



Globally consistent influences of seasonal precipitation limit grassland biomass response to elevated CO₂

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1 **Globally consistent influences of seasonal precipitation limit grassland**
2 **biomass response to CO₂**

3

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42

43 **Abstract**

44 Rising atmospheric carbon dioxide concentration ($[\text{CO}_2]$) should stimulate biomass
45 production directly via biochemical stimulation of carbon assimilation and indirectly via
46 water savings caused by increased plant water use efficiency¹. Because of these water
47 savings², the CO_2 fertilisation effect should be stronger in drier sites³, yet large differences
48 among experiments in grassland biomass response to elevated CO_2 appear unrelated to annual
49 precipitation^{2,4}, preventing useful generalisations. Here we show that, as predicted, the impact
50 of elevated CO_2 on biomass production in 19 globally-distributed temperate grassland
51 experiments reduces as mean precipitation in seasons other than spring increases but,
52 unexpectedly, rises as mean spring precipitation increases. Moreover, because sites with high
53 spring precipitation also tend to have high precipitation at other times, these effects of spring
54 and non-spring precipitation on the CO_2 response offset each other, constraining the response
55 of ecosystem productivity to rising CO_2 . This explains why previous analyses were unable to
56 discern a reliable trend between site dryness and the CO_2 fertilisation effect^{2,4}. Thus, the CO_2
57 fertilisation effect in temperate grasslands worldwide will be constrained by their natural
58 rainfall seasonality such that the stimulation of biomass by rising CO_2 could be substantially
59 less than anticipated.

60 **Introduction**

61 The capacity of the biosphere to absorb carbon as the atmospheric concentration of CO₂
62 ([CO₂]) increases is a crucial yet uncertain factor in climate science⁵. The fundamental
63 physiology is simple; photosynthesis of most plants is not saturated at current [CO₂], so
64 increasing [CO₂] should stimulate biomass production¹. Additionally, increasing [CO₂]
65 reduces stomatal aperture, increasing plant water-use efficiency and, by maintaining higher
66 soil moisture storage, increasing productivity in water-limited ecosystems¹. Together with
67 other minor indirect effects, these two mechanisms produce the CO₂ fertilisation effect on
68 biomass (CFE), defined as the elevated CO₂ (eCO₂)-driven increase in biomass production as
69 percentage of that in control plots. However, models currently ‘disagree strongly’⁶ on the
70 size of the positive CO₂–productivity feedback indicating that the processes driving eCO₂
71 responses are not well characterised, leading to argument as to the strength of the CFE^{7,8}.
72 The CFE measured in experiments that manipulate [CO₂] varies substantially among studies
73^{2,9} and is considerably lower in open-air experiments than expected from leaf-level and
74 enclosure studies, even for crop plants¹⁰. Various factors have been proposed to influence the
75 magnitude of the CFE^{2,4,9-11}, but none have explained the large variation observed among
76 experiments. Grasslands occupy over 29% of ice-free land and are consequently important
77 components of the global carbon budget, so the large degree of unexplained variation (~300%
78 CV¹¹) in grassland biomass response to eCO₂ limits our ability to estimate future carbon
79 cycling.

80 Indirect effects caused by changes in plant water-use efficiency can have a pivotal, and
81 sometimes dominant, influence on the overall biomass response to eCO₂^{1,3,4}. These indirect
82 effects likely relate to precipitation patterns and soil moisture conditions¹² and might explain
83 why CFE responds strongly to precipitation at particular sites and why the mean CFE varies
84 even among similar sites. Despite having a firm theoretical basis, attempts to use water

85 availability to explain CFE have yielded little success^{2,9,11}, and individual studies have
86 countered the theory^{13,14} suggesting the opposite, that water scarcity can partially limit CFE.
87 We propose that these apparent contradictions are caused by precipitation having different
88 effects on the CFE at different times of year¹⁵. Previous work has demonstrated that the
89 seasonal balance of rainfall predicts the CFE at a single site¹⁵, so we suspected that a similar
90 influence might extend across sites. Here, we test the hypothesis that differences in mean
91 CFE among sites are related to site differences in the seasonal precipitation totals.

