. Precipitation data were derived from the NCDC Rhinelander station (477113). Annual PPT was the sum of measurement at daily base for a calendar year. LAI estimates refer to the methods applied in the Oak-Ridge deciduous sweetgum sites (the protocols).
Florida scrub-oak woodland	For 16 octagonal OTC chambers (at 2.5m H × 3.45m D ₁ × 3.66m D ₂), 8 plots with eCO ₂ treatment were randomly assigned* ¹ . Shoots were counted and stem basal diameters measured at 2–5 cm height. Biomass allometric equations were developed using data from three destructive harvests to calculate aboveground biomass. ANPP was estimated as average biomass increment for eCO ₂ and control plots, respectively. Precipitation data were derived from the weather station located at the John F. Kennedy Space Center (the location of the study site). Annual PPT was the sum of daily-based measurements for a calendar year.
Duke loblolly pine plantation	For the FACE prototype (plots 7-8 since 1994) and the replicated experiment (plots 1–6 since 1996) of 30m diameter rings, 4 plots received eCO ₂ treatment. Empirical allometric equations and wood density were used to calculate wood biomass (stems, branches, coarse roots) based on tree diameters and heights. Tree diameter was measured annually using dendrobands, and height measured in every 5 years and averaged for each year. Leaf litterfall was collected using masses. For 1996-2004, ANPP was estimated as annual increment of wood plus litterfall biomass, averaged for eCO ₂ and control plots, respectively. For 1994-1995, only wood NPP are available ²² , which was converted to aboveground NPP based on the average fraction of woody NPP to ANPP (0.55) of following years (1997-1999). Precipitation data were from site measurements and a nearby NCDC (311677) station (when site data were not available). Annual PPT was the sum of daily based measurements for a calendar year. LAI estimates of pines ²⁶ depend on measurements and modeling. The optical gap fraction measurements were taken using a LAI-2000 canopy analyzer (Li-Cor, Lincoln, NE, USA). Fresh leaf litter samples were collected and measured optically for leaf area (DIAS, Decagon Devices Inc., Pullman, WA, USA) and oven dried for dry mass. The leaf area and dry mass of the samples were used to determine Specific Leaf Area (SLA, cm ² g ⁻¹), which was also scaled by the ratio of canopy LAI of pines. The dry mass of leaf litter collected through a year and SLA were used to estimate annual leaf area production (L _{prod}). The leaf area loss (L _{loss}) was calculated using litter mass at the time of collection and SLA. A continuous leaf area gain (L _{gain}) was estimated by L _{prod} multiplying the relative leaf area expansion (L _{exp}). L _{exp} was calculated based on relative new needle elongation monitored continuously at lower, middle and upper canopy and the proportional LAI for the position, scaled for the canopy. The dynamic LAI was the previous LAI plus the balance between L _{gain} and L _{loss} . The LAI before the experimental years was estimated using empirical allometric equations.

Oak Ridge sweetgum plantation	<p>Five 25-m diameter plots were laid out in 1997, comprised 2 plots with eCO₂ and 3 plots with ambient CO₂. Dendrobands were set for measuring tree diameters at 1.3m height. Tree basal area (BA) was calculated from the diameter and summed for a plot. Using data from destructive harvests and other measurements, allometric equations were developed to estimate biomass of wood (stem & branches) and coarse roots with BA, tree height, taper index and wood density. Leaf biomass was collected every 2 weeks using 5 baskets in each plot. ANPP*² was estimated as mean annual increment of biomass (wood, coarse roots, leaf) for eCO₂ and control plots. ANPP data of 1998-1999 were from the publication⁷, while 2000-2008 from the Oak-Ridge website. Precipitation data of 1998-1999 were from the NCDC Oak Ridge station (406750) and other years from the site measurements. Annual precipitation was the sum of daily based measurements for a calendar year. The LAI estimates involved the following process⁵⁵: PAR sensors (LI-190SB, LI-COR, Lincoln, Neb., USA) were mounted to measure PAR above canopy and near the center of each plot at 2 m above the ground. For the period of leaf production, the fractional transmission of PAR (\bar{Z}) was calculated and used to estimate LAI based on the relationship between LAI and \bar{Z}. Leaf litter was collected in litter traps continuously through growing season until all leaves fell. The data was used to estimate lost leaf mass over time. The fresh leaves were collected at each meter of canopy depth to measure their leaf area (LI-3100 area meter, LI-COR, Lincoln, Neb., USA) and dry mass, then the leaf mass per unit area (LMA) of each layer was estimated. A canopy-averaged LMA was calculated by weighting the LMA of each 1-m layer by the proportion of total leaf area (LAI) in that layer. The lost leaf area was calculated using the litter mass data and LMA. The LAI through the year was estimated as the difference of the transmittance-based LAI and the lost leaf area.</p>
Australia mature evergreen eucalypt woodland	<p>Six circular plots (490 m² each) were established in 2010, comprised 3 plots subjected to free-air CO₂ enrichment treatment receiving extra 150 ppm CO₂ input using a computer-controlled pre-dilution method and maintaining CO₂ level at ~550 ppm, while other 3 plots under ambient CO₂ (~ 400 ppm). <i>Eucalyptus tereticornis</i> Sm. is the dominant tree species and counts for 98% of the overstory basal area of the sites. Understory vegetation is a diverse mixture of forbs, graminoids and shrubs. The diameters of all trees in the plots were measured at 1.3m height at approximately monthly intervals using manual band dendrometers to monitor stem diameter changes. A species-specific allometric equation for <i>Eucalyptus tereticornis</i> was applied to convert diameter increments to aboveground biomass increment. Of a total of 146 trees measured across the ambient and elevated plots, measurements of 87 trees were used by excluding those of suppressed and deformed trees. Eight circular fine-mesh traps each at ~0.2 m² were randomly placed in each plot and litterfall was collected monthly to estimate foliage and twig production. Litter was sorted into leaf, twigs, bark, and other materials. In addition, consumption of overstory leaf by insect herbivores was estimated based on insect frass data collected from the circular fine-mesh traps, and a relationship between frass mass and insect-consumed leaf mass³¹. Understory aboveground production was estimated based on biomass harvest, taken between 2015 and 2017*³. In this study, ANPP was estimated as the sum of production in stem, foliage, twigs, bark, seeds, insect consumption, and understory plants.</p>

Note: All harvested live biomass materials were taken to laboratories, separated (often for different purposes), dried and weighted for values of dry organic matter.

*1. There were 8 additional plots established as unchambered controls, but the data were not used in this analysis.

*2. To be consistent with the Duke FACE data, coarse root (woody root) biomass was included in calculating aboveground biomass increment.

