

1 **Rhizodeposition under drought and consequences for soil communities** 2 **and ecosystem resilience**

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11 12 **Abstract**

13 *Background*

14 Rhizodeposition is the release of organic compounds from plant roots into soil. Positive
15 relationships between rhizodeposition and soil microbial biomass are commonly
16 observed. Rhizodeposition may be disrupted by increasing drought however the effects
17 of water stress on this process are not sufficiently understood.

18 *Scope*

19 We aimed to provide a synthesis of the current knowledge of drought impacts on
20 rhizodeposition. The current scarcity of well-defined studies hinders a quantitative
21 meta-analysis, but we are able to identify the main effects of water stress on this process
22 and how changes in the severity of drought may produce different responses. We then
23 give an overview of the links between rhizodeposition and microbial communities, and
24 describe how drought may disrupt these interactions.

25 *Conclusions*

26 Overall, moderate drought appears to increase rhizodeposition per gram of plant, but
27 under extreme drought rhizodeposition is more variable. Concurrent decreases in plant
28 biomass may lessen the total amount of rhizodeposits entering the soil. Effects on
29 rhizodeposition may be strongly species-dependant therefore impacts on soil
30 communities may also vary, either driving subsequent changes or conferring resilience
31 in the plant community. Advances in the study of rhizodeposition are needed to allow a
32 deeper understanding of this plant-soil interaction and how it will respond to drought.

33

34 **Key words:** rhizodeposition; root exudation; drought; soil microbial community; roots;
35 resilience

36 **Introduction**

37 Terrestrial plants and soils are inextricably linked and rarely operate independently.
38 They exhibit a wide range of positive and negative feedbacks on each other and other
39 trophic levels (Ehrenfeld et al. 2005; Wardle et al. 2004). One important link between
40 plants and soils is rhizodeposition, whereby organic compounds in many forms are
41 released into the soil by plant roots, and differentially used by various components of
42 the soil community including both microorganisms and soil fauna. Many questions
43 remain about how human-induced environmental changes affect rhizodeposition
44 (Bardgett et al. 2013; Wardle et al. 2004).

45 Amongst these environmental changes, more frequent or intense drought, due to
46 climate change and intensification of agriculture, threatens the availability of water and
47 increases vulnerability to soil erosion (Field et al. 2014; Mishra and Singh 2010).
48 Increasing droughts are predicted for a number of different regions including central
49 Europe, Southern Europe and the Mediterranean, Southern Africa, Central America and
50 Mexico, North-eastern Brazil, and South Australia and New Zealand (Dai 2011; Field et
51 al. 2014; Li et al. 2009). Consequently, water stress, and its impacts on soils, will be
52 widespread across the globe. However, the mechanisms by which drought impacts soils,
53 and consequently the species living in them, are not yet sufficiently understood to be
54 able to predict at what stage water stress becomes a major driver of ecosystem change
55 (McDowell et al. 2008).

56 Soils have a crucial role in maintaining ecosystem function and ecosystem
57 services (such as food security) due to the tight link between soil properties and the
58 productivity and sustainability of both agricultural and natural ecosystems (Lal 2009;
59 Pimentel 2006). Specifically, soil microbial diversity is positively correlated with the
60 provision of ecosystem services (Delgado-Baquerizo et al. 2016). The focus of this
61 review is on the impact of drought on rhizodeposition and the potential knock-on effects
62 on soil microbial community structure and resilience. A fuller understanding of this
63 subject will be useful both for predicting climate impacts in natural and agricultural
64 systems. Further, it may be possible to manipulate these feedbacks, for example by
65 encouraging populations of specific types of microorganisms that are known to have
66 beneficial effects on plant populations, such as through increasing plant growth or
67 suppression of pathogens, in order to increase resilience of ecosystems (Dennis et al.
68 2010) and preserve biodiversity in natural habitats and increase food security (van der
69 Putten et al. 2013).

70

71 **Rhizodeposition - an important plant-soil linkage**

72 Rhizodeposits are made up of a wide array of compounds, including ions (e.g. H^+ , OH^- ,
73 HCO_3^-), sugars, amino acids, enzymes, organic acids and mucilage (Bais et al. 2006).
74 They may be released actively or passively (Dennis et al. 2010) and in addition to
75 substances released from healthy roots (sometimes distinguished as root exudates) they
76 can include compounds released from senescing roots, including tissue of dead roots
77 (Neumann and Römheld 2007). The composition and amount of these compounds vary
78 between species of plants and even across the lifetime of an individual (Bais et al.
79 2006). Rhizodeposition is involved in many different types of interactions between
80 plants and other groups of species. For example, rhizodeposits allow communication
81 between plants, allelopathy, interactions between parasitic plants and their hosts, and
82 defence from pathogens (Bais et al. 2006).

83 Estimates of the amount of carbon (C) fixed during photosynthesis that is lost
84 through rhizodeposition are between 2 and 11% (Jones et al. 2004; Jones et al. 2009;
85 Pinton et al. 2007). Rhizodeposition is often calculated as the mass of carbon released
86 per mass of plant (root or total) per day. A recent study, using ^{13}C labelling with four
87 grass species grown in pots, found rates of between 14 and 48 $\mu g C g^{-1}$ root dry mass
88 day^{-1} , varying by species and soil fertility (Baptist et al. 2015). Rhizodeposition can also
89 be calculated per unit area of soil, and a review of data presented in Kuzyakov *et al.*
90 (2000) calculated that 400–600 $kg C ha^{-1}$ is added to the soil through rhizodeposition
91 for grasses and cereals during the vegetation period (Jones et al. 2009).

92 It may initially seem like a bad strategy for plants to lose carbon through their
93 roots. However, rhizodeposition may be advantageous for plants, as it can increase the
94 uptake of nutrients from the rhizosphere (Jones et al. 2004). One main way this occurs
95 is through stimulation of soil microorganisms, which tend to be carbon-limited.
96 Therefore the addition of an easily accessible C source into the soil (from the
97 rhizodeposits) leads to increased activity of soil microbes and increased decomposition
98 of soil organic matter (SOM). A review of the importance of rhizodeposition for carbon
99 turnover found that a high proportion of rhizodeposits are bioavailable, as
100 microorganisms rapidly respire 64-86% of these substances (Hütsch et al. 2002). This
101 well-documented phenomenon is called the “priming effect” (Kuzyakov and Domanski
102 2000), and one way that this has been demonstrated is by greater soil microbial activity

103 (i.e. CO₂ efflux) in soils that have plants growing in them compared with bare soils
104 (Dijkstra and Cheng 2007).

105 The priming effect may be particularly significant in soils of low nutrient
106 availability, where increased microbial activity and higher production of extracellular
107 enzymes can enable the release of nutrients previously retained in the SOM, for use by
108 microbes and plants (Dijkstra et al. 2013). For example, in nitrogen-limited soils, the
109 priming effect can lead to increased availability in soil N, as shown by an experiment
110 which added glucose (to represent root exudates) to soil and found increased activity of
111 proteases and total soluble N (Asmar et al. 1994). In a field situation, rhizodeposition of
112 carbon from temperate forest tree species was shown to stimulate soil N cycling, via an
113 increase in extracellular enzymes (Brzostek et al. 2013). Similarly, increased exudation
114 due to elevated CO₂ and temperature was shown to increase N cycling (via enhanced
115 microbial activity) in low N soils in experiments with *Pinus taeda* and *Picea asperata*
116 (Phillips et al. 2011; Yin et al. 2014). The links between roots, rhizodeposition, soil
117 organic matter and microbial communities are summarised in Figure 1.

