Rewetting of soil: Revisiting the origin of soil CO2 emissions

Romain Barnard, Steven Blazewicz, Mary Firestone

HAL Id: hal-03137091
https://hal.inrae.fr/hal-03137091

Submitted on 16 Jun 2022

1

2

3 **Rewetting of soil: revisiting the origin of soil CO₂ emissions**

4

5 Romain L. Barnard[1*], Steven J. Blazewicz[2], Mary K. Firestone[3]

6

7

8 [1] Agroécologie, AgroSup Dijon, INRAE, Univ. Bourgogne, Univ. Bourgogne Franche-Comté,

9 F-21000 Dijon, France

10

11 [2] Lawrence Livermore National Laboratory, 7000 East Avenue, Livermore, CA 94550, USA

12

13 [3] Department of Environmental Science, Policy and Management, University of California,

14 Berkeley, 140 Mulford Hall, Berkeley CA 94720, USA

15

16

17

18 *Corresponding author:

19 Romain Barnard, romain.barnard@inrae.fr, phone +33 380 69 37 45

Abstract

Rewetting dry soils is associated with a burst of microbial activity and mineralization, which manifests itself as a pulse in soil CO_2 emissions, long-known as the Birch effect. In arid and semi-arid systems, soil CO_2 losses upon rewetting at the end of extended dry periods can contribute a significant fraction to the overall carbon (C) budget. Microbial biomass is one of the sources of mineralized C, as was demonstrated over 30 years ago (Kieft et al., 1987). The present paper offers a perspective on how the field has progressed since the 1987 paper was published in *Soil Biology & Biochemistry*, what it means in terms of current concerns about global climate change, and the needs and potential emphases of future research. Many studies since 1987 have addressed the origin of this CO_2 pulse, finding multiple possible C sources involving both biotic and abiotic processes. We propose that the magnitude of the rewetting event ($\Delta\psi$) determines the relative contribution from the array of substrates that contribute to the soil CO_2 pulse upon rewetting. The magnitude of the CO_2 pulse is likely related to soil physical characteristics and to the size of the available C pool, which is partly controlled by plants. Further, the relative contributions of the mechanisms generating soil CO_2 pulses upon rewetting are likely to be modified by climate change. To understand and predict the magnitude of soil CO_2 pulses upon rewetting, we advocate continued cross-disciplinary research involving soil microbial ecology, soil physics, soil chemistry, as well as increased integration and recognition of the importance of plant-soil interactions in controlling the soil C pools contributing to soil CO_2 pulses.

Introduction

The ecology of soil rewetting is especially relevant to drylands, which include arid, semi-arid and dry sub-humid subtypes. Drylands represent 45% of terrestrial surface (i.e. 66.7×10^6 km^2) and carry 39% of the world population (Prăvălie, 2016; Huang et al., 2017; Plaza et al., 2018). Soil wet-up is particularly important for terrestrial ecosystems in Mediterranean and savanna climates that experience sustained periods of very low or no rainfall, followed by significant rainfall. Mediterranean climates (dry summers and wet winters) occur between 30° and 45° latitude and are found in Africa, Europe, western South America, Southwest and West Australia, and western North America, for a total area of ∼3×10^6 km^2. Savanna climates occur between and 25° and 30° latitude, and include almost half the surface of Africa, large areas of Central & South America, eastern India, southeast Asia, eastern and northern Australia, totaling ∼33×10^6 km^2.

Rewetting of dry soil can have global consequences. At the ecosystem scale it results in a large soil CO_2 efflux pulse, also known as the Birch effect, named after H.F. Birch who reported mineralization peaks upon rewetting soils in East Africa (Birch, 1958). However, the phenomenon had already been documented 35 years earlier by soil microbiologists (Waksman and Starkey, 1923; Winogradsky, 1924). Its putative mechanisms at the soil microbial scale started gaining attention in the 1980s (Bottner, 1985). The sudden increase in microbial activity upon rewetting triggers a burst in carbon (C) and nitrogen (N) mineralization (Miller et al., 2005; Xiang et al., 2008; Borken and Matzner, 2009; Dijkstra et al., 2012). The amount of C emitted due to rain pulses is comparable in magnitude to the net annual CO_2 exchange of many terrestrial ecosystems (Xu et al., 2004). In ecosystems that are characterized by distinct dry-wet seasons, the CO_2 pulses associated with rewetting can represent a large part of the annual C budget (Jarvis

67 et al., 2007; Ma et al., 2012; Rey et al., 2017). For example, following intense rainfall, up

68 to 20 % of the annual CO_2 flux from soil to atmosphere occurred in an African savanna

69 ecosystem (Fan et al., 2015). While a rapid change in soil water potential results in an

70 overall microbial reactivation, it exposes soil microorganisms to a radical change in

71 environmental conditions. The soil dry-down and subsequent rewetting provide such an

72 extreme change in microbial environment, that bacterial and fungal death commonly

73 results (Blazewicz et al., 2014; Blazewicz et al., 2020).

74   The 1987 study by Kieft et al. was designed to investigate the fate of soil microbial

75 biomass C after the rapid rewetting of a dry soil. Using two Californian soils from a

76 Mediterranean-type climate, Kieft and his colleagues found a net loss of microbial biomass

77 C upon rewetting, that could be due to the death of microbial cells or the rapid

78 decomposition of the microbial solutes; the authors favoured the latter explanation.

79 Mechanisms of C loss, the nature of the lost C, and changes in microbial community

80 composition or relation to biogeochemical functioning were not investigated. However,

81 by opening the microbial 'black box' in the general context of dry-wet cycles, this study

82 brought attention to the large influence that rapid increases in soil water content can

83 exert on microbial and terrestrial ecosystem functioning. Exploration of the processes

84 comprising the Birch effect has been a particularly active field of research lately, as global

85 change impacts precipitation cycles worldwide. In many regions, especially under

86 Mediterranean climates, more extreme climate conditions increase the contrast between

87 dry and wet conditions to which ecosystems are exposed. It has been more than three

88 decades since the Kieft et al. study was published; here we provide a perspective on the

89 current status of the field, its importance in the context of global change, and areas in need

90 of more research.

91

What is wet-up and where does it occur?

92

93   We use the term wet-up to describe a real or simulated precipitation input of liquid
94   water to dry soil causing a large and rapid change in soil water potential ($\Delta\psi$). The
95   magnitude of the change in water potential is a determinant of the size of the resulting
96   soil CO_2 efflux pulse (Lado-Montserrat et al., 2014). Here we suggest that the addition of
97   liquid water to a very dry soil causes CO_2 pulses that differ not only in rate/magnitude but
98   also in available carbon sources and impact on microbial physiology and survival
99   depending on the magnitude of the water potential increase. Since soil wet-up includes a
100   prominent biological component, we focus on the biologically active zone of the soil, i.e.
101   between 0 and ~50 cm depth; this zone can experience rapid rewetting from very dry
102   conditions, depending on presence of macropores, surface cracking, and soil texture.
103   While we will not concentrate on other inputs of moisture in this article, it is important to
104   note that in arid and semi-arid ecosystems, several other processes can introduce
105   moisture to dry surface soil. For example, surface litter decomposition occurs in response
106   to fog and dew events and even as a result of high relative humidity, particularly in
107   combination with UV-mediated degradation of exposed surface litter (Dirks et al., 2010;
108   Jacobson et al., 2015). Adsorption of water from atmospheric humidity has been
109   demonstrated to extend into soil (perhaps to a depth of 5 cm) over a range of atmospheric
110   relative humidity (20-60%) and to stimulate CO_2 production (McHugh et al., 2015). Thus,
111   transient episodes of decomposition at or near the soil surface occur in arid and semi-arid
112   ecosystems in response to non-precipitation events (fog, dew, sorption from atmospheric
113   humidity) and can drive CO_2 fluxes that are significant in ecosystem C budgets (Dirks et
114   al., 2010). Recognition and understanding of the importance of these alternative means of
115   increasing soil moisture (non-rainfall) has developed over the past 30 years and are
116   important advances in the subject.

117   We present a perspective that primarily addresses rewetting dynamics of soil near

118   the soil surface and in the rooting zone of shallow-rooted plants. Under laboratory

119   conditions, drying-rewetting cycles resulted in the release of "old" C from soil layers

120   below 20 cm (Schimel et al., 2011). While macropore flow of incident rain water might

121   result in the wet-up of soil deeper than 20 cm, rapid rewetting of soil by rainfall will be

122   most important near the surface of soil and generally play a less important role in the

123   mobilization of deep old soil carbon.

124

125   **C released upon rewetting: origin and mechanisms**

126   The CO_2 pulse upon rewetting typically exhibits a pattern of very high rates during

127   the first minutes and hours after rewetting and this response declines over time (Kim et

128   al., 2012). The origin of the CO_2 pulse upon rewetting soil can be both abiotic and biotic.