*3. In this study, understory aboveground production for 2013 and 2014 was estimated using average ratios of understory NPP plus respiration to understory GPP based on understory NPP of 2015 and 2016 with available understory GPP and respiration data for all years²⁹.

Table S2b. Descriptions of experimental sites of grassland ecosystems, experimental designs, data collections and estimation methods

Site	Plot designs, data, and methods estimating ANPP and annual precipitation
Wyoming mixed grass prairie (C ₃ /C ₄)	Plots were circular with a 3.3 m diameter. Each treatment (control and eCO ₂)* ¹ was applied to 5 plots. Plant aboveground biomass was measured annually in mid-July when near its maximum, which was sampled by clipping half the quadrats in a harvest area (1.5 m ² per plot). Vegetation include C ₃ and C ₄ grasses and C ₃ forbs. ANPP was estimated as aboveground biomass per square meters, averaged for eCO ₂ and control plots, respectively. Precipitation data were from PHACE site measurements. Annual precipitation was the sum of daily measurements for a calendar year.
Tasmania mixed native grassland (C ₃ /C ₄)	1.5 m FACE rings, 3 replicate plots were designed for ambient CO ₂ and eCO ₂ only treatments* ² . Vegetation includes perennial C ₃ , C ₄ grasses and forbs. Above-ground biomass was sampled annually by clipping to 2mm above the ground surface at the end of summer in one quadrat (20 x20 cm ²) randomly located in each plot. ANPP was estimated as aboveground biomass per square meters, averaged for eCO ₂ and control plots, respectively. Precipitation for each year started from March 1 st (autumn). Annual precipitation was the sum of seasonal precipitation totals of autumn, winter, spring and summer (data were derived from the publication).
Colorado shortgrass steppe (C ₃ /C ₄)	Six open-top chambers (4.5 m D x 3.8 m H) were set in 6 plots* ³ , 3 with eCO ₂ and 3 controls. Aboveground biomass was sampled by clipping half the quadrats in a harvest area (1.73m ²) of each chamber in late July. ANPP was estimated as above-ground biomass per m ² for eCO ₂ and control plots, respectively. Precipitation data were from the site measurements. Annual precipitation was the sum of daily-based measurements for a calendar year.
Jasper Ridge annual grassland	Of 32 plots* ⁴ at 2 m in diameter, each was divided into 4 equal quadrants for multifactorial treatments. The control and eCO ₂ only treatments were replicated at 8 plots, respectively. Aboveground biomass was harvested at the time of peak biomass in an area (141 cm ²) in a quadrant, averaged for estimating ANPP for the treatment. Annual precipitation was summed from daily site measurements for a calendar year.
Cedar Creek perennial prairie (C ₃ /C ₄)	Among 296 individual plots (2 x 2 m ²) in six 20-m diameter rings* ⁵ , 90 plots exposed to eCO ₂ only and 90 control to ambient CO ₂ . A strip (10x100cm) was clipped at just above the soil surface. Two harvests occurred in early June and August in the first 11 experimental years, then the harvest routine changed to once a year in August. For consistency, only the first 11 years' data were used because growth responses to eCO ₂ in June and August were different (based on the data) and different harvest rotations affect estimates of biomass responses to eCO ₂ . The mean value of two harvests was used for each plot. In most years, all plots were sampled, while in some years, only 80% or 50% plots were sampled. ANPP was estimated as harvested aboveground biomass per m ² , averaged for all plots with eCO ₂ and ambient CO ₂ treatments respectively. C ₃ and C ₄ data were derived from subplots that were planted with only C ₃ or C ₄ species for a comparison analysis (Fig. S2). Precipitation data were derived from nearby weather station NCDC Cedar (211390). Annual precipitation was the sum of daily-based measurements for a calendar year.
Kansas tallgrass prairie (dominated by C ₄)	Open-top chambers (4.5m D x 4.0m H) with three replicates for eCO ₂ and three for ambient CO ₂ treatment* ⁶ . For 1989-1990, sampling was made in late May and mid-September by clipping to ground level from two subplots (0.2 x 0.5m) in each plot. For 1991-1996, peak live biomass was sampled in early August by clipping two subplots (50 x 100cm). ANPP was estimated as harvested aboveground biomass per m ² , averaged for all plots with eCO ₂ and ambient CO ₂ , respectively. Precipitation data were derived from nearby weather station NCDC Manhattan (144972). Annual precipitation was the sum of daily-based measurements for a

	calendar year. Leaf area was estimated for each species or species group using a leaf area meter (LI-COR, Model LI-3100) immediately after separation of the samples.
Swiss calcareous grassland	Among 24 plots (each 1.27 m ²), 8 plots selected randomly for eCO ₂ treatments with SACC* ⁷ , and 8 for screened ambient CO ₂ . Samples were collected in the center area (0.82 cm ²) of each plot by clipping at a height of 5 cm aboveground in June and the end of October. ANPP was estimated only using the data of June (peak aboveground biomass) for eCO ₂ and ambient treatments. Annual precipitation was from the data table of the publication (see Table S1b), which was the sum of monthly totals for a calendar year.
Swiss meadows	An eCO ₂ and a control plot (18m diameter) were set in each of 3 experimental blocks. Fixed plots (10m ²) of monoculture and bi-species swards (sub-subplots) were fertilized with low or high N level* ⁸ . Aboveground biomass from the central sample area (1m ²) was harvested at 0.05m height. There were two cutting frequencies (6-8 times & 4 times) for 1993-95, but one (5 times) for 1996-02. ANPP was the mean biomass of the cutting frequencies and sums through growing seasons. ANPP of low and high N levels was also averaged, resulting in 3 replicates for eCO ₂ and control treatment. Precipitation data were from a publication (1993-1995) and weather station of WMO Zurich (646066600) (1996-2002) as both datasets were matched. Annual precipitation was the sum of monthly data for a calendar year.

Note: All harvested live biomass materials were taken to laboratories, separated (often based on different purposes), dried and weighted for values of dry organic matter.

*1. Treatments also replicated three times for ambient CO₂-no chamber sites, although that data were not used in this analysis.

*2. The experimental site had established 12 FACE rings, including eCO₂ and warming experiments. Only the replicates from the plots of eCO₂ and ambient CO₂ (without warming) were used in the analysis.

*3. The pasture for the experiment was divided into three blocks, and three 15.5 m² circular plots per block were randomly selected for the experimental treatments, including an ambient chamber CO₂ treatment, an elevated chamber CO₂ treatment, and an unchambered control plot of equal ground area. Only the data from chambered eCO₂ and chambered ambient CO₂ were used in this analysis.