92 **Experimental results**

93 Using data from 19 grassland CO₂-manipulation experiments and a total of 163 experimental
94 years (Table S1), we show that the differences among experiments in mean CFE are
95 explained extremely well by a stimulatory effect of precipitation in spring and a suppressive
96 effect of precipitation at other times of the year (Fig. 1). The experiments were distributed
97 throughout temperate zones in North America, Europe, Asia and Australasia, covering a wide
98 range of grassland types and environmental factors (Table S1). The mean CFE of these
99 experiments was 9.0±1.7% (mean±SEM) at an average enrichment level of 243 μmol CO₂
100 mol⁻¹ and an average ambient [CO₂] of 375 μmol mol⁻¹, but variation in CFE among
101 experiments was large, with site-mean CFE ranging from -7.1% to +20.0% (Table S1). We
102 used simple and multiple regression analyses to determine whether variation in mean CFE
103 among sites was related to climatic and site factors. We tested the impact on CFE of mean
104 annual, autumn, winter, spring and summer precipitation over the study period at each site,
105 with the seasons defined as being three calendar months in duration with 1 March being the
106 first day of spring in the Northern Hemisphere and autumn in the Southern Hemisphere. We
107 also tested the effects on the mean CFE of mean annual temperature, mean shoot nitrogen
108 content, mean soil C to N ratio, mean annual aboveground biomass production, the
109 proportion of C₄ plants at each site, the CO₂ enrichment level and the fumigation technique

110 (chambers versus FACE technology). Importantly, variation among experiments in the mean
111 CFE was not explained by any of the tested site variables (Fig. 2), but 74.7% of the variation
112 in CFE among sites was explained by a two-factor model that incorporated mean spring
113 precipitation and the mean summed precipitation at other times of the year (i.e. “non-spring
114 precipitation”, $r^2=0.747$, $F_{2,16}=23.6$, $P<0.00002$; Table S2). Site-mean CFE was enhanced by
115 decreasing non-spring precipitation ($P=0.0002$; Fig. 1), but the effect of low precipitation in
116 spring was negative, i.e. the opposite pattern ($P<0.00001$; Fig. 1). Thus, the mean CFE for a
117 site was determined by the combination of the stimulatory effect of higher spring
118 precipitation and the stimulatory effect of lower non-spring precipitation (Fig. 1).
119 Considering the range of spring and non-spring precipitation values, the influence of spring
120 and non-spring precipitation on the CFE are relatively evenly balanced, such that their
121 impacts tend to be similar in scale but opposite in influence.

122 Data from both the experimental sites and a worldwide precipitation grid covering temperate
123 grassland show that sites that are wetter in spring also tend to be wetter during the rest of the
124 year (Fig. 3, Fig. S1) and hence the contrasting impact of precipitation in spring and non-
125 spring periods constrains the CFE (Fig. 3). This offsetting influence of average spring versus
126 average non-spring precipitation on the CFE explains why mean annual precipitation by itself
127 is a very poor predictor of the CFE (Fig. 2; $r^2=0.02$, $P=0.68$) and why earlier analyses failed
128 to discern any substantial effect of overall site wetness or dryness (usually described by
129 annual metrics) on the degree of stimulation of biomass across sites with markedly different
130 aridity levels. Importantly, none of the other potential predictor variables significantly
131 improved the predictive capacity of the two-factor model (Tables S2-S4) nor were they
132 strongly correlated with the two predictors (Fig. S2), indicating that the observed relationship
133 is unlikely to be mediated by these factors. This offsetting mechanism also explains why the
134 CFE observed in field experiments is mostly lower than anticipated.

135 Certain site characteristics such as the proportion of C₄ species in a community^{16,17} and N
136 availability^{18,19} can influence the CFE within a site, but our analysis indicates that these
137 ecosystem traits, as well as factors such as mean annual temperature and the degree of CO₂
138 enrichment, had little influence on the differences in CFE among grassland experiments.
139 Further, fumigation technique (chambered versus FACE experiments) had no significant
140 impact on the CFE (Fig. S3). We suggest that the amount and seasonal distribution of
141 precipitation shape important, relatively stable community and ecosystem properties at a
142 particular site, determining the site's average or 'inherent' CFE. We believe such properties
143 to be the result of long-term (multi-year and evolutionary) processes and their effect on the
144 biomass CO₂ response differ fundamentally from that of shorter-term physiological
145 mechanisms.