118 In addition to changes to the amount of rhizodeposition, the composition of
119 rhizodeposits varies by plant species and can also change in response to nutrient
120 availability (Carvalhais et al. 2011). For example, in response to low phosphorus
121 availability, the concentration of organic acids in rhizodeposits has been shown to
122 increase in *Lupinus albus* (Johnson et al. 1994; Neumann and Römheld 1999), *Brassica*
123 *napus* (Hoffland et al. 1992) and *Medicago sativa* (Lipton et al. 1987). Some species
124 even produce special root formations called proteoid roots which release compounds,
125 including acid phosphatases and carboxylate organic anions, that can mobilise nutrients,
126 particularly mineral phosphorus bound to metal cations (such as iron, aluminium and
127 calcium) (Watt and Evans 1999). However, understanding the net effects of
128 rhizodeposits on soil nutrient cycles is complex, as greater nutrient availability may be
129 accompanied by higher competition between plants and microorganisms for those
130 nutrients, and the possibility of increased growth of pathogens (Jones et al. 2004). It
131 should be noted that soil microbes also have the ability to influence rhizodeposition, not
132 only respond to it, and have been shown to induce root exudation of amino acids
133 (Phillips et al. 2004).

134 Besides the significant input of carbon into the soil, rhizodeposition can have
135 impacts on soil structure in a number of different ways. For example, rhizodeposits can
136 increase soil aggregate stability through the release of polysaccharides and proteins that

137 have binding properties (Bardgett et al. 2014; Bronick and Lal 2005; Gregory 2006;
138 Morel et al. 1991; Traore et al. 2000). This can have further impacts on the
139 susceptibility of the soil to water run-off and erosion, which is increased in areas of low
140 soil aggregate stability (Barthès and Roose 2002). During drying-rewetting cycles,
141 addition of polygalacturonic acid, a root mucilage analogue, increased water repellency
142 of soils leading to greater stability of the soil structure (Czarnes et al. 2000). Mucilage
143 can also contain phospholipid surfactants (such as phosphatidylcholines) that can reduce
144 soil water surface tension (Read et al. 2003). Micro-engineering of soil pores by
145 microorganisms and plant roots, has been visualised using synchrotron-radiation
146 microtomography (three-dimensional reconstruction), showing changes towards a soil
147 structure that is more porous, aggregated and ordered (Feeney et al. 2006). Soil
148 microbial communities may be altered by such changes in the physical properties of the
149 soil, but also directly due to the potential occurrence of antimicrobial compounds within
150 rhizodeposits. The presence of such compounds is presumed to help protect the
151 rhizosphere from attack by pathogens (Bais et al. 2006; Sobolev et al. 2006; Walker et
152 al. 2003b).

153 Whilst the importance of rhizodeposition for interactions of plants with soils and
154 their communities has now been realised, there remains much to be understood about
155 how changing environmental conditions, including drought, affect this linkage. In a
156 review of drought impacts on trees, it was suggested that drought will decrease
157 rhizodeposition (Brunner et al. 2015), but so far, in the wider literature, this has not
158 been sufficiently evaluated. Although there are little data on this subject, advances in
159 techniques for measuring rhizodeposition are enabling greater insight into the process.
160 With the current urgency to increase understanding about this process, we therefore
161 believe that now is an excellent time to summarise the current state of understanding on
162 the impact of drought on rhizodeposition and we describe areas of general consensus,
163 and highlight where future research should focus.

164

165 **Challenges in measuring drought impacts on rhizodeposition**

166 Drought may impact rhizodeposition by changing the amount or composition of
167 rhizodeposits, both of which may then affect microbial communities. There is still a
168 relatively limited literature on how water stress impacts rhizodeposition, and it is
169 difficult to assess, as there is no standardised drought treatment. This means that the
170 duration of water stress differs for each study, as does the reduction in water, and the

171 evaporative demand. Other challenges arise due to the differing methods used to
172 measure rhizodeposition.

173 A variety of techniques have been developed in order to measure the process and
174 how it responds to drought. Earlier studies usually measured rhizodeposits of plants
175 grown in hydroponic conditions or axenic cultures (highly-controlled conditions without
176 microorganisms). In hydroponic systems water stress is induced by the addition of
177 polyethylene glycol (PEG) which can be used to modify the osmotic potential of
178 nutrient solution culture (Blum 1989; Song et al. 2012). Advantages of these types of
179 experiments are that they allow close control over the study system and have fewer
180 factors that can interfere with rhizodeposit composition. However, they suffer from the
181 unnaturalness of the growth environment, as there is no soil, and therefore also no soil
182 microbes, and they also have a tendency to underestimate exudation (Jones et al. 2004).

183 Recent studies commonly use pulse or continuous isotope labelling (e.g. ^{14}C ,
184 ^{13}C) to partition C into its different pools (Cheng and Gershenson 2007; Neumann et al.
185 2009). However, these types of studies are expensive and difficult to perform in natural
186 systems (Kuzyakov and Domanski 2000; Neumann et al. 2009) and may overestimate
187 root exudation (Meharg 1994). Differences in the natural abundance of isotopes to
188 distinguish plant-derived and soil-derived material, detect large differences in carbon
189 budgets (Cheng and Gershenson 2007), however a possible problem with all isotope
190 studies is that measurement of plant-derived carbon in the soil may not discriminate
191 between increased exudation and decreased microbial activity (Dijkstra and Cheng
192 2007), or between C exuded from living roots and C from dead roots (Jones et al. 2004).

193 A number of recently developed methods measure rhizodeposits (and exudates
194 in particular) from roots of plants growing in soil, such as by using modified rhizoboxes
195 (Oburger et al. 2013) with collection by micro-suction cups connected to a vacuum, or
196 placement of filter paper onto the roots surface (Neumann and Römheld 2007). Another
197 method involves excavating an individual root and placing it within a cuvette containing
198 a carbon-free nutrient solution (Phillips et al. 2008). This does expose plants to some
199 disturbance, but it is much more similar to natural conditions than hydroponics
200 experiments, and more affordable than isotope labelling. However, in general, the lack
201 of simple methods to measure rhizodeposition in the field creates a major bottleneck for
202 increasing our knowledge about this process. For more details on methods for
203 measuring rhizodeposition see the reviews by Kuzyakov and Domanski (2000),
204 Vranova *et al.* (2013) and Oburger and Schmidt (2016).

205 As plants experience water stress, the initial impact includes a reduction in
206 photosynthesis due to stomatal closure, a decrease in mesophyll conductance and, under
207 long-term drought, biochemical limitations such as decreasing enzyme activity (Bota et
208 al. 2004; Chaves 1991; Chaves et al. 2003; Flexas et al. 2004; Grassi and Magnani
209 2005). Therefore, due to the knock on-effect on growth, a common effect of drought is
210 to reduce plant biomass (Brunner et al. 2015; Jaleel et al. 2009; Penuelas et al. 2007;
211 Zhao and Running 2010) and changes in rhizodeposition that may be due primarily to
212 concurrent changes in biomass must be carefully interpreted. Where this is the case, this
213 does not diminish the potential impact on the soil microbial community, but it is
214 important to also understand if there are changes in the rhizodeposition activity of the
215 roots, in addition to changes in mass.