*5. The BioCON experiment was designed to manipulate multifactorial experiments including elevated CO₂, N addition, soil warming, and species diversity. A factorial 232 design with three replicate rings and 296 individual split-split plots (subplots) for replicated experiments with combined factors. For this analysis, only the data from control and eCO₂ only plots (~89-94 plots) were used.

*6. The experiment had treatments replicated three times consisted of ambient CO₂-no chamber (A), ambient CO₂ with chamber (CA), and eCO₂ with chamber (CE). The data from CA and CE were used in this analysis.

*7. The site used Screen-Aided CO₂ Control (SACC) technology for eCO₂ exposure system, which is a middle ground between FACE and traditional OTC and superior to OTCs for minimizing microclimate impacts. There were 24 plots in the experiment, and 8 plots were randomly and assigned for unscreened ambient control plots (C), screened ambient plots (A), and eCO₂ plots (E), respectively. Only data from A and E plots were used in this analysis.

*8. The experiment was designed as split-split plot for testing growth responses to multifactorial treatments, including eCO₂, N addition, cutting frequency and species. All sub-subplots were fertilized with N either at a low (10-14 g N m²) or high (40-56 g N m²) level and had monoculture species (*Trifolium repens* L or *Lolium perenne* L) or mixed bi-species. In this analysis, only the data from monoculture subplots of *Lolium perenne* L were used, which were averaged for cutting frequencies and N additions for comparing growth responses under eCO₂ and ambient CO₂ conditions.

Table S3a. Linear regression equations between ANPP enhancement ratios (EAPP) and annual precipitation (iPPT, mm) over multiple experimental years within individual experimental sites, represented by regression lines in Fig. 1a and 1b. Bold values represent statistically significant at $*p=0.1$,

Within woody ecosystems	Regression equations	R^2	n	p
Nevada desert shrub	EAPP = $0.9428 + 3.0264e^{-3} * iPPT$	0.93	4	0.03
Wisconsin aspen-poplar forests	EAPP = $-0.0196 + 1.6628e^{-3} * iPPT$	0.77	6	0.02
Florida scrub oak	EAPP = $-0.0455 + 1.3414e^{-3} * iPPT$	0.34	8	0.13
Duke loblolly pine plantation	EAPP = $0.8736 + 3.3229e^{-4} * iPPT$	0.26	11	0.10
Oak Ridge sweetgum plantation	EAPP = $0.8475 + 1.8295e^{-4} * iPPT$	0.34	11	0.06
EucFACE eucalyptus woodland	EAPP = $0.8499 + 2.4420e^{-4} * iPPT$	0.76	4	0.12
Within grassland ecosystems				
Wyoming mixed grass prairie	EAPP = $1.4361 - 7.1258e^{-4} * iPPT$	0.35	8	0.10
Tasmania mixed native grassland	EAPP = $1.9923 - 2.0597e^{-3} * iPPT$	0.23	9	0.19
Colorado shortgrass steppe	EAPP = $1.9903 - 1.3653e^{-3} * iPPT$	0.67	5	0.09
Jasper Ridge annual grassland	EAPP = $1.4329 - 5.1607e^{-4} * iPPT$	0.16	5	0.50
Cedar Creek perennial prairie	EAPP = $1.3270 - 2.1515e^{-4} * iPPT$	0.20	10	0.20
Kansas tallgrass prairie	EAPP = $1.6261 - 5.0930e^{-4} * iPPT$	0.42	8	0.08
Swiss calcareous grassland	EAPP = $1.4021 - 2.1220e^{-4} * iPPT$	0.13	6	0.49
Swiss meadows	EAPP = $1.4318 - 2.7922e^{-4} * iPPT$	0.69	10	< 0.01

Table S3b. Linear regression equations between ANPP enhancement ratios (EAPP) and growing season precipitation (mPPT, mm) aggregated for months over multiple experimental years within individual experimental sites (Fig. S3.). The growing season is set from March to September in the Northern Hemisphere and September to March in the Southern Hemisphere (†), or uses site data if available. Bold values represent statistically significant at $*p=0.1$.

Within woody ecosystems	Regression equations	R^2	n	p	mPPT
Nevada desert shrub	EAPP = $1.0644 + 7.3998e^{-3} * \text{mPPT}$	0.74	4	0.14	Site data ⁹
Wisconsin aspen-poplar forests	EAPP = $0.2519 + 1.7369e^{-3} * \text{mPPT}$	0.77	6	0.04	3 - 9
Florida scrub oak	EAPP = $0.9874 + 4.9857e^{-4} * \text{mPPT}$	0.03	8	0.69	3 - 9
Duke loblolly pine plantation	EAPP = $1.1601 + 1.3991e^{-4} * \text{mPPT}$	0.04	11	0.55	3 - 9
Oak Ridge sweetgum plantation	EAPP = $0.9262 + 1.9776e^{-4} * \text{mPPT}$	0.23	11	0.14	3 - 9
†EucFACE eucalyptus woodland	EAPP = $0.7698 + 5.3430e^{-4} * \text{mPPT}$	0.62	4	0.21	9 - 3
Within grassland ecosystems					
Wyoming mixed grass prairie	EAPP = $1.3418 - 5.6902e^{-4} * \text{mPPT}$	0.17	8	0.31	3 - 9
†Tasmania mixed native grassland	EAPP = $1.8849 - 2.6811e^{-3} * \text{mPPT}$	0.16	9	0.28	9 - 3
Colorado shortgrass steppe	EAPP = $1.8927 - 1.3653e^{-3} * \text{mPPT}$	0.74	5	0.06	Site data ³⁷
Jasper Ridge annual grassland	EAPP = $1.3799 - 2.0665e^{-3} * \text{mPPT}$	0.13	5	0.56	3 - 9
Cedar Creek perennial prairie	EAPP = $1.2838 - 2.3054e^{-4} * \text{mPPT}$	0.14	11	0.26	3 - 9
Kansas tallgrass prairie	EAPP = $1.5193 - 4.8957e^{-4} * \text{mPPT}$	0.43	8	0.07	3 - 9
Swiss calcareous grassland	EAPP = $1.3359 - 2.5438e^{-4} * \text{mPPT}$	0.14	6	0.46	3 - 9
Swiss meadows	EAPP = $1.3647 - 3.1483e^{-4} * \text{mPPT}$	0.51	10	0.02	3 - 9

Note: † is for sites located in Southern Hemisphere.