146 First, a site that tends to have wet springs will have communities biologically equipped to
147 take advantage of eCO₂. Repeatedly, experiments show grasslands are more responsive to
148 changes in spring precipitation than to changes at other times of year^{20,21}, so that spring
149 precipitation is the best predictor of grassland productivity²² and has a disproportionate
150 influence on community properties key to ecosystem function²³. Thus, the strong impact of
151 spring precipitation on the CFE is most likely mediated via positive relationships with plant
152 species richness^{17,24,25}, leaf-area-index, meristem density²⁶, microbial community function²⁷
153 and ecosystem resource availability, all of which boost the CFE. Additionally, the strong
154 effect of spring precipitation is robust to variation in the definition of spring by about 20 days
155 (Fig. S4). The *a priori* definition of spring we used here (i.e. "calendar spring" 1 March-31
156 May in the Northern Hemisphere, 1 September – 30 November in the Southern Hemisphere)
157 is at the early edge of that range, indicating the importance of including late-spring
158 precipitation for explaining variation in CFE. This agrees with the fact that altering our
159 definition of spring by advancing the commencement date by only 10 days dramatically

160 reduced our ability to explain the variation in CFE among sites, whereas delaying the
161 commencement of spring by up to 20 days had little effect on the predictive power of spring
162 precipitation (Fig. S4). Such a strong effect of advancing the definition of spring onset by
163 only 10 days is surprising since the season was defined to span three months, but it indicates
164 the importance of capturing the amount of precipitation that falls within the entirety of the
165 spring period. This suggests that the amount of precipitation that falls while the grassland is
166 in its maximum growth period affects key properties of the community and/or ecosystem, as
167 suggested elsewhere²⁰⁻²³. We also tested the effect of site-specific “growing-season”
168 precipitation (Table S1) using both broad and narrow definitions of the growing season (see
169 Methods for details) but this analysis explained far less of the variation in CFE among sites
170 than the spring/non-spring analysis. This is because definitions of growing seasons often
171 extend far into the summer period, combining periods in which precipitation has opposing
172 effects on the CFE (Fig. 1). In addition, we tested the effect of varying the duration of spring
173 between one month and six months, but again, none of the models approached the ability of
174 the spring/non-spring model to describe the variation in CFE. Thus, while the exact timing of
175 the onset of warmer conditions conducive to active growth will vary from site to site and year
176 to year, the traditional definition of the three-month spring period clearly captures the impact
177 of precipitation on important ecosystem properties that have real and measurable effects on
178 productivity.

179 Second, a considerable proportion of the CFE is obtained from the anti-transpirant effects of
180 eCO₂, which are most pronounced in drier sites^{1,3,4}. Therefore, a site that tends to be wet in
181 seasons other than spring has limited opportunities for the benefits of the water-saving effects
182 of eCO₂ to be realised simply because the soil in such sites will tend to be moist even when
183 not exposed to eCO₂. Thus, the CFE reduces as non-spring precipitation increases, exactly as
184 predicted from theory^{1,3,4}. The combination of these two factors determines the site’s inherent

185 ability to respond to eCO₂. Importantly, it is a site's mean precipitation in the spring and non-
186 spring periods that determines the mean strength of the CFE. Long-term precipitation
187 averages have a far greater impact on crucial community and ecosystem properties such as
188 plant community composition than shorter-term deviations from the average²⁸, indicating
189 that ecosystem properties link the mean CFE with precipitation, rather than the immediate
190 effects of precipitation on carbon assimilation rates. Thus, increasing spring precipitation
191 increases a site's tendency to possess community traits that boost the response to eCO₂.
192 Unravelling the mechanisms whereby this occurs should now become a key goal of global
193 change ecology and will require concerted, global observational and experimental efforts.
194 The fact that the models with the greatest ability to explain the variation among sites were
195 those that included the entirety of the spring period suggests that processes occurring
196 belowground prior to shoot emergence and those occurring during the early stages of biomass
197 formation are key to understanding the mean CFE response of a system.