216

217 **Data analysis of current literature**

218 Following an extensive review of the literature, we summarise the few studies that have
219 measured the effects of drought on rhizodeposition, shown in Table 1. Data were
220 obtained directly from values shown in text or tables, or taken from figures using
221 GetData Graph Digitizer software. It should be noted that some studies measured or
222 calculated rhizodeposition (or an equivalent measure) at more than one time point. Here,
223 we present the results for the longest duration of drought. Different studies expressed
224 rhizodeposition in slightly different ways, depending on the method used, with some
225 measuring total organic carbon and others measuring soluble organic carbon. To enable
226 easy comparison between studies we calculate effect sizes of the drought treatment for
227 each study. Effect sizes were calculated as the natural log of the response ratio (Hedges
228 et al. 1999), therefore: effect size = $\ln(\text{treatment mean} / \text{control mean})$.

229 These effect sizes are shown for rhizodeposition (amount of organic carbon) per
230 individual (or plot, in one case) (Fig. 2) and per gram of plant biomass (Fig. 3). For this
231 second measurement total plant biomass was used where possible, but in two cases only
232 shoot mass was directly measured. In the first instance, root biomass was estimated to
233 be 25% of total biomass, and total biomass was back-calculated (Henry et al. 2007), but
234 for the second study rhizodeposition was calculated per gram of shoot biomass
235 (Somasundaram et al. 2009) and this is indicated on Table 1 and Figure 3. The use of
236 effect sizes allows us to compare all types of study, but it is possible that drought effects
237 on root: shoot ratios could alter results slightly for those calculating rhizodeposition
238 relative to shoot mass. Positive values of the effect size indicate that the drought

239 treatment increased rhizodeposition. The mean effect size was calculated and the 95 %
240 confidence intervals around this mean were estimated using bootstrapping (1000
241 iterations). If these confidence intervals did not overlap with zero, the mean effect size
242 was considered significant ($P < 0.05$) (Trap et al. 2015).

243 Additionally, we have approximately quantified the *drought intensity* of each
244 study by multiplying the duration (in days) by the reduction in water relative to the
245 control (as a proportion). For example, a study in which water-stressed plants received
246 50% less water than the control plants for 10 days would be given a drought intensity
247 score of 5 (10×0.5). The data in Figures 2 and 3 are ordered by this drought intensity in
248 order to visualise if there is any change in response with increasing drought. We tested
249 if there were correlations between the change in rhizodeposition and the drought
250 intensity using simple linear regressions in R (R Core Team, 2014).

251

252 **Variable responses of rhizodeposition to drought**

253 In general, it is evident that there are variable results about how drought affects
254 rhizodeposition, with both positive and negative effects having been recorded and no
255 clear patterns relating to methods for measuring rhizodeposition or study systems (Table
256 1). A summary of how rhizodeposition responses varied in response to drought is shown
257 in Figures 2 and 3 and in online resource 1 (Fig. S1). In particular, the response to
258 drought on rhizodeposition per individual was very variable (Fig. 2), and showed no
259 relationship with the strength of the drought treatment (online resource Fig. S1). The
260 mean effect size was positive (0.125), but this was not significant (95% CIs: -0.327,
261 0.514).

262 Most studies in this review demonstrate a decrease in plant biomass under water
263 stress, which whilst not a surprising finding (Brunner et al. 2015), does emphasise the
264 importance of this measurement when attempting to determine the mechanisms behind
265 any physiological changes in rhizodeposition. Therefore the ability to conserve biomass
266 (especially roots) may be one of the most important factors for maintenance of
267 rhizodeposition under water stress. Indeed, in studies that found evidence of a decrease
268 in rhizodeposition per individual, a corresponding decrease in biomass was
269 overwhelmingly suggested as the explanation, and when accounted for, the effect often
270 disappeared. This is an important consideration when determining the effects on soils
271 and their communities, and a change in plant biomass, specifically root biomass, offers
272 a compelling and simple explanation for finding lower total rhizodeposition (per

273 individual) under drought. In fact, it has been suggested that plants may have little
274 control over regulation of rhizodeposition, overall and during abiotic stress such as
275 drought (Jones et al. 2004). The significance of plant biomass on rhizodeposition has
276 been previously demonstrated, for example, differences in rhizosphere priming effects
277 of soybean (*Glycine max*) and sunflower (*Helianthus annuus*) on decomposition of SOM
278 in two soil types (an organically farmed soil and an annual grassland) were
279 predominantly explained by differences in plant biomass (Dijkstra et al. 2006). We
280 recommend that future studies on rhizodeposition aim to measure both root and shoot
281 biomass. While it may be presumed that root biomass will better correlate with
282 rhizodeposition, there is not enough data to be sure of this. Also, changes in
283 rhizodeposition patterns may likely occur before a change in overall plant biomass, so
284 biomass should not be used as a replacement for measuring rhizodeposition directly.

285 We also assessed impacts on rhizodeposition when measured relative to the mass
286 of the plant. In this case, water stress tended to cause an increase in rhizodeposition
287 relative to controls (Fig. 3), with a mean effect size of 0.667 (95% CIs: 0.1582, 1.2747).
288 Previous work has shown that drought may stimulate root metabolic activity, in order to
289 buffer the negative impacts of water stress in the short term (Gargallo-Garriga et al.
290 2014). Therefore, a first possible explanation for higher rhizodeposition under drought
291 is that up-regulation of this process can offset the direct negative impacts on plants. This
292 may be through an increase in lubrication to help the roots move through the dry soil
293 and maintain root-soil contact (Henry et al. 2007; Nguyen 2003; Vranova et al. 2013;
294 Walker et al. 2003a). Mucilage is the main component within rhizodeposits that is
295 believed to have an important role in lubrication however this was not usually measured
296 separately in the studies brought together in this review. One study that did measure
297 mucilage production was an experiment using maize, exposed to 21 days of drought in a
298 greenhouse experiment. In this case there was a reduction in rhizodeposition of
299 mucilage (of almost 30%) in water stressed soil, despite a three-fold increase in carbon
300 release, demonstrating that the drought responses of different components of
301 rhizodeposits may be uncoupled, and not always in the direction that is predicted
302 (Somasundaram et al. 2009).

303 A second explanation for signs of increased rhizodeposition under drought is
304 that the water stress induces higher root mortality and lower cell membrane integrity,
305 leading to increased leakage of solutes which are a source of carbon and cannot be
306 easily distinguished from increased rhizodeposition of carbon (Henry et al. 2007). This

307 could in fact be an explanation for the discrepancy between mucilage production and
308 overall carbon release mentioned previously (Somasundaram et al. 2009). Similarly,
309 damaged roots may have less reabsorption of rhizodeposits, further increasing the
310 amount of carbon that is measured (Henry et al. 2007). Therefore, higher measurements
311 of released C may be observed as a general response to stress, at least in the short term.
312 However, over longer periods measured C would likely decrease unless roots were able
313 to recover. Clearly, it is important for future studies to differentiate between these two
314 conflicting explanations as the first (up-regulation) indicates tolerance and high
315 likelihood of recovery and the second (root damage and death) indicates susceptibility
316 and lower likelihood of recovery. Additionally, during a single drought event, increased
317 carbon inputs may initially be due to up-regulation and later because of root damage.

318 A further area of uncertainty is that, as mentioned earlier, in many studies,
319 rhizodeposition is not measured directly, thus decreases in available soil carbon could
320 be due to an increase in soil microorganism activity, rather than a decrease in
321 rhizodeposition. In the one study that we reviewed that found decreased rhizodeposition
322 in the absence of lower plant biomass (Gorissen et al. 2004), this was measured as a
323 decrease in the plant-derived C in the soluble fraction of soil. It is possible that higher
324 microbial activity was involved in this finding. Alternatively it could indicate that the
325 species in that study (*Calluna vulgaris*) responds to water stress by down-regulating
326 rhizodeposition and conserving carbon.