Table S4. Linear regression equations between mean site EAPP ($EAPP_{AV}$) and mean annual precipitation (MAP) across multiple woody and grassland ecosystems, represented by regression lines in Fig. 2. The logistic equation between LAI enhancement ratios (ELAI) and ANPP enhancement ratios (EAPP), represented by the logistic curve in Fig. 3; data from different experimental sites and years were used for curve fitting.

Across-ecosystems	Regression equations	R^2	n	p
Woody & Grassland ecosystems	$EAPP_{AV} = 1.3952 - 2.1564e^{-4} * MAP$	0.28	14	0.0523
Woody ecosystems	$EAPP_{AV} = 1.4721 - 2.3307e^{-4} * MAP$	0.39	6	0.1824
Grassland ecosystems	$EAPP_{AV} = 1.2751 - 1.4642e^{-4} * MAP$	0.38	8	0.1031
ELAI-EAPP relationships				
Logistic function	$EAPP = 0.96 + 0.79 / (1 + \text{EXP}(10.93 - 9.84 * \text{ELAI}))$	0.82	38	<0.0001

Table S5. Fine root productivity of forest and grassland ecosystems under ambient and elevated CO₂ concentration, and enhancement ratios

Site	Year	Fine root productivity (g/m ²)		Enhancement ratio	Data Reference
		aCO ₂	eCO ₂		
Wisconsin aspen-poplar forest	2001	25	43	1.73	http://facedata.ornl.gov/npp-cdiac.html . More site information refers to Table S1a
	2002	29	51	1.77	
	2003	45	58	1.28	
Duke loblolly pine forest	1996	52	94	1.81	http://facedata.ornl.gov/npp-cdiac.html . More site information refers to Table Sa1
	1997	31	73	2.35	
	1998	31	73	2.35	
	1999	32	37	1.17	
	2000	33	48	1.45	
	2001	33	48	1.45	
	2002	33	48	1.45	
Oak Ridge sweetgum plantation	1998	157	172	1.09	http://facedata.ornl.gov/npp-cdiac.html . More site information refers to Table S1a
	1999	239	286	1.20	
	2000	270	536	1.98	
	2001	414	853	2.06	
	2002	245	802	3.27	
	2003	149	317	2.12	
	2004	209	372	1.78	
	2005	96	342	3.54	
	2006	102	254	2.49	
	2007	137	237	1.72	
	2008	105	107	1.02	
Wyoming mixed grass prairie (C ₃ /C ₄)	2007	125	175	1.39	Mueller <i>et al.</i> ⁷ . More site information refers to Table S1b
	2008	239	238	1.00	
	2009	228	296	1.30	
	2010	287	425	1.48	
	2011	418	450	1.08	
	2012	258	348	1.35	
Jasper Ridge annual grassland	1999	192	231	1.20	Dukes <i>et al.</i> ⁴⁰ . More site information refers to Table S1
	2000	343	322	0.94	
	2001	376	276	0.73	
	2002	339	215	0.63	
	2003	276	256	0.93	
Kansas tallgrass prairie (C ₄)	1990	115	272	2.37	Owensby <i>et al.</i> ⁴³ . More site information refers to Table S1
	1991	178	209	1.18	
	1992	281	330	1.18	
	1993	244	216	0.89	
	1994	102	196	1.92	
	1995	138	252	1.83	

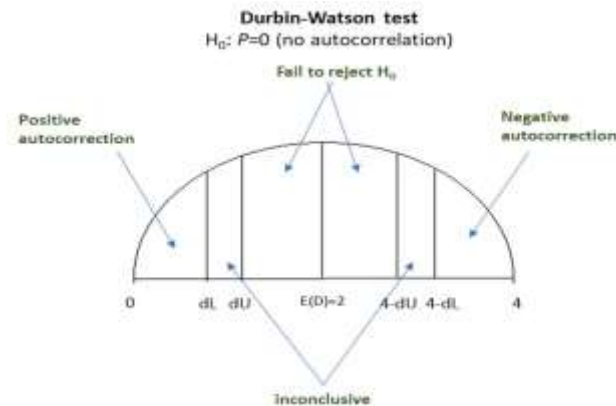
Table S6. The Durbin-Watson test for temporal autocorrelation in ANPP data.

Experimental sites	Sampled years n	Durbin-Watson Test (D)		Critical values (at 1% significant level)		APPa			APPe		
		D (APPa)	D (APPe)	dL	dU	4-D	Evaluation	Result	4-D	Evaluation	Result
<i>Woody ecosystem</i>											
Wisconsin aspen forest	6	3.395	2.926	0.390	1.142	0.605	$dL < 4-D < dU$	inconclusive	1.074	$dL < 4-D < dU$	inconclusive
Florida scrub-oak woodland	8	2.547	2.515	0.497	1.003	1.453	$4-D > dU$	no autocorrelation	1.485	$4-D > dU$	no autocorrelation
Duke loblolly pine forest	11	1.271	1.350	0.653	1.010		$D > dU$	no autocorrelation		$D > dU$	no autocorrelation
Oak Ridge sweetgum forest	11	1.024	1.263	0.653	1.010		$D > dU$	no autocorrelation		$D > dU$	no autocorrelation
Australia Eucalyptus woodland	4	2.357	2.786	0.286	1.264	1.643	$4-D > dU$	no autocorrelation	1.214	$dL < 4-D < dU$	inconclusive
<i>Grassland ecosystem</i>											
Wyoming mixed grass prairie	8	1.733	1.447	0.497	1.003		$D > dU$	no autocorrelation		$D > dU$	no autocorrelation
Colorado shortgrass steppe	5	2.923	2.621	0.343	1.186	1.077	$dL < 4-D < dU$	inconclusive	1.379	$4-D > dU$	no autocorrelation
Jasper Ridge annual grassland	5	2.385	3.285	0.343	1.186	1.615	$4-D > dU$	no autocorrelation	0.715	$dL < 4-D < dU$	inconclusive
Cedar Creek perennial prairie	11	1.867	1.886	0.653	1.010		$D > dU$	no autocorrelation		$D > dU$	no autocorrelation
Kansas tallgrass prairie	8	1.804	2.646	0.497	1.003		$D > dU$	no autocorrelation	1.354	$4-D > dU$	no autocorrelation
Swiss calcareous grassland	6	2.689	2.625	0.390	1.142	1.311	$4-D > dU$	no autocorrelation	1.375	$4-D > dU$	no autocorrelation
Swiss meadows	10	1.172	0.978	0.604	1.001		$D > dU$	no autocorrelation		$dL < D < dU$	inconclusive

Note: D is the Durbin-Watson test for autocorrelation. The value of D always lies between 0 and 4. If D is close to 2 there is no autocorrelation (see below illustration). The critical value dL and dU is the Lower critical value and the Upper critical value at a given significant level, respectively. When the test value $D < 2$, D is evaluated by dL and dU; while when $D > 2$, 4-D is evaluated by dL and dU. When $D < dL$ a positive autocorrelation is present, while $4-D < dL$ a negative autocorrelation is present. When D falls into the range of dL and dU, or 4-dU and 4-dL, the result is inconclusive.

$$D = \frac{\sum_{t=2}^n (e_t - e_{t-1})^2}{\sum_{t=1}^n e_t^2}$$

Where $e_t = y_t - \hat{y}_t$ are the residuals from the ordinary least squares fit, and y_t is the time sequence of data measured over experimental years.