198 In short, we found that it is the *tendency* of a site to receive more or less precipitation than
199 another site in spring or in the rest of the year, as indicated by the average values, that
200 influences the site's mean CFE, rather than a direct link between each precipitation event and
201 CO₂-related growth stimulation. This is supported by the fact that interannual variation in
202 CFE within each site was poorly described by the combination of spring and non-spring
203 precipitation (Fig. S5). Within each site, the annual CFE can be affected by a variety of
204 factors, including deviation from the climatic average as well as lags and legacies of
205 responses to treatments in previous years. For instance, a strong stimulation of biomass
206 production in one year could deplete soil nutrient stocks, leading to suppressed responses in
207 subsequent years²⁹. Similarly, conditions that limit growth in one year could lead to the
208 accumulation of nutrients and lead to strong growth responses in subsequent years. In both of
209 these scenarios, the annual CFE values will be divorced from the contemporaneous

210 precipitation since the CFE will be partly dependent upon the climatic conditions of
211 antecedent years, such as occurs with other ecosystem processes³⁰⁻³³. However, over longer
212 periods the site average CFE should tend towards the inherent CFE for that location, which is
213 determined by the combination of average values of spring and non-spring precipitation.

214 **Geographical extrapolation**

215 The ability to describe variation in CFE among grassland sites allows us to project the
216 potential CFE of a site from easily obtained climatic variables (Fig. 3), as is possible for
217 ANPP^{34,35}. By doing this for temperate grasslands worldwide, we found that most grasslands
218 occur in sites in which the combination of spring and non-spring precipitation leads to a low
219 CFE (Fig. 3). Although there is substantial geographic variation in the potential CFE of
220 temperate grasslands, the projected CFE is below 10% in large areas across all continents
221 (Fig. 4), constrained by the seasonality of precipitation in those locations (Fig. 3). The
222 average expected CFE of temperate grasslands from our projections is $6.0 \pm 0.03\%$, one-third
223 lower than that observed in the experiments (Fig. 1) because of the global prevalence of
224 temperate grasslands in sites with low spring precipitation but moderate precipitation at other
225 times of year (Fig. 3). Thus, predicting eCO₂ effects on grassland biomass production by
226 averaging experimental results without the geographical extrapolation would lead to
227 overestimation of the CFE.

228 **Conclusions**

229 Clearly, predicting carbon feedbacks to the atmosphere is a global research priority³⁶ and the
230 CFE is a dominant uncertainty in projecting biosphere feedback effects on the growth of
231 atmospheric [CO₂]. We show consistent, biome-wide, interactions of the CFE with
232 precipitation seasonality that suggest the CFE in grasslands is likely to be less than would be
233 predicted by models that do not accurately represent these counteracting influences of

234 precipitation at different times of year ⁶. Targeted experiments in underrepresented grassland
235 areas, especially the neglected tropical areas and those predicted to have low CFE, would be
236 an efficient way of refining and confirming our capacity to project the impact of eCO₂ on
237 grasslands around the world. Together with a thorough examination of belowground biomass
238 responses to eCO₂ and how biomass responses translate into ecosystem carbon balance, this
239 will be the next important step in improving global predictions of carbon feedbacks from
240 terrestrial ecosystems.
241

