

1 **Differential Effects of Extreme Drought on Production and Respiration: Synthesis and**
2 **Modeling Analysis**

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14 **Running title:** differential effects of drought on production and respiration
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23 **Abstract:** Extremes in climate may severely impact ecosystem structure and function, with both
24 the magnitude and rate of response differing among ecosystem types and processes. We
25 conducted a modeling analysis of the effects of extreme drought on two key ecosystem processes,
26 production and respiration, and to provide broader context we complemented this with a
27 synthesis of published results across multiple ecosystems. The synthesis indicated that across a
28 broad range of biomes gross primary production (GPP) generally was more sensitive to extreme
29 drought (defined as proportional reduction relative to average rainfall periods) than was
30 ecosystem respiration (ER). Furthermore, this differential sensitivity between production and
31 respiration increased as drought severity increased and occurred only in grassland ecosystems
32 but not in evergreen needle-leaf and broad-leaf forests or woody savannahs. The modeling
33 analysis was designed to better understand the mechanisms underlying this pattern and focused
34 on four grassland sites arrayed across the Great Plains, USA. Model results consistently showed
35 that net primary productivity (NPP) was reduced more than heterotrophic respiration (Rh) by
36 extreme drought (i.e., 67% reduction in annual ambient rainfall) at all four study sites. The
37 sensitivity of NPP to drought was directly attributable to rainfall amount, whereas sensitivity of
38 Rh to drought was driven by soil drying, reduced carbon (C) input and a drought-induced
39 reduction in soil C content, a much slower process. However, differences in reductions in NPP
40 and Rh diminished as extreme drought continued due to a gradual decline in the soil C pool
41 leading to further reductions in Rh. We also varied the way in which drought was imposed in the
42 modeling analysis, either as reductions in rainfall event size (ESR) or by reducing rainfall event
43 number (REN). Modeled NPP and Rh decreased more by ESR than REN at the two relatively
44 mesic sites but less so at the two xeric sites. Our findings suggest that responses of production

45 and respiration differ in magnitude, occur on different timescales and are affected by different
46 mechanisms under extreme, prolonged drought.

47

48 **1 Introduction**

49 The hydrological cycle is forecast to be intensified by climate warming, leading to increased
50 drought frequency and severity, especially in water-limited ecosystems (IPCC, 2007). Responses
51 of ecosystem processes to drought, especially carbon (C) fluxes, are critical given that any net
52 change of ecosystem C balance acts as a feedback to climate change. Many studies have reported
53 ecosystem responses to climate extremes. For example, Ciais et al. (2005) reported that heat and
54 severe drought caused an unprecedented continental scale reduction in primary productivity with
55 ecosystem respiration decreasing concurrently. In contrast, by analyzing observational data from
56 a global network of eddy flux towers, Schwarm et al. (2010) found that global mean gross
57 primary production (GPP) was more sensitive to a drought event than respiration. In a long-term
58 field experiment, Jentsch et al. (2011) imposed an extreme drought in a constructed grassland
59 and reported the opposite - that drought decreased soil respiration without reducing net primary
60 production (NPP). Finally, by decreasing throughfall in a Mediterranean evergreen forest,
61 Mission et al. (2010) reported a greater reduction in GPP than that in ecosystem respiration (ER),
62 especially soil respiration. Such divergent responses of ecosystem productivity and respiration
63 to extreme drought suggests that greater mechanistic understanding is needed with regard to how
64 these two key C cycling processes are likely to respond to climate extremes.

65 Drought can affect production and respiration through both common and unique
66 mechanisms. Drought lowers plant C uptake by reducing stomatal conductance and leaf area, and
67 by increasing soil water deficit (Bréda et al., 2006), whereas soil water deficits and reduced
68 substrate availability can reduce ecosystem respiration (Luo and Zhou, 2006). Although there are
69 now many studies that have reported C cycling responses to both natural and experimentally

70 imposed droughts in a variety of biomes (e.g., Reichstein et al., 2002, Ciais et al., 2005,
71 Schwalm et al., 2012), these have not been synthesized to determine if there are any general
72 patterns of production and respiration responses to extreme drought across terrestrial biomes (but
73 see Schwalm et al., 2010). Identifying such patterns is key for determining if general
74 mechanisms underlie production and respiration responses.

75 One critical limitation to both observational and experimental studies is that they are all
76 conducted at short time scales - from seasonal to annual in length - whereas ecological responses
77 to drought over the longer term are likely to be more complex (Anderson et al., 2011). This is
78 especially true for heterotrophic respiration, which is affected by drought induced reductions in
79 the soil C pool as a function of lower GPP (Mission et al., 2010). Knowing how ecosystems
80 respond to long-term, extreme drought is important given that climate models predict an increase
81 in the frequency and magnitude of these events in the future (Dai, 2011). It has been
82 hypothesized that although the sensitivity of production and respiration to drought may differ
83 initially, they will eventually become equivalent as carbon cycle processes equilibrate over time
84 (Luo and Weng, 2011). Such long-term response patterns of ecosystems to drought are difficult
85 to reveal in experiments or observational studies but can be explored by ecosystem modeling
86 (Luo et al., 2011).

87 Drought has often been imposed in global change experiments by reducing each rainfall
88 event amount (Yahdjian and Sala, 2006, Mission et al., 2010, Cherwin and Knapp, 2012).
89 However, as climate models have predicted decreases in rainfall frequency in the future, drought
90 could also occur due to declines in rainfall event number (e.g., Báez et al. 2013). These two
91 different types of drought may affect ecosystem functions differently. For example, Harper et al.
92 (2005) observed more drought-induced reduction on aboveground NPP (ANPP) and soil CO₂

93 flux under natural drought caused by reducing rainfall event number and size than simply
94 altering the size of each rainfall event. This drought-event size interaction has also been observed
95 in shortgrass steppe where experimental droughts only reduced ANPP when rainfall events were
96 frequent and small rather than few but large (Cherwin and Knapp, 2012).

97 Our objectives were 2-fold. First, we determined if general patterns of drought effects on
98 production and respiration exist across multiple biomes based on published papers of both
99 observational and experimental studies. Second, we used an ecosystem model to examine
100 mechanisms possibly underlying differential sensitivity of production and respiration in four
101 different grassland types over a rainfall gradient in Central US Great Plains. In the modeling
102 analysis, we assessed responses of NPP and heterotrophic respiration (Rh) to a long-term severe
103 drought imposed by either reducing the size or the number of individual rainfall events. In
104 addition to assessing responses over longer time scales and mechanistically, we also compared
105 responses in these sites to identical treatments, thus overcoming a weakness of syntheses of
106 published studies that each impose drought in different ways and of different magnitudes and
107 measure responses uniquely (Luo et al. 2011).

108

109 **2 Materials and Methods**

110

111 **2.1 Synthesis methods and data analysis**

112 We searched ISI's Web of Science using these search strings: '(drought OR severe drought OR
113 extreme drought) AND (ecosystem fluxes OR ecosystem carbon balance)', 'drought AND NEE
114 AND eddy covariance', '(precipitation OR drought OR rainfall) AND net ecosystem exchange
115 AND manipulation' and 'drought AND NPP AND respiration' to identify both observational and
116 manipulative studies of drought effects on ecosystem C fluxes over global terrestrial biomes. We

117 also used 'rain forest AND eddy flux AND drought' to search for studies focused more
118 appropriately on seasonal droughts in rain forest dry seasons. We reviewed the most relevant
119 studies in which GPP and ER were reported in both drought and normal years or dry and wet
120 seasons for rain forest (Table 3 and Table S1).

121 Drought was categorized as extreme drought when ecosystems experienced more than a
122 40% decrease in annual precipitation relative to the long term average, as moderate drought with
123 less than a 40% but more than a 25% rainfall decrease, and minor drought with less than 25%
124 precipitation reduction. The drought sensitivity of production as estimated by GPP and
125 respiration estimated by ER for each study site was calculated as the drought induced absolute
126 reduction relative to the normal year divided by GPP or ER in the normal years (i.e. $\Delta\text{GPP}\% =$
127 $(\text{GPP}_{\text{normal}} - \text{GPP}_{\text{drought}})/\text{GPP}_{\text{normal}}$ or $\Delta\text{ER}\% = (\text{ER}_{\text{normal}} - \text{ER}_{\text{drought}})/\text{ER}_{\text{normal}}$). The differential
128 sensitivities were also assessed based on ecosystem types. The ecosystems were divided into
129 grassland, evergreen needle-leaf forest (ENF), broad-leaf forest (BF) and woody savannahs (WS).
130 One open shrubland, one oak woodland and one pine woodland were not included into the data
131 analysis due to limited sample size. The significance between $\Delta\text{GPP}\%$ and $\Delta\text{ER}\%$ was tested
132 using paired-sample T test. Seasonal drought effects on $\Delta\text{GPP}\%$ and $\Delta\text{ER}\%$ in rainforest were
133 not included in this analysis because of different responses and underlying mechanisms. Thus,
134 seasonal drought effects in rainforest are discussed separately in this study.

135

136 **2.2 Modeling analyses**

137 **2.2.1 Model description**

138 The terrestrial ecosystem model (TECO) is a process-based ecosystem model and was designed
139 to examine ecosystem responses to climatic perturbations including elevated CO₂, warming and
140 altered precipitation (Luo et al., 2008, Weng and Luo, 2008). The algorithms applied in TECO

141 are described in detail by Weng and Luo (2008). Here we provide a brief description, focusing
142 on mechanisms related to drought.