129   Abiotic processes include solubilization of carbonates (depending on carbonate

130   concentration in soils), CO_2 displacement from the soil pores to the atmosphere by water,

131   as well as the quantitatively low degassing of CO_2 dissolved in rain and soil degassing due

132   to the decrease in barometric pressure over time (Lee et al., 2004; Barnard et al., 2015).

133   However, in non-carbonate-rich soils, abiotic processes generate less CO_2 than do the

134   biotic processes, which are the main contributors of the soil CO_2 pulse upon rewetting.

135   The nature and sources of the C compounds that are mineralized upon rewetting a dry

136   soil has been extensively explored and somewhat fervently argued. Here we highlight the

137   most prevalent sources and mechanisms that fuel the C mineralization pulse: compatible

138   solutes; microbial necromass; changes in water film connectivity; sustained extracellular

139   enzyme activity during dry-down; C desorption from mineral surfaces; and disruption of

140   aggregates. Each of these is discussed below.

141   Compatible solutes, accumulated by microbial cells in response to drying, were

142   suggested by Kieft et al. (1987) as candidate compounds fueling the soil CO_2 efflux pulse;

143   this substrate pool was also addressed by later studies (Halverson et al., 2000; Fierer and

144   Schimel, 2003; Schimel et al., 2007). Soil microorganism accumulation of compatible

145   solutes within their membrane-bound cells reduces cell dehydration, but cells are

146   required to rapidly dispose of them upon rewetting, or face membrane rupture

147   (plasmoptysis). These processes will release solutes, such as proline, glutamine, glycine

148   betaine, and trehalose into the soil (Kempf and Bremer, 1998; Halverson et al., 2000;

149   Welsh, 2000; Warren, 2019) and these can be assimilated and mineralized rapidly by

150   other microorganisms. Some of the earlier studies focusing on the intracellular

151   accumulation of compatible solutes as soil gets drier, found no evidence for osmolytes as

152   a significant C-source (Boot et al., 2013; Kakumanu et al., 2013). More recent evidence

153   (Warren, 2014; Warren, 2016) for this mechanism however provides some support.

154   While some studies detected no increased amount of compatible solutes in the soil upon

155   rewetting (Williams and Xia, 2009; Warren, 2014), recent studies have reported an

156   accumulation of osmolytes in microbial communities during dry periods (Chowdhury et

157   al., 2019; Malik et al., 2019; Slessarev et al., 2020). The elusive nature of osmolytes may

158   be related to: (i) their low residence time in the soil, as they are produced and consumed

159   at measurable rates even in moist soils (Warren, 2019), albeit at lower rates than in dry

160   soils (Warren et al, unpubl. data); and (ii) their probable specificity to a microbial

161   community. Some microbes may not accumulate compatible solutes and instead undergo

162   passive water loss, especially under conditions of rapid drying (Potts, 1994). Possible

163   fates of these plasmolyzed cells are death from water loss, death upon rewetting, or

164   survival of both desiccation and re-wetting.

165

166   Microbial death due to the rapid water potential increase (from very negative

167   values to zero or nearly zero) upon rewetting was also invoked by Kieft et al. (1987) as a

168   possible source of C substrates. Dead microbial cells can provide mineralizable substrates

169   upon rewetting a dry soil, arising from cells that died during the previous dry-down

170   period or as a direct result of the rewetting. Evidence for this mechanism has been

171   presented by measuring gross rates of bacterial death and growth upon rewetting

172   (Blazewicz et al., 2014; Blazewicz et al., 2020). High bacterial mortality was documented

173   to have occurred within the first three hours after a rewetting event. The authors noted

174   that some of the mortality is likely to have occurred during the dry-down process but the

175   microbial necromass remained largely intact until the wet-up event.

176   Bacteriophage predation may also contribute to cell death after rewetting. Phages

177   infect a large proportion of soil bacteria (Williamson et al., 2007) and can become lytic

178   when soil conditions become favorable for the growth of their hosts (Williamson et al.,

179   2017). Indeed, viral abundance in the soil has been shown to be correlated with soil water

180   content (Williamson et al., 2005), possibly due to the effects of soil water content on

181   bacterial numbers as well as on the adsorption of viruses in the soil (Zhao et al., 2008).

182   Viral diffusion/advection is also enhanced by soil wetting, increasing the chances of virus-

183   host encounter and attachment. At this time, however, there is no direct evidence for wet-

184   up-associated predation as a significant mechanism of cell death and labile C input.

185   Similarly, eukaryotic predation may contribute to microbial mortality upon soil wetting,

186   but, to our knowledge, this has not been demonstrated.

187   Upon rewetting a dry soil, microorganisms have to access and then metabolize

188   organic substrates. Connectivity of soil water films is gradually lost as soils dry and this

189   restricts diffusional access to substrate (Manzoni et al., 2012) but enhances bacterial

190   coexistence and diversity (Carson et al., 2010) by limiting competitive exclusion (Wang

191 and Or, 2013; Šťovíček et al., 2017b). Conversely, rewetting a soil restores water film

192 connectivity (Smith et al., 2017), providing conditions for highly competitive and mobile

193 microorganisms to access substrates and to thrive, thereby generating a soil CO_2 efflux

194 pulse (see modelling study by Evans et al., 2016).

195 Another possible source of substrates during rewetting requires sustained

196 extracellular enzyme activity during dry-down (Miller et al., 2005; Schimel et al., 2017).

197 The reduction in microbial activity as soils dry can lead to a net increase in substrate that

198 may become available to soil microorganisms upon rewetting (Lawrence et al., 2009;

199 Zhang et al., 2014; Fraser et al., 2016). However, a recent study found no evidence for

200 sustained exoenzyme activity in drying soils (Homyak et al., 2018).

201 Soluble organic compounds in the soil can associate with minerals, particularly

202 during dry periods (Qualls, 2000). Upon rewetting, the desorption of organic compounds

203 from mineral surfaces can become a source of C (Blankinship and Schimel, 2018) as

204 changes in pH and ionic strength can directly affect organic matter-mineral binding

205 (Clarke et al., 2011; Newcomb et al., 2017).

206 In dryland ecosystems, photodegradation of surface litter increases the

207 breakdown of carbon compounds to substrates that can be metabolized by

208 microorganisms upon rewetting (Austin and Vivanco, 2006; Baker and Allison, 2015; Day

209 et al., 2018). Although photodegradation alone cannot explain differences in

210 decomposition rates across an aridity gradient (Brandt et al., 2010), it enhances soil CO_2

211 emissions upon soil rewetting (Ma et al., 2012).

212 Disruption of organic matter occlusion in soil aggregates is another physical

213 consequence of rewetting that can enhance substrate availability. Rewetting a dry soil can

214 break up aggregates, exposing organic substrates that were previously occluded (Denef

215   et al., 2001a; Cosentino et al., 2006; Borken and Matzner, 2009; Navarro-García et al.,

216   2012).

217   Modeling has provided solid insight into the mechanisms that drive the soil CO_2

218   pulse associated with rewetting. Most modeling studies have focused on the sources of

219   soil organic matter at a large scale (Lawrence et al., 2009) and were not designed to take

220   into account the biophysical mechanisms at the pore-scale. The gap between pore physics,

221   soil organic matter cycling and microbiology has been bridged, using empirical models

222   and simplified model systems (Moyano et al., 2013; Manzoni et al., 2016; Tecon and Or,

223   2017), yet challenges remain (Baveye et al., 2018). Recent modeling efforts support the

224   coexistence of physical as well as microbiological processes as drivers of the rewetting

225   soil CO_2 pulse (Zhang et al., 2014; Evans et al., 2016; Šťovíček et al., 2017b; Yan et al.,

226   2018).

227   The question of which C sources fuels the Birch effect has been under discussion

228   for many decades. It is an important topic in the context of global change, as rainfall

229   patterns and amounts change in areas around the globe, potentially impacting the C

230   budget of ecosystems (Kim et al., 2012; Vargas et al., 2012).

231

232   **Soil microbial response**

233   Ascribing the CO_2 released upon rewetting to a particular source of C can be akin

234   to the Indian parable of six blind men examining an elephant, each of them failing to

235   consider the multiple facets of the objective truth while experiencing it from their own

236   limited perspective. Many C sources contribute to the soil CO_2 pulse upon rewetting

237   (Unger et al., 2010; Evans et al., 2016). Apart from carbonate solubilization, CO_2 emissions

238   from the soil upon rewetting are driven by coupled biophysical or biochemical

mechanisms, in which soil microorganisms act as catalysts, conditional upon whether or not they have access to substrate.

