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Rewetting of soil: revisiting the origin of soil CO_2 emissions

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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. $66.7\text{x}10^6$ 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 ~$3\text{x}10^6$ 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 ~$33\text{x}10^6$ 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 et al., 2007; Ma et al., 2012; Rey et al., 2017). For example, following intense rainfall, up to 20 % of the annual CO_2 flux from soil to atmosphere occurred in an African savanna ecosystem (Fan et al., 2015). While a rapid change in soil water potential results in an overall microbial reactivation, it exposes soil microorganisms to a radical change in environmental conditions. The soil dry-down and subsequent rewetting provide such an extreme change in microbial environment, that bacterial and fungal death commonly results (Blazewicz et al., 2014; Blazewicz et al., 2020).

The 1987 study by Kieft et al. was designed to investigate the fate of soil microbial biomass C after the rapid rewetting of a dry soil. Using two Californian soils from a Mediterranean-type climate, Kieft and his colleagues found a net loss of microbial biomass C upon rewetting, that could be due to the death of microbial cells or the rapid decomposition of the microbial solutes; the authors favoured the latter explanation. Mechanisms of C loss, the nature of the lost C, and changes in microbial community composition or relation to biogeochemical functioning were not investigated. However, by opening the microbial 'black box' in the general context of dry-wet cycles, this study brought attention to the large influence that rapid increases in soil water content can exert on microbial and terrestrial ecosystem functioning. Exploration of the processes comprising the Birch effect has been a particularly active field of research lately, as global change impacts precipitation cycles worldwide. In many regions, especially under Mediterranean climates, more extreme climate conditions increase the contrast between dry and wet conditions to which ecosystems are exposed. It has been more than three decades since the Kieft et al. study was published; here we provide a perspective on the current status of the field, its importance in the context of global change, and areas in need of more research.

What is wet-up and where does it occur?

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

We present a perspective that primarily addresses rewetting dynamics of soil near the soil surface and in the rooting zone of shallow-rooted plants. Under laboratory conditions, drying-rewetting cycles resulted in the release of "old" C from soil layers below 20 cm (Schimel et al., 2011). While macropore flow of incident rain water might result in the wet-up of soil deeper than 20 cm, rapid rewetting of soil by rainfall will be most important near the surface of soil and generally play a less important role in the mobilization of deep old soil carbon.

C released upon rewetting: origin and mechanisms

The CO_2 pulse upon rewetting typically exhibits a pattern of very high rates during the first minutes and hours after rewetting and this response declines over time (Kim et al., 2012). The origin of the CO_2 pulse upon rewetting soil can be both abiotic and biotic. Abiotic processes include solubilization of carbonates (depending on carbonate concentration in soils), CO_2 displacement from the soil pores to the atmosphere by water, as well as the quantitatively low degassing of CO_2 dissolved in rain and soil degassing due to the decrease in barometric pressure over time (Lee et al., 2004; Barnard et al., 2015). However, in non-carbonate-rich soils, abiotic processes generate less CO_2 than do the biotic processes, which are the main contributors of the soil CO_2 pulse upon rewetting. The nature and sources of the C compounds that are mineralized upon rewetting a dry soil has been extensively explored and somewhat fervently argued. Here we highlight the most prevalent sources and mechanisms that fuel the C mineralization pulse: compatible solutes; microbial necromass; changes in water film connectivity; sustained extracellular enzyme activity during dry-down; C desorption from mineral surfaces; and disruption of aggregates. Each of these is discussed below.

