1   **Faster turnover of new soil carbon inputs under increased atmospheric CO_2**

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27   **Faster turnover of new soil carbon inputs under increased atmospheric CO_2**

28

29   **Abstract**

30   Rising levels of atmospheric CO_2 frequently stimulate plant inputs to soil, but the

31   consequences of these changes for soil carbon (C) dynamics are poorly understood. Plant-

32   derived inputs can accumulate in the soil and become part of the soil C pool ("new soil C"), or

33   accelerate losses of pre-existing ("old") soil C. The dynamics of the new and old pools will

34   likely differ and alter the long-term fate of soil C, but these separate pools, which can be

35   distinguished through isotopic labeling, have not been considered in past syntheses. Using

36   meta-analysis, we found that while elevated CO_2 (ranging from 550 to 800 parts per million

37   by volume) stimulates the accumulation of new soil C in the short term (< 1 year), these

38   effects do not persist in the longer term (1 - 4 years). Elevated CO_2 does not affect the

39   decomposition or the size of the old soil C pool over either temporal scale. Our results are

40   inconsistent with predictions of conventional soil C models and suggest that elevated CO_2

41   might increase turnover rates of new soil C. Because increased turnover rates of new soil C

42   limit the potential for additional soil C sequestration, the capacity of land ecosystems to slow

43   the rise in atmospheric CO_2 concentrations may be smaller than previously assumed.

44

45   **Introduction**

46   Because soils are one of the largest natural sources of the greenhouse gas CO_2 (Raich &

47   Schlesinger, 1992), they play a crucial role in determining the future trajectory of climate

48   change. Yet, the response of soil C dynamics to future atmospheric conditions remains

49   uncertain. Numerous studies have found that rising CO_2 concentrations stimulate plant growth

50   (Ainsworth & Long, 2005). If the resulting increase in soil C input increases the size of the

51   soil C pool, soils may slow the rise in atmospheric CO_2 concentrations (Thornton *et al.*,

52   2007). However, long-term changes in soil C stocks are determined by the balance between

the input of new organic matter to soil pools, and the decomposition of soil organic matter

(Hungate *et al.*, 1995). Many CO_2 enrichment experiments do not directly measure C fluxes or

the fate of recently added plant detritus vs. soil organic matter that is already present, possibly

limiting their predictive power for the response of soil C stocks to rising atmospheric CO_2

(Cardon *et al*., 2001). A recent meta-analysis used a data-model assimilation approach to

show that CO_2 enrichment increases decomposition rates of both new plant inputs and soil

organic matter (van Groenigen *et al.,* 2014). However, without separate measurements of both

these C pools, estimates of decomposition rates could in theory be affected by the structure of

the soil C model used to analyze experimental data (Georgiou *et al.,* 2015; van Groenigen *et

al.,* 2015).

The dynamics of different C pools can be assessed through isotopic labeling, in which

the isotopic composition of the totality of recently fixed C differs from pre-existing soil C

(hereafter "old soil C"). With this approach, we can determine the amount of soil C derived

from the cumulative plant inputs since labeling began (i.e., "new soil C"; Keith *et al*., 1986;

Balesdent *et al.*, 1987). A similar approach enables us to determine what fraction of total soil

CO_2 respiration is derived from decomposition of old C (Rochette *et al.*, 1999), and these

results can be combined to assess the net C storage in an ecosystem (Pendall *et al.,* 2005).

Results vary from studies that use isotopic labeling to quantify CO_2 effects on soil C

dynamics, making it difficult to infer global responses from individual experiments. A

quantitative synthesis of results across a wide range of studies can overcome this problem.

Thus, we used meta-analysis (Osenberg *et al.*, 1999) of results from 28 published studies to a)

summarize the effect of atmospheric CO_2 enrichment on new and old C stocks in mineral soil,

on soil respiration rates and soil C input rates, and to b) explore the factors that shaped the

responses to CO_2 enrichment.