In arid and semi-arid systems, adaptation to cyclic dry-down and rewetting enables soil functions to be carried out under alternating contrasting environmental conditions. Soil microorganisms seem to have evolved life strategies related to prolonged dry periods followed by rapid rewetting (Placella et al., 2012; Barnard et al., 2013; Evans and Wallenstein, 2014). At the seasonal scale, microbial strategies during dry-down differ from strategies during rewetting (Evans et al., 2014). Soil microorganisms that are able to sustain activity longer as soils dry down may access easily degradable organic matter under less intense competitive conditions, while the other microorganisms that are not able to maintain activity under dry conditions have already entered a state of reduced activity, or even dormancy (including formation of spores). This mechanism could support the existence of taxa (e.g. bacteria belonging to the Sphingomonadaceae, Comamonadaceae and Oxalobacteraceae; Aanderud et al., 2015) that are present in low relative abundance in the soil (Lennon and Jones, 2011; Meisner et al., 2018). The duration of the dry period can affect the response to subsequent rewetting (Barnard et al., 2015), especially in microbial communities that have not evolved in contrasting dry-wet conditions (Meisner et al., 2015; Meisner et al., 2017). For example, in soils where microbes are not adapted to drought or cyclic dry periods, a lag period before exponential microbial growth has been detected, the duration of which depended on the intensity of drying (Meisner et al., 2017). Indeed, altered precipitation patterns before rewetting impacted not only the community structure of the microorganisms that were active upon rewetting, but also of those that were not, as they were recruited into the active bacterial pool (Engelhardt et al., 2019).

263   The importance of microbial death as a source of C for the CO_2 pulse has been

264   measured using quantitative ^{18}O stable isotope probing. Upon rewetting a soil from a

265   Mediterranean climate, initial bacterial growth was detected in select taxa dominated by

266   Proteobacteria (*Azotobacter, Pseudomonas, Vibrio*) and Firmicutes (*Streptococcus,*

267   *Clostridium, Mycoplasma*) while mortality was taxonomically widespread (Blazewicz et

268   al., 2020). In addition, the density-dependence of growth upon rewetting contrasted with

269   density independence of mortality, supporting the hypothesis that population-level

270   biological interactions, such as competition and predation, likely controlled the growth

271   rates of taxa but not their death (Blazewicz et al., 2020).

272

273   A number of studies have shown differential sensitivity of soil bacterial taxa to dry-

274   down and rewetting; this differential sensitivity is conserved at phylum and class

275   phylogenetic groupings (Lennon et al., 2012; Placella et al., 2012; Barnard et al., 2013,

276   2015; Engelhardt et al., 2018). This phylogenetic coherence reflects the evolutionary

277   roots of microbial tolerance to drying and rewetting in microorganisms that are

278   indigenous to and more common in semi-arid soil systems. The functional response of

279   arid and semi-arid systems to dry-wet cycles can thus be expected to be deterministic and

280   predictable (Averill et al., 2016). The two flagship phyla are Actinobacteria, which are

281   commonly abundant in arid soils and include many taxa that are resistant to low moisture

282   conditions (Goodfellow and Williams, 1983; Zvyagintsev et al., 2007) and Acidobacteria,

283   a versatile group that can be adapted to changing environments (Eichorst et al., 2018);

284   taxa from the Acidobacteria group have been found to dynamically track soil water

285   conditions, flourishing rapidly upon rewetting (Placella et al., 2012; Barnard et al., 2013).

286   Dry-down typically increases the relative abundance of the present or potentially active

287   thick-walled, Gram-positive, high G+C content, spore-forming, and EPS-producing

bacterial groups (e.g. Actinobacteria, Firmicutes) but decreases that of thin-walled, Gram-negative or fast-growing groups such as Acidobacteria, Verrucomicrobia or Chloroflexi (Placella et al., 2012; Angel and Conrad, 2013; Barnard et al., 2013; Maestre et al., 2015; Zhou et al., 2016; Šťovíček et al., 2017a; Ochoa-Hueso et al., 2018). Upon rewetting, different bacterial groups respond on a variable timeframe that likely reflects their ability to have formed spores during the dry period, thus being potentially ready for a quick response and rapid growth (Keijser et al., 2007; Placella et al., 2012; Barnard et al., 2013; Sinai et al., 2015). Taxon-specific growth documented by quantitative stable isotope probing has shown that members of the Bacillales order of Firmicutes grew within 3h of rewetting a dry Mediterranean soil, followed in the first 24h by β-proteobacteria of the Burkholderia order (Blazewicz et al., 2020). Fungi generally display an overall greater resistance to desiccation-hydration cycles than bacteria (Bapiri et al., 2010; Curiel Yuste et al., 2011; Barnard et al., 2015), likely due to their hyphal network structure and frequent mutualistic strategies (de Boer et al., 2005), which complement other drought-resistance traits that can also be found in bacteria, such as production of extracellular polymeric substances (EPS) and heat-shock proteins (Crowther et al., 2014). As a consequence, the fungal community displays a higher stability than the overall bacterial community during dry-down and subsequent rewetting (de Vries et al., 2018).

In temperate climates, contrasting dry and wet conditions arise during a period of drought, i.e. water limitations outside the normal climatic envelope. Since the temperate soil biosphere may not be well-adapted to these extreme conditions, its response to drying and rewetting is expected to be more stochastic and less predictable than that of highly-adapted arid and semi-arid systems, although a trait-based phylogenetic framework could help predict microbial responses (Lennon et al., 2012; Amend et al., 2016). Drought legacy experiments have shown that in some systems having been

313 exposed to past drought conditions can shape the response of soil microbial communities

314 to subsequent drought or rewetting (Bouskill et al., 2013; Göransson et al., 2013; Hawkes

315 et al., 2017; Meisner et al., 2018), with consequences that can extend to soil processes

316 (Evans and Wallenstein, 2012; Martiny et al., 2017) as well as plant communities (Lau and

317 Lennon, 2012; Meisner et al., 2013; Kaisermann et al., 2017).

318   The intensity and duration of dry conditions determine the response of soils to

319 rewetting (Zhang et al., 2019). After a severe dry period, soil rewetting triggers a larger

320 CO_2 pulse (Xu et al., 2004; Cable et al., 2008; Göransson et al., 2013; Barnard et al., 2015),

321 which is consistent with a greater loss of C in carbon-rich ecosystems that experience

322 more pronounced dry-wet events (Canarini et al., 2017). Under extreme conditions (i.e.

323 dry soil for a long period of time or large $\Delta\psi$), maintaining metabolic functions upon

324 rewetting may become more challenging than under more favorable conditions and there

325 may be a greater frequency of microbial death and subsequent larger relative

326 contribution of compatible solutes to the soil CO_2 pulse. However, the speed of dry-down

327 should also be considered. When dry-down is slow, more compatible solutes accumulate

328 in the soil relative to depolymerization products generated by exoenzymes (Warren,

329 2016). In addition, microbial production of extracellular polymeric substances (EPS),

330 such as exopolysaccharides, can both retain water during soil drying and slow down

331 rewetting of the habitats of microbial cells. (Roberson and Firestone, 1992).

332   Maximum compatible solute concentration in soil microbes occurred at relatively

333 high ψ (-5 MPa) under slow dry-down conditions (Warren, 2016), compared to the

334 estimated -14 MPa at which microbial activity ceases in the soil (Manzoni et al., 2012).

335 Thus, compatible solute accumulation can only protect indigenous soil organisms from

336 dry down events of limited magnitude.

The physical effects of rewetting on soil aggregates are expected to become relevant once the point at which large soil aggregates become disrupted is reached (Lado-Montserrat et al., 2014). Rewetting aggregates with a large $\Delta\psi$ would enable access to C pools that were previously inaccessible, i.e. occluded organic matter. How big an upshock, i.e. the size of $\Delta\psi$, is required to access occluded organic matter? As water travels down the soil profile, the vapor phase front likely influences microbial cell metabolism, but liquid water is required to disrupt soil aggregates. Does the disruption threshold depend on the size of $\Delta\psi$ or is it an absolute threshold of ψ (i.e. soil water potential falling below the threshold during dry-down and rising above it upon rewetting)? While the dryness reached by the soil can play a role, the size of $\Delta\psi$ seems to be the most relevant parameter (Xu et al., 2004; Chowdhury et al., 2011; Lado-Montserrat et al., 2014). Estimating this parameter could provide a metric of sensitivity of ecosystems to intense dry periods. Soil CO_2 emission rates before rewetting are significantly negatively correlated with the post-rewetting rates (Kim et al., 2012) and can be predicted from rewetting-related changes in soil moisture (Rey et al., 2017). Thus, the soil water content within the preceding years could possibly be used as a proxy to estimate the relative contribution of rewetting events to the overall C budget in systems that experience seasonally dry climatic conditions. Moreover, the speed of soil rewetting frames the impact of the event; this would depend on soil physico-chemical characteristics, among which texture (including preferential flow paths) and soil salinity are important (Cable et al., 2008; Chowdhury et al., 2011) as well as EPS content which can influence soil repellency as well as speed of rewetting (Seaton et al., 2019).

We propose that: (i) all the previously discussed substrates potentially contribute to soil CO_2 pulse upon rewetting, but that their relative contributions depend on climate,

361 soil type and magnitude of water potential upshock $\Delta\psi$; and (ii) exceeding a threshold in

362 dry-wet $\Delta\psi$ is required to mobilize occluded organic matter (Fig. 1).