Compatible solutes, accumulated by microbial cells in response to drying, were suggested by Kieft et al. (1987) as candidate compounds fueling the soil CO_2 efflux pulse; this substrate pool was also addressed by later studies (Halverson et al., 2000; Fierer and Schimel, 2003; Schimel et al., 2007). Soil microorganism accumulation of compatible solutes within their membrane-bound cells reduces cell dehydration, but cells are required to rapidly dispose of them upon rewetting, or face membrane rupture (plasmoptysis). These processes will release solutes, such as proline, glutamine, glycine betaine, and trehalose into the soil (Kempf and Bremer, 1998; Halverson et al., 2000; Welsh, 2000; Warren, 2019) and these can be assimilated and mineralized rapidly by other microorganisms. Some of the earlier studies focusing on the intracellular accumulation of compatible solutes as soil gets drier, found no evidence for osmolytes as a significant C-source (Boot et al., 2013; Kakumanu et al., 2013). More recent evidence (Warren, 2014; Warren, 2016) for this mechanism however provides some support. While some studies detected no increased amount of compatible solutes in the soil upon rewetting (Williams and Xia, 2009; Warren, 2014), recent studies have reported an accumulation of osmolytes in microbial communities during dry periods (Chowdhury et al., 2019; Malik et al., 2019; Slessarev et al., 2020). The elusive nature of osmolytes may be related to: (i) their low residence time in the soil, as they are produced and consumed at measurable rates even in moist soils (Warren, 2019), albeit at lower rates than in dry soils (Warren et al, unpubl. data); and (ii) their probable specificity to a microbial community. Some microbes may not accumulate compatible solutes and instead undergo passive water loss, especially under conditions of rapid drying (Potts, 1994). Possible fates of these plasmolyzed cells are death from water loss, death upon rewetting, or survival of both desiccation and re-wetting.

Microbial death due to the rapid water potential increase (from very negative values to zero or nearly zero) upon rewetting was also invoked by Kieft et al. (1987) as a possible source of C substrates. Dead microbial cells can provide mineralizable substrates upon rewetting a dry soil, arising from cells that died during the previous dry-down period or as a direct result of the rewetting. Evidence for this mechanism has been presented by measuring gross rates of bacterial death and growth upon rewetting (Blazewicz et al., 2014; Blazewicz et al., 2020). High bacterial mortality was documented to have occurred within the first three hours after a rewetting event. The authors noted that some of the mortality is likely to have occurred during the dry-down process but the microbial necromass remained largely intact until the wet-up event.

Bacteriophage predation may also contribute to cell death after rewetting. Phages infect a large proportion of soil bacteria (Williamson et al., 2007) and can become lytic when soil conditions become favorable for the growth of their hosts (Williamson et al., 2017). Indeed, viral abundance in the soil has been shown to be correlated with soil water content (Williamson et al., 2005), possibly due to the effects of soil water content on bacterial numbers as well as on the adsorption of viruses in the soil (Zhao et al., 2008). Viral diffusion/advection is also enhanced by soil wetting, increasing the chances of virus-host encounter and attachment. At this time, however, there is no direct evidence for wet-up-associated predation as a significant mechanism of cell death and labile C input. Similarly, eukaryotic predation may contribute to microbial mortality upon soil wetting, but, to our knowledge, this has not been demonstrated.

Upon rewetting a dry soil, microorganisms have to access and then metabolize organic substrates. Connectivity of soil water films is gradually lost as soils dry and this restricts diffusional access to substrate (Manzoni et al., 2012) but enhances bacterial coexistence and diversity (Carson et al., 2010) by limiting competitive exclusion (Wang and Or, 2013; Šťovíček et al., 2017b). Conversely, rewetting a soil restores water film connectivity (Smith et al., 2017), providing conditions for highly competitive and mobile microorganisms to access substrates and to thrive, thereby generating a soil CO_2 efflux pulse (see modelling study by Evans et al., 2016).

Another possible source of substrates during rewetting requires sustained extracellular enzyme activity during dry-down (Miller et al., 2005; Schimel et al., 2017). The reduction in microbial activity as soils dry can lead to a net increase in substrate that may become available to soil microorganisms upon rewetting (Lawrence et al., 2009; Zhang et al., 2014; Fraser et al., 2016). However, a recent study found no evidence for sustained exoenzyme activity in drying soils (Homyak et al., 2018).