143 TECO is composed of four major sub-models that represent canopy processes, plant
144 growth, C transfer, and soil water dynamics. The canopy photosynthesis-transpiration submodel
145 is a two-leaf model with multiple canopy layers, derived primarily from Wang and Leuning
146 (1998), to simulate canopy energy balance, canopy photosynthesis and conductance. For each
147 layer, foliage is divided into sunlit and shaded leaves. Leaf photosynthesis and transpiration are
148 estimated by coupling the Farquhar photosynthesis (Farquhar et al., 1980) and Ball-Berry
149 stomata-conductance model (Ball et al., 1987). In the plant growth submodel, allocation of
150 photosynthetic assimilates depends on growth rate of leaves, stems and roots following
151 ALPHAPHA model (Denison and Loomis, 1989), and varies with phenology following CTEM
152 (Arora and Boer, 2005). Phenology is represented by seasonal variation in leaf area index (LAI).
153 Leaf onset is determined by growing degree days and leaf senescence is induced by low
154 temperature and low soil water content. The C transfer submodel simulates movement of C from
155 plant to soil C pools in three layers through litterfall and the decomposition of litter and soil
156 organic C. Carbon fluxes from litter and soil carbon pools are based on residence time of each C
157 pool and C pool sizes (Luo and Reynolds, 1999).

158 The soil water dynamics submodel has ten soil layers and simulates the dynamics of soil
159 water content based on precipitation, evaporation, transpiration and runoff. Evaporation is
160 determined by water content of the first soil layer and evaporative demand of the atmosphere.
161 Transpiration is regulated by stomatal conductance and soil water content of layers where roots
162 are present. When precipitation exceeds water recharge to soil water holding capacity, runoff
163 occurs. In this study, a soil moisture scalar, ω , is the most important parameter because the

164 reduction in precipitation directly affects soil water content and thus the soil moisture scalar. In
165 TECO, relative soil water content is defined as $\omega = (W_{\text{soil}} - W_{\text{min}}) / (W_{\text{max}} - W_{\text{min}})$ where W_{max} is soil
166 water holding capacity, W_{min} is the permanent wilting point and W_{soil} is soil water content.
167 Photosynthesis and plant growth rate are reduced whenever ω is less than 0.3.

168

169 **2.2.2 Study sites**

170 The sites selected for the modeling analysis are the Konza Prairie Biological Station (Konza), the
171 Hays Agricultural Research Center (Hays), the High Plains Grasslands Research Center
172 (Cheyenne), and the Sevilleta National Wildlife Refuge (Sevilleta). The four grasslands are
173 distributed along mean annual temperature (MAT) and mean annual precipitation (MAP)
174 gradients (Table 1). Cheyenne has the lowest mean annual temperature among the four sites
175 (Table 1). Sevilleta has much coarser soil texture than the other three grasslands.

176

177 **2.2.3 Modeling scenarios**

178 The objective of this experimental simulation was to use the long-term records of rainfall to
179 model extreme drought effects on ecosystem C dynamics. Therefore, the long-term records of
180 daily rainfall data were collected from weather stations closest to each grassland. The periods of
181 rainfall data were 1982-2010 for Konza, 1949-2010 for Hays and Sevilleta and 1949-2011 for
182 Cheyenne. The four meteorological variables (solar radiation, air temperature, soil temperature,
183 and relative humidity) used to drive the model were from year 2007 for Konza, Cheyenne, and
184 Sevilleta, and from year 2006 for Hays, repeated for each rainfall year. In order to simulate the
185 effects of extreme drought, the annual rainfall amount was reduced to 33% of ambient rainfall by
186 two approaches. One was to reduce each rainfall event size (ESR) by 67% of ambient rainfall

187 (AMB), and the other was to reduce rainfall event number (REN) to achieve the same 67%
188 reduction in annual rainfall as ESR. The REN treatment resulted in intermittent periods with no
189 rain events and thus increased precipitation variability compared with ESR treatment. These two
190 treatments allowed us to explore the differential effects of drought and increased rainfall
191 variability on ecosystem C dynamics in different grassland ecosystems along the MAT and MAP
192 gradients. The selection of 67% rainfall reduction in the model was based on analysis of long-
193 term rainfall records in central US grasslands. Multi-year drought similar to 67% rainfall
194 reduction occurred but only for 4-6 times in a 70-year record for semi-arid Colorado and 108-
195 year record for mesic Kansas (data not shown).

196

197 **2.2.4 Statistical analysis**

198 The linear regressions were conducted in SigmaPlot version 12. A student's t-test for the slope
199 difference between ambient condition and rainfall reduction treatments was conducted in SAS
200 software (SAS Institute Inc., Cary, NC, USA). A multiple regression between relative reduction
201 in Rh (dependent variable) and relative reduction in soil water content (SWC), NPP and soil C
202 content (independent variables) was performed to assess the relative contribution to drought-
203 induced reduction in Rh from each of the three factors. The regression model is

204 $\Delta Rh = a * \Delta SWC + b * \Delta NPP + c * \Delta Soil\ C + \epsilon$. The relative contributions are calculated as $a * \Delta SWC /$
205 $\Delta Rh * 100\%$, $b * \Delta NPP / \Delta Rh * 100\%$ and $c * \Delta Soil\ C / \Delta Rh * 100\%$.

206

207 **3 Results**

208 **3.1 Model validation**

209 The TECO model was driven by meteorological data from eddy flux towers for Konza tallgrass
210 prairie and Sevilleta desert grassland and from meteorological stations for the Hays and

211 Cheyenne mixed-grass prairie sites. Meteorological data include hourly solar radiation, air
212 temperature, soil temperature, precipitation and relative humidity from 2007 - 2010. For Hays,
213 meteorological data in 2006 were used, instead of 2007 due to its incomplete record. The model
214 was validated against daily net ecosystem CO₂ exchange (NEE) from eddy flux towers during
215 2007 -2010 at Konza and Sevilleta (Fig. 1), along with biometric data including ANPP and soil
216 respiration measured at these grasslands (Table 2). For all the variables, the modeled results were
217 in good agreement with observational data (Fig. 1 and Table 2).

218

219 **3.2 Differential drought effects on production and respiration and mechanisms: Literature** 220 **synthesis**

221 We synthesized results from 39 studies that included grasslands, deciduous broad-leaf forests,
222 evergreen needle-leaf forests, woody savanna and shrubland (Table S1). Eleven out of the 39
223 study sites experienced extreme drought (i.e., >40% below long-term average rainfall), 10 sites
224 experienced moderate drought and 18 sites were subject to minor drought. GPP was more
225 sensitive to drought than ER under extreme and moderate drought (Fig. 2a). Minor drought had
226 no differential impacts on GPP or ER. Drought had greater impact on GPP than ER in grassland
227 ecosystems, whereas in forest and woody savannah ecosystem drought did not have differential
228 impact (Fig. 2b).

229 For the five study sites with data available, seasonal drought in rainforest had only a
230 limited impact on GPP (Table 3) likely because the tree root systems had access to an adequate
231 water supply in deep soil layers. Respiration, especially heterotrophic respiration was reduced
232 due to drying of the surface soil. As a consequence, ecosystem carbon uptake actually increased
233 under seasonal drought in tropical rainforests.

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3.3 Modeled drought effect on ecosystem C variables

Both extreme drought treatments decreased annual NPP, heterotrophic respiration (Rh), NEE and soil C content with similar patterns over modeled years in each of the four grasslands (Fig. 3 and Fig. S1). The relative reduction in NPP was consistently greater than in Rh in all the grassland sites, but the difference diminished over time due to continued decreases in Rh with drought (Fig. 3a-h). Annual GPP and ER showed similar drought responses to annual NPP and Rh, respectively (Fig. S2). However, in order to reveal directional change in Rh, we used annual NPP and Rh in the model analysis. The differential responses of NPP and Rh to drought caused NEE to increase (more ecosystem CO₂ release), but the drought-induced change in NEE decreased over time (Fig. 3i-l). Drought-induced reduction in soil C content also increased over time, the same as Rh in all the study sites (Fig. 3m-p).

Annual NPP, Rh, NEE and soil C content responded differently to the two different drought types (Fig. S1, Fig. 3 and Table S2). In the tallgrass prairie and the Hays mixed-grass prairie, annual NPP, Rh, and soil C content decreased more under ESR than under REN, whereas annual NPP, Rh, and soil C content decreased less under ESR than under REN in the Cheyenne mixed-grass prairie and the desert grassland (Sevilleta). Differential responses of NEE to the two drought types were contingent upon year. Overall, Sevilleta had the greatest inter-annual variability (23%, 19%, and 29% average coefficient of variation over the two rainfall treatments) whereas the mixed grass site near Cheyenne had the lowest inter-annual variability (10%, 12%, and 17% average coefficient of variation over the two rainfall treatments) for relative reductions in NPP, Rh, and soil C, respectively with drought.

257 **3.4 Controls on annual C fluxes and the long-term impacts of drought**

258 Annual NPP increased with increasing rainfall amounts for all the grasslands under each of the
259 three rainfall scenarios (ambient, ESR and REN) (Fig. 4a-d). The slopes of change in NPP were
260 greater under the drought scenarios than that under ambient conditions (Table S3). Annual NEE
261 decreased with rainfall (Fig. 4i-l). The slopes were negative and smaller under drought
262 treatments than under ambient condition (Table S3). Annual Rh was not related to rainfall under
263 drought scenarios, but a positive linear relationship with rainfall was noted under ambient
264 conditions for all grasslands (Fig. 4e-h). The interannual variation in the relative reduction in
265 NPP negatively correlated with annual rainfall amount in all grassland sites except for Cheyenne
266 (Fig. 5) and the relative reduction in Rh was positively correlated with drought-induced relative
267 reductions in soil C content (Fig. 6).