363

364 **Importance of plants**

365   Plants are the primary contributors to the quantity and quality of C entering soil

366 and the size and composition of the available C pool controls the magnitude of the CO_2

367 pulse. Many of the studies investigating the nature of the C fueling the CO_2 pulse upon

368 rewetting were undertaken in systems that were devoid of live plants at the time of

369 rewetting (Borken and Matzner, 2009). This reflects the fact that wet-up studies, and the

370 $\Delta\psi$ associated with substantial CO_2 pulses, require extremely dry soils, in which annual

371 plants are generally no longer alive. However, the plants that were present during a

372 growing period immediately preceding the dry-down may affect the microbial response

373 to rewetting as: (i) labile C pools support CO_2 pulses ; (ii) above- and below-ground litter

374 from semi-arid ecosystems can generate a large and labile pool of soil organic C that is

375 present during the dry season ; and (iii) the presence of plants can impact the number and

376 size of soil aggregates (Blankinship et al., 2016). Thus, plants may have been absent in

377 many studies due either to the soil-centric focus of the researchers and the question, or

378 due to the absence of living plants at the time of rewetting. For example, in Mediterranean

379 systems the annual plant cover is often dead by the end of the dry season, when the first

380 rains constitute the largest soil water potential upshocks.

381   Nevertheless, plants matter, whether dead or alive. Dry episodes can take place

382 during the growing season without killing plant cover. In systems in which live plants are

383 present, dry-wet cycling directly impacts plant-derived soil labile C inputs, both in their

384 quantity, generally increasing exudation under moderate drought but having a more

385 variable effect under intense drought (Preece and Peñuelas, 2016), and quality (Preece

386   and Peñuelas, 2016; Gargallo-Garriga et al., 2018), with consequences on ecosystem

387   functioning (Oikawa et al., 2014; Canarini and Dijkstra, 2015; Williams and de Vries,

388   2019). Dry-wet cycles can also affect plant N uptake, hydraulic redistribution (Fu et al.,

389   2018) and trapping of windblown soil particles (Ravi et al., 2010), which all likely interact

390   with major processes involved in the soil CO_2 pulse upon rewetting (Wang et al., 2015).

391   Root exudation is of particular relevance, as it not only provides a direct labile C source

392   for soil microorganisms, but can also contribute to shaping the root microbiome (Naylor

393   and Coleman-Derr, 2017; Hartman and Tringe, 2019), a major driver of the soil CO_2 pulse

394   upon rewetting.

395   Dry soils as well as those subject to infrequent watering events can hamper plant-

396   microbial coupling by impeding the transfer of recent photo-assimilates from the roots to

397   soil microorganisms (Ruehr et al., 2009; Fuchslueger et al., 2014; Engelhardt et al., 2018;

398   Karlowsky et al., 2018). This may be due to reduced rhizodeposition rates (but see Preece

399   and Peñuelas, 2016) or to challenging microbial access to rhizodeposits under diminished

400   water film connectedness (Moyano et al., 2013; Fuchslueger et al., 2014; Tecon and Or,

401   2016; von Rein et al., 2016; Karlowsky et al., 2018). The plant-microbial interaction

402   component of the mechanisms underlying the soil CO_2 efflux pulse upon rewetting may

403   also vary with depth (Engelhardt et al., 2018).

404   Few experiments have addressed rewetting events during the spring in

405   Mediterranean systems, when the plants are still alive, actively growing and the high flux

406   of rhizodeposits to the soil exerts a strong influence on soil microbial activity (Curiel Yuste

407   et al., 2007; Ma et al., 2012). The seasonal component of microbial response to changes in

408   water availability has been documented in several studies (Cruz-Martínez et al., 2009; Bell

409   et al., 2014; Zhao et al., 2016). The plant-microbial interaction component of the soil CO_2

410   pulse after rewetting may vary seasonally and experiments exploring rewetting after dry

411   spring periods could provide a valuable perspective.

412   We propose that the origin of the C released upon soil rewetting (Fig. 2) is mainly

413   controlled by three factors: the magnitude of the rewetting upshock ($\Delta\psi$), soil physical

414   characteristics, and ecosystem productivity (NEP). The $\Delta\psi$ controls the pool of microbial-

415   derived C, i.e. compatible solutes and dead cells. Soil physics controls pore connectivity,

416   which in turn controls access to microbial- and plant-derived C. NEP controls the pool of

417   plant-derived labile C which determines much of the soil enzyme pool.

418   Dry-wet cycles can impact soil C stabilization both positively and negatively

419   (Bailey et al., 2019). A few dry-wet cycles increase the turnover of aggregates (i.e. as they

420   are broken down then formed again), releasing inter-aggregate particulate organic matter

421   and decreasing stabilization of fresh organic matter within the aggregate structure (Denef

422   et al., 2001b). However, aggregates become slake-resistant with time, and more dry-wet

423   cycles result in increased microaggregate stability (Denef et al., 2001a; Rahman et al.,

424   2018). Dry-wet cycles increase microbial biomass C turnover, as microbial C lost through

425   microbial death is replaced. Recent studies have proposed that enhanced microbial

426   turnover under dry-wet cycles could result in an increased contribution of previously

427   stable organic matter to microbial C (Lopez-Sangil et al., 2018; Schimel, 2018).

428

429   **Conclusion**

430   The large CO_2 pulse that is produced by rapid rewetting of very dry soil results

431   from biological, physical and chemical mechanisms. The past 30+ years of research in this

432   area provides an excellent example of integration across the subdisciplines of soil science.

433   We suggest that significant future advances on the topic will be facilitated by greater

434   inclusion and recognition of plant-microbe soil interactions.

447 **References**

448 Aanderud, Z.T., Jones, S.E., Fierer, N., Lennon, J.T., 2015. Resuscitation of the rare
449 biosphere contributes to pulses of ecosystem activity. Frontiers in Microbiology 6, 24.

450 Amend, A.S., Martiny, A.C., Allison, S.D., Berlemont, R., Goulden, M.L., Lu, Y., Treseder,
451 K.K., Weihe, C., Martiny, J.B., 2016. Microbial response to simulated global change is
452 phylogenetically conserved and linked with functional potential. The ISME Journal 10,
453 109-118.

454 Angel, R., Conrad, R., 2013. Elucidating the microbial resuscitation cascade in biological
455 soil crusts following a simulated rain event. Environmental Microbiology 15, 2799-2815.

456 Austin, A.T., Vivanco, L., 2006. Plant litter decomposition in a semi-arid ecosystem
457 controlled by photodegradation. Nature 442, 555-558.

458 Averill, C., Waring, B., Hawkes, C.V., 2016. Historical precipitation predictably alters the
459 shape and magnitude of microbial functional response to soil moisture. Global Change
460 Biology 22, 1957-1964.

461 Bailey, V.L., Pries, C.H., Lajtha, K., 2019. What do we know about soil carbon
462 destabilization? Environmental Research Letters 14.

463 Baker, N.R., Allison, S.D., 2015. Ultraviolet photodegradation facilitates microbial litter
464 decomposition in a Mediterranean climate. Ecology 96.

465 Bapiri, A., Bååth, E., Rousk, J., 2010. Drying–rewetting cycles affect fungal and bacterial
466 growth differently in an arable soil. Microbial Ecology 60, 419-428.

467 Barnard, R.L., Osborne, C.A., Firestone, M.K., 2013. Responses of soil bacterial and fungal
468 communities to extreme desiccation and rewetting. The ISME Journal 7, 2229-2241.

469 Barnard, R.L., Osborne, C.A., Firestone, M.K., 2015. Changing precipitation pattern alters
470 soil microbial community response to wet-up under a Mediterranean-type climate. The
471 ISME Journal 9, 947-957.

472 Baveye, P.C., Otten, W., Kravchenko, A., Balseiro-Romero, M., Beckers, E., Chalhoub, M.,
473 Darnault, C., Eickhorst, T., Garnier, P., Hapca, S., Kiranyaz, S., Monga, O., Mueller, C.W.,
474 Nunan, N., Pot, V., Schluter, S., Schmidt, H., Vogel, H.J., 2018. Emergent properties of
475 microbial activity in heterogeneous soil microenvironments: Different research
476 approaches are slowly converging, yet major challenges remain. Frontiers in
477 Microbiology 9, 1929.

478 Bell, C.W., Tissue, D.T., Loik, M.E., Wallenstein, M.D., Acosta-Martinez, V., Erickson, R.A.,
479 Zak, J.C., 2014. Soil microbial and nutrient responses to 7 years of seasonally altered
480 precipitation in a Chihuahuan Desert grassland. Global Change Biology 20, 1657-1673.

481 Birch, H.F., 1958. The effect of soil drying on humus decomposition and nitrogen
482 availability. Plant and Soil 10, 9-31.

483 Blankinship, J.C., Fonte, S.J., Six, J., Schimel, J.P., 2016. Plant versus microbial controls on
484 soil aggregate stability in a seasonally dry ecosystem. Geoderma 272, 39-50.