327 Amongst the studies that measured rhizodeposition using pulse-labelling with
328 ^{13}C or ^{14}C (which comprised the majority of studies), rhizodeposition per gram of plant
329 decreased as the intensity of drought increased (linear model, effect size of
330 rhizodeposition \sim drought intensity, $F_{1,7} = 5.757$, $P = 0.048$). This indicates that carbon
331 inputs may be augmented under low to moderate water stress, but this becomes less
332 likely under more extreme and prolonged water stress, perhaps after a threshold level of
333 water stress has been reached. Similar patterns have been shown with other root
334 responses to drought, for example fine root length and the live-to-dead ratio of fine
335 roots were shown to increase under moderate drought, but then decrease with further
336 water stress in beech saplings (*Fagus sylvatica*) (Zang et al. 2014). It has been
337 suggested that fine root production may initially compensate for root mortality, but that
338 root growth stops in extreme drought conditions (Brunner et al. 2015; Gaul et al. 2008),
339 and this level of drought may be when the soil water matrix potentials approaches -0.12
340 MPa (Gaul et al. 2008). This definition of extreme drought is used later when

341 considering the interactions between rhizodeposition and microorganisms under
342 different drought regimes (Fig. 4).

343 Our analysis hints at a split in responses between dicots and monocots, therefore
344 future studies to investigate if there are differences in rhizodeposition responses to
345 drought between these two groups of plants are warranted. For the studies we have
346 analysed here, rhizodeposition per gram of plant is either decreased or unaffected by
347 water stress for dicots, however for monocots it is either unaffected or increased (Table
348 1). Similarly, there may be differences in responses between plants in natural versus
349 agricultural systems. We found that cultivated species appeared quite resistant to
350 drought with regard to rhizodeposition per gram of plant, with no negative effects
351 reported, and most species showing no change. For wild species, rhizodeposition per
352 gram of plant was more affected by water stress, with negative impacts reported for
353 some species (Table 1). For this comparison, species included as “cultivated” were the
354 crops *Brassica napus*, *Triticum aestivum*, *Zea mays*, *Glycine max*, plus *Medicago sativa*
355 *Lolium perenne* and *Agropyron cristatum* which are commonly grown for forage.

356 With such a small sample of studies it is not yet possible to be definitive about
357 these findings, or indeed about the overall impacts of drought on rhizodeposition, and in
358 fact it seems that water stress has different effects depending on the plant species or
359 variety involved. Interspecific differences in responses can be best shown by studies in
360 which the same drought treatment has varying effects on different species, for example
361 by increasing exudation of *Lolium perenne* and *Festuca arundinacea*, and having no
362 effect on *Medicago sativa* (Sanaullah et al. 2012). The reasons for these species
363 differences may relate to differences in species strategies for responding to stress
364 (stress-avoiding versus stress-tolerating), and also differences in root traits, for example,
365 *M. sativa* is a legume species, therefore has different requirements for soil nutrients. It
366 may also be expected that more diverse plant communities will have greater
367 rhizodeposition, as there is some evidence that root biomass increases with plant
368 diversity (Mommer et al. 2015; Ravenek et al. 2014).

369 There may be changes in composition of rhizodeposits in response to drought.
370 *Brassica napus* seedlings grown in an axenic system with 24 hours of water stress
371 showed a shift in the composition of soluble organic carbon towards a lower proportion
372 of amino acids (7% in droughted plants compared to 28% in controls) and exuded more
373 sterols per root dry mass and a higher number of types of polar lipids (Svenningsson et
374 al. 1990). Crested wheatgrass (*Agropyrum cristatum*) undergoing a 35 day drought

375 treatment in axenic conditions had increased levels of succinic acid in the rhizodeposits
376 (Henry et al. 2007), and amongst two varieties of maize (*Zea mays*) grown in
377 hydroponics, water stress induced by exposure to a polyethylene glycol (PEG) solution
378 for 24 hours led to an increase in the amount of organic acids in rhizodeposits, and in
379 the more drought tolerant variety there was found to be higher concentrations of
380 proteases and catalases (Song et al. 2012).

381 More information about the effects of drought on rhizodeposits composition is
382 needed as changes in the quality of rhizodeposits (i.e. how easily they can be used as an
383 energy source) may help to explain microbial responses, and even shape microbial
384 community structure (as discussed in the following section). These types of questions
385 may benefit from the use of metabolomics techniques, which are now being adapted for
386 use with rhizodeposits and will help assess how specific compounds link plants to their
387 rhizosphere community (van Dam and Bouwmeester 2016). It is important to remember
388 that changes in rhizodeposition reflect only one way that plants respond to drought, and
389 should be considered amongst other plant responses. Overall, drought appears to
390 increase rhizodeposition per gram of plant, but when taking into account the likely
391 concurrent decrease in plant biomass, the effect on the carbon inputs to the soil and
392 overall soil C sequestration may not be so marked.

393

394 **Effects of rhizodeposits on microorganisms**

395 The variability of the effects of drought on rhizodeposition may make it difficult to
396 anticipate how a particular plant species or community will respond to drought,
397 however, effects of rhizodeposition on microorganisms are far more predictable.
398 Therefore information about rhizodeposition responses for a given plant species or
399 community may enable predictions about the impacts on soil microorganisms beneath
400 those plant communities.

401 Rhizodeposition effects on soils can be studied in the field by trenching (cutting
402 the roots from a channel of soil around the base of a tree) and girdling (removing a strip
403 of bark from the entire circumference of the trunk, disrupting phloem transport). In
404 general, rhizodeposition increases microbial biomass due to the additional inputs of
405 carbon into the soil (Paterson 2003). Such experiments have consistently shown positive
406 correlations between the amount of rhizodeposition (often shown by total organic
407 carbon in the soil) and microbial biomass (Dannenmann et al. 2009; Zeller et al. 2008)
408 and soil respiration (Högberg et al. 2001; Subke et al. 2004). Positive correlations

409 between root mass or activity and soil microbial biomass have also been shown in
410 studies on forest die-back which compare living and dead trees (Xiong et al. 2011), and
411 in studies comparing soil containing living roots with bare soil (Loeppmann et al. 2016)
412 and comparisons of rhizosphere soil with bulk soil (Finzi et al. 2015).

413 The effect of rhizodeposition on soil communities has also been studied in the
414 lab, where solutions containing the compounds found in rhizodeposits can be added to
415 soils in microcosms. These experiments have shown similar responses to the trenching
416 and girdling experiments, such as an increase in microbial biomass and phosphatase
417 activity in the rhizosphere of *Lolium perenne* (Paterson et al. 2007), and a 450%
418 increase in the number of cultivatable bacteria following addition of maize root
419 mucilage to soil (Benizri et al. 2007).