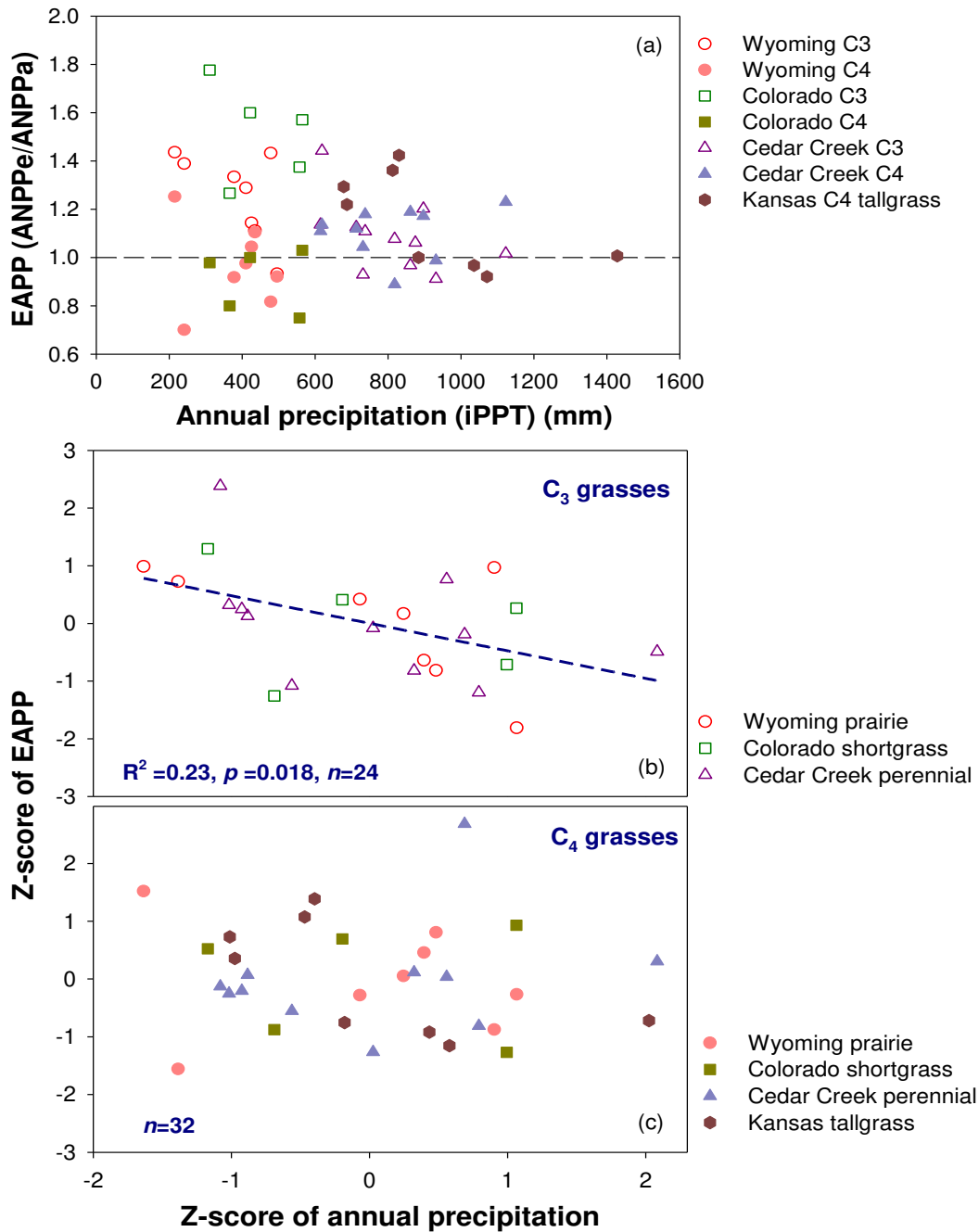


Fig. S1. Responses of C₃ and C₄ grasses to eCO₂. (a) EAPP responses of C₃ and C₄ grasses to annual precipitation (iPPT); (b) the Z-score analysis for C₃ grasses, and a linear regression; and (c) the Z-scores analysis for C₄ grasses; there is not an obvious relationship between EAPP and iPPT.