268 Contribution from reduced soil C to drought sensitivity of Rh increased over time and
269 contributions from both reduced NPP and soil water content decreased over time (Fig. 7). In
270 general, reductions in NPP and soil water content contributed more than reduction in soil C in
271 the early years, whereas their relative importance switched later on (Fig. 7) due to gradually
272 increased reduction in soil C content.

273

274 **4 Discussion**

275 Our synthesis and modeling analysis both revealed that production (GPP and NPP) was more
276 sensitive to moderate to severe drought than respiration (ER and Rh). Furthermore, this
277 differential sensitivity between production and respiration increased as drought severity
278 increased and occurred only in grassland ecosystems but not in evergreen needle-leaf and broad-
279 leaf forests or woody savannahs. In the modeling analysis, NPP was reduced more than Rh by

280 extreme drought. However, the difference between NPP and Rh (i.e., NEE) diminished over time
281 with drought over multiple years. Our findings suggest that responses of production and
282 respiration to drought differ in magnitude, occur on different timescales and are affected by
283 different mechanisms under extreme, prolonged drought. Additionally, the finding of different
284 responses to drought types indicates the diverse interactive effects on ecosystem functions
285 between rainfall variability and rainfall amount.

286

287 **4.1 General patterns of drought effects on production and respiration**

288 In the literature synthesis, GPP and ER responded differently to extreme and moderate drought,
289 but not to minor drought, which suggests that moderate to extreme drought may override other
290 confounding factors, for example site characteristics, climate conditions, and dominant plant
291 species. However, during minor drought, evidence indicates that the responses of GPP and ER
292 were largely regulated by topographic position and soil texture (Kljun et al., 2006), drought-
293 associated high summer radiation (Granier et al., 2007) and high summer temperature (Welp et
294 al., 2007), along with a lagged effect from previous soil water condition (Welp et al., 2007). A
295 broad range of ecosystems were included in the synthesis (Table S1), for example grasslands,
296 deciduous broad-leaf forests, evergreen needle-leaf forests, woody savanna and shrubland. Thus,
297 the general pattern of such differential responses is representative and robust across biomes.
298 When synthesized data were analyzed based on ecosystem types, differential responses of
299 production and respiration were not found in forest ecosystems. There are two possibly main
300 reasons. The rooting systems of forests could partially relieve drought stress on production by
301 tapping deep soil water (Kerhoulas et al., 2013) and secondly, most of the forest ecosystems only
302 experienced moderate or minor drought in the synthesized studies. On the other hand, most of

303 the grassland ecosystems went through extreme drought and do not have deep rooting systems,
304 together resulting in the differential responses.

305 In contrast to the general pattern, however, in rainforest ecosystems where dry seasons
306 occur annually, seasonal drought had limited effects on GPP due to adequate water supply from
307 deep soil layers and hydraulic redistribution by deep roots. Therefore, rainforest GPP is generally
308 controlled more by factors such as solar radiation (Bonafant et al., 2008) rather than precipitation.
309 Indeed, previous modeling studies that included deep water supply and hydraulic redistribution
310 closely captured the seasonal drought effects in rain forest (Baker et al., 2008). Even though trees
311 in other ecosystems were also able to tap deep soil water (e.g., Kerhoulas et al., 2013), GPP was
312 still reduced due to drought-increased vapor pressure deficit which causes leaf stomata to
313 partially close (Kolb et al., 2013).

314

315 **4.2 Mechanisms underlying differential response of production and respiration to drought**

316 In agreement with the synthesis results, the modeling analysis revealed the general pattern that
317 production (GPP and NPP) was more drought sensitive than respiration (ER and Rh). The
318 underlying mechanisms were explored in the model analysis of four grasslands over a rainfall
319 gradient ranging from 240 to 860 mm. The greater sensitivity of modeled NPP to extreme
320 drought that we observed (Fig. 3) at all four sites was due to different controls of the two
321 ecosystem C variables. In grassland ecosystems, production generally increases linearly or
322 asymptotically with rainfall amount (e.g., Fig. 4; Sala et al., 1988; Huxman et al., 2004).
323 Therefore, in the extreme drought treatments NPP declined almost linearly with precipitation
324 amount. However, heterotrophic respiration, which is the mineralization of litter and soil C, is a
325 C pool-controlled ecological process that is often regulated by soil temperature over the long

326 term in addition to soil water content and substrate availability in the short term (Luo and Zhou,
327 2006, Vargas et al., 2010). Therefore, drought-induced reductions in NPP, soil water content and
328 soil C content all contributed to the reduction in Rh. Responses of NPP and soil water content
329 were prompt and contributed significantly to reduced Rh in the early years, especially in the most
330 mesic site. However, their contributions generally decreased over time due to increased relative
331 importance of reduction in soil C content. As a consequence, Rh was less impacted than NPP in
332 the short-term and the difference gradually disappears over time. Even though reduction in soil C
333 content is relative smaller to short-term drought than NPP and soil water content, its smaller
334 reduction played more important role than NPP and soil water content due to its high correlation
335 with Rh, especially in the arid sites.

336 The model analysis also showed that the reduction in Rh increased during long-term
337 drought due to diminishment of soil C pool size. The decrease in the soil C pool could be caused
338 by drought-reduced NPP, the primary source of soil C. To our knowledge, we are not aware of
339 any empirical studies that reported long-term effects of drought on soil C and Rh. However,
340 space-for-time studies provide indirect evidence regarding ecosystem C dynamics under long-
341 term climatic changes (Luo et al., 2011). For example, soil C declined linearly with decreasing
342 precipitation in observations along precipitation gradients (Anderson et al., 2011; Talmon et al.,
343 2011), which indirectly supports model results indicating a long-term drought-induced decrease
344 in soil C content. This long-term decline in soil C content could cause the difference between the
345 drought sensitivities of production and respiration to diminish gradually over time. Due to these
346 differential responses over longer timescales, our modeling results showed that grassland
347 ecosystems all released CO₂ to the atmosphere during drought, but the amount of released CO₂
348 decreased over time as soil C pools declined. The model results, however, would benefit from

349 long-term field experiments to provide direct support for these results. This exploration of
350 ecosystem sensitivity dynamics over the long term is critical for global change studies because
351 many ecological responses are strongly regulated by slow processes (Luo et al., 2011).

352 Our model results also showed that Sevilleta and Cheyenne had the largest and least
353 inter-annual variation, respectively, in the relative reduction of NPP and Rh. Soil texture has
354 long been known to affect plant productivity through the inverse soil texture effect (Noy-Meir,
355 1973) and has the potential to interact with rainfall regimes to mediate the impacts of drought
356 (Weng and Luo, 2008). The much larger inter-annual variability in relative reduction in NPP and
357 Rh in Sevilleta could be explained by coarse-textured soils because lower average water
358 availability can amplify drought effects (Paruelo et al., 1999). The low variability and lack of
359 correlation between rainfall and relative reduction in NPP at Cheyenne may have occurred
360 because the lower average temperatures for this site relative to the other three (Table 1) resulted
361 in less evaporation, and thus increased available water for plants and constrained the inter-annual
362 variation in sensitivity to drought. These results emphasize the need for multi-site long-term
363 drought experiments, because inter-annual variation in precipitation as well as lagged effects
364 from soil water storage likely play important roles in regulating ecosystem responses to climate
365 extremes (Granier et al., 2007).

366 The mechanisms associated with drought responses in forest ecosystems are likely to be
367 similar to those in grasslands. The primary responses of forests to drought are to reduce
368 productivity and respiration due to water deficit (Dale et al., 2001) and the responses of
369 production and respiration could be different. However, it is also likely that the mechanisms
370 could be more complicated in forest ecosystems than in grasslands and consequently have
371 different long-term effects. For example, deep rooting systems in forest ecosystems could buffer

372 drought effect on production in forest ecosystems; drought associated increase in solar radiation
373 might increase production as we found in rainforest; hydraulic lifting by tree roots could also
374 alleviate drought effect on C processes. As we found out in our synthesis, drought had similar
375 effects on both production and respiration in forest ecosystems (Fig. 2b). As a consequence, the
376 long-term response pattern may be different from that in the grassland ecosystems. Therefore, it
377 is critical to include above possible mechanisms when simulating long term drought effect in
378 forest ecosystem.

379

380 **4.3 Drought attributes and differential responses of production and respiration**

381 In our modeling analyses, total annual rainfall in the two reduced rainfall treatments was the
382 same. Drought imposed by reducing every event (ESR treatment) was characterized by lower
383 rainfall event size (1/3 of ambient rainfall), but ambient rainfall frequency. In comparison, the
384 REN treatment was characterized by ambient rainfall event size but lower frequency, and longer
385 dry intervals between rain events. Responses of NPP and Rh to these treatments were contingent
386 on grassland type, with greater reductions in NPP and Rh when drought was caused by every
387 rain event becoming smaller (ESR scenario) at the two most mesic and productive grasslands
388 (Konza and Hays) However, REN also caused in reduction in both NPP and Rh. Knapp et al.
389 (2002) also observed that lower frequency in rainfall events without changing total rainfall in a
390 mesic tallgrass prairie resulted in less production than ambient rainfall frequency. However, if
391 annual precipitation amount was low (1/3 of ambient rainfall in our study), the larger rainfall
392 event size under REN relative to ESR could lead to higher soil water content and consequently
393 higher production (Fig. S1a and b) in mesic grasslands. More water was stored in deep soil layers
394 under ambient rainfall event size compared to lower rainfall event size in ESR, which decreased

395 evaporative loss to the atmosphere and increased water availability to plants. Lower rainfall
396 frequency (i.e. REN treatment), however, led to lower NPP in xeric grasslands (Fig. S1c and d).
397 Frequent small rainfall events (the ESR treatment) can potentially alleviate chronic water stress,
398 whereas the longer dry period under REN inhibited early leaf and root development and
399 consequently decreased production. In addition, different levels of rainfall frequency could affect
400 its effect size (Heisler-White et al., 2009). Responses of Rh to the two drought types are
401 consistent with those of NPP, indicating NPP controls the responses of Rh to different drought
402 types.