Soluble organic compounds in the soil can associate with minerals, particularly during dry periods (Qualls, 2000). Upon rewetting, the desorption of organic compounds from mineral surfaces can become a source of C (Blankinship and Schimel, 2018) as changes in pH and ionic strength can directly affect organic matter-mineral binding (Clarke et al., 2011; Newcomb et al., 2017).

In dryland ecosystems, photodegradation of surface litter increases the breakdown of carbon compounds to substrates that can be metabolized by microorganisms upon rewetting (Austin and Vivanco, 2006; Baker and Allison, 2015; Day et al., 2018). Although photodegradation alone cannot explain differences in decomposition rates across an aridity gradient (Brandt et al., 2010), it enhances soil CO_2 emissions upon soil rewetting (Ma et al., 2012).

Disruption of organic matter occlusion in soil aggregates is another physical consequence of rewetting that can enhance substrate availability. Rewetting a dry soil can break up aggregates, exposing organic substrates that were previously occluded (Denef et al., 2001a; Cosentino et al., 2006; Borken and Matzner, 2009; Navarro-García et al., 2012).

Modeling has provided solid insight into the mechanisms that drive the soil CO_2 pulse associated with rewetting. Most modeling studies have focused on the sources of soil organic matter at a large scale (Lawrence et al., 2009) and were not designed to take into account the biophysical mechanisms at the pore-scale. The gap between pore physics, soil organic matter cycling and microbiology has been bridged, using empirical models and simplified model systems (Moyano et al., 2013; Manzoni et al., 2016; Tecon and Or, 2017), yet challenges remain (Baveye et al., 2018). Recent modeling efforts support the coexistence of physical as well as microbiological processes as drivers of the rewetting soil CO_2 pulse (Zhang et al., 2014; Evans et al., 2016; Šťovíček et al., 2017b; Yan et al., 2018).

The question of which C sources fuels the Birch effect has been under discussion for many decades. It is an important topic in the context of global change, as rainfall patterns and amounts change in areas around the globe, potentially impacting the C budget of ecosystems (Kim et al., 2012; Vargas et al., 2012).

Soil microbial response

Ascribing the CO_2 released upon rewetting to a particular source of C can be akin to the Indian parable of six blind men examining an elephant, each of them failing to consider the multiple facets of the objective truth while experiencing it from their own limited perspective. Many C sources contribute to the soil CO_2 pulse upon rewetting (Unger et al., 2010; Evans et al., 2016). Apart from carbonate solubilization, CO_2 emissions 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).

The importance of microbial death as a source of C for the CO_2 pulse has been measured using quantitative ^{18}O stable isotope probing. Upon rewetting a soil from a Mediterranean climate, initial bacterial growth was detected in select taxa dominated by Proteobacteria (*Azotobacter, Pseudomonas, Vibrio*) and Firmicutes (*Streptococcus, Clostridium, Mycoplasma*) while mortality was taxonomically widespread (Blazewicz et al., 2020). In addition, the density-dependence of growth upon rewetting contrasted with density independence of mortality, supporting the hypothesis that population-level biological interactions, such as competition and predation, likely controlled the growth rates of taxa but not their death (Blazewicz et al., 2020).