420 It is well established that the composition of rhizodeposits is specific to different
421 plant species, and that this in turn can affect the structure and function of microbial
422 populations associated with the rhizosphere (Berg and Smalla 2009). In general,
423 rhizodeposits appear to have different effects on bacteria and fungi. Changes in
424 microbial community structure, towards dominance of fungi over bacteria, have been
425 shown by experimental addition of compounds commonly found in rhizodeposits
426 (Griffiths et al. 1999). Also, a comparison of the microorganisms found below
427 *Arabidopsis thaliana* and *Medicago truncatula*, showed that an increase in fungal
428 diversity (and biomass) was due to specific C compounds having differing effects on the
429 relative abundance of fungal species (Broeckling et al. 2008). Another study
430 demonstrated that rhizosphere bacterial community structure was significantly affected
431 by the composition of rhizodeposits produced by four different plant species (Haichar et
432 al. 2008). A change in fungal: bacterial ratio may affect a range of ecosystem processes,
433 such as carbon sequestration (due to slower turnover of fungi), a change in soil
434 aggregation (as fungi tend to increase aggregation via mechanical and chemical means)
435 and litter decomposition (as fungi are able to decompose lignin while bacteria are not)
436 (Boer et al. 2005; Guggenberger et al. 1999; Six et al. 2006; Strickland and Rousk 2010;
437 Van Der Heijden et al. 2008).

438 Rhizodeposition may also have differing impacts on microorganisms dependent
439 on whether they are r- or K-strategists. The easily degraded, low-molecular compounds
440 that are released from roots are quickly consumed by fast-growing r-strategists, so may
441 respond quickly to changes in the amount of rhizodeposition. In contrast, slow-growing
442 K-strategists are less well adapted to utilising rhizodeposits (Fierer et al. 2007;

443 Loepmann et al. 2016), and may therefore be more resistant to changes in this carbon
444 source. Soil microbial communities have generally been found to contain a large
445 amount of functional redundancy, and it has been suggested that any initial loss of soil
446 species richness is unlikely to impact soil carbon cycling (Nielsen et al. 2011).
447 However, studies addressing this question are still relatively uncommon therefore the
448 identification of general responses and feedbacks of microbial functional types to
449 changes in rhizodeposition may still assist with predictions of soil community
450 sensitivity under water stress.

451 Changes in rhizodeposition may also impact soil fauna, as studies using ^{13}C
452 labelling and natural abundance stable isotopes have shown that soil animals get most of
453 their carbon from the roots (either directly or indirectly), and not from the leaf litter as
454 previously believed (Pollierer et al. 2007; Scheunemann et al. 2015). Also, carbon
455 derived from root exudates has been shown to reach the third trophic level (predatory
456 mites) via soil microorganisms (Ruf et al. 2006).

457

458 **Role of plant-soil microbe interactions in ecosystem resilience**

459 The capacity for an ecosystem to recover from a disturbance, such as drought, is called
460 its resilience (Holling 1973) and depends on the resilience of its component parts,
461 including plants and soils. Plant species show varying levels of resilience and resistance
462 (the ability to remain unchanged) to water stress, and survival and recovery is strongly
463 linked to the individual's capacity to maintain membrane stability (Chaves and Oliveira
464 2004) and is somewhat independent from the soil community. Microbial community
465 structure and function have been shown to be more resistant and resilient to changes in
466 precipitation compared with plants (Cruz-Martinez et al. 2009; Curiel Yuste et al. 2014;
467 Williams 2007). This high soil microbial resilience is due to a complex mixture of biotic
468 and abiotic factors including their functional redundancy, rapid growth and high
469 adaptive capabilities (Griffiths and Philippot 2013; Shade et al. 2012) and the ability of
470 some microorganisms to synthesise protective chemicals that can increase tolerance to
471 osmotic stress (Schimel et al. 2007). However, a meta-analysis found evidence that
472 differences in soil microbial composition remain evident for a few years following
473 disturbance (Allison and Martiny 2008). There is evidence that the extent of soil
474 community changes may vary depending on the long-term climate of a habitat (Averill
475 et al. 2016; Clark et al. 2009), and that resistance of soil microbial communities may be
476 greater in habitats that are more prone to extremes of precipitation (Evans and

477 Wallenstein 2012; Hawkes and Keitt 2015). This is presumably due to selection
478 pressures during initial soil microbial community assembly (Curiel Yuste et al. 2014).
479 For example, drying-rewetting cycles did not affect bacterial composition in a drought-
480 prone grassland, but did in an oak forest which experiences water stress less frequently
481 (Fierer et al. 2003).

482 Such drought-adapted soil communities may confer advantages on plants in
483 those soils and allow them to maintain processes such as rhizodeposition. For example,
484 populations of *Brassica rapa* grown under drought conditions were shown to maintain
485 higher fitness when grown in association with a drought adapted microbial community
486 (Lau and Lennon 2012). Additionally, plant growth promoting (PGPR) bacteria can
487 stimulate plant growth via a range of mechanisms including nitrogen fixation,
488 production of phytohormones and nutrient solubilisation, and indirectly through
489 pathogen suppression (Bais et al. 2006; Bulgarelli et al. 2013). PGPR bacteria may
490 therefore contribute to improving plant adaptation to drought and have been shown to
491 increase above-ground growth of various species under water stress including
492 grapevines (Rolli et al. 2015), tomato and pepper seedlings (Mayak et al. 2004) pea
493 (Belimov et al. 2009) and drought sensitive pepper (Marasco et al. 2012). Ethylene is a
494 phytohormone that is produced by plants under a range of stresses, including drought,
495 and inhibits plant growth. Some microorganisms can interfere with ethylene production,
496 by producing the enzyme ACC deaminase, thus maintaining plant growth (Bulgarelli et
497 al. 2013; Glick et al. 2007).

498 In addition to effects of microbes on plants, changes in the amount or
499 composition of rhizodeposits by water-stressed plants may affect soil microbial
500 community composition through recruitment or population increases of microorganisms
501 that are drought tolerant. There is evidence of changes in rhizodeposits leading to
502 changes in soil communities (Bakker et al. 2013; Bulgarelli et al. 2013). For example,
503 experimental application of different glucose substrates to microcosms altered the soil
504 bacteria community composition (Eilers et al. 2010). In light of our observation that
505 plants are able to respond to moderate drought by increasing relative levels of
506 rhizodeposition (per gram of root biomass), high resistance of soil communities may be
507 linked to the presence of plants with this capacity. For example, there may be fewer
508 negative effects for the soil microorganisms under plants that can maintain or up-
509 regulate rhizodeposition, as the relative increase in C inputs may offset any decrease in
510 living root biomass. Conversely for plant species that cannot increase rhizodeposition in

511 response to drought, changes in soil microbial communities may be more likely to
512 occur. In Figure 4 we summarise the direct and indirect (via rhizodeposition) effects of
513 moderate and extreme drought on microbial communities, and how this may impact
514 ecosystem resistance and resilience.

515

516 **Conclusions**

517 In this review we found that the overall trend is for drought to lead to an increase in
518 carbon release per gram of plant, however it is clear that water stress produces varied
519 responses in rhizodeposition. The ability of plants to maintain rhizodeposition may be
520 largely mediated by the drought tolerance of the particular plant species or community
521 involved. The consequent effects of water stress on plant biomass are also important, as
522 an increase in root growth is expected under moderate drought, which would lead to
523 increased rhizodeposition. This indicates that it may be important to maintain diversity
524 in plant communities in order to ensure some resistant species are present and soil
525 inputs through rhizodeposition can continue. However, there are currently very few
526 studies investigating this link between plant diversity and rhizodeposition inputs into
527 water stressed soils, and this represents an opportunity for future work.