Methods

Data Collection

We extracted results for soil C content and CO_2 fluxes from atmospheric CO_2 enrichment studies conducted in the field, in growth chambers, or in glass houses. For studies reporting new soil C contents, we also extracted data on soil C input proxies. We used Web of Science (Thompson Reuters) for an exhaustive search of journal articles published before June 2016, using search terms "CO_2" for article title, and "soil AND carbon" and "isotop* OR label*" for article topic. To be included in our dataset, studies had to meet several criteria:

1. Studies needed to include at least two CO_2 treatments: ambient (between 350–400 ppmV) and increased (550–800 ppmV).

2. Plants and soils needed to have distinctive isotopic composition in each of the treatments. Such differences in isotopic composition were established in one of two ways. First, experiments exploited the difference in C_3 and C_4 plants; the abundance of ^{13}C relative to ^{12}C is less in plant tissue than in atmospheric CO_2 due to isotope discrimination, with C_4 plants discriminating less than C_3 plants (Farquhar *et al*., 1989). Thus, growing C_3 plants on soil developed under C_4-vegetation (or vice versa) creates a difference in isotopic signature between plants and soil. Second, some experiments grew plants under an atmosphere with CO_2 that had a different composition from atmospheric CO_2 under natural conditions. This was achieved through ^{13}C or ^{14}C labeling of CO_2 in glass houses, growth chambers or field experiments. In all cases, the contribution of each source to the total soil C pool was calculated using an isotopic mixing model with two end members, i.e. new plant material and old soil C (Keith *et al*., 1986; Balesdent *et al.*, 1987). Using the same approach, the contribution of old soil C respiration to soil CO_2 efflux was determined as well (Rochette *et al.*, 1999). Because root respiration and CO_2 derived from new C input have a similar isotopic signature, isotopic labeling usually cannot distinguish between the contributions of these two

104   sources to soil CO_2 efflux. As such, we did not quantify CO_2 production derived from the

105   decomposition of new soil C.

106   3. Plants needed to be labeled using methods that distributed the isotope among all plant

107   parts. Therefore, we excluded studies that applied a single pulse of ^{14}C-CO_2 or ^{13}C-CO_2 to

108   plants, because this approach results in a distribution of labeled C that does not correspond to

109   the distribution of total C across different plant parts (Kuzyakov & Domanski, 2000).

110   4. Means and sample sizes had to be available for both ambient and increased CO_2 treatments

111   to be included in our dataset. Estimates of variance were tabulated when available but were

112   not required for inclusion in the analysis.

113   We found 31 papers that met our requirements. One study was excluded because no

114   new soil C input was detected in either the control or the increased CO_2 treatment. Another

115   study was excluded because it assumed temporal variation in the old soil C end member; this

116   approach prohibited direct comparisons with new and old C stocks in other studies in our

117   dataset. Finally, one study was excluded because low image resolution prevented extraction of

118   graphical data (see Data S1). Out of the remaining 28 papers, 18 papers reported new soil C

119   stocks; 18 papers reported soil C input proxy data; 14 papers reported old soil C respiration

120   rates; and 7 papers reported old soil C stocks (Table 1).

121   We extracted final observations on soil C contents (only 1 experiment reported soil

122   C data for more than one time point). Although this was not a requirement for a study to be

123   included in our dataset, all soil C measurements in our dataset were from mineral soil layers.

124   We averaged observations of old soil C respiration rates over time. For each study, we also

125   tabulated experimental duration, plant species, and the type of experimental facility that was

126   used to increase CO_2 concentrations. Experiment duration (i.e. the time period during which

127   soil C input was isotopically labeled) varied between 6 days and 4 years (Table 1, Data S2-5).

Soil C input proxies

For each study we choose the proxy that we assumed was most indicative of net primary productivity (NPP), while taking into account the experimental design (Table 1). In studies on newly seeded plants that lasted less than one growing season, the incorporation of aboveground litter in mineral soil was likely to be minimal. In these cases we used standing root biomass, which we assumed was an estimate of belowground NPP. For experiments that determined new soil C in root ingrowth cores (Hoosbeek *et al.,* 2004; Phillips *et al.,* 2012), we used root growth as the proxy. In several longer-term experiments, aboveground biomass was periodically harvested (e.g. van Kessel *et al.,* 2000) or aboveground litter was removed (Cardon *et al.,* 2001; Heath *et al.,* 2005), which minimized the input of aboveground biomass. Because root growth data were not available for these studies, we used standing root biomass as a proxy. For longer-term (1-4 years) experiments without litter removal or biomass harvesting (Olszyk *et al.,* 2003) we used total plant biomass. For all experiments, we only included proxies of C input from the time point closest to the corresponding new-soil C measurements. For all experiments < 1 year, soil C input proxies were measured at the same time as new-soil C stocks.