403

404 **4.4 Implications for future experimental studies**

405 Our findings have several important implications for field experiments. First, reported
406 observations and manipulative climate change studies are often short term. The snapshot of
407 observed responses, therefore, may not be representative of long-term response, especially when
408 slow ecological processes are involved. Second, many manipulated drought experiments only
409 decrease event sizes. Our results showed that reduced rainfall event number had differential
410 effects on ecological processes than simply decreasing the size of each rain event. Future
411 experiments should impose drought through different patterns of rainfall size, different levels of
412 frequency and intensity. Third, other components of ecosystem C processes should be assessed
413 in global change experiments in addition to production. Different ecosystem C variables are
414 likely to have different response patterns to imposed perturbation. In order to provide
415 information on positive or negative feedbacks of terrestrial biomes to climate change,
416 measurements of both production and respiration are needed.

417

418 **4.5 Model limitations**

419 Ecosystem carbon models have often been used as a tool to investigate effects of global changing
420 on ecosystem carbon cycling (Norby and Luo, 2004; Parton et al., 2007; Luo et al., 2008;
421 Schwalm et al., 2010b; Grant et al., 2011). At present, most of the models, however, do not
422 represent photosynthetic and respiratory acclimation (Smith and Dukes, 2013), mortality
423 (McDowell et al., 2013), and species shift (Sebastia et al., 2008) well yet due to limited
424 understanding. As a consequence, their regulations may not be well captured in the modeling
425 results when models are used to simulate long-term effects of climate changing factors on
426 ecosystems. In this study, we used data from space-for-time studies to support our model results.
427 For example, soil C declined linearly with decreasing precipitation in observations along
428 precipitation gradients (Anderson et al., 2011; Talmon et al., 2011), which is consistent with our
429 modeling results indicating a long-term drought-induced decrease in soil C content. This
430 consistency between model and empirical studies suggest that the responses of ecosystem
431 variables to extreme climatic changes are unlikely to be overridden by biotic adaptation
432 (Anderson et al. 2011). Rather, the extent of the responses might be attenuated or exacerbated
433 (Smith 2011, Reichstein et al., 2013). Nonetheless, further research is needed to incorporate
434 acclimation, adaptation and vegetation change into ecosystem models to improve ecological
435 forecasting.

436 Vegetation mortality due to carbon starvation or hydraulic failure or both (McDowell et
437 al., 2008) is likely to occur if the drought is severe enough and can therefore have legacy effect
438 on most aspects of ecosystem carbon cycling (Liu et al., 2011). It is difficult for ecosystem
439 models to accurately capture plant mortality due to the lack of thorough understanding on the
440 mechanisms (Xu et al., 2013, McDowell et al., 2013, Reichstein et al., 2013). Mortality in

441 grasslands differs from that in forest ecosystems. In a forest ecosystem, when large area of
442 mortality occurs, the whole ecosystem would have to start over from secondary succession.
443 However, grasslands are characterized by the high recovery potential of plant growth and they
444 would recover to their original states in a very short time and had less impact on carbon cycling
445 than forest ecosystems (Reichstein et al., 2013).

446 Another limitation in our study is possible model bias due to only one ecosystem model
447 was used. A multiple-model inter-comparisons (MI) would be nice to test the robustness of our
448 main conclusion that extreme drought had differential effect on production and respiration in
449 grassland ecosystems. However, it is not our focus of this study. Nonetheless, findings from
450 previous multiple model analysis can provide evidence for the robustness of our conclusion. For
451 example, using four ecosystem C models, Luo et al. (2008) explored potential individual and
452 interactive effects of climate warming, altered precipitation amount and elevated CO₂
453 concentration across a broad range of biomes. They found that half precipitation reduced net
454 primary production more than heterotrophic respiration, and as a result decreased net ecosystem
455 production.

456

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462

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703

704 **Table 1** Key climate, plant, and soil characteristics of four grassland ecosystem types located
 705 within the US America Great Plains

	Konza	Hays	Cheyenne	Sevilleta
Latitude	39°05'N	38°53'N	41°11'N	34°20'N
Longitude	96°35'W	99°23'W	104°54'W	106°43'W
Grassland Type	Tallgrass	Southern mixed-grass	Northern mixed-grass	Desert/shortgrass
MAT (°C)	12.9	12.0	7.6	13.3
MAP (mm)	860	577	384	242
Soil Texture	Silty Clay Loam ¹	Silty Clay Loam ¹	Fine-loamy ²	Sandy Loam ³

1: Heislter-White et al., 2009; 2: Carrillo et al., 2011; 3: Muldavin et al., 2008;

706

707 **Table 2** Comparisons between modeled and measured aboveground net primary production
 708 (ANPP) and soil respiration (Rs).

	ANPP(g m ⁻²)		Monsoon Rs* (g C m ⁻²)	
	Observed	Modeled	Observed	Modeled
Konza	461 (134) ^a	488 (38)	-	-
Hays	300(-) ^b	342 (46)	-	-
Cheyenne	130 (25) ^c	163 (15)	-	-
Sevilleta	140 (3) ^d	165 (2)	63 (3) ^e	81 (8)

709 a: mean ANPP from 1984-1998 (Knapp et al., 2006); b: Long term mean ANPP (Heisler-White
 710 et al., 2009); c: PHACE measurement (Personal communication); d: average in 2007 and 2008
 711 (Thomey et al., 2011); e: average in 2007 and 2008 (Vargas et al., 2012). Values in the
 712 parentheses are standard errors across years. ‘-’ mean that values were not available. ‘*’
 713 monsoon Rs is cumulative soil respiration during monsoon season from July through September
 714 in Sevilleta desert grassland.

715

716 **Table 3** Synthesis of published studies in differential responses of GPP and ER to extreme seasonal drought in tropical rainforest

Site	Biome type	Results	Mechanisms	Reference	Note
Tapajos km83, Brazil	Amazonian rain forest	Seasonal drought did not impact GPP, but decreased ER	Deep rooting depth buffered drought stress on GPP	Saleska et al., 2003; Goulden et al., 2004	Eddy flux
Tapajos km67, Brazil	Amazonian rain forest	Seasonal drought reduced GPP less than ER	Adequate water supply for photosynthesis during dry season	Hutyra et al., 2007	Eddy flux
French Guiana, South America	Neotropical rainforest	Seasonal drought increased GPP, but reduced ER	Drought-associated higher incident radiation increased GPP	Bonal et al., 2008	Eddy flux
Sardinilla, Panama	Plantation	Seasonal drought reduced both GPP and ER by similar amount	Deep rooting depth buffered drought stress on GPP	Wolf et al., 2011	Eddy flux
Xishuangbanna, China	Tropical rain forest	Seasonal drought reduced less on GPP than on ER	Deep rooting depth alleviated drought stress on GPP	Zhang et al., 2010	Eddy flux

717

718 **Figure legends**

719 **Figure 1** Comparisons between observed daily net ecosystem CO₂ exchange (NEE) from eddy
720 flux data and modeled daily NEE in Konza tallgrass prairie and Sevilleta desert grassland from
721 2007 to 2010. Open black circles represent observed daily NEE. Black solid lines represent
722 modeled daily NEE.

723 **Figure 2** Synthesized published observational and experimental results on sensitivity of gross
724 primary production (GPP) and ecosystem respiration (ER) to drought severity (a) and to drought
725 in different ecosystem types (b). The ecosystems were divided into grassland, evergreen needle-
726 leaf forest (ENF), broad-leaf forest (BF) and woody savannahs (WS). One open shrubland, one
727 oak woodland and one pine woodland were not included into the data analysis due to limited
728 sample size. Numbers represent the number of studies included, ** represents significant ($P <$
729 0.05) difference and * represents marginally significant difference ($P < 0.1$).

730 **Figure 3** Drought-induced reductions in net primary production (NPP), heterotrophic respiration
731 (Rh), NEE and soil C content along modeled years in four North American grasslands (Konza: a,
732 e, i and m; Hays: b, f, j and n; Cheyenne: c, g, k and o; Sevilleta: d, h, l and p). ESR is rainfall
733 event size reduction and REN is reduced rainfall event number. Figures a-d show reduction in
734 NPP and Rh under ESR. Figures e-h show reduction in NPP and Rh under REN. Figures 3i- l
735 show reduction in NEE and Figures m- p showed reduction in soil C content.

736 **Figure 4** Relationships between annual precipitation and annual C fluxes under the three rainfall
737 scenarios (AMB: ambient rainfall; ESR: rainfall event size reduction; REN: reduced event
738 number) in four North American grasslands (Konza: a, e and i; Hays: b, f and j; Cheyenne: c, g
739 and k; Sevilleta: d, h and l). Figures a-d show relationship between precipitation and NPP.