528 Clearly, much more information about the effects of water stress on
529 rhizodeposition is needed in order to assess which habitats are most at risk from
530 increased drought. It does not seem possible to generalise on the basis of individual
531 plant species, therefore this should be a research focus, particularly now that methods
532 are becoming available to provide this information in field situations. There may be
533 differences in responses between natural and agricultural systems, and we have shown
534 preliminary indications that crop species may be able to maintain rhizodeposition (per
535 gram of plant) better than wild species. There may also be opportunities for particular
536 plant species to be cultivated or promoted in order to protect ecosystems from drought
537 effects, such as in agricultural ecosystems. Also, agricultural systems tend to be much
538 less nutrient limited, which may change how rhizodeposition responds to drought
539 (Baptist et al. 2015; Bardgett et al. 2013; Henry et al. 2007). Therefore, forthcoming
540 research should investigate the interaction between soil nutrients and water stress in
541 order to better predict how systems of different soil fertility will respond, and if there
542 are ways to mitigate drought impacts by altering the soil nutrient status. As agricultural
543 land is often irrigated, and nutrients may be added at similar set concentrations between

544 farms, there may be a narrower range of possible interactions of soil water and soil
545 nutrient status, making this a simpler study system.

546 Future work should also concentrate on assessing changes in the composition of
547 rhizodeposits and determining if there are threshold levels of drought which provoke
548 large changes in rhizodeposition, as it appears that the intensity of water deficit is also
549 important in controlling plant responses. In all of these examples of directions for
550 upcoming research, studies should aim to use drought treatments that are realistic,
551 quantifiable and reproducible, in order to be of maximum usefulness. Care should be
552 taken to measure impacts on plant biomass (both root and shoot) and to present
553 rhizodeposition as the amount of carbon inputs per individual or unit area, and also
554 standardised by plant biomass.

555 Overall, there may be large changes in the quantity and composition of soil
556 inputs under water stress and such differences may have knock-on effects on microbial
557 communities. It is therefore important to further investigate the role of rhizodeposition
558 as an important driver of soil microbial community change under drought.

559

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565 **Figures**

566

567 **Fig. 1** Schematic diagram showing interactions between rhizodeposits, soil
568 microorganisms and soil organic matter. Under moderate and short-term drought
569 conditions, if rhizodeposition increases (as was shown to be generally the case) there
570 could be increases in the amount of carbon released into the soil, leading to a positive
571 feedback loop with the microbial community. SOM decomposition may be increased
572 both through the direct effect of higher enzyme release from rhizodeposition, and
573 indirectly via the microbial community. During more severe or longer-term drought the
574 positive feedback loop would stop due to cessation of root growth, or even root death

575

576 **Fig. 2** Rhizodeposition per individual, shown as the effect size $-\ln(\text{treatment mean} /$
577 $\text{control mean})$ – separated by the method used (pulse labelling, continuous labelling and
578 direct measurement) and ordered by the intensity of the drought treatment (duration of
579 treatment multiplied by the reduction in water relative to the control), with the values
580 for this metric shown below each bar. Bars represent data from the nine studies from
581 Table 1, and for studies with data for multiple species bars are shown touching each
582 other. Asterisks (*) show a significant effect ($P < 0.05$) of drought on rhizodeposition,
583 as stated in the original article, and NS denotes no significant effect

584

585 **Fig. 3** Rhizodeposition per gram of plant, shown as the effect size $-\ln(\text{treatment mean}$
586 $/ \text{control mean})$ – separated by the method used (pulse labelling, continuous labelling
587 and direct measurement) and ordered by the intensity of the drought treatment (duration
588 of treatment multiplied by the reduction in water relative to the control), with the values
589 for this metric shown below each bar. Bars represent data from the nine studies from
590 Table 1, and for studies with data for multiple species bars are shown touching each
591 other. Asterisks (*) show a significant effect ($P < 0.05$) of drought on rhizodeposition,
592 as stated in the original article, and NS denotes no significant effect. † Note that for
593 Henry *et al.* (2007) total biomass was estimated rather than measured directly, and for
594 Somasundaram *et al.* (2009) rhizodeposition was calculated per gram of shoot biomass

595

596

597 **Fig. 4** Schematic diagram showing how interactions between rhizodeposition and the
598 microbial community affect ecosystem resistance and resilience under moderate and

599 extreme drought. Extreme drought refers to water stress leading to large-scale root
600 mortality without replacement from new root growth. Under moderate drought there are
601 more likely to be positive relationships (+) between drought, rhizodeposition, microbial
602 community. Under more extreme droughts, relationships may be more variable and less
603 predictable (+/-) but positive relationships are unlikely to be maintained over prolonged
604 periods of time.

Table 1 Summary of drought effects on rhizodeposition. Studies are listed in chronological order (1 – Svenningsson *et al.*, 1990, 2 – Palta and Gregory, 1997, 3 – Gorissen *et al.*, 2004, 4 – Henry *et al.*, 2007, 5 – Somasundaram *et al.*, 2009, 6 – Sanaullah *et al.*, 2012, 7 – Zhu and Cheng, 2013, 8 – Fuchslueger *et al.*, 2014, 9 – Canarini & Dijkstra, 2015). The effects of drought on plant biomass and rhizodeposition (per individual and per gram of plant) are shown by the following symbols: ↑ is an increase, ↓ is a decrease and = shows no significant difference. The effect size – calculated as $\ln(\text{treatment mean} / \text{control mean})$ – is shown beneath each symbol. The effect on plant biomass is normally reported for total biomass unless not stated in the original article. For Sanaullah *et al.* (2012) effect of drought is reported separately for shoot and root, but rhizodeposition is calculated per gram of total plant biomass. † Note that for Henry *et al.* (2007) total biomass was estimated rather than measured directly, and for Somasundaram *et al.* (2009) rhizodeposition was calculated per gram of shoot biomass. Abbreviations: SWC = soil water content, FC = field capacity.

Species (age)	Drought treatment / control treatment	Drought duration	Method of measurement	Effect on plant biomass (plant biomass measured)	Effect on rhizodeposition effect size	
					per individual	per gram of plant
<i>Brassica napus</i> ¹ (25 days)	No water / optimum water	1 day	Direct measurements in lab (axenic conditions)	= (total)	= 0.747	= 0.740
<i>Triticum aestivum</i> ² (64 days)	3.9% SWC / 7.1% SWC	56 days	¹³ C pulse labelled in pot	↓ (total)	↓ -0.521	= -0.145

<i>Calluna vulgaris</i> ³ (multiple years old)	52% lower rainfall / normal rainfall	56 days	¹⁴ C pulse-labelled in field (UK)	= (total)	↓ -0.615	↓ -0.629
<i>Calluna vulgaris</i> ³ (multiple years old)	97% lower rainfall / normal rainfall	56 days	¹⁴ C pulse-labelled in field (Denmark)	= (total)	↓ -1.376	↓ -1.025
<i>Agropyron cristatum</i> ⁴ (70 days)	75% less water / optimum water	35 days	Direct measurements in lab (axenic conditions)	↓ (shoot only - marginal)	= 0.326	↑† 0.519
<i>Zea mays</i> ⁵ (21 days)	-100 kPa Ψ_{soil} / -20 kPa Ψ_{soil}	21 days	¹³ C pulse labelled in pot	↓ (shoot only)	↑ 1.185	↑† 2.545
<i>Lolium perenne</i> ⁶ (70 days)	30% FC / 70% FC	40 days	¹⁴ C pulse-labelled in pot	= / = (shoot / root)	↑ 1.040	↑ 1.975
<i>Festuca arundinacea</i> ⁶ (70 days)	As above	As above	As above	↓ / = (shoot / root)	↑ 0.566	↑ 1.661
<i>Medicago sativa</i> ⁶ (70 days)	As above	As above	As above	↓ / = (shoot / root)	↑ 0.108	= 0.292
Mixture of previous three species ⁶ (70 days)	As above	As above	As above	= / ↓ (shoot / root)	↑ 0.500	↑ 2.093