Meta-analysis

We quantified the effect of increased CO_2 on new soil C, soil C input proxies, old C respiration and old soil C by calculating the natural log of the response ratio (r), a metric commonly used in meta-analyses (Hedges et al., 1999; Osenberg et al., 2001):

$$\ln r = \ln(V_{ic}/V_{ac})$$

where V is the value for new soil C, soil C input proxies, old C respiration or old soil C under increased (ic) or ambient (ac) CO_2 conditions. We performed a mixed-effects meta-analysis in R, using the rma.mv function in the "metafor" package (Viechtbauer *et al.*, 2010), including "paper" as a random effect (because several papers contributed more than one effect size), and

154   weighting $\ln r$ by the inverse of its variance. We estimated missing variances using the average

155   coefficient of variation across the dataset. To ease interpretation, the results from all our

156   analyses were back-transformed and reported as the percentage change under increased

157   CO_2 $((r - 1) \times 100)$.

158   Several factors have been suggested to affect the response of plant growth and soil C

159   dynamics to CO_2 enrichment: 1) type of vegetation (Ainsworth *et al.,* 2005), 2) the CO_2

160   fumigation technology used (De Graaff *et al.,* 2006), 3) experiment duration (Norby *et al.,*

161   2010), 4) soil texture (Procter *et al.,* 2015), 5) age of the vegetation (Körner *et al.,* 2005), and

162   6) N availability (van Groenigen *et al.,* 2006). To test whether these factors affected CO_2

163   responses, we categorized each study based on plant type (that is, woody vs. herb),

164   experimental facility (greenhouse, GH, and growth chamber, GC vs. open top chamber, OTC

165   and free air CO_2 enrichment, FACE), and study duration (< 1 year vs. 1-4 years). We based

166   our cut-off point on expected abrupt changes in soil C input over time; in the first growing

167   season of an experiment isotopically labeled input mostly consists of root exudates and fine

168   root turnover (Norby *et al.*, 1987), whereas in longer studies, dead coarse root material and

169   aboveground litter will contribute as well (Hobbie *et al.,* 2004). One study reported respiration

170   data for more than 1 year. For this study, we time-averaged the short-term and longer-term

171   responses separately, and included them as two separate comparisons in our dataset**.** For each

172   study we also tabulated the age of vegetation (number of years at the start of the isotopic

173   labeling) and clay content. When studies reported soil texture class but not the exact clay

174   content, we estimated clay content as the mean of the minimum and maximum value of that

175   texture class according to the soil textural triangle

176   (http://en.wikipedia.org/wiki/File:SoilTextureTriangle.jpg). In addition, we categorized

177   studies on soil C stocks and respiration rates according to isotopic labeling method and we

178   categorized soil C input studies according to the type of proxy that was used (Table 1).

179   We selected our meta-analytic models using the same approach as Terrer *et al.*

180   (2016). Briefly, we analyzed the data with all possible models that could be constructed using

181   combinations of the experimental factors described above as main effects, using the "glmulti"

182   package in R. The relative importance of the factors was then calculated as the sum of Akaike

183   weights derived for all the models in which the factor occurred.

184   We assessed the effect of N availability using studies that included multiple N levels

185   in a full factorial design, comparing CO_2 responses between high vs. low N treatments. The

186   interaction between CO_2 enrichment and soil N availability was calculated according to

187   Lajeunesse (2011):

188    $\ln i = \ln r_{+N} - \ln r_{-N}$

189   with $\ln i$ as the natural log of the interaction term, $\ln r_{+N}$ as $\ln r$ in the high N treatment,

190   and $\ln r_{-N}$ as $\ln r$ in the low N treatment.

191   Models were fitted according to the Knapp and Hartung (2003) method; 95%

192   confidence intervals (CI) of treatment effects were based on critical values from a t-

193   distribution. For all analyses, we inferred an effect of CO_2 if the 95% CI of the mean effect

194   size did not overlap 0. We used a Wald test to determine whether treatment effects were

195   statistically different between study categories.

196

197   **Results**

198   Averaged across the entire data set, elevated CO_2 tended to increase new soil C contents

199   (+14.4%, $P = 0.12$). The effect of elevated CO_2 on new soil C was best predicted by

200   experiment duration and soil texture; the sum of Aikake weights indicate that other predictors

201   were of minor importance (Fig. 1). Based on these results, we calculated treatment effects for

202   short- and longer-term experiments, using experiment duration as the sole moderator in our

203   model. Experimentally elevated CO_2 only stimulated new soil C accumulation in short-term

204   experiments (Fig. 2a and Table S1). The effect of elevated CO_2 on new C also depended on

205 soil texture; treatment effects on new soil C decreased with clay content (Table S1). We found

206 similar results when we analyzed our data using a model that included both moderators (Fig.