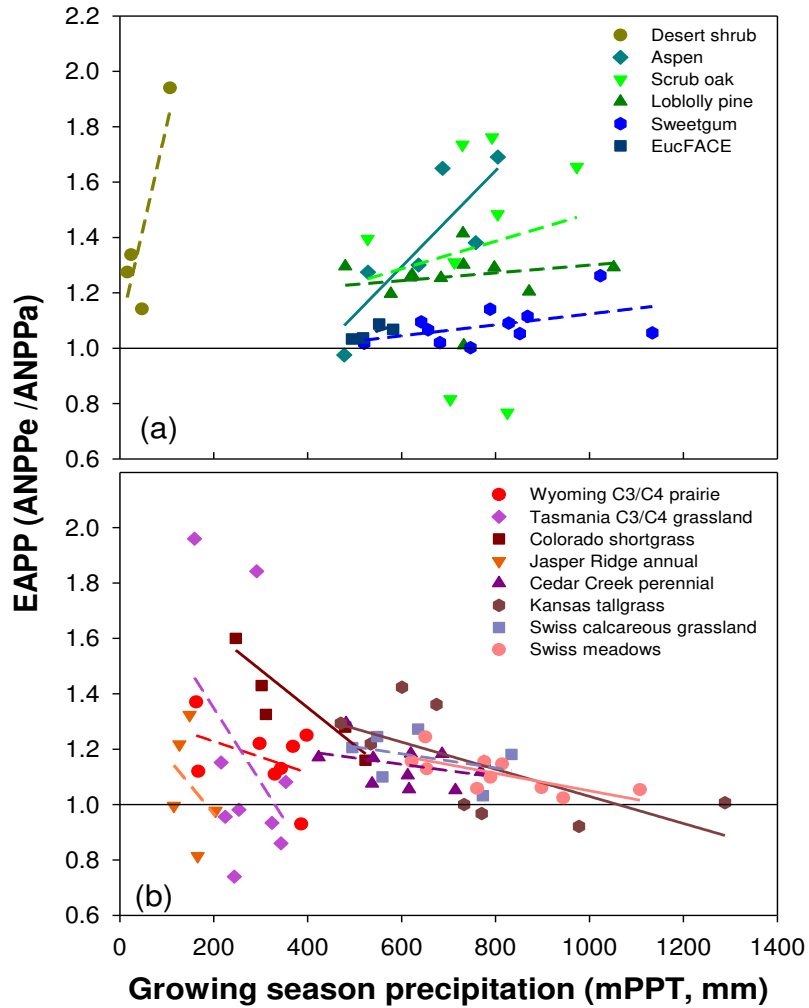


Fig. S2. Relationships between eCO₂ enhancement of ANPP and growing season precipitation (Table S3b). EAPP is enhancement ratio of ANPP under eCO₂ (ANPPe) and ambient CO₂ (ANPPa) treatments. (a) EAPP responses to growing season precipitation (mPPT) over multiple experimental years within woody ecosystems, and (b) within grassland ecosystems. At $*p = 0.1$, solid lines represent statistically significant regressions, dashed lines not significant (Table S3a).

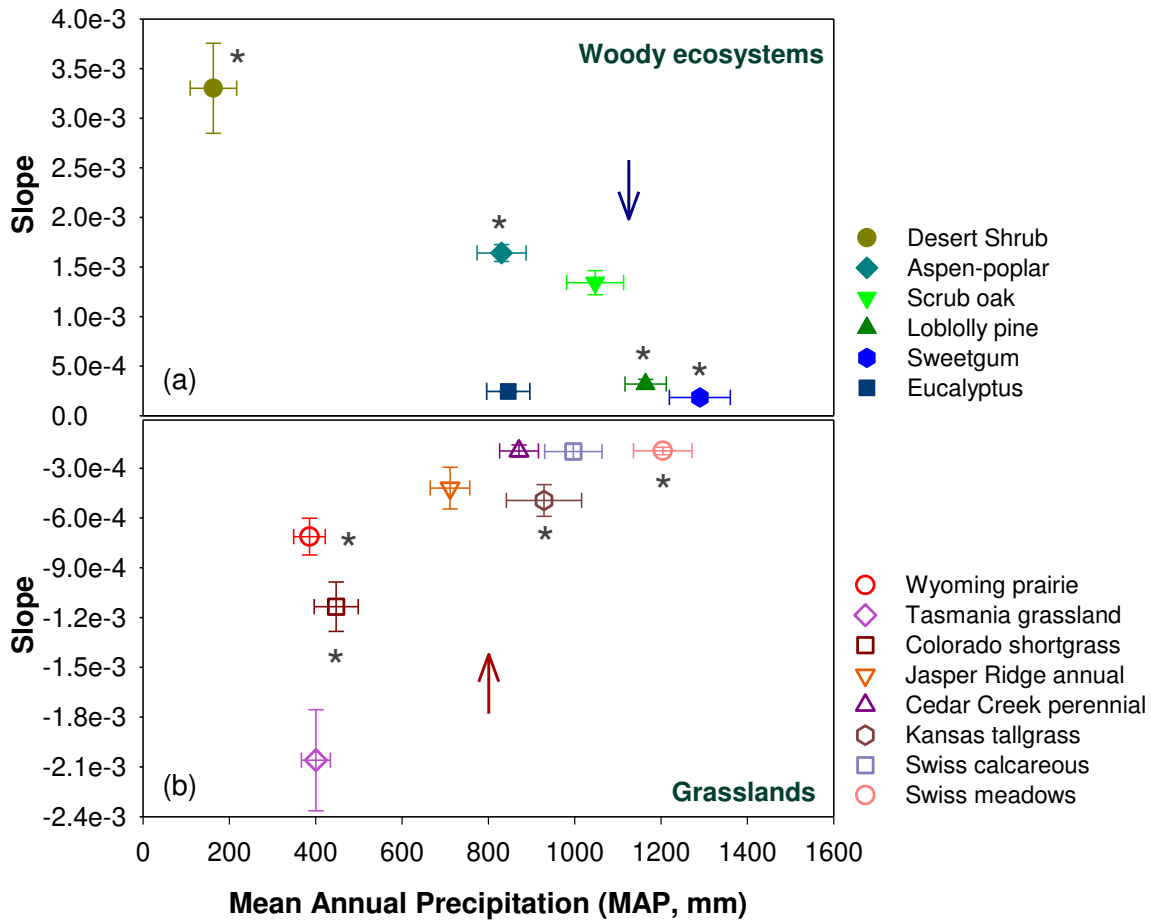


Fig. S3. Sensitivity of ANPP enhancement to annual precipitation (slope). Slopes ($\Delta EAPP / \Delta iPPT$ mm⁻¹) of linear functions of EAPP-iPPT (Fig. 1a and 1b and Table S3a) across (a) woody and (b) grassland ecosystems. A positive slope means EAPP increasing with increasing iPPT at a given site; 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.