485 Blankinship, J.C., Schimel, J.P., 2018. Biotic versus abiotic controls on bioavailable soil
486 organic carbon. Soil Systems 2, 10.

487 Blazewicz, S.J., Hungate, B.A., Koch, B.J., Nuccio, E.E., Morissey, E., Schwartz, E., Pett-
488 Ridge, J., Firestone, M.K., 2020. Taxon-specific microbial growth and mortality patterns
489 reveal distinct temporal population responses to rewetting in a California grassland soil.
490 The ISME Journal in press.

491 Blazewicz, S.J., Schwartz, E., Firestone, M.K., 2014. Growth and death of bacteria and
492 fungi underlie rainfall-induced carbon dioxide pulses from seasonally dried soil. Ecology
493 95, 1162-1172.

494 Boot, C.M., Schaeffer, S.M., Schimel, D., 2013. Static osmolyte consentrations in microbial
495 biomass during seasonal drought in a California grassland. Soil Biology and
496 Biochemistry 57, 356-361.

497 Borken, W., Matzner, E., 2009. Reappraisal of drying and wetting effects on C and N
498 mineralization and fluxes in soils. Global Change Biology 15, 808-824.

499 Bottner, P., 1985. Response of microbial biomass to alternate moist and dry conditions
500 in a soil incubated with ^{14}C and ^{15}N-labelled plant material. Soil Biology and
501 Biochemistry 17, 329–337.

502 Bouskill, N.J., Lim, H.C., Borglin, S., Salve, R., Wood, T.E., Silver, W.L., Brodie, E.L., 2013.
503 Pre-exposure to drought increases the resistance of tropical forest soil bacterial
504 communities to extended drought. The ISME Journal 7, 384-394.

505 Brandt, L.A., King, J.Y., Hobbie, S.E., Milchunas, D.G., Sinsabaugh, R.L., 2010. The Role of
506 Photodegradation in Surface Litter Decomposition Across a Grassland Ecosystem
507 Precipitation Gradient. Ecosystems 13, 765-781.

508 Cable, J.M., Ogle, K., Williams, D.G., Weltzin, J.F., Huxman, T.E., 2008. Soil texture drives
509 responses of soil respiration to precipitation pulses in the Sonoran desert: Implications
510 for climate change. Ecosystems 11, 961-979.

511 Canarini, A., Dijkstra, F.A., 2015. Dry-rewetting cycles regulate wheat carbon
512 rhizodeposition, stabilization and nitrogen cycling. Soil Biology and Biochemistry 81,
513 195-203.

514 Canarini, A., Kiaer, L.P., Dikstra, F.A., 2017. Soil carbon loss regulated by drought
515 intensity and available substrate: A meta-analysis. Soil Biology and Biochemistry 112,
516 90-99.

517 Carson, J.K., Gonzalez-Quinones, V., Murphy, D.V., Hinz, C., Shaw, J.A., Gleeson, D.B., 2010.
518 Low pore connectivity increases bacterial diversity in soil. Applied and Environmental
519 Microbiology 76, 3936-3942.

520   Chowdhury, N., Yan, N., Islam, M.N., Marschner, P., 2011. The extent of drying influences
521   the flush of respiration after rewetting in non-saline and saline soils. Soil Biology and
522   Biochemistry 43, 2265-2272.

523   Chowdhury, T.R., Lee, J.-Y., Bottos, E.M., Brislawn, C.J., White III, R.A., Bramer, L.M.,
524   Brown, J., Zucker, J.D., Kim, Y.-M., Jumpponen, A., Rice, C.W., Fansler, S.J., Metz, T.O.,
525   McCue, L.A., Callister, S.J., Song, H.-S., Jansson, J.K., 2019. Metaphenomic responses of a
526   native prairie soil microbiome to moisture perturbations. mSystems 4, E00061-00019.

527   Clarke, C.E., Aguilar-Carrillo, J., Roychoudhury, A.N., 2011. Quantification of drying
528   induced acidity at the mineral–water interface using ATR-FTIR spectroscopy.
529   Geochimica et Cosmochimica Acta 75, 4846-4856.

530   Cosentino, D., Chenu, C., Le Bissonnais, Y., 2006. Aggregate stability and microbial
531   community dynamics under drying-wetting cycles in a silt loam soil. Soil Biology and
532   Biochemistry 38, 2053-2062.

533   Crowther, T.W., Maynard, D.S., Crowther, T.R., Peccia, J., Smith, J.R., Bradford, M.A., 2014.
534   Untangling the fungal niche: the trait-based approach. Frontiers in Microbiology 5, 579.

535   Cruz-Martínez, K., Suttle, K.B., Brodie, E.L., Power, M.E., Andersen, G.L., Banfield, J.F.,
536   2009. Despite strong seasonal responses, soil microbial consortia are more resilient to
537   long-term changes in rainfall than overlying grassland. The ISME Journal 3, 738-744.

538   Curiel Yuste, J., Baldocchi, D.D., Gershenson, A., Goldstein, A., Misson, L., Wong, S., 2007.
539   Microbial soil respiration and its dependency on carbon inputs, soil temperature and
540   moisture. Global Change Biology 13, 2018-2035.

541   Curiel Yuste, J., Penuelas, J., Estiarte, M., Garcia-Mas, J., Mattana, S., Ogaya, R., Pujol, M.,
542   Sardans, J., 2011. Drought-resistant fungi control soil organic matter decomposition and
543   its response to temperature. Global Change Biology 17, 1475-1486.

544   Day, T.A., Bliss, M.S., Tomes, A.R., Ruhland, C.T., Guenon, R., 2018. Desert leaf litter decay:
545   Coupling of microbial respiration, water-soluble fractions and photodegradation. Global
546   Change Biology 24, 5454-5470.

547   de Boer, W., Folman, L.B., Summerbell, R.C., Boddy, L., 2005. Living in a fungal world:
548   impact of fungi on soil bacterial niche development. FEMS Microbiology Reviews 29,
549   795-811.

550   de Vries, F.T., Griffiths, R.I., Bailey, M., Craig, H., Girlanda, M., Gweon, H.S., Hallin, S.,
551   Kaisermann, A., Keith, A.M., Kretzschmar, M., Lemanceau, P., Lumini, E., Mason, K.E.,
552   Oliver, A., Ostle, N., Prosser, J.I., Thion, C., Thomson, B., Bardgett, R.D., 2018. Soil bacterial
553   networks are less stable under drought than fungal networks. Nature Communications
554   9, 3033.

555   Denef, K., Six, J., Bossuyt, H., Frey, S.D., Elliott, E.T., Merckx, R., Paustian, K., 2001a.
556   Influence of dry-wet cycles on the interrelationship between aggregate, particulate
557   organic matter, and microbial community dynamics. Soil Biology and Biochemistry 33,
558   1599-1611.

559 Denef, K., Six, J., Paustian, K., Merckx, R., 2001b. Importance of macroaggregate dynamics
560 in controlling soil carbon stabilization: short-term effects of physical disturbance
561 induced by dry-wet cycles. Soil Biology and Biochemistry 33, 2145-2153.

562 Dijkstra, F.A., Augustine, D.J., Brewer, P., von Fischer, J.C., 2012. Nitrogen cycling and
563 water pulses in semiarid grasslands: are microbial and plant processes temporally
564 asynchronous? Oecologia 170, 799-808.

565 Dirks, I., Navon, Y., Kanas, D., Dumbur, R., GrÜNzweig, J.M., 2010. Atmospheric water
566 vapor as driver of litter decomposition in Mediterranean shrubland and grassland
567 during rainless seasons. Global Change Biology 16, 2799-2812.

568 Eichorst, S.A., Trojan, D., Roux, S., Herbold, C., Rattei, T., Woebken, D., 2018. Genomic
569 insights into the Acidobacteria reveal strategies for their success in terrestrial
570 environments. Environmental Microbiology 20, 1041-1063.

571 Engelhardt, I.C., Blazewicz, S.J., Barnard, R.L., 2019. Effects of contrasting precipitation
572 patterns on the trajectory of actively growing and inactive microbial communities after
573 rewetting. Soil Biology and Biochemistry 134, 172-174.

574 Engelhardt, I.C., Welty, A., Blazewicz, S.J., Bru, D., Rouard, N., Breuil, M.C., Gessler, A.,
575 Galiano, L., Miranda, J.C., Spor, A., Barnard, R.L., 2018. Depth matters : effects of
576 precipitation regime on soil microbial activity upon rewetting of a plant-soil system. The
577 ISME Journal 12, 1061-1071.

578 Evans, S., Dieckmann, U., Franklin, O., Kaiser, C., 2016. Synergistic effects of diffusion and
579 microbial physiology reproduce the Birch effect in a micro-scale model. Soil Biology and
580 Biochemistry 93, 28-37.