207 S1).

208   Within the experiments that measured new soil C, elevated CO_2 increased soil C input

209 proxies by 40.7% ($P < 0.001$), with positive effects both in short- and longer-term

210 experiments (Fig. 2b). The effects of elevated CO_2 on soil C input proxies did not depend on

211 experiment duration or any of the other model predictors (Fig. 2b, Fig. S2). When we limited

212 our analysis to studies conducted in the field (that is, FACE and OTC studies), we found

213 similar results: the effect of elevated CO_2 on new soil C contents in short-term experiments

214 was significantly higher than in longer-term experiments, but elevated CO_2 increased C input

215 proxies regardless of experimental duration (Table S1).

216   The average effect of elevated CO_2 on soil C input in longer-term studies was strongly

217 affected by the data from one study (Cardon *et al.,* 2001) which reported exceptionally strong

218 positive CO_2 effects (178 - 343%, see table S3). Excluding the results from this study from

219 our analysis lowered CO_2 effects on soil C input proxies for longer-term studies to a similar

220 level as those for short-term studies, whereas CO_2 effects on new soil C stocks remained

221 largely unchanged (Fig. S3). Averaged across the entire data set, elevated CO_2 did not affect

222 old soil C respiration ($P = 0.99$) and old soil C stocks ($P = 0.16$). Treatment effects on old soil

223 C respiration and old soil C stocks were not affected by any of the model predictors (Fig. 2cd,

224 Figs. S4-S5).

225   Within studies that included N availability treatments, elevated CO_2 increased the soil

226 C input proxy more strongly at high N levels (Table 2). The effect of elevated CO_2 on old soil

227 C stocks tended to be more positive at high N levels ($P = 0.11$); we found no $CO_2 \times N$

228 interactions for the other response variables.

229

230 **Discussion**

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231 Our results show that elevated CO_2 did not affect new soil C contents in longer-term

232 experiments. At the same time, our finding that elevated CO_2 increased soil C input proxies

233 both in short- and longer-term experiments indicate that CO_2 enrichment stimulated soil C

234 input regardless of experiment duration. Increased soil C input with no concomitant increase

235 in new soil C storage can only be explained by increased decomposition rates. Thus, our

236 results strongly suggest that faster decomposition of new C under increased CO_2 negated the

237 higher soil C input rates, thereby limiting the potential for longer-term soil C storage.

238 Experiments included in our dataset show that elevated CO_2 also increases soil C input

239 proxies other than the ones used in our analysis, such as litter production (Gielen *et al.,* 2005),

240 NPP (McCarthy *et al.,* 2010), photosynthetic rate (Heath *et al.,* 2005) and fine root turnover

241 (Lukac *et al.,* 2003; Trueman & Gonzalez-Meler, 2005) both in the short- and longer term.

242 Similarly, a recent meta-analysis shows that elevated CO_2 increases fine root production and

243 litter fall regardless of experimental duration (Dieleman *et al.,* 2010). Thus, several lines of

244 evidence suggest continued positive effects of elevated CO_2 on soil C input. This provides

245 further support for our interpretation that the lack of an effect of elevated CO_2 on new soil C

246 accumulation is not due to decreasing treatment effects on soil C input over time, but rather to

247 an increase in decomposition rates under elevated CO_2.

248   Our finding that new soil C is unresponsive to elevated CO_2 - despite increased C

249 input to soil - is inconsistent with the idea that more rapid C turnover through soil is an

250 artifact of the model structure used to infer rates of soil C turnover (Georgiou *et al.,* 2015; van

251 Groenigen *et al.,* 2015). Rather, finding that elevated CO_2 increased C input to soil with no

252 effect on the size of the new soil C pool supports the interpretation that elevated CO_2

253 increases the turnover rate of new soil C (Phillips *et al.,* 2012; van Groenigen *et al.,* 2014).