242 **Methods**

243 We collected annual aboveground biomass data from the 19 experiments listed in Table S1,
244 all of which were either open-top chamber (OTC) or Free Air CO₂ Enrichment (FACE)
245 experiments located outdoors with plants growing in the soil (i.e. not in pots). We used all
246 experiments for which annual aboveground biomass data were available either directly from
247 the researchers or from published results. Where experiments included factors other than CO₂
248 manipulation, such as warming or precipitation removal, we only used the control (ambient)
249 levels of the other factors and therefore examined the CO₂ response independent of other
250 experimental factors, essentially treating each experiment as a single-factor experiment. The
251 SwissFACE experiment included differing levels of nutrient application as a treatment. We
252 used data from the lower level of nutrient application, which was merely sufficient to replace
253 the nutrients removed during regular biomass harvests. We first calculated the annual CO₂
254 fertilisation effect (CFE) as the difference in annual aboveground biomass production
255 between elevated CO₂ and control plots, expressed as a percentage of biomass of control
256 plots. The difference in biomass between elevated and control plots was corrected for any
257 pre-existing difference where these data were available. Most experiments harvested or
258 measured aboveground biomass once per year but where biomass was harvested more
259 frequently, the individual harvest values were summed at the plot level to obtain the annual
260 aboveground biomass values.

261 Daily precipitation was obtained from each site individually using data collected on site with
262 automatic weather stations (most sites) or from a nearby meteorological weather station
263 (Kansas and Hungary). In both instances, the weather station was within ~2.5 km of the
264 experimental site. At the Swiss FACE site, the locally-collected precipitation data contained
265 short gaps in the record, amounting to ~5% of the total record, so we used data from the
266 nearest meteorological weather station to interpolate the missing values. We used the daily

267 precipitation data to calculate seasonal precipitation totals for each year at each site. The
268 seasons were defined to commence on 1 March (spring in the northern hemisphere, autumn in
269 the southern), 1 June (summer in the northern hemisphere, winter in the southern), 1
270 September (autumn in the northern hemisphere, spring in the southern) and 1 December
271 (winter in the northern hemisphere, summer in the southern). The seasonal precipitation total
272 was defined as the sum of daily precipitation over the season in each year and this value was
273 then averaged over all years for which the experiment ran. Annual precipitation was defined
274 as the sum of autumn, winter, spring and summer precipitation totals, with the year
275 commencing on 1 September in the Northern Hemisphere and 1 March in the Southern
276 Hemisphere. The year was defined this way so that it was the year preceding the biomass
277 harvest, which normally occurred in late summer or very early autumn. The seasonal and
278 annual precipitation totals were calculated in the same manner for all experiments.

279 Characteristics of each experiment to be used as potential drivers of the CFE were supplied by
280 the experimental team from each site or obtained from published values for each experiment.
281 Mean CO₂ enrichment was obtained from annual enrichment values, using annual CO₂ values
282 for elevated and ambient/control plots, then averaged for each site over all years of each
283 experiment. Mean site aboveground biomass production was calculated as the annual
284 aboveground biomass produced in ambient/control plots of each experiment, averaged over
285 all years of the experiment. The proportion of C₄ plants at each site was calculated as the
286 aboveground biomass contribution of C₄ plants as a proportion of total aboveground biomass
287 in control plots in each experiment, averaged over all years of the experiment. Mean shoot N
288 was calculated as the mean percent N of aboveground biomass in control plots for each
289 experiment, again averaged over all years for which data were available. Site fertility was
290 also calculated as total soil nitrogen content and soil carbon to nitrogen ratio, but each of
291 these variables had a discontinuous distribution and were thought not to be the most reliable

292 predictors of fertility given that some of the sites were located on organic-rich soils.
293 Nonetheless, all three of these fertility indicators were used in turn in the below analyses,
294 with negligible effects on the analysis outcome, thus shoot N was selected for final analyses.
295 Relationships between the CFE and potential drivers were determined by multiple regression
296 analyses using R³⁷. Beginning with all possible combinations of the five precipitation metrics
297 (annual, autumn, winter, spring and summer precipitation totals) and the other six potential
298 drivers (mean annual temperature, mean shoot N, mean annual aboveground biomass
299 production, proportion C₄, mean CO₂ enrichment and fumigation technique), we ranked the
300 resultant models using the Akaike Information Criterion corrected for finite sample size
301 (AIC_c), using the MuMIN package of R³⁸. Model competitiveness was determined by
302 observation of the difference in AIC_c between each model and the lowest value of AIC_c
303 obtained (Δ AIC_c). Models were ranked in ascending Δ AIC_c value and a distinction between
304 competitive and non-competitive models was made by observing any obvious breaks in the
305 sequence of ascending Δ AIC_c. A single two-factor model containing annual and spring
306 precipitation totals was clearly superior to other models and had a 15% probability of being
307 the best model among all possible models, with next most competitive model only having a
308 7% probability of being the best model (Table S2), so no coefficient averaging was
309 necessary. This model had an r^2 value of 0.75 ($P < 0.00002$) but because spring and annual
310 precipitation were significantly correlated ($r^2 = 0.88$), we replaced the annual precipitation
311 term with non-spring precipitation (i.e. the total precipitation in seasons other than spring),
312 which was less strongly correlated with spring precipitation ($r^2 = 0.78$). We also calculated the
313 variance inflation factor (VIF) as an additional test of collinearity and the VIF was 2.6 for the
314 spring + non-spring precipitation model, approximately half the value for the spring + annual
315 precipitation model (VIF=4.5), indicating the model incorporating non-spring precipitation
316 had a substantially lower impact from collinearity, and far below 5, the VIF value generally