A number of studies have shown differential sensitivity of soil bacterial taxa to dry-down and rewetting; this differential sensitivity is conserved at phylum and class phylogenetic groupings (Lennon et al., 2012; Placella et al., 2012; Barnard et al., 2013, 2015; Engelhardt et al., 2018). This phylogenetic coherence reflects the evolutionary roots of microbial tolerance to drying and rewetting in microorganisms that are indigenous to and more common in semi-arid soil systems. The functional response of arid and semi-arid systems to dry-wet cycles can thus be expected to be deterministic and predictable (Averill et al., 2016). The two flagship phyla are Actinobacteria, which are commonly abundant in arid soils and include many taxa that are resistant to low moisture conditions (Goodfellow and Williams, 1983; Zvyagintsev et al., 2007) and Acidobacteria, a versatile group that can be adapted to changing environments (Eichorst et al., 2018); taxa from the Acidobacteria group have been found to dynamically track soil water conditions, flourishing rapidly upon rewetting (Placella et al., 2012; Barnard et al., 2013). Dry-down typically increases the relative abundance of the present or potentially active 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 exposed to past drought conditions can shape the response of soil microbial communities to subsequent drought or rewetting (Bouskill et al., 2013; Göransson et al., 2013; Hawkes et al., 2017; Meisner et al., 2018), with consequences that can extend to soil processes (Evans and Wallenstein, 2012; Martiny et al., 2017) as well as plant communities (Lau and Lennon, 2012; Meisner et al., 2013; Kaisermann et al., 2017).

The intensity and duration of dry conditions determine the response of soils to rewetting (Zhang et al., 2019). After a severe dry period, soil rewetting triggers a larger CO_2 pulse (Xu et al., 2004; Cable et al., 2008; Göransson et al., 2013; Barnard et al., 2015), which is consistent with a greater loss of C in carbon-rich ecosystems that experience more pronounced dry-wet events (Canarini et al., 2017). Under extreme conditions (i.e. dry soil for a long period of time or large $\Delta\psi$), maintaining metabolic functions upon rewetting may become more challenging than under more favorable conditions and there may be a greater frequency of microbial death and subsequent larger relative contribution of compatible solutes to the soil CO_2 pulse. However, the speed of dry-down should also be considered. When dry-down is slow, more compatible solutes accumulate in the soil relative to depolymerization products generated by exoenzymes (Warren, 2016). In addition, microbial production of extracellular polymeric substances (EPS), such as exopolysaccharides, can both retain water during soil drying and slow down rewetting of the habitats of microbial cells. (Roberson and Firestone, 1992).

Maximum compatible solute concentration in soil microbes occurred at relatively high ψ (-5 MPa) under slow dry-down conditions (Warren, 2016), compared to the estimated -14 MPa at which microbial activity ceases in the soil (Manzoni et al., 2012). Thus, compatible solute accumulation can only protect indigenous soil organisms from 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, soil type and magnitude of water potential upshock $\Delta\psi$; and (ii) exceeding a threshold in dry-wet $\Delta\psi$ is required to mobilize occluded organic matter (Fig. 1).

Importance of plants

Plants are the primary contributors to the quantity and quality of C entering soil and the size and composition of the available C pool controls the magnitude of the CO_2 pulse. Many of the studies investigating the nature of the C fueling the CO_2 pulse upon rewetting were undertaken in systems that were devoid of live plants at the time of rewetting (Borken and Matzner, 2009). This reflects the fact that wet-up studies, and the $\Delta\psi$ associated with substantial CO_2 pulses, require extremely dry soils, in which annual plants are generally no longer alive. However, the plants that were present during a growing period immediately preceding the dry-down may affect the microbial response to rewetting as: (i) labile C pools support CO_2 pulses ; (ii) above- and below-ground litter from semi-arid ecosystems can generate a large and labile pool of soil organic C that is present during the dry season ; and (iii) the presence of plants can impact the number and size of soil aggregates (Blankinship et al., 2016). Thus, plants may have been absent in many studies due either to the soil-centric focus of the researchers and the question, or due to the absence of living plants at the time of rewetting. For example, in Mediterranean systems the annual plant cover is often dead by the end of the dry season, when the first rains constitute the largest soil water potential upshocks.