254   Why does increased atmospheric CO_2 stimulate the decomposition of new soil C?

255 Rising levels of atmospheric CO_2 increase the supply of labile C root exudates (Phillips *et al.*,

256 2011) and the release of labile C by mycorrhizae (Cheng *et al.,* 2012), which can stimulate the

257   decomposition of plant litter by saprotrophs (Phillips *et al.*, 2012; De Graaff *et al.,* 2010). This

258   explanation is consistent with direct measurements of higher *in situ* litter decomposition rates

259   with increased atmospheric CO_2 compared to ambient CO_2 (Cotrufo *et al.,* 2005; Cheng *et al*.,

260   2012; Carrillo *et al*., 2014) and with non-girdled trees compared to girdled trees (Subke *et al.,*

261   2004). Furthermore, increased CO_2 can improve the efficiency of water use by plants, which

262   reduces soil water loss through transpiration and increases soil water content (Field *et al.*,

263   1995; van Groenigen *et al.*, 2011). This response stimulates decomposition rates in

264   ecosystems where low water availability constrains the activity of soil microbes and their

265   access to substrate (Hungate *et al.*, 1997; Pendall *et al.*, 2003). We note that this latter

266   mechanism will only have a limited impact in experiments where irrigation minimizes the

267   effects of elevated CO_2 on soil moisture contents.

268   Our analysis suggests that increased turnover of new C could be a general response to

269   atmospheric CO_2 enrichment. Nonetheless, increased CO_2 stimulated new C accumulation in

270   the short-term. This positive treatment effects on new soil C in experiments < 1 year might

271   reflect an adjustment period, where microbial activity and decomposition rates did not fully

272   respond following a step increase in soil C input rates under elevated CO_2. The change in

273   composition of soil C input over time may have played a role as well. In short-term

274   experiments, plant inputs to soil will consist mostly of root exudates (Norby *et al.*, 1987); the

275   positive effect of CO_2 on new soil C in these experiments likely reflects increased root

276   exudation. Over time, isotopically labelled root litter, mycorrhizal tissue and leaves contribute

277   to soil C input as well (Hobbie *et al.*, 2004). Indeed, increased CO_2 has been shown to

278   stimulate the decomposition of these types of plant input (Cheng, 1999; Cheng *et al.*, 2012;

279   Phillips *et al.,* 2012).

280   Our findings of faster decomposition rates with increased CO_2 are corroborated by

281   studies that did not include an isotopic C label. For instance, increased CO_2 has been shown to

282   increase the ability of microbes to decompose soil organic matter (Nie *et al.*, 2013), and to

11

283   stimulate the activity of enzymes associated with decomposition of both recalcitrant (Carney

284   *et al.*, 2007) and labile soil organic matter (Kelley *et al.*, 2011). However, it should be noted

285   that our analysis only pertains to mineral soils; to the best of our knowledge, no study has

286   reported CO_2 responses of old and new C in organic layers. This is important, because

287   experimentally elevated CO_2 can increase litter fall and stimulate C accumulation in forest

288   floors, thereby forming a minor additional C sink (Drake *et al.*, 2011).

289   A recent synthesis of data from a much larger set of mostly longer-term CO_2

290   experiments (n=53, average experiment duration of 6.8 years) that used a mass balance

291   approach to estimate changes in soil C dynamics found that elevated CO_2 increases the

292   decomposition of both new and old soil C (van Groenigen *et al.*, 2014). Our new findings

293   confirm those earlier results for the new, but not the old, soil C pool. The lack of a significant

294   treatment effect on old C respiration might be due to low statistical power; the small sample

295   size (n=8 for experiments 1-4 years) and high variance associated with the respiration of old

296   soil C (Fig. 2c, Table S1) limit our ability to detect treatment effects. The large variation in

297   treatment effects may be caused by among-system variation in the recalcitrance and physical

298   protection of the old soil C. Moreover, old soil C stocks are large compared to new soil C

299   stocks and they are characterized by high spatial variability, making it difficult to detect

300   changes in pool size (Hungate *et al.*, 1995). The impact of spatial variability may be reduced

301   through long-term experiments involving planted communities on homogenized soils. Large

302   differences in isotopic signatures between recently fixed C and old C may improve sensitivity

303   as well (Ogle & Pendall, 2015). Clearly, additional studies are needed to identify the soil

304   properties determining the turnover of old soil C under increased CO_2.

305   We do not know what caused the negative correlation between clay content and the

306   effect of elevated CO_2 on new soil C stocks. This result seems counter-intuitive, as clay

307   minerals are generally expected to promote soil C accumulation (Six *et al.*, 2002). One

308   possible explanation is that the soil disturbance inherent to all experiments in our data set

309   released previously physically protected C. Experiments that trace soil C input under both

310   ambient and elevated CO_2 conditions involve continuous isotopic labelling of CO_2 (which can

311   be achieved in greenhouses), or replacing vegetation (i.e. by using soil that developed under

312   vegetation with a different photosynthetic pathway than that of the experimental vegetation).