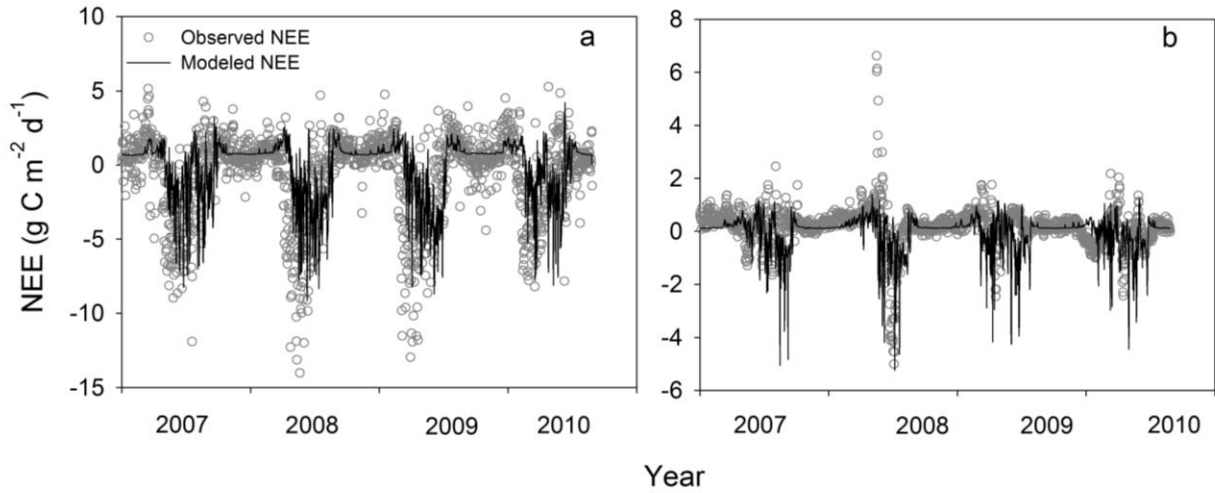
740 Figures e-h show relationship between precipitation and Rh. Figures i-l show relationship
741 between precipitation and NEE.

742 **Figure 5** Relationships between annual precipitation and drought-induced relative reduction
743 (calculated as absolute change caused by drought divided by NPP under the ambient condition)
744 in NPP in four North American grasslands (Konza: a; Hays: b; Cheyenne: c; Sevilleta: d). Open
745 circles represent ESR treatment. Solid circles represent REN treatment.

746 **Figure 6** Relationships between drought-induced relative reduction (calculated as absolute
747 change caused by drought divided by soil C under the ambient condition) in soil C content and
748 relative reduction (calculated as absolute change caused by drought divided by Rh under the
749 ambient condition) in Rh in four North American grasslands (Konza: a; Hays: b; Cheyenne: c;
750 Sevilleta: d). Open circles represent ESR treatment. Solid circles represent REN treatment.

751 **Figure 7** Relative contributions to drought sensitivity of Rh from reductions in soil C content,
752 NPP and soil water content under both rainfall reduction treatments in four North American
753 grasslands (Konza: a and b; Hays: c and d; Cheyenne: e and f; Sevilleta: g and h). Solid line
754 represents contribution from reduction in soil C, dotted line represents contribution from
755 reduction in NPP and dashed line represents contribution from reduction in soil water content.

756



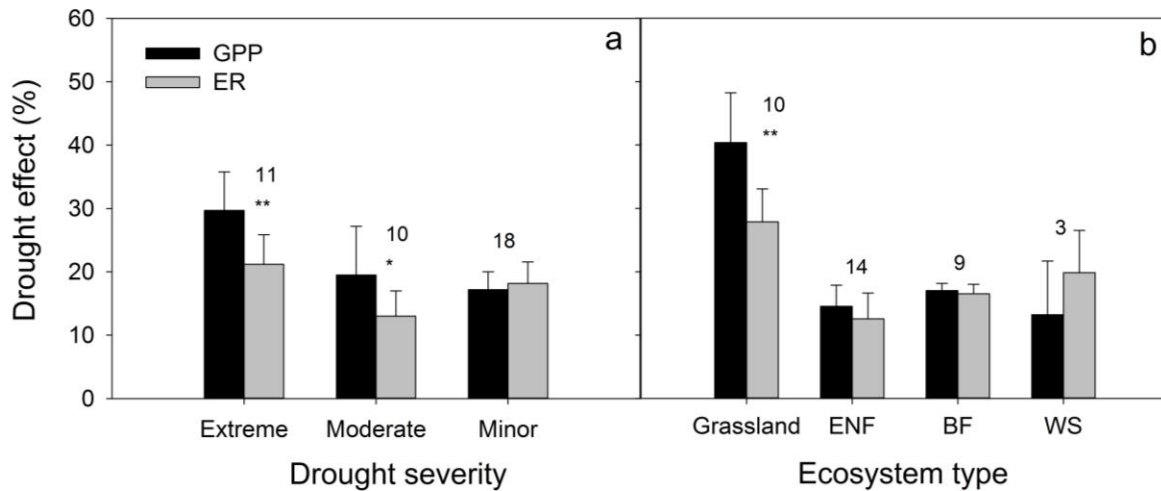
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758

759 **Fig. 1** Comparisons between observed daily NEE from eddy flux data and modeled daily NEE in

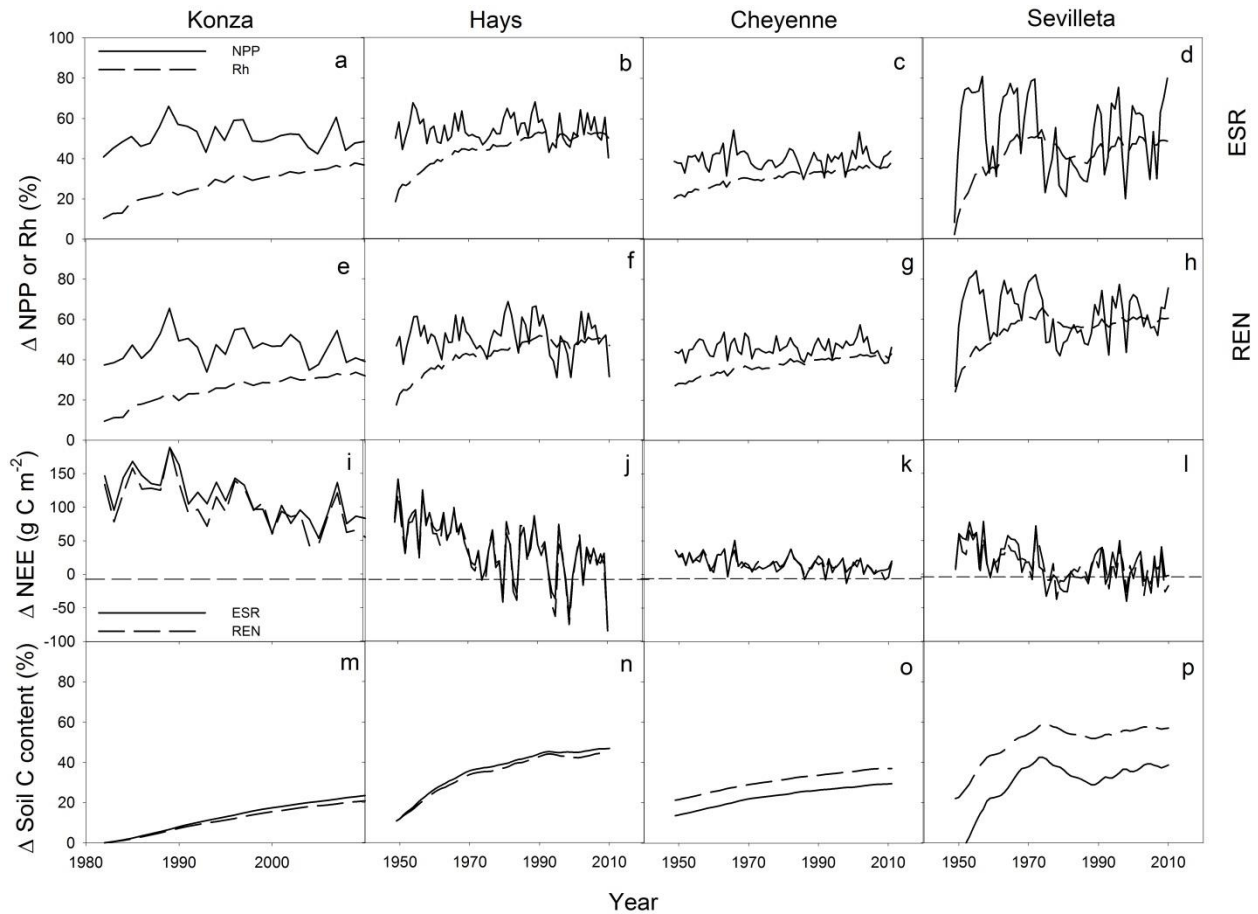
760 Konza tallgrass prairie (a) and Sevilleta desert grassland (b) from 2007 to 2010. Overall, the