<i>Helianthus annuus</i> ⁷ (67 days)	10% SWC / 25% SWC	12 dry-rewetting cycles (3 days each)	¹³ C continuously- labelled in pot	↓ (total)	↓ -0.755	= -0.309
<i>Glycine max</i> ⁷ (68 days)	16% SWC / 25% SWC	12 dry-rewetting cycles (3 days each)	¹³ C continuously- labelled in pot	= (total)	= 0.039	= 0.128
Mountain meadow - mostly perennial grasses and herbs ⁸ (multiple years)	14.1% SWC / 38.8% SWC	56 days	¹³ C pulse labelled in field	= (total)	↑ 1.486	↑ 1.504
<i>Triticum aestivum</i> ⁹ (~68 days)	30% FC / 60% FC	21 days	¹³ C continuously- labelled in pot	↓ (total)	↓ -0.981	= -0.012

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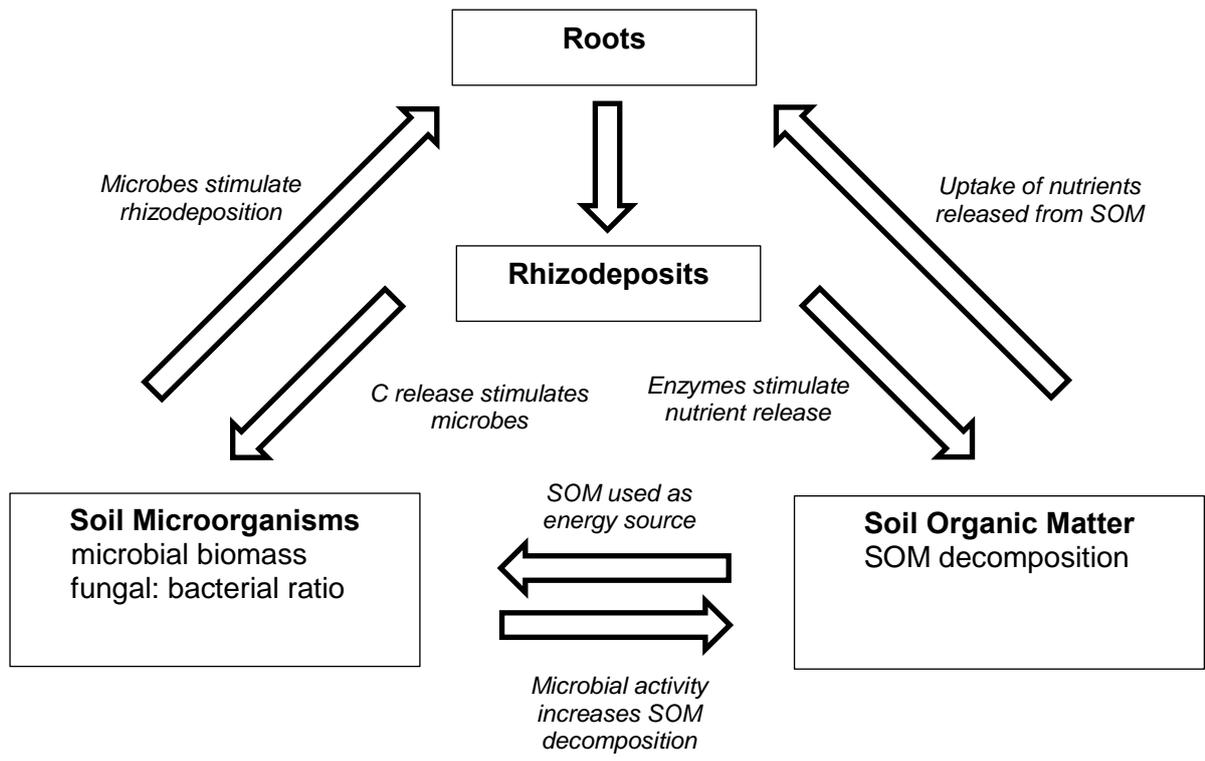
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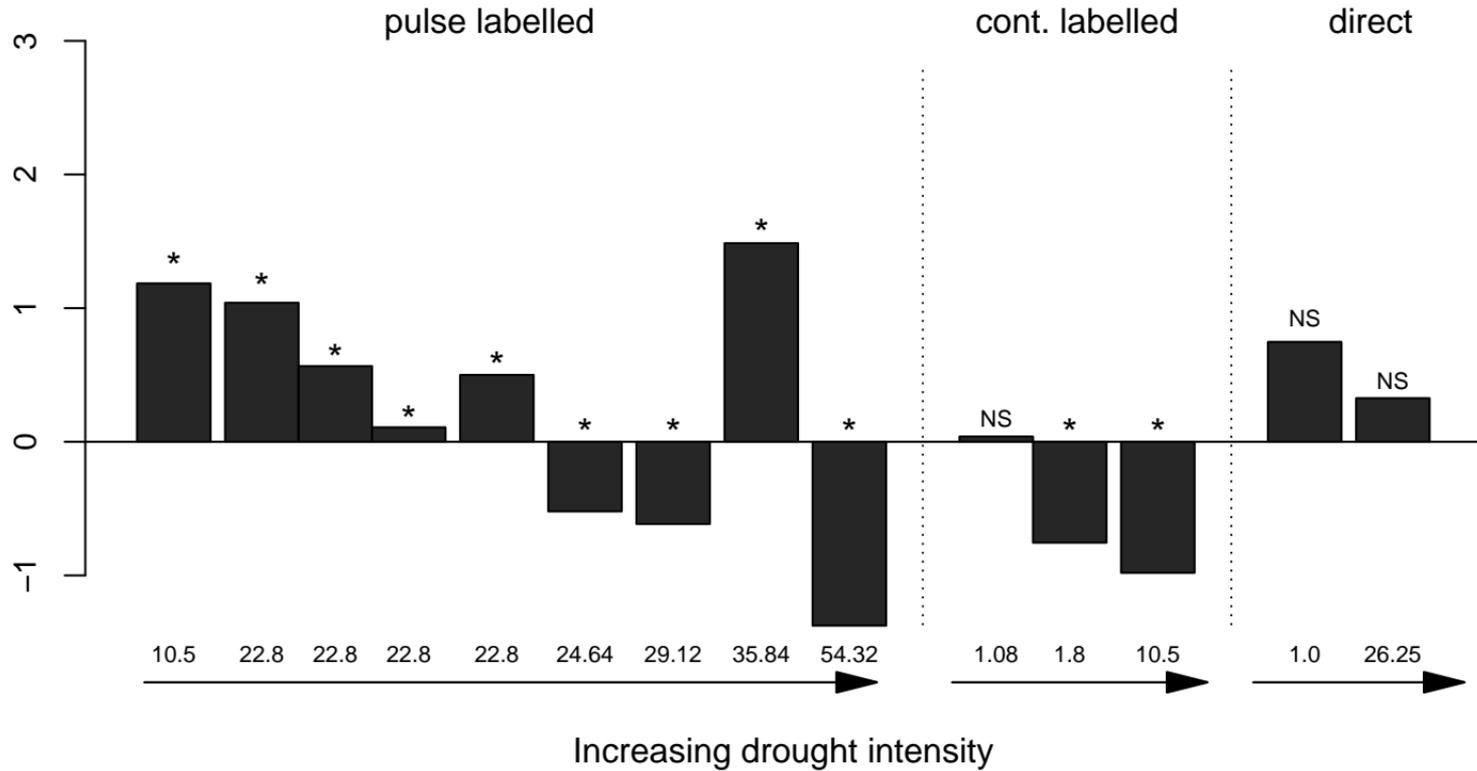