581 Evans, S.E., Wallenstein, M.D., 2012. Soil microbial community response to drying and
582 rewetting stress: does historical precipitation regime matter? Biogeochemistry 109,
583 101-116.

584 Evans, S.E., Wallenstein, M.D., 2014. Climate change alters ecological strategies of soil
585 bacteria. Ecological Letters.

586 Evans, S.E., Wallenstein, M.D., Burke, I.C., 2014. Is bacterial moisture niche a good
587 predictor of shifts in community composition under long-term drought? Ecology 95,
588 110-122.

589 Fan, Z., Neff, J.C., Hanan, N.P., 2015. Modeling pulsed soil respiration in an African
590 savanna ecosystem. Agricultural and Forest Meteorology 200, 282-292.

591 Fierer, N., Schimel, J.P., 2003. A proposed mechanism for the pulse in carbon dioxide
592 production commonly observed following the rapid rewetting of a dry soil. Soil Science
593 Society of America Journal 67, 798-805.

594 Fraser, F.C., Corstanje, R., Deeks, L.K., Harris, J.A., Pawlett, M., Todman, L.C., Whitmore,
595 A.P., Ritz, K., 2016. On the origin of carbon dioxide released from rewetted soils. Soil
596 Biology and Biochemistry 101, 1-5.

597   Fu, C., Wang, G., Bible, K., Goulden, M.L., Saleska, S.R., Scott, R.L., Cardon, Z.G., 2018.
598   Hydraulic redistribution affects modeled carbon cycling via soil microbial activity and
599   suppressed fire. Global Change Biology 24, 3472-3485.

600   Fuchslueger, L., Bahn, M., Fritz, K., Hasibeder, R., Richter, A., 2014. Experimental drought
601   reduces the transfer of recently fixed plant carbon to soil microbes and alters the
602   bacterial community composition in a mountain meadow. New Phytologist 201, 916-
603   927.

604   Gargallo-Garriga, A., Preece, C., Sardans, J., Oravec, M., Urban, O., Penuelas, J., 2018. Root
605   exudate metabolomes change under drought and show limited capacity for recovery.
606   Scientific Reports 8, 12696.

607   Goodfellow, M., Williams, S.T., 1983. Ecology of Actinomycetes. Annual Review of
608   Microbiology 37, 189-216.

609   Göransson, H., Godbold, D.L., Jones, D.L., Rousk, J., 2013. Bacterial growth and respiration
610   responses upon rewetting dry forest soils: Impact of drought-legacy. Soil Biology and
611   Biochemistry 57, 477-486.

612   Halverson, L.J., Jones, T.M., Firestone, M.K., 2000. Release of intracellular solutes by four
613   Soil bacteria exposed to dilution stress. Soil Science of America Journal 64, 1630-1637.

614   Hartman, K., Tringe, S.G., 2019. Interactions between plants and soil shaping the root
615   microbiome under abiotic stress. Biochem J 476, 2705-2724.

616   Hawkes, C.V., Waring, B.G., Rocca, J.D., Kivlin, S.N., 2017. Historical climate controls soil
617   respiration responses to current soil moisture. Proceedings of the National Academy of
618   Sciences, USA 114, 6322-6327.

619   Homyak, P.M., Blankinship, J.C., Slessarev, E.W., Schaeffer, S.M., Manzoni, S., Schimel, J.P.,
620   2018. Effects of altered dry season length and plant inputs on soluble soil carbon.
621   Ecology 99, 2348-2362.

622   Huang, J., Li, Y., Fu, C., Chen, F., Fu, Q., Dai, A., Shinoda, M., Ma, Z., Guo, W., Li, Z., Zhang, L.,
623   Liu, Y., Yu, H., He, Y., Xie, Y., Guan, X., Ji, M., Lin, L., Wang, S., Yan, H., Wang, G., 2017.
624   Dryland climate change: Recent progress and challenges. Reviews of Geophysics 55,
625   719-778.

626   Jacobson, K., van Diepeningen, A., Evans, S., Fritts, R., Gemmel, P., Marsho, C., Seely, M.,
627   Wenndt, A., Yang, X., Jacobson, P., 2015. Non-rainfall moisture activates fungal
628   decomposition of surface litter in the Namib Sand Sea. PLoS One 10, e0126977.

629   Jarvis, P., Rey, A., Petsikos, C., Wingate, L., Rayment, M., Pereira, J., Banza, J., David, J.,
630   Miglietta, F., Borghetti, M., Manca, G., Valentini, R., 2007. Drying and wetting of
631   Mediterranean soils stimulates decomposition and carbon dioxide emission: the "Birch
632   effect". Tree Physiology 27, 929-940.

633   Kaisermann, A., de Vries, F.T., Griffiths, R.I., Bardgett, R.D., 2017. Legacy effects of
634   drought on plant-soil feedbacks and plant-plant interactions. New Phytologist 215,
635   1413-1424.

636   Kakumanu, M.L., Cantrell, C.L., Williams, M.A., 2013. Microbial community response to
637   varying magnitudes of desiccation in soil: A test of the osmolyte accumulation
638   hypothesis. Soil Biology and Biochemistry 57, 644-653.

639   Karlowsky, S., Augusti, A., Ingrisch, J., Uddin Akanda, M.K., Bahn, M., Gleixner, G., 2018.
640   Drought-induced accumulation of root exudates supports post-drought recovery of
641   microbes in mountain grassland. Frontiers in Plant Science 9, 1593.

642   Keijser, B.J.F., Ter Beek, A., Rauwerda, H., Schuren, F., Montijn, R., van der Spek, H., Brul,
643   S., 2007. Analysis of Temporal Gene Expression during Bacillus subtilis Spore
644   Germination and Outgrowth. Journal of Bacteriology 189, 3624-3634.

645   Kempf, B., Bremer, E., 1998. Uptake and synthesis of compatible solutes as microbial
646   stress responses to high-osmolality environments. Archives of Microbiology 170, 319-
647   330.

648   Kieft, T.E., Soroker, E., Firestone, M.K., 1987. Microbial biomass response to a rapid
649   increase in water potential when dry soil is wetted. Soil Biology and Biochemistry 19,
650   119–126.

651   Kim, D.G., Vargas, R., Bond-Lamberty, B., Turetsky, M.R., 2012. Effects of soil rewetting
652   and thawing on soil gas fluxes: a review of current literature and suggestions for future
653   research. Biogeosciences 9, 2459-2483.

654   Lado-Montserrat, L., Lull, C., Bautista, I., Lidón, A., Herrera, R., 2014. Soil moisture
655   increment as a controlling variable of the "Birch effect". Interactions with the pre-
656   wetting soil moisture and litter addition. Plant and Soil 379, 21-24.

657   Lau, J.A., Lennon, J.T., 2012. Rapid responses of soil microorganisms improve plant
658   fitness in novel environments. Proceedings of the National Academy of Sciences, USA
659   109, 14058-14062.

660   Lawrence, D., Neff, J.C., Schimel, D., 2009. Does adding microbial mechanisms od
661   decomposition improve soil organic matter models? A comparison of four models using
662   data from pulsed rewetting experiment. Soil Biology and Biochemistry 41, 1923-1934.

663   Lee, X., Wu, H.J., Sigler, J., Oishi, C., Siccama, T., 2004. Rapid and transient response of soil
664   respiration to rain. Global Change Biology 10, 1017-1026.

665   Lennon, J.T., Aanderud, Z.T., Lehmkuhl, B.K., Schoolmaster, D.R., 2012. Mapping the niche
666   space of soil microorganisms using taxonomy and traits. Ecology 93, 1867-1879.

667   Lennon, J.T., Jones, S.E., 2011. Microbial seed banks: the ecological and evolutionary
668   implications of dormancy. Nature Reviews Microbiology 9, 119-130.

669   Lopez-Sangil, L., Hartley, I.P., Rovira, P., Casals, P., Sayer, E.J., 2018. Drying and rewetting
670   conditions differentially affect the mineralization of fresh plant litter and extant soil
671   organic matter. Soil Biology and Biochemistry 124, 81-89.

672 Ma, S., Baldocchi, D.D., Hatala, J.A., Detto, M., Curiel Yuste, J., 2012. Are rain-induced
673 ecosystem respiration pulses enhanced by legacies of antecedent photodegradation in
674 semi-arid environments? Agricultural and Forest Meteorology 154-155, 203-213.

675 Maestre, F.T., Delgado-Baquerizo, M., Jeffries, T.C., Eldridge, D.J., Ochoa, V., Gozalo, B.,
676 Quero, J.L., Garcia-Gomez, M., Gallardo, A., Ulrich, W., Bowker, M.A., Arredondo, T.,
677 Barraza-Zepeda, C., Bran, D., Florentino, A., Gaitan, J., Gutierrez, J.R., Huber-Sannwald, E.,
678 Jankju, M., Mau, R.L., Miriti, M., Naseri, K., Ospina, A., Stavi, I., Wang, D., Woods, N.N.,
679 Yuan, X., Zaady, E., Singh, B.K., 2015. Increasing aridity reduces soil microbial diversity
680 and abundance in global drylands. Proceedings of the National Academy of Sciences,
681 USA 112, 15684-15689.