761 TECO model can reproduce observed NEE.



762

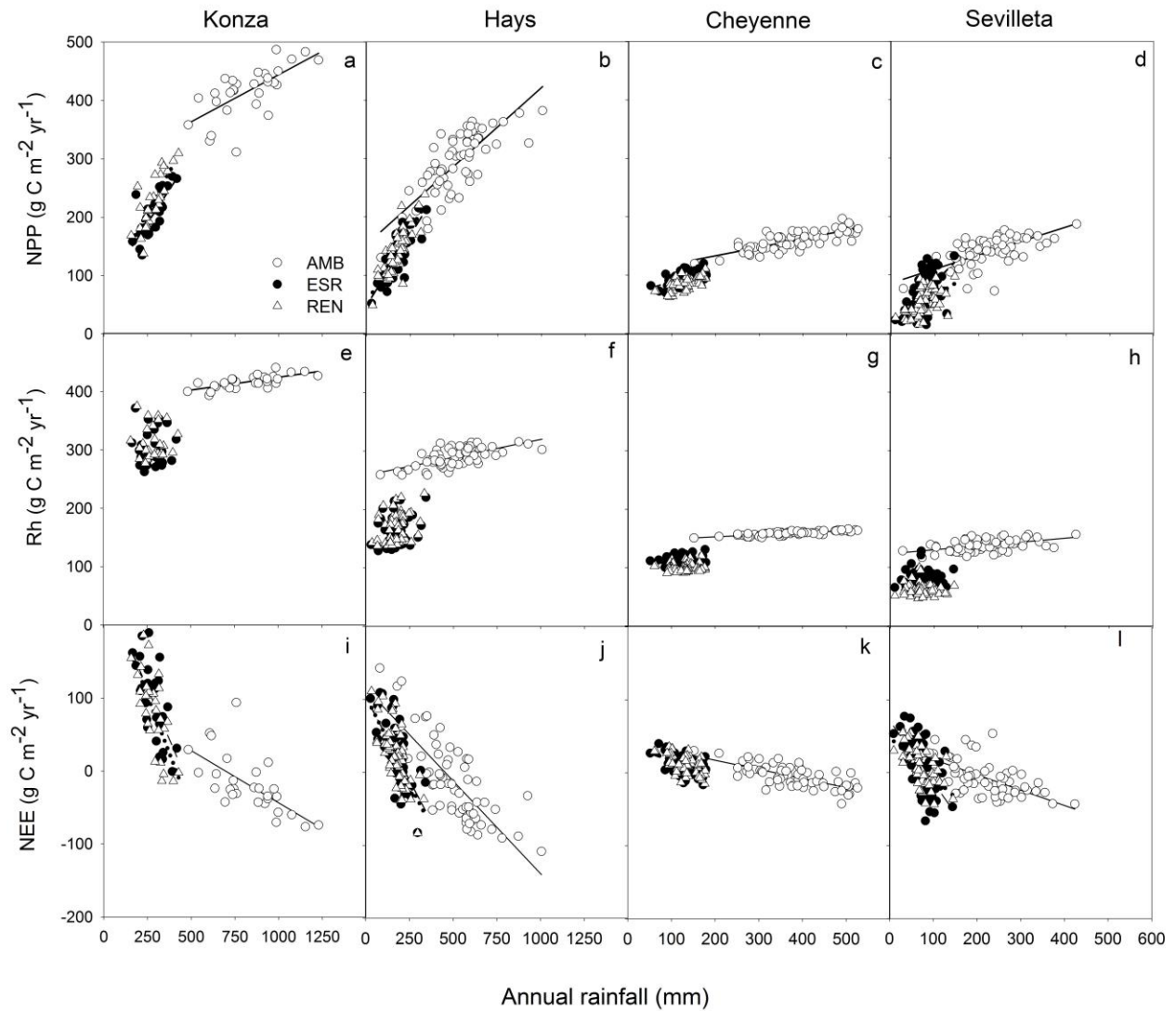
763 **Fig. 2** Synthesized published observational and experimental results on sensitivity of gross
 764 primary production (GPP) and ecosystem respiration (ER) to drought severity (a) and to drought
 765 in different ecosystem types (b). The ecosystems were divided into grassland, evergreen needle-
 766 leaf forest (ENF), broad-leaf forest (BF) and woody savannahs (WS). One open shrubland, one
 767 oak woodland and one pine woodland were not included into the data analysis due to limited
 768 sample size. Numbers represent the number of studies included, ** represents significant ($P <$
 769 0.05) difference and * represents marginally significant difference ($P < 0.1$).



770

771 **Fig. 3** Drought-induced reductions in modeled annual NPP, Rh, NEE and soil C content over
 772 time in four North American grasslands (Konza: a, e, i and m; Hays: b, f, j and n; Cheyenne: c, g,
 773 k and o; Sevilleta: d, h, l and p). Absolute reduction in NEE was calculated as the difference in
 774 NEE between drought treatments and ambient condition. Relative reduction in NPP, Rh and soil
 775 C content were presented and calculated as absolute reduction divided by ambient condition.
 776 Differential effects of long-term droughts diminish over time as soil C content decreases.

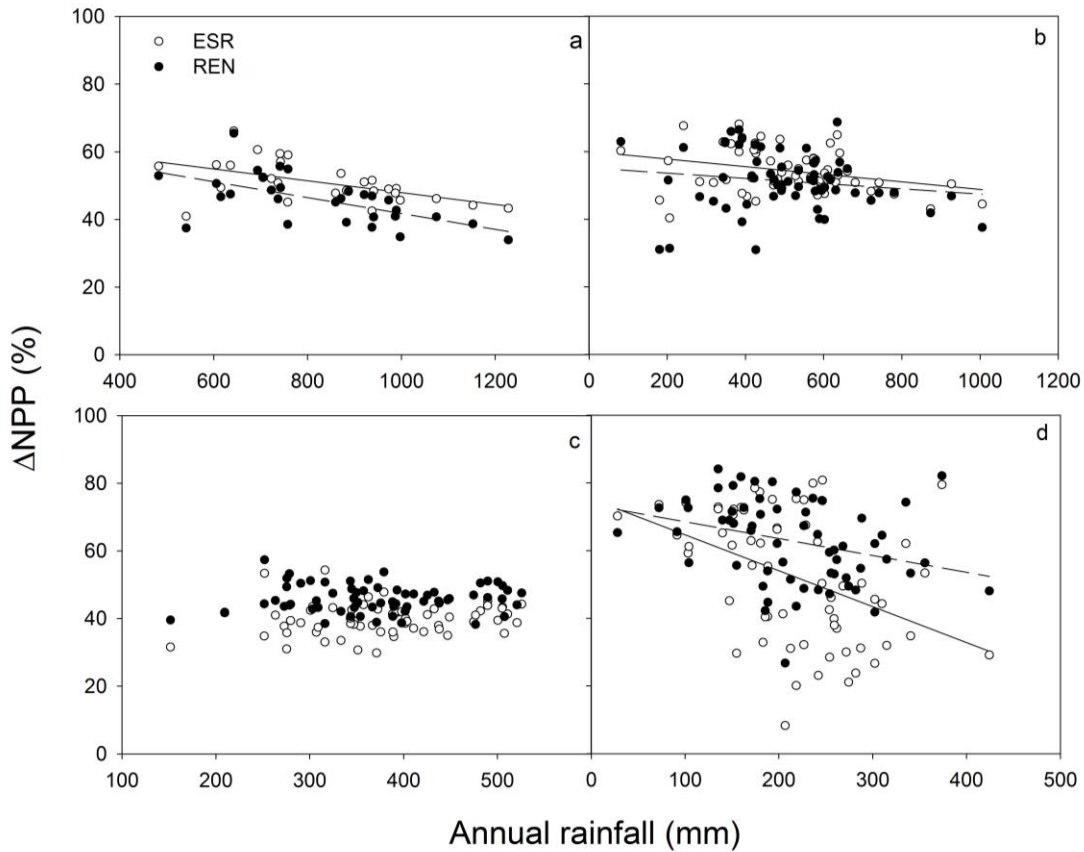
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779 **Fig. 4** Relationships between annual rainfall and annual C fluxes under the three rainfall
 780 scenarios (AMB: ambient rainfall; ESR: rainfall event size reduction; REN: reduced event
 781 number) in four North American grasslands (Konza: a, e and i; Hays: b, f and j; Cheyenne: c, g
 782 and k; Sevilleta: d, h and l). Annual rainfall determined grassland ecosystem carbon fluxes.