317 believed to cause concern ³⁹. However, collinearity can influence interpretation of a multiple
318 regression relationship and affect predictions using a model containing collinear predictor
319 variables. Therefore, we first tested whether the strength of the regression was influenced by
320 the incorporation of both spring and non-spring precipitation by regressing non-spring
321 precipitation against spring precipitation, calculating the residuals between the non-spring
322 values and the regression line and using these residual values in the model instead, following
323 the method of Harrell ⁴⁰. This has the advantage of retaining the information contained in the
324 predictor variable, but removing any collinearity between it (non-spring precipitation) and the
325 remaining term (spring precipitation; $r^2 < 0.01$). This model had an identical r^2 value (0.747,
326 $P < 0.00002$) to that of the original model containing spring and non-spring precipitation,
327 indicating that the original model is robust and, importantly, its interpretation not subject to
328 error from collinearity. Second, collinearity can inflate the errors involved in making
329 predictions but only if predictions involve predictor variables that are not similarly correlated
330 ⁴⁰. Thus, predictions using the model containing spring and non-spring precipitation would be
331 unreliable if spring and non-spring precipitation were not correlated in the dataset used for
332 predictions. Therefore, we tested the relationship between spring and non-spring precipitation
333 using the entire gridded dataset of mean spring and non-spring precipitation for all temperate
334 grasslands globally (Fig. S1). The relationship between spring and non-spring precipitation
335 was almost identical in the global temperate grassland dataset (regression coefficient =
336 0.27 ± 0.1) as in the dataset used to construct the model (regression coefficient = 0.28 ± 0.05).
337 Since collinearity does not affect predictions made using new data that have the same degree
338 of collinearity as the original data ⁴⁰, we are confident that the predictions using this model
339 are robust and appropriate.

340 Therefore, we examined the influence of spring and non-spring precipitation on the CFE by
341 multiple linear regression, also testing for an interaction between spring and non-spring

342 precipitation on the CFE, which was found to be non-significant ($P=0.24$). Further, we tested
343 the relationship between mean CFE and all combinations between spring and non-spring
344 precipitation and the other six potential, non-precipitation predictors (mean annual
345 temperature, mean shoot N, proportion C_4 , mean CO_2 enrichment and fumigation technique,
346 Table S3) using the same methods as above. Finally, we used a hierarchical approach, adding
347 each of the non-precipitation predictors in turn to the two-factor model and testing whether
348 this led to a significant improvement in model performance using analysis of variance (Table
349 S4). We also tested the performance of the seven-term model containing all of these
350 predictors (Table S4). None of the resultant three-factor models significantly improved model
351 performance and neither did the seven-term model (Table S4), thus the most parsimonious
352 model under all tests remained the two-factor model. Partial regression analysis was used to
353 determine the effects, with 95% confidence limits, of spring and non-spring precipitation
354 totals on the mean site CFE using the *effects* package in R⁴¹.