682 Malik, A.A., Swenson, T., Weihe, C., Morrison, E., Martiny, J.B.H., Brodie, E.L., Northen,
683 T.R., Allison, S.D., 2019. Physiological adaptations of leaf litter microbial communities to
684 long-term drought. bioRxiv doi 10/1101/631077.

685 Manzoni, S., Moyano, F., Kätterer, T., Schimel, J., 2016. Modeling coupled enzymatic and
686 solute transport controls on decomposition in drying soils. Soil Biology and
687 Biochemistry 95, 275-287.

688 Manzoni, S., Schimel, J.P., Porporato, A., 2012. Responses of soil microbial communities
689 to water stress: results from a meta-analysis. Ecology 93, 930-938.

690 Martiny, J.B., Martiny, A.C., Weihe, C., Lu, Y., Berlemont, R., Brodie, E.L., Goulden, M.L.,
691 Treseder, K.K., Allison, S.D., 2017. Microbial legacies alter decomposition in response to
692 simulated global change. The ISME Journal 11, 490-499.

693 Meisner, A., de Deyn, G.B., de Boer, W., van der Putten, W.H., 2013. Soil biotic legacy
694 effects of extreme weather events influence plant invasiveness. Proceedings of the
695 National Academy of Sciences, USA 110, 9835-9838.

696 Meisner, A., Jacquiod, S., Snoek, B.L., ten Hooven, F.C., van der Putten, W.H., 2018.
697 Drought legacy effects on the composition of soil fungal and prokaryote communities.
698 Frontiers in Microbiology 9, 294.

699 Meisner, A., Leizeaga, A., Rousk, J., Bååth, E., 2017. Partial drying accelerates bacterial
700 growth recovery to rewetting. Soil Biology and Biochemistry 112, 269-276.

701 Meisner, A., Rousk, J., Bååth, E., 2015. Prolonged drought changes the bacterial growth
702 response to rewetting. Soil Biology and Biochemistry 88, 314-322.

703 Miller, A.E., Schimel, J.P., Meixner, T., Sickman, J.O., Melack, J.M., 2005. Episodic rewetting
704 enhances carbon and nitrogen release from chaparral soils. Soil Biology and
705 Biochemistry 37, 2195-2204.

706 Moyano, F.E., Manzoni, S., Chenu, C., 2013. Responses of soil heterotrophic respiration to
707 moisture availability: An exploration of processes and models. Soil Biology and
708 Biochemistry 59, 72-85.

709 Navarro-García, F., Casermeiro, M.Á., Schimel, J.P., 2012. When structure means
710 conservation: Effect of aggregate structure in controlling microbial responses to
711 rewetting events. Soil Biology and Biochemistry 44, 1-8.

712 Naylor, D., Coleman-Derr, D., 2017. Drought Stress and Root-Associated Bacterial
713 Communities. Front Plant Sci 8, 2223.

714 Newcomb, C.J., Qafoku, N.P., Grate, J.W., Bailey, V.L., De Yoreo, J.J., 2017. Developing a
715 molecular picture of soil organic matter-mineral interactions by quantifying organo-
716 mineral binding. Nature Communications 8, 396.

717 Ochoa-Hueso, R., Collins, S.L., Delgado-Baquerizo, M., Hamonts, K., Pockman, W.T.,
718 Sinsabaugh, R.L., Smith, M.D., Knapp, A.K., Power, S.A., 2018. Drought consistently alters
719 the composition of soil fungal and bacterial communities in grasslands from two
720 continents. Global Change Biology 24, 2818-2827.

721 Oikawa, P.Y., Grantz, D.A., Chatterjee, A., Eberwein, J.E., Allsman, L.A., Jenerette, G.D.,
722 2014. Unifying soil respiration pulses, inhibition, and temperature hysteresis through
723 dynamics of labile soil carbon and O_2. Journal of Geophysical Research: Biogeosciences
724 119, 521-536.

725 Placella, S.A., Brodie, E.L., Firestone, M.K., 2012. Rainfall-induced carbon dioxide pulses
726 result from sequential resuscitation of phylogenetically clustered microbial groups.
727 Proceedings of the National Academy of Sciences, USA 109, 10931-10936.

728 Plaza, C., Zaccone, C., Sawicka, K., Mendez, A.M., Tarquis, A., Gasco, G., Heuvelink, G.B.M.,
729 Schuur, E.A.G., Maestre, F.T., 2018. Soil resources and element stocks in drylands to face
730 global issues. Scientific Reports 8, 13788.

731 Potts, M., 1994. Dessication tolerance of prokaryotes. Microbiological Reviews 58, 755-
732 805.

733 Prăvălie, R., 2016. Drylands extent and environmental issues. A global approach. Earth-
734 Science Reviews 161, 259-278.

735 Preece, C., Peñuelas, J., 2016. Rhizodeposition under drought and consequences for soil
736 communities and ecosystem resilience. Plant and Soil 409, 1-17.

737 Qualls, R.G., 2000. Comparison of the behavior of soluble organic and inorganic nutrients
738 in forest soils. Forest Ecology and Management 138, 29-50.

739 Rahman, M.T., Guo, Z.C., Zhang, Z.B., Zhou, H., Peng, X.H., 2018. Wetting and drying cycles
740 improving aggregation and associated C stabilization differently after straw or biochar
741 incorporated into a Vertisol. Soil and Tillage Research 175, 28-36.

742 Ravi, S., Breshears, D.D., Huxman, T.E., D'Odorico, P., 2010. Land degradation in
743 drylands: Interactions among hydrologic–aeolian erosion and vegetation dynamics.
744 Geomorphology.pdf 116, 236-245.

745 Rey, A., Oyonarte, C., Morán-López, T., Raimundo, J., Pegoraro, E., 2017. Changes in soil
746 moisture predict soil carbon losses upon rewetting in a perennial semiarid steppe in SE
747 Spain. Geoderma 287, 135-146.

748 Roberson, B., Firestone, M.K., 1992. Relationship between desiccation and
749 exoplysaccharide production in a soil *Pseudomonas* sp. Applied and Environmental
750 Microbiology 58, 1284-1291.

751 Ruehr, N.K., Offerman, C., Gessler, A., Winkler, B.J., Ferrio, J.P., Buchmann, N., Barnard,
752 R.L., 2009. Effects of drought on allocation of recent carbon: From beech leaves to soil
753 respiration. New Phytologist 184, 950-961.

754 Schimel, J., Balser, T.C., Wallenstein, M.D., 2007. Microbial stress-response physiology
755 and its implications for ecosystem function. Ecology 88, 1386-1394.

756 Schimel, J., Becerra, C.A., Blankinship, J., 2017. Estimating decay dynamics for enzyme
757 activities in soils from different ecosystems. Soil Biology and Biochemistry 114, 5-11.

758 Schimel, J.P., 2018. Life in dry soils: effects of drought on soil microbial communities and
759 processes. Annual Review of Ecology, Evolution, and Systematics 49, 409-432.

760 Schimel, J.P., Wetterstedt, J.Å.M., Holden, P.A., Trumbore, S.E., 2011. Drying/rewetting
761 cycles mobilize old C from deep soils from a California annual grassland. Soil Biology and
762 Biochemistry 43, 1101-1103.

763 Seaton, F.M., Jones, D.L., Creer, S., George, P.B.L., Smart, S.M., Lebron, I., Barrett, G.,
764 Emmett, B.A., Robinson, D.A., 2019. Plant and soil communities are associated with the
765 response of soil water repellency to environmental stress. Science of the Total
766 Environment 687, 929-938.

767 Sinai, L., Rosenberg, A., Smith, Y., Segev, E., Ben-Yehuda, S., 2015. The molecular timeline
768 of a reviving bacterial spore. Molecular Cell 57, 695-707.

769 Slessarev, E.W., Lin, Y., Jiménez, B., Homyak, P.M., Chadwick, O.A., D'Antonio, C.M.,
770 Schimel, J.P., 2020. Cellular and extracellular C contributions to respiration after wetting
771 dry soil. Biogeochemistry 147, 307-324.

772 Smith, A.P., Bond-Lamberty, B., Benscoter, B.W., Tfaily, M.M., Hinkle, C.R., Liu, C., Bailey,
773 V.L., 2017. Shifts in pore connectivity from precipitation versus groundwater rewetting
774 increases soil carbon loss after drought. Nature Communications 8, 1335.

775 Šťovíček, A., Azatyan, A., Soares, M.I.M., Gillor, O., 2017a. The Impact of hydration and
776 temperature on bacterial diversity in arid soil mesocosms. Fronters Microbiology 8,
777 1078.

778 Šťovíček, A., Kim, M., Or, D., Gillor, O., 2017b. Microbial community response to
779 hydration-desiccation cycles in desert soil. Scientific Reports 7, 45735.