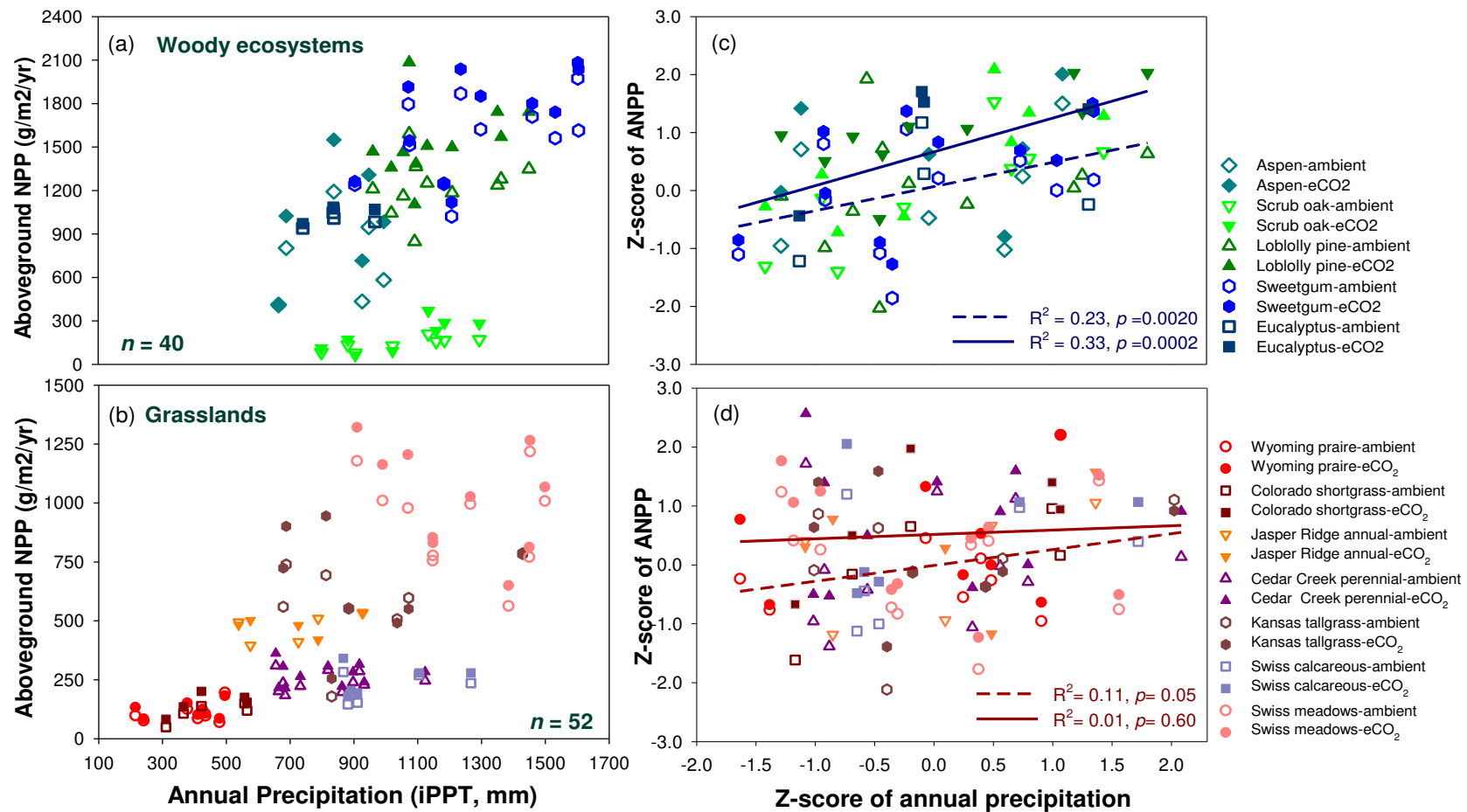


Figure S4. Direct responses of ANPP to iPPT under ambient CO₂ (open symbols) and eCO₂ (solid symbols) in (a) woody and (b) grassland ecosystems ($n=40$ and $n=53$, respectively). Not all sites have ANPP values as some only reported ANPP response ratios (EAPP). Z-score analyses of ANPP responses to iPPT and regression lines under ambient CO₂ (dashed line) and eCO₂ (solid line) in (c) woody and (d) grassland ecosystems. The regressions of Z-scores are statistically significant for both treatments in woody ecosystems; in grassland ecosystems, a positive relationship between ANPP and iPPT occurs under ambient CO₂ but not under eCO₂ treatments, although eCO₂ enhances ANPP.