313   As such, all these experiments required a substantial amount of soil disturbance. Undisturbed

314   clay soils contain relatively large amounts of physically protected C (Six *et al.,* 2002). When

315   soil disturbance breaks up soil aggregates, much of this C becomes available to microbes

316   (Hassink *et al.,* 1993). Thus, disturbed clay soils have relatively large and active microbial

317   communities that might be better adapted to decompose the increased amount of soil C input

318   under elevated CO_2 than soils with low clay contents. Alternatively, clay content may

319   correlate with soil properties that were not considered in this analysis (because they weren't

320   always reported) but that may affect decomposition rates (e.g. nutrient availability, soil

321   moisture).

322   Elevated CO_2 stimulated soil C input proxies more strongly under high than under low

323   N inputs, but this response did not result in additional new soil C storage. These results are

324   consistent with a recent study showing that N additions increase decomposition of new soil C

325   input (Chen *et al.,* 2014). Nonetheless, several studies found that N additions stimulate total

326   soil C storage under elevated CO_2 (e.g. Hungate *et al.,* 2009; Luo *et al.,* 2006, van Groenigen

327   *et al.,* 2006). In combination with our finding that N addition does not stimulate new soil C

328   storage under elevated CO_2, this suggests that N addition stimulates net soil C storage by

329   reducing old soil C decomposition (e.g. Cheng & Johnson*,* 1998; Cardon *et al.,* 2001). This

330   explanation is consistent with our finding that high N additions tended to increase old C

331   stocks under elevated CO_2. However, because this result is based on a small dataset (n=11)

332   and is only marginally significant, it requires additional experimental work to be tested more

333   thoroughly.

334   Two important limitations of our analysis must be noted. First, the experiments in our

335   dataset only lasted 4 years at the most, whereas soil C storage is a process that occurs on

336   decadal timescales. Elevated CO_2 can increase the input of new C into slowly cycling or

337   passive C pools (Jastrow *et al.,* 2005; Iversen *et al.,* 2011), a response that could stimulate

338   new soil C storage over time frames longer than the spans of most experiments. As such, we

339   can only speculate about the extent to which our results are representative for responses on

340   longer time scales. However, a recent global synthesis of soil ^{14}C data shows that current soil

341   C models actually overestimate the incorporation of new C in soil with rising CO_2

342   concentrations (He *et al.,* 2016), suggesting that our finding of increased turnover rates also

343   may apply to longer time scales in real-world ecosystems.

344   Second, our dataset does not include field experiments in undisturbed natural

345   ecosystems, or systems with a continuous management history. However, our findings are

346   supported by longer-term studies in both continuously managed and natural ecosystems. For

347   instance, Marhan *et al.* (2010) combined soil ^{13}C data with inverse modelling to show that 5

348   years of elevated CO_2 increased the decomposition rate of both old and new soil C in cropland

349   by increasing soil moisture contents. Longer-term CO_2 enrichment studies on natural

350   ecosystems often include an isotopic C tracer in the high CO_2 treatment only. Several of these

351   studies found that new C is predominantly allocated to soil C pools with high turnover rates.

352   For instance, Taneva *et al.* (2006) found in a *Pinus taeda* plantation that after 8 years of

353   elevated atmospheric CO_2, the majority of soil-respired CO_2 was derived from pools with a

354   turnover rate of less than 35 days. Importantly, meta-analyses suggest that on average,

355   increased plant growth under elevated CO_2 does not result in additional soil C storage unless

356   nutrients are also added (e.g. De Graaff *et al.,* 2006; van Groenigen *et al.,* 2006). Together,

357   these results strongly suggests that our finding of increased decomposition rates is

358   transferrable to a wide range of ecosystems.

359   Conventional soil C models assume that decomposition rates (k) are not directly

360   affected by rising CO_2 levels (Friedlingstein *et al.,* 2006; Luo *et al.,* 2016). However, our

361   results (and those of other recent syntheses, e.g. van Groenigen *et al.*, 2014) indicate that k

362   might increase under elevated CO_2. This inconsistency between models and real-world

363   responses can potentially be avoided when models explicitly represent the relation between

364   microbial dynamics and decomposition rates and the interactions between various C

365   pools. Indeed, microbe-centered models (i.e., models in which decomposition is determined

366   by the size and activity of the microbial biomass, both of which are modeled explicitly)

367   predict less new soil C accumulation following an increase in atmospheric CO_2 than

368   conventional models (Wieder *et al.,* 2015; Wutzler *et al.*, 2013; Sulman *et al.*, 2014).