780 Tecon, R., Or, D., 2016. Bacterial flagellar motility on hydrated rough surfaces controlled
781 by aqueous film thickness and connectedness. Scientific Reports 6, 19409.

782   Tecon, R., Or, D., 2017. Biophysical processes supporting the diversity of microbial life in
783   soil. FEMS Microbiology Reviews.

784   Unger, S., Máguas, C., Pereira, J.S., David, T.S., Werner, C., 2010. The influence of
785   precipitation pulses on soil respiration – Assessing the "Birch effect" by stable carbon
786   isotopes. Soil Biology and Biochemistry 42, 1800-1810.

787   Vargas, R., Collins, S.L., Thomey, M.L., Johnson, J.E., Brown, R.F., Natvig, D.O., Friggens,
788   M.T., 2012. Precipitation variability and fire influence the temporal dynamics of soil CO_2
789   efflux in an arid grassland. Global Change Biology 18, 1401-1411.

790   von Rein, I., Gessler, A., Premke, K., Keitel, C., Ulrich, A., Kayler, Z.E., 2016. Forest
791   understory plant and soil microbial response to an experimentally induced drought and
792   heat-pulse event: the importance of maintaining the continuum. Global Change Biology
793   22, 2861-2874.

794   Waksman, S.A., Starkey, R.L., 1923. Partial sterilization of soil, microbiological activities
795   and soil fertility: II. Soil Science 16, 247–268.

796   Wang, G., Or, D., 2013. Hydration dynamics promote bacterial coexistence on rough
797   surfaces. The ISME Journal 7, 395-404.

798   Wang, L., Manzoni, S., Ravi, S., Riveros-Iregui, D., Caylor, K., 2015. Dynamic interactions
799   of ecohydrological and biogeochemical processes in water-limited systems. Ecosphere 6,
800   art133.

801   Warren, C.R., 2014. Response of osmolytes in soil to drying and rewetting. Soil Biology
802   and Biochemistry 70, 22-32.

803   Warren, C.R., 2016. Do microbial osmolytes or extracellular depolymerisation products
804   accumulate as soil dries? Soil Biology and Biochemistry 98, 54-63.

805   Warren, C.R., 2019. Isotope pool dilution reveals rapid turnover of small quaternary
806   ammonium compounds. Soil Biology and Biochemistry 131, 90-99.

807   Welsh, D.T., 2000. Ecological signifiance of compatible solute accumulation by micro-
808   organisms: from single cells to global climate. FEMS Microbiology Reviews 24, 263-290.

809   Williams, A., de Vries, F.T., 2019. Plant root exudation under drought: implications for
810   ecosystem functioning. New Phytologist.

811   Williams, M.A., Xia, K., 2009. Characterization of the water soluble soil organic pool
812   following the rewetting of dry soil in a drought-prone tallgrass prairie. Soil Biology and
813   Biochemistry 41, 21-28.

814   Williamson, K.E., Fuhrmann, J.J., Wommack, K.E., Radosevich, M., 2017. Viruses in soil
815   ecosystems: An unknown quantity within an unexplored territory. Annual Review of
816   Virology 4, 201-219.

817   Williamson, K.E., Radosevich, M., Smith, D.W., Wommack, K.E., 2007. Incidence of
818   lysogeny within temperate and extreme soil environments. Environmental Microbiology
819   9, 2563-2574.

820   Williamson, K.E., Radosevich, M., Wommack, K.E., 2005. Abundance and diversity of
821   viruses in six Delaware soils. Applied and Environmental Microbiology 71, 3119-3125.

822   Winogradsky, S., 1924. Sur la microflora autochtone de la terre arable. Comptes-rendus
823   hebdomadaires des séances de l'Académie des Sciences (Paris) D178, 1236-1239.

824   Xiang, S.-R., Doyle, A., Holden, P.A., Schimel, J.P., 2008. Drying and rewetting effects on C
825   and N mineralization and microbial activity in surface and subsurface California
826   grassland soils. Soil Biology and Biochemistry 40, 2281-2289.

827   Xu, L., Baldocchi, D.D., Tang, J., 2004. How soil moisture, rain pulses, and growth alter the
828   response of ecosystem respiration to temperature. Global Biogeochemical Cycles 18,
829   GB4002.

830   Yan, Z., Bond-Lamberty, B., Todd-Brown, K.E., Bailey, V.L., Li, S., Liu, C., Liu, C., 2018. A
831   moisture function of soil heterotrophic respiration that incorporates microscale
832   processes. Nature Communications 9, 2562.

833   Zhang, X., Niu, G.-Y., Elshall, A.S., Ye, M., Barron-Gafford, G.A., Pavao-Zuckerman, M.,
834   2014. Assessing five evolving microbial enzyme models against field measurements
835   from a semiarid savannah-What are the mechanisms of soil respiration pulses?
836   Geophysical Research Letters 41, 6428-6434.

837   Zhao, B., Zhang, H., Zhang, J., Jin, Y., 2008. Virus adsorption and inactivation in soil as
838   influenced by autochthonous microorganisms and water content. Soil Biology and
839   Biochemistry 40, 649-659.

840   Zhao, Q., Jian, S., Nunan, N., Maestre, F.T., Tedersoo, L., He, J., Wei, H., Tan, X., Shen, W.,
841   2016. Altered precipitation seasonality impacts the dominant fungal but rare bacterial
842   taxa in subtropical forest soils. Biology and Fertility of Soils 53, 231-245.

843   Zhou, X., Fornara, D., Ikenaga, M., Akagi, I., Zhang, R., Jia, Z., 2016. The resilience of
844   microbial community under drying and rewetting cycles of three forest soils. Frontiers
845   in Microbiology 7, 1101.

846   Zvyagintsev, D.G., Zenova, G.M., Doroshenko, E.A., Gryadunova, A.A., Gracheva, T.A.,
847   Sudnitsyn, I.I., 2007. Actinomycete growth in conditions of low moisture. Biology
848   Bulletin 34, 242-247.
849

850

Figure legends

852

853 Figure 1. Proposed mechanisms fueling soil CO_2 efflux pulse upon rewetting.

854

855 Figure 2. Main drivers (gray) of the mechanisms releasing CO_2 upon rewetting a dry soil,

856 involving interactions between soil microorganisms (blue, center), plants (green, left) and

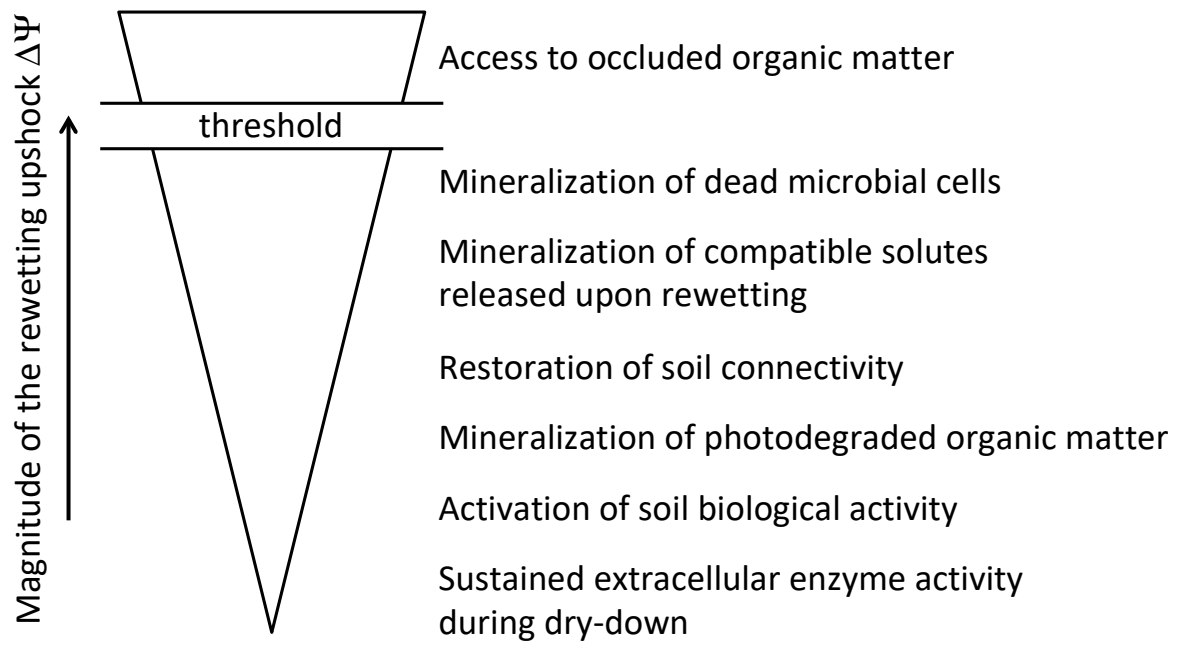857 soil physico-chemical properties (red, right).

858   Figure 1

859

860

861

862

863   Figure 2

864

865

866