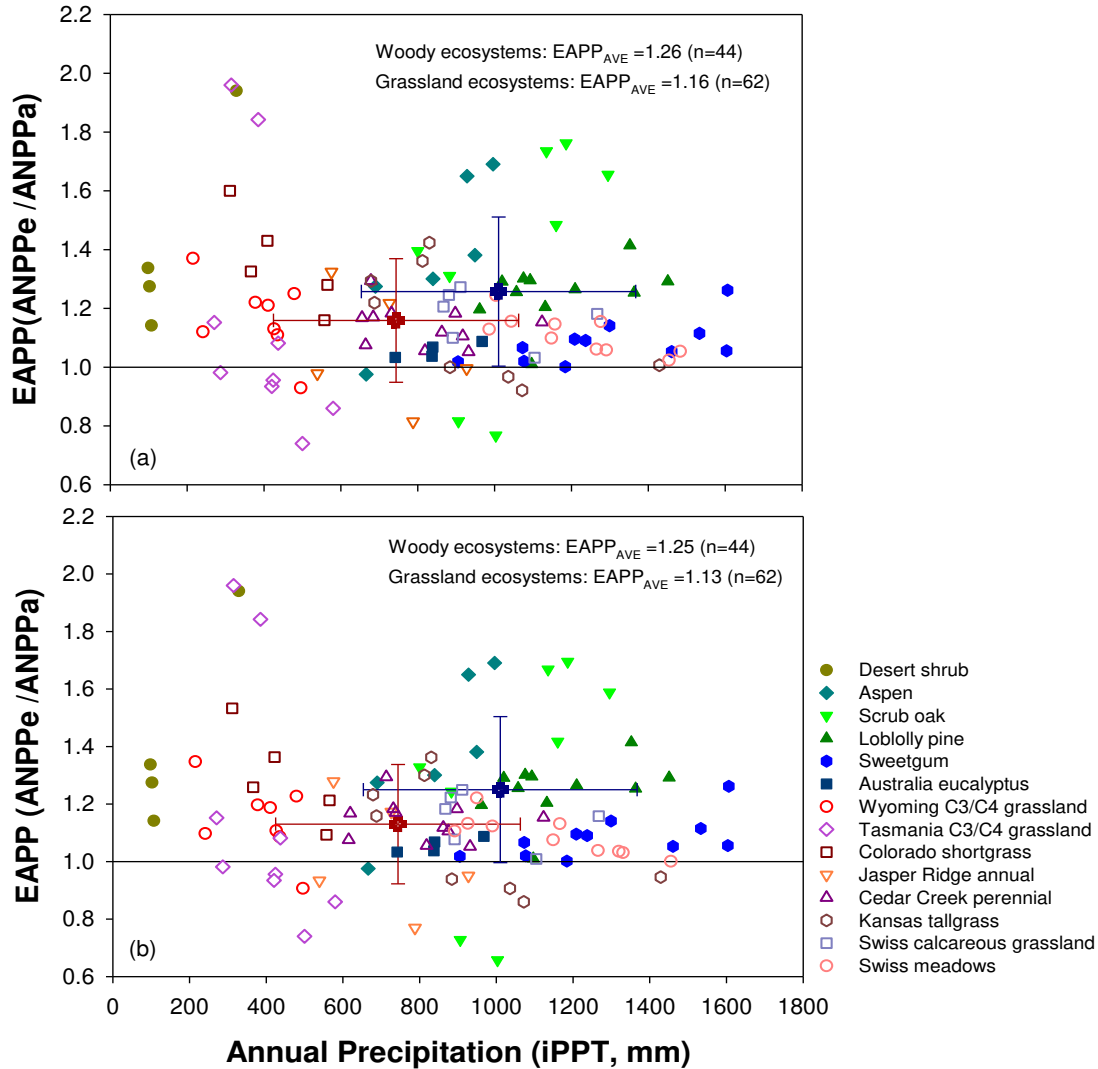


Fig. S5. Mean ANPP enhancements affected by eCO_2 levels. (a) Mean values of EAPP for all sampling years and all sites ($EAPP_{AVE}$) of woody (solid symbols) and grassland (open symbols) ecosystems; EAPP responses to iPPT are significantly different between woody and grassland ecosystems (t -test: $p = 0.044$); (b) $EAPP_{AVE}$ of woody and grassland ecosystems after adjusting higher eCO_2 concentrations used in grassland experiments and the scrub-oak site to 550 ppm based on the Farquhar model (Fig. S6); EAPP responses to iPPT are significantly different between woody and grassland ecosystems (t -test: $p = 0.015$). Error bars represent standard deviations (SDs).

Effect of intercellular CO₂ level on canopy photosynthesis

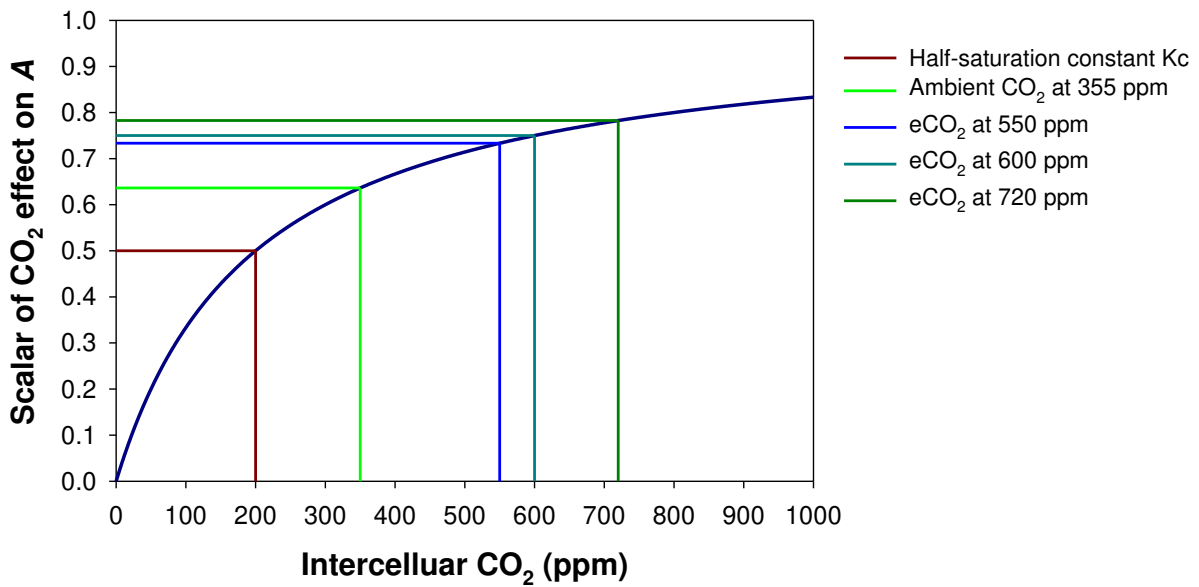


Fig. S6. Effects of CO₂ levels on canopy photosynthetic rates illustrated by the Farquhar model. Y-axis shows the impact (scalar) of intercellular CO₂ levels on canopy photosynthesis rates, given an assumption of optimal intercellular CO₂ level being close to the atmospheric level. Relatively higher CO₂ concentrations were used in 6 enrichment experiments of grassland ecosystems (600-720 ppm) compared to the CO₂ concentration (~550 ppm) used in woody ecosystems.

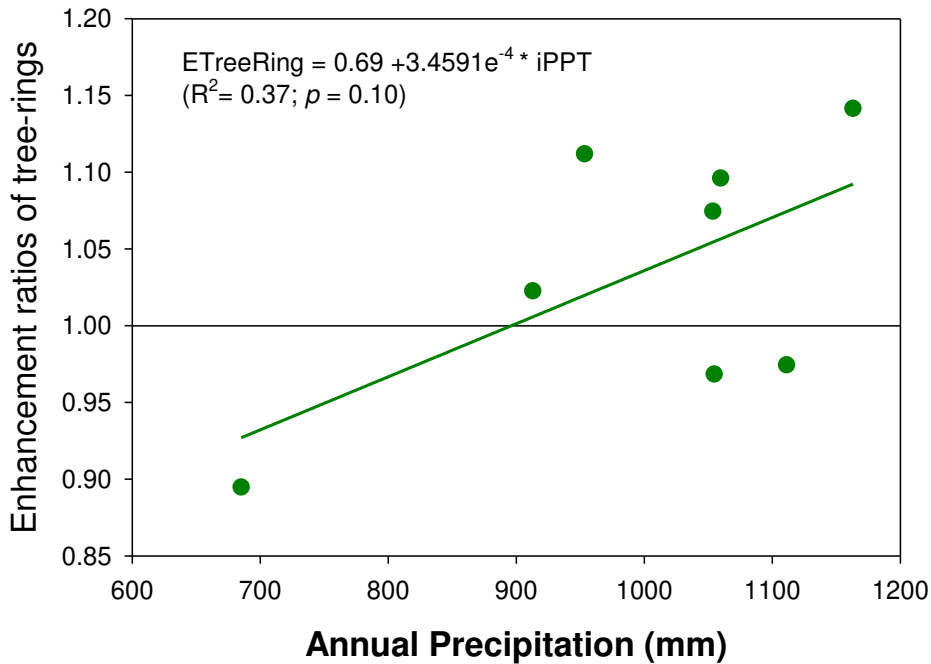


Fig. S7. The eCO₂ enhancements in tree-ring increments at a mature European beech forest located in the Swiss Canopy Crane (SCC) FACE site (operated from 2001 to 2008). ETreeRing is enhancement ratios of standardized tree rings under eCO₂ vs. ambient CO₂ treatments, and the mean of enhancement ratios of two dominant canopy tree species, *Fagus sylvatica* and *Quercus petraea*. The crowns of study trees with eCO₂ treatments were exposed to eCO₂ at ~550 ppm during daylight hours throughout the growing season. The annual precipitation data were from the weather station located in Basel, Switzerland.

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