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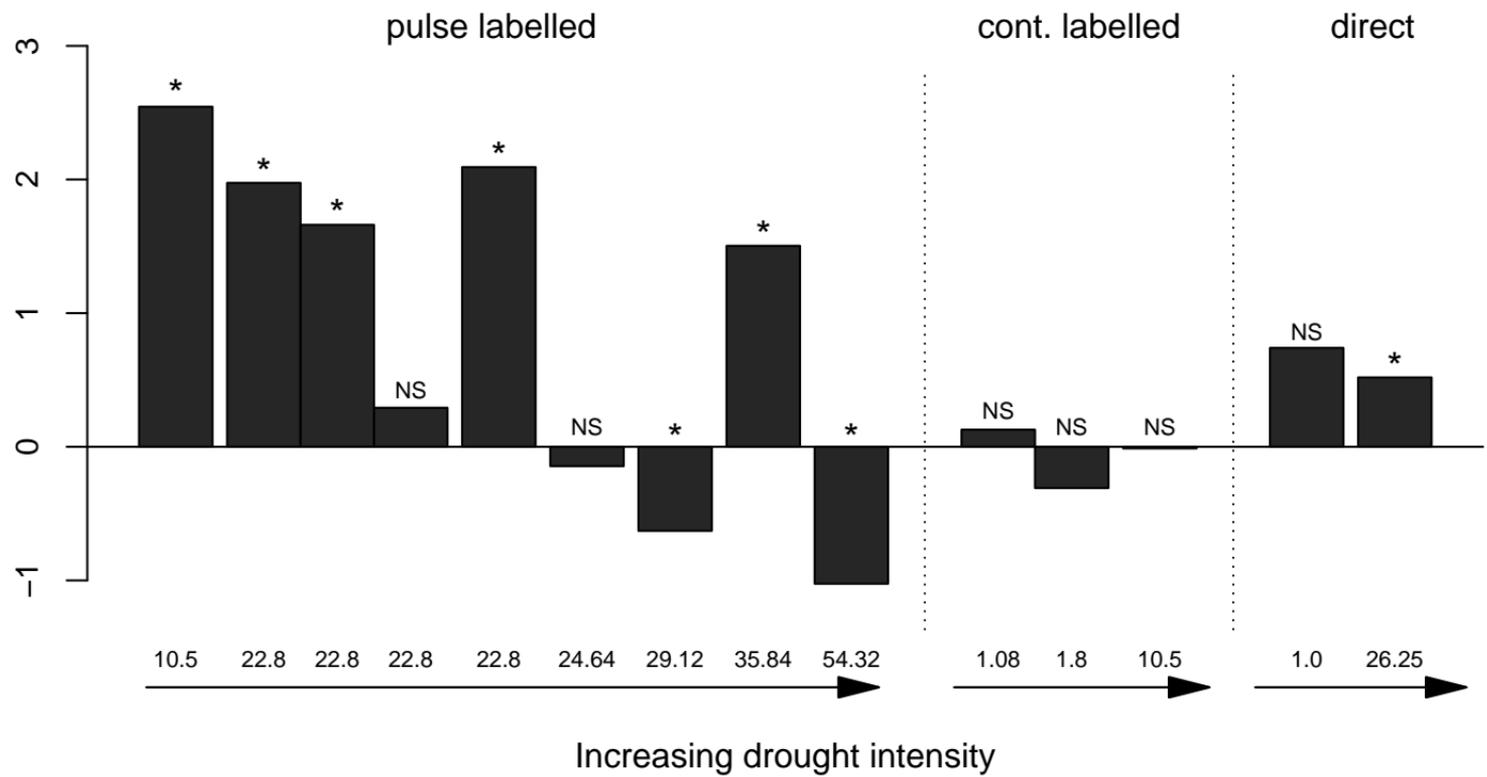
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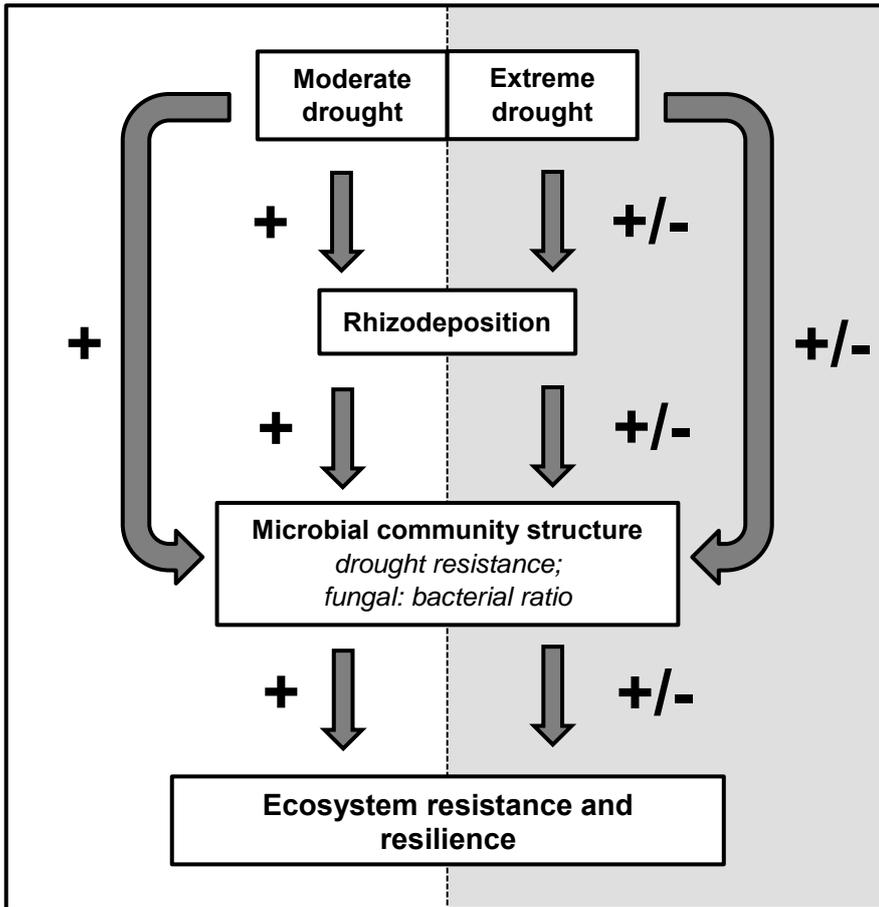


Effect size (rhizodeposition per individual)



Effect size (rhizodeposition per gram of plant)





Electronic Supplementary Material

Fig. S1. (a) Rhizodeposition per individual and (b) rhizodeposition per gram of plant, as the logged effect size, plotted against the intensity of drought (duration \times reduction in water). Each point represents data from the nine studies from Table 1, and for studies with data for multiple species, different species are shown as separate points. Studies are colour-coded by the method used to measure rhizodeposition: white – direct measurements, light grey – pulse labelling, dark grey – continuous labelling.