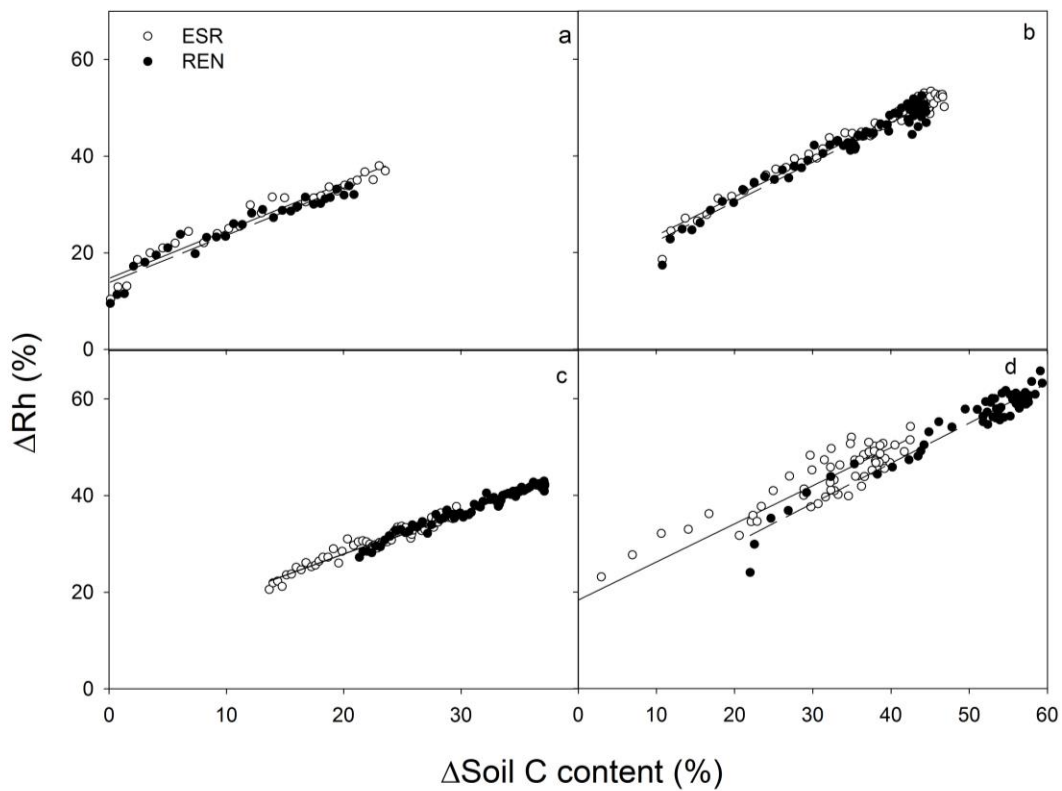
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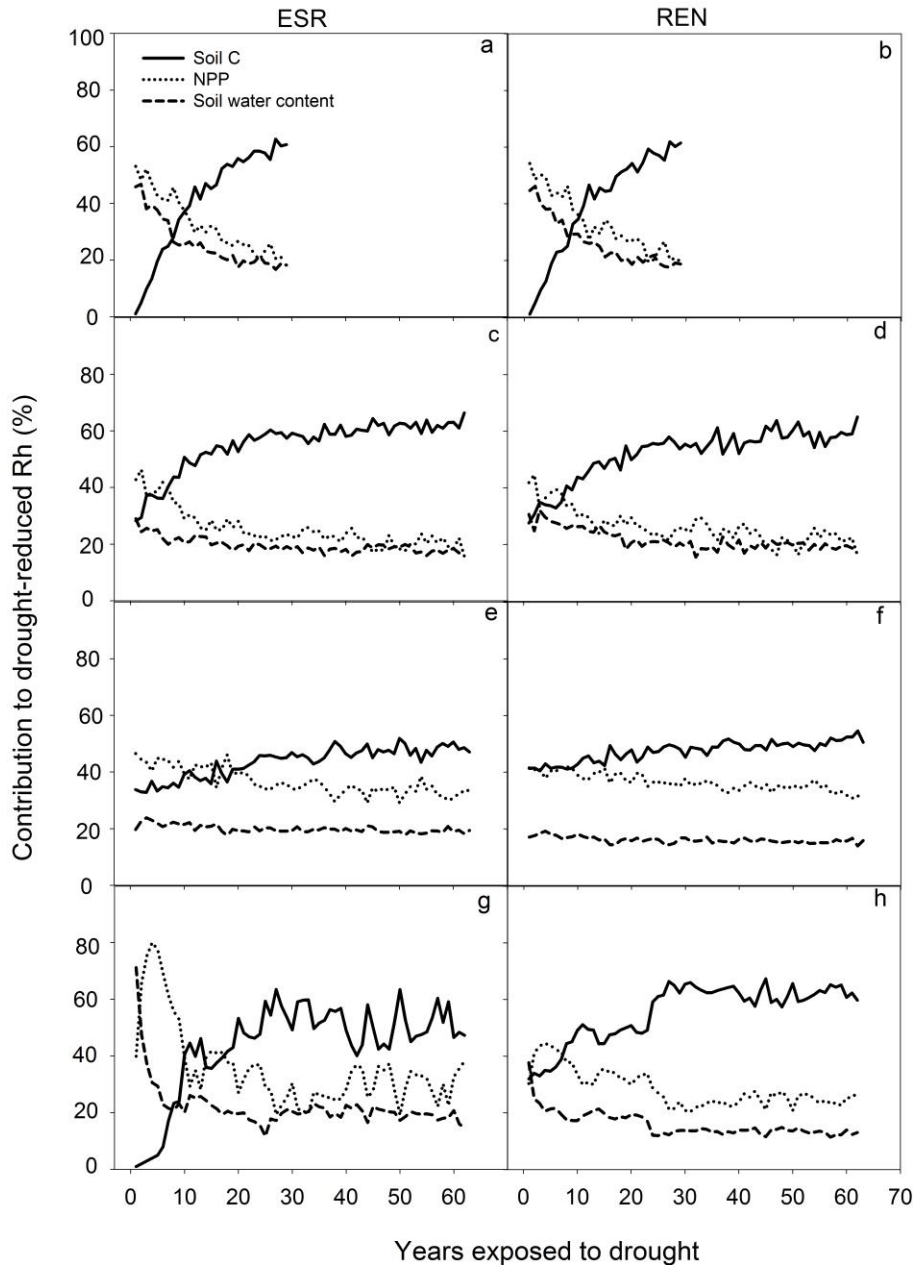
785 **Fig. 5** Relationships between annual rainfall and drought-induced relative reduction in NPP in
 786 four North American grasslands (Konza: a; Hays: b; Cheyenne: c; Sevilleta: d). Open circles
 787 represent ESR treatment. Solid circles represent REN treatment. Variation in drought-induced
 788 relative reduction in NPP was significantly related to annual precipitation for all but the northern
 789 mixed grass site (Cheyenne).

790



791

792 **Fig. 6** Relationships between drought-induced relative reduction in soil C content and relative
 793 reduction in Rh in four North American grasslands (Konza: a; Hays: b; Cheyenne: c; Sevilleta:
 794 d). Open circles represent ESR treatment. Solid circles represent REN treatment. Drought-
 795 induced reductions in soil C were significantly and positively related to Rh reduction.



796

797 **Fig. 7** Relative contributions to drought sensitivity of Rh from reductions in soil C content, NPP
 798 and soil water content under both rainfall reduction treatments in four North American
 799 grasslands (Konza: a and b; Hays: c and d; Cheyenne: e and f; Sevilleta: g and h). Solid line
 800 represents contribution from reduction in soil C, dotted line represents contribution from
 801 reduction in NPP and dashed line represents contribution from reduction in soil water content.

802 **Supporting information**

803
804 Figure S1 Drought-induced reductions in NPP and Rh along modeled years in four North
805 American grasslands (Konza: a, e, i and m; Hays: b, f, j and n; Cheyenne: c, g, k and o; Sevilleta:
806 d, h, l and p). ESR is rainfall event size reduction and REN is reduced rainfall event number.
807 Solid line represents ESR treatment and dash line represents REN treatment.

808
809 Figure S2 Drought-induced reductions in GPP and ER along modeled years in four North
810 American grasslands (Konza: a and e; Hays: b and f; Cheyenne: c and g; Sevilleta: d and h). ESR
811 is rainfall event size reduction and REN is reduced rainfall event number. Solid line represents
812 GPP and dash line represents ER.

813

814 **Table S1** Literature review of differential responses of production and respiration to drought in field observations and manipulative
 815 experiments across different biomes

816
 817

Site	Biome type	Results	Mechanisms	Reference	Note
European forests and one grassland	Pine, oak, beech, spruce, fir, juniper, and grassland	In most sites, extreme drought induced more reduction in GPP than ER except a few Mediterranean ecosystems where the drought effect was smaller for GPP than ER	Not specified	Cias et al., 2005	Eddy flux
East coast of japan	Temperate evergreen and deciduous broadleaved tree	GPP was reduced more than ER	Not specified	Kosugi et al., 2005	Eddy flux
Saskatchewan Canada	Southern boreal forests including aspen, spruce and jack pine	In aspen, first-year drought suppressed ER, but enhanced GPP whereas second- and third-year drought reduced GPP and ER with more reduction in GPP; In spruce and jack pine forests, drought did not significant affected GPP and ER	The enhanced GPP in aspen was due to warmer spring in that year; the lack of response to drought in the two coniferous forests was because of summer rainfall, low topographic position and low soil water holding capacity	Kljun et al., 2006	Eddy flux
European forests	Beech, Douglas-fir, Scots pine, Spruce, mixed coniferous	Drought inhibited GPP greater than ER	Not specified	Granier et al., 2007	Eddy flux
Hungaria	Semi-arid sandy grassland	Drought is more effective in reducing plant CO ₂ uptake than in reducing ER	Uncoupled heterotrophic respiration to photosynthesis is more resistant to drought	Nagy et al., 2007	Eddy flux
Southern Portugal	Evergreen oak woodland, grassland, and eucalyptus plantation	Severe drought affected more GPP than ER	Not specified	Pereira et al., 2007	Eddy flux

Interior Alaska, USA	Black spruce and aspen	GPP was reduced in the two forests, but ER increased	Drought-associated temperature increase might cause ER to rise	Welp et al., 2007	Eddy flux
Northwest Ohio, USA	Oak and red maple	Greater suppression of GPP than of ER by drought	Drought caused lower leaf area, lower apparent quantum yield and lower canopy conductance	Noormets et al., 2008	Eddy flux
Global network of eddy flux towers	Grassland, forest, shrubland, wetland, savannas	Overall, production is 50% more sensitive than respiration to drought, with a few exceptions	Not specified	Schwalm et al., 2010	Eddy flux
Kendall grassland, USA	Semi-desert grassland	Drought reduced more gpp than ER	Not specified	Scott et al., 2010	Eddy flux
Southern Portugal	semi-natural Mediterranean grassland	Drought reduced GPP more than ER	Not specified	Jongen et al., 2011	Eddy flux
Western North America	Grassland, evergreen needle forest (ENF), woody savannas	GPP of grassland and ENF were more sensitive to drought, whereas in woody savannas GPP was less sensitive	Not specified	Schwalm et al., 2012	Eddy flux
Inner-Mongolia, China	Arid grassland	GPP was more sensitive to seasonal drought than ER	None but suggested drought might have lasted longer for assimilation than respiration in this ecosystem	Yang and Zhou, 2013	Eddy flux
Southwestern US	Ponderosa pine and grassland	GPP was more sensitive to summer drought than ER in the forest, but less sensitive in the grassland/shrubland	Not specified	Kolb et al., 2013	Eddy flux
France	Mediterranean evergreen oak forest	Drought inhibited GPP greater than ER	Shallow soil water content was not strongly affected by drought and thus soil respiration was less affected than GPP	Misson et al., 2010	Manipulative experiment
Wyoming, USA	High Plains Grassland	GPP was more sensitive to reduced rainfall than ER	Not specified	Chimner et al., 2010	Manipulative experiments
Northern Arizona	Desert grassland, pinyon-juniper, ponderosa pine forest, mixed conifer forest	Precipitation reduction did not impact both GPP and ER	Not specified	Wu et al., 2011	Manipulative experiments
Cairngorms, Scotland	Grassland	Drought reduced more reduction in GPP than in ER	Not specified	Johnson et al., 2011	Manipulative experiment
Southern California	Coastal grassland	Imposed drought reduced GPP more than ER	Not specified	Potts et al., 2012	Manipulative experiment