Nevertheless, plants matter, whether dead or alive. Dry episodes can take place during the growing season without killing plant cover. In systems in which live plants are present, dry-wet cycling directly impacts plant-derived soil labile C inputs, both in their quantity, generally increasing exudation under moderate drought but having a more variable effect under intense drought (Preece and Peñuelas, 2016), and quality (Preece and Peñuelas, 2016; Gargallo-Garriga et al., 2018), with consequences on ecosystem functioning (Oikawa et al., 2014; Canarini and Dijkstra, 2015; Williams and de Vries, 2019). Dry-wet cycles can also affect plant N uptake, hydraulic redistribution (Fu et al., 2018) and trapping of windblown soil particles (Ravi et al., 2010), which all likely interact with major processes involved in the soil CO_2 pulse upon rewetting (Wang et al., 2015). Root exudation is of particular relevance, as it not only provides a direct labile C source for soil microorganisms, but can also contribute to shaping the root microbiome (Naylor and Coleman-Derr, 2017; Hartman and Tringe, 2019), a major driver of the soil CO_2 pulse upon rewetting.

Dry soils as well as those subject to infrequent watering events can hamper plant-microbial coupling by impeding the transfer of recent photo-assimilates from the roots to soil microorganisms (Ruehr et al., 2009; Fuchslueger et al., 2014; Engelhardt et al., 2018; Karlowsky et al., 2018). This may be due to reduced rhizodeposition rates (but see Preece and Peñuelas, 2016) or to challenging microbial access to rhizodeposits under diminished water film connectedness (Moyano et al., 2013; Fuchslueger et al., 2014; Tecon and Or, 2016; von Rein et al., 2016; Karlowsky et al., 2018). The plant-microbial interaction component of the mechanisms underlying the soil CO_2 efflux pulse upon rewetting may also vary with depth (Engelhardt et al., 2018).

Few experiments have addressed rewetting events during the spring in Mediterranean systems, when the plants are still alive, actively growing and the high flux of rhizodeposits to the soil exerts a strong influence on soil microbial activity (Curiel Yuste et al., 2007; Ma et al., 2012). The seasonal component of microbial response to changes in water availability has been documented in several studies (Cruz-Martínez et al., 2009; Bell et al., 2014; Zhao et al., 2016). The plant-microbial interaction component of the soil CO_2

pulse after rewetting may vary seasonally and experiments exploring rewetting after dry spring periods could provide a valuable perspective.

We propose that the origin of the C released upon soil rewetting (Fig. 2) is mainly controlled by three factors: the magnitude of the rewetting upshock ($\Delta\psi$), soil physical characteristics, and ecosystem productivity (NEP). The $\Delta\psi$ controls the pool of microbial-derived C, i.e. compatible solutes and dead cells. Soil physics controls pore connectivity, which in turn controls access to microbial- and plant-derived C. NEP controls the pool of plant-derived labile C which determines much of the soil enzyme pool.

Dry-wet cycles can impact soil C stabilization both positively and negatively (Bailey et al., 2019). A few dry-wet cycles increase the turnover of aggregates (i.e. as they are broken down then formed again), releasing inter-aggregate particulate organic matter and decreasing stabilization of fresh organic matter within the aggregate structure (Denef et al., 2001b). However, aggregates become slake-resistant with time, and more dry-wet cycles result in increased microaggregate stability (Denef et al., 2001a; Rahman et al., 2018). Dry-wet cycles increase microbial biomass C turnover, as microbial C lost through microbial death is replaced. Recent studies have proposed that enhanced microbial turnover under dry-wet cycles could result in an increased contribution of previously stable organic matter to microbial C (Lopez-Sangil et al., 2018; Schimel, 2018).

Conclusion

The large CO_2 pulse that is produced by rapid rewetting of very dry soil results from biological, physical and chemical mechanisms. The past 30+ years of research in this area provides an excellent example of integration across the subdisciplines of soil science. We suggest that significant future advances on the topic will be facilitated by greater inclusion and recognition of plant-microbe soil interactions.

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Figure legends

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

Figure 2. Main drivers (gray) of the mechanisms releasing CO_2 upon rewetting a dry soil, involving interactions between soil microorganisms (blue, center), plants (green, left) and soil physico-chemical properties (red, right).

Figure 1