355 Additionally, we tested the impact of precipitation in and out of the growing season, as
356 opposed to in and out of spring, using a two-factor model and growing season dates estimated
357 for each site individually. We used both broad and narrow definitions of growing season as
358 either the period encompassing non-trivial aboveground growth (broad) or the period of
359 maximum aboveground biomass production (narrow). The variation among sites in mean
360 CFE was very poorly explained by the combination of growing season and non-growing
361 season precipitation, whether the broad ($r^2=0.06$, $F_{2,16}=0.5$, $P=0.6$) or narrow ($r^2=0.08$,
362 $F_{2,16}=0.7$, $P=0.5$) definition of growing season was used. Further, neither growing season
363 (broad definition, $r^2=0.04$, $F_{1,17}=0.7$, $P=0.4$; narrow definition, $r^2=0.05$, $F_{1,17}=0.8$, $P=0.4$),
364 nor non-growing season precipitation (broad definition, $r^2=0.02$, $F_{1,17}=0.4$, $P=0.5$; narrow
365 definition, $r^2=0.04$, $F_{1,17}=0.7$, $P=0.4$) were correlated with annual CFE of a site, nor was the
366 proportion of precipitation received during the growing season (broad definition, $r^2=0.003$,

367 $F_{1,17}=0.05$, $P=0.8$; narrow definition, $r^2=0.04$, $F_{1,17}=0.07$, $P=0.8$). Hence, variation in the CFE
368 among sites was not related to growing season precipitation.

369 We tested the impact of varying the definition of spring by either advancing or delaying the
370 commencement date from 1 March/September by 10, 20, 30 or 45 days and testing the impact
371 this alteration had on the performance of the two-factor spring/non-spring model. The
372 duration of the spring period was maintained at 90 days for all comparisons. Since
373 precipitation data were only available as monthly values for 3 of the 19 experiments, the
374 spring adjustment analysis was done using the remaining 16 of the sites. Advancing the
375 definition of spring substantially reduced the two-factor model's ability to explain variation
376 among sites in mean CFE (Fig. S4). In contrast, delaying the definition of spring by up to 20
377 days had little impact on model performance but longer delays caused it to decline (Fig. S4).
378 Therefore, we maintained our definition of spring as commencing on 1 March (Northern
379 Hemisphere) or 1 September (Southern Hemisphere).

380 Data conformed to the assumptions of the statistical tests involved, as tested by investigation
381 of residuals, leverage and normality as well as using Box-Cox plots using the MASS package
382 in R⁴². The only exception was mean annual biomass production of control plots, in which
383 the single datapoint from the site in Ireland exerted excessive leverage on the relationship
384 with CFE. Therefore, this single datapoint was removed from subsequent analyses.

385 We conducted mapping and spatial analyses in ArcMap 10.3 and ESRI, USA. The 8 km
386 AVHRR global land cover classification⁴³ product provided moderate oversampling of land
387 cover classification for wooded grasslands, grasslands and croplands that we determined to
388 be representative of the model target. We added land cover class, spring and non-spring
389 precipitation to CFE modelled values using the *Sample* and *Spatial Join* (nearest geodesic)
390 tools respectively. Spring and non-spring precipitation values were calculated from a 10' grid
391 of monthly precipitation values obtained from the Climatic Research Unit at the University of

392 East Anglia CRU CL v. 2.0 database, which is available (<http://www.cru.uea.ac.uk/data>)
393 under the Open Database License (ODbL). These values were used to calculate the local CFE
394 from the spring + non-spring multiple regression model. We mapped all CFE values for
395 locations meeting model parameters for climate zone and land cover. We visualised the limits
396 of model precipitation parameters by interpolating total precipitation data (*Ordinary Kriging*)
397 and classifying the resulting raster with masks applied to tropic and polar zones. Calculations
398 using the geographically projected values of CFE only included those sites that fell within the
399 range of spring and non-spring precipitation values observed in the experimental sites.

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

402 **Data availability**

403 All data generated or analysed during this study are included in this published article (and its
404 supplementary information files) with the exception of the gridded GIS data, which are
405 available from <https://crudata.uea.ac.uk/cru/data/hrg/tmc/> for the precipitation data and from
406 <http://glcf.umd.edu/data/landcover/data.shtml> for the landcover data.