369   This meta-analysis, synthesizing results across 28 studies, suggests that enhanced

370   turnover rates of new soil C with increased atmospheric CO_2 might be common. Therefore,

371   future assessments of terrestrial feedbacks to climate change should consider the effects of

372   increased atmospheric CO_2 on microbial processes such as soil C turnover.

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380

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25

Figures

Fig. 1 Model-averaged importance of the predictors of the CO_2 enrichment effect on new soil C stocks. The importance is based on the sum of Akaike weights derived from model selection using AICc (Akaike's Information Criteria corrected for small samples). Cut-off is set at 0.8 (dashed line) to differentiate important from non-essential predictors.

645
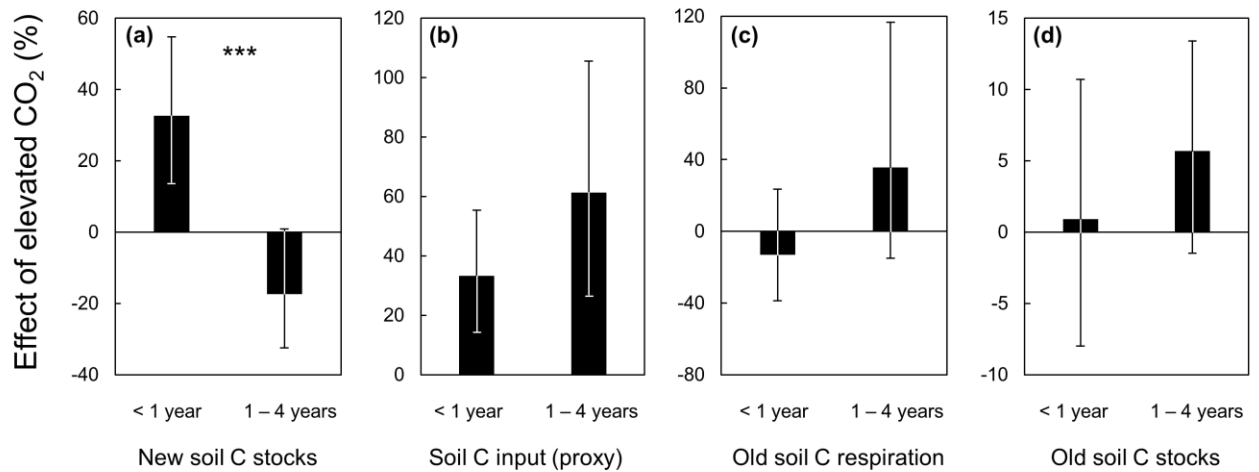
Fig. 2 Results of a meta-analysis on the response of new soil C stocks, soil C input proxies, old soil C respiration and old soil C stocks to increased levels of atmospheric CO_2 for short (< 1 year) and longer-term (1-4 years) studies. (a) Change in new soil C stocks for short-term studies (n=32) and longer-term studies (n=24); (b) Change in soil C input proxies for short-term (n=32) and longer-term studies (n=24); (c) Change in respiration of old soil C for short-term (n=21) and longer-term studies (n=8); (d) Change in old C stocks for short-term studies (n=10) and longer-term studies (n=24). Error bars indicate 95% confidence intervals. *** indicates treatment responses that are significantly different between study categories at *P* < 0.001.

655

Table 1 Overview of CO$_2$ enrichment experiments included in our meta-analysis; responses that were reported in each study are indicated by '●'.