818 Table S2 Results (p values) of paired-sample T test in reduction of C variable (Δ NPP, Δ Rh,
 819 Δ NEE, Δ Soil C) between the two drought types (even size reduction and reduced event number)
 820 in the four grassland sites

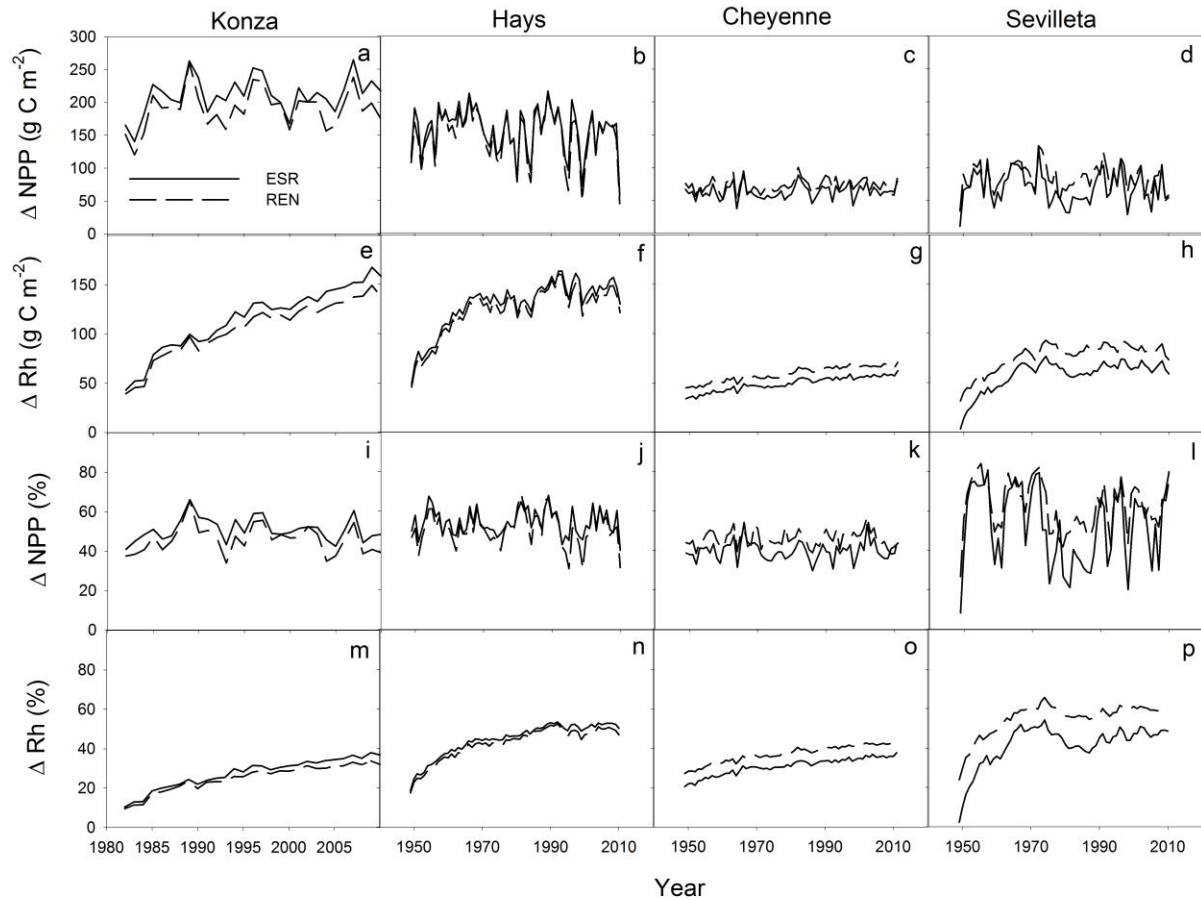
Sites	Konza	Hays	Cheyenne	Sevilleta
NPP	0	0	0	0
Rh	0	0	0	0
NEE	0	0.044	0.098	0.412
Soil C	0	0	0	0

821

822 Table S3 Slopes of the linear regression between rainfall and C variables (NPP, Rh, and NEE) in
 823 each of three rainfall scenarios, and the significance (p) in slope difference between ambient and
 824 rainfall treatments. “-” means not applicable.

Sites		Konza		Hays		Cheyenne		Sevilleta	
Rainfall scenarios		Slopes	p	Slopes	p	Slopes	p	Slopes	p
Rainfall vs. NPP	Ambient	0.16	-	0.27	-	0.15	-	0.24	-
	ESR	0.46	0.002	0.48	0.0016	0.23	0.0646	0.75	<.0001
	REN	0.55	0.0001	0.5	0.0011	0.23	0.0858	0.46	<.0001
Rainfall vs. Rh	Ambient	0.04	-	0.06	-	0.04	-	0.07	-
	ESR	-	-	-	-	-	-	-	-
	REN	-	-	-	-	-	-	-	-
Rainfall vs. NEE	Ambient	-0.14	-	-0.25	-	-0.12	-	-0.21	-
	ESR	-0.56	0.0005	-0.45	0.0076	-0.23	0.0443	-0.85	<.0001
	REN	-0.63	<.0001	-0.48	0.0028	-0.23	0.0309	-0.55	0.001

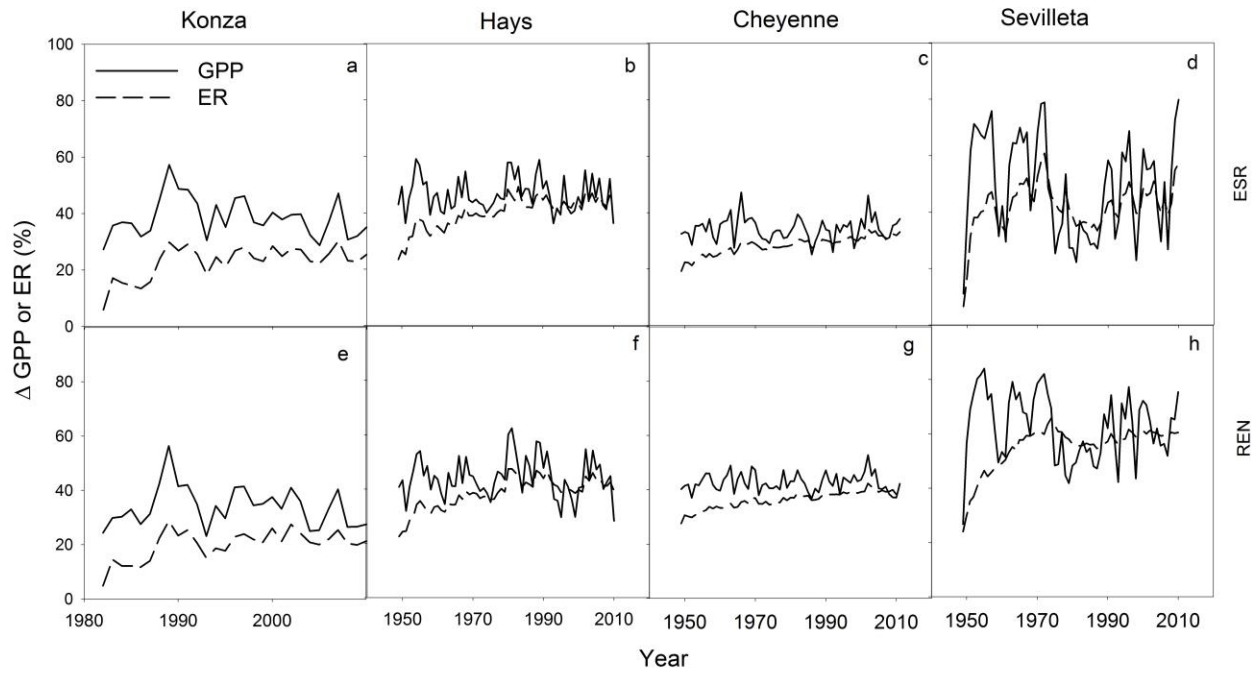
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827

828 Figure S1 Drought-induced reductions in NPP and Rh along modeled years in four North
 829 American grasslands (Konza: a, e, i and m; Hays: b, f, j and n; Cheyenne: c, g, k and o; Sevilleta:
 830 d, h, l and p). ESR is rainfall event size reduction and REN is reduced rainfall event number.
 831 Solid line represents ESR treatment and dash line represents REN treatment.

832



833

834 Figure S2 Drought-induced reductions in GPP and ER along modeled years in four North
 835 American grasslands (Konza: a and e; Hays: b and f; Cheyenne: c and g; Sevilleta: d and h). ESR
 836 is rainfall event size reduction and REN is reduced rainfall event number. Solid line represents
 837 GPP and dash line represents ER.