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580 **Author contributions**

581 S.L., J.A.L., M.J.H. and S.F. conceived the research idea and designed the study with
582 assistance from P.C.D.N. and K.H., while M.J.H., S.L., P.C.D.N., J.A.L. and S.F. did the
583 analysis and together with A.L. and P.B.R. led the writing of the manuscript. A.F. did the
584 mapping and all geographical analyses. P.C.D.N., M.J.H., J.A.L., L.C.A., D.B., N.R.C., J.D.,
585 J.K., A.L., P.N., C.B., P.B.R., S.W. and J.S. contributed unpublished data. All authors
586 contributed to the final version of the manuscript.

587 **Competing interests**

588 The authors declare no competing interests

589 **Additional information**

590 **Supplementary information** is available for this paper at...

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593

594 **Figure legends**

595 **Fig. 1. The impact of seasonal precipitation on the CO₂-fertilisation effect (CFE).** Partial
596 regression plots showing the influence on the CO₂ fertilisation effect attributable to spring
597 and non-spring precipitation across nineteen grassland elevated CO₂ experiments. The black
598 line shows the modelled effect with 95% confidence bands shown in red.

599

600 **Fig. 2. The carbon dioxide fertilisation effect (CFE) across nineteen temperate grassland**
601 **experiments as a function of different potential drivers.** Each point is the mean percentage
602 stimulation of aboveground annual biomass production by elevated CO₂, the CO₂ fertilisation
603 effect (CFE), for a particular site. Relationships between each driver and the CFE were
604 analysed by simple regression, with associated r^2 and P values shown in each panel, n=19
605 independent experiments. Abbreviations: MAP, mean annual precipitation, MAT, mean
606 annual temperature, Shoot N, the mean nitrogen content of aboveground biomass in control
607 plots; Proportion C₄, the mean proportion of biomass contributed by C₄ species, Enrichment,
608 the mean CO₂ enrichment level, AG Biomass, the mean aboveground biomass of control
609 plots.

610

611 **Fig. 3. Predicted CFE of aboveground biomass for given spring and non-spring**
612 **precipitation values.** Predictions used the formula $CFE (\%) = 2.94 + 0.135 \text{ spring}$
613 $\text{precipitation (mm)} - 0.035 \text{ non-spring precipitation (mm)}$. The CFE is for a CO₂ enrichment
614 of 243 $\mu\text{mol mol}^{-1}$ above an ambient [CO₂] of 375 $\mu\text{mol mol}^{-1}$. Suppression of biomass is
615 shown as red, stimulation of biomass shown in blue. Contours show the probability density of
616 particular combinations of spring and non-spring precipitation for temperate grasslands
617 worldwide, most of which lie within a range in which CFE is predicted to be low. The

618 nineteen experiments used in this analysis are plotted to show their combination of spring and
619 non-spring precipitation values, details provided in Table S1.

620

621 **Fig. 4. Modelled CO₂ fertilisation effect (CFE) in temperate grasslands.** **A**, Modelled
622 CFE for temperate grassland, using the formula $CFE (\%) = 2.94 + 0.135 \text{ spring precipitation (mm)} - 0.035 \text{ non-spring precipitation (mm)}$, for a CO₂ enrichment of 243 $\mu\text{mol mol}^{-1}$ above
623 an ambient [CO₂] of 375 $\mu\text{mol mol}^{-1}$. Grey areas fall outside the precipitation limits of this
624 analysis. White areas are not temperate zones or not grasslands. **B**, Frequency distribution of
625 modelled CFE in temperate grassland sites within the precipitation range used to construct
626 the model. **C**, Frequency distributions of modelled CFE as for (b) for Europe, Asia, North
627 America and the Southern Hemisphere. Mean CFE (\pm SEM) for each region is 5.9 \pm 0.03%
628 (Europe, n=14,604 grid-squares), 4.1 \pm 0.05 (Asia, n=24,944 grid-squares), 8.9 \pm 0.05% (North
629 America, n=13,764 grid-squares) and 7.5 \pm 0.05% (Southern Hemisphere, n=9,027 grid-
630 squares).
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