657

Reference	System/species	Duration in years[a]	Label[b]	Facility[c]	New C	C input proxy[d]	Old C resp.	Old C
Billes *et al*., 1993	*Triticum aestivum*	0.08	C-14	GC	●	● (RB)		
Butterly *et al.,* 2015	*Triticum aestivum / Pisum sativum*	0.27	C-13	FACE	●	● (RB)		
Cardon *et al.,* 2001	California grassland	1.8	C$_3$/C$_4$	OTC	●	● (RB)	●	●
Carrillo *et al.,* 2014	*Bouteloua gracilis*	0.18	C-13	GC			●	
Carrillo *et al.,* 2016	*Bouteloua gracilis / Pascopyrum smithii*	0.18	C-13	GC	●	● (RB)	●	●
Cheng & Johnson, 1998	*Triticum aestivum*	0.08	C$_3$/C$_4$	GC			●	
Cheng *et al.,* 2000	*Helianthus annuus*	0.15	C$_3$/C$_4$	GC	●	● (RB)	●	
Cotrufo & Gorissen, 1997	*Lolium perenne /Agrostis capillaris Festuca ovina*	0.15	C-14	GC	●	● (RB)		
Heath *et al.,* 2005	*Fagus sylvatica / Quercus rober Carpinus betulus /Betual pendula Abies alba / Pinus sylvestris*	1.3	C$_3$/C$_4$	GH	●	● (RB)		●
Hobbie *et al.,* 2004	*Pseudotsuga mensiezii*	4.0	C-13	OTC	●			●
Hoosbeek *et al.,* 2004	*Populus alba Populus euramericana Populus nigra*	0.67	C$_3$/C$_4$	FACE	●			●
Hungate *et al.,* 1997	California grassland	1.5	C-13	FACE			●	
Ineson *et al.,* 1996	*Betula pendula*	0.5	C$_3$/C$_4$	FACE	●	● (RB)		
Kuikman *et al.,* 1991	*Triticum aestivum*	0.13	C-14	GC	●	● (RB)	●	
Lin *et al.,* 1999	*Pseudotsuga mensiezii*	1.3	C-13	OTC			●	
Lukac *et al.*, 2003	*Poplar plantation*	0.67	C$_3$/C$_4$	FACE		● (RG)		
Martens *et al.,* 2009	*Triticum aestivum*	0.12	C-14	FACE	●	● (RB)		
Nie *et al.,* 2015	*Bouteloua gracilis*	0.08	C-13	GC	●	● (RB)	●	
Nie & Pendall, 2016	*Bouteloua gracilis / Hesperostipa comata*	0.06	C-13	GC			●	
Olszyk *et al.,* 2003	*Pseudotsuga mensiezii*	4.0	C-13	OTC		● (TB)		
Paterson *et al.,* 2008	*Lolium perenne*	0.18	C-13	GC			●	
Pendall *et al.,* 2003	Colorado grassland	2.6	C$_3$/C$_4$	FACE			●	
Phillips *et al.,* 2012	*Pinus taeda*	1	C-13[e]	FACE	●	● (RG)		●
Rouhier *et al.,* 1996	*Castanea sativa*	0.02	C-14	GC	●	● (RB)		
Trueman & Gonzalez-Meler, 2005	*Populus deltoids*	4.0	C-13	GH			●	
Van Ginkel *et al*., 1997	*Lolium perenne*	0.12	C-14	GC	●	● (RB)	●	
Van Ginkel *et al*., 2000	*Lolium perenne*	0.23	C-14	GC	●	● (RB)		
Van Kessel *et al.,* 2000	*Lolium perenne / Trifolium repens*	4.0	C$_3$/C$_4$	FACE	●	● (RB)		●

658 [a] Number of years during which the soil in the study received isotopically labeled C input.

659 [b] C-14 = isotopic labelling by ^{14}C-CO$_2$; C-13 = isotopic labelling by ^{13}C-CO$_2$; C$_3$/C$_4$ = isotopic labelling by using a shift in C$_3$ vs. C$_4$ vegetation.

660 [c] FACE = Free Air Carbon dioxide Enrichment; GC= Growth Chamber; GH = Greenhouse; OTC=Open Top Chamber.

661 [d] RB= root biomass, TB= total biomass, RG = root growth.

662 [e] This study created a difference in isotopic signature between old soil C and new soil C input by switching soils between ambient and elevated CO$_2$ treatments.

663 **Table 2** Effect of elevated CO_2 for low and high N addition treatments, and the $CO_2 \times N$
664 interaction term in $CO_2 \times N$ factorial experiments for all response variables included in our
665 analysis.

Response variable	CO_2 effect at low N (%)			CO_2 effect at high N (%)			$CO_2 \times N$ interaction (%)			n
		95% CI			95% CI			95% CI		
	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	
New soil C stocks	-11.7	-31.2	13.3	-2.3	-24.0	25.5	6.7	-12.2	29.8	18
Soil C input (proxy)	43.8	10.2	87.8	60.0	22.2	109.4	13.4	1.2	27.1	18
Old soil C respiration	-5.2	-46.7	68.8	-5.3	-45.8	65.4	-3.0	-48.5	82.9	6
Old soil C stocks	5.5	-4.4	16.3	7.6	-2.4	18.5	2.7	-0.8	6.3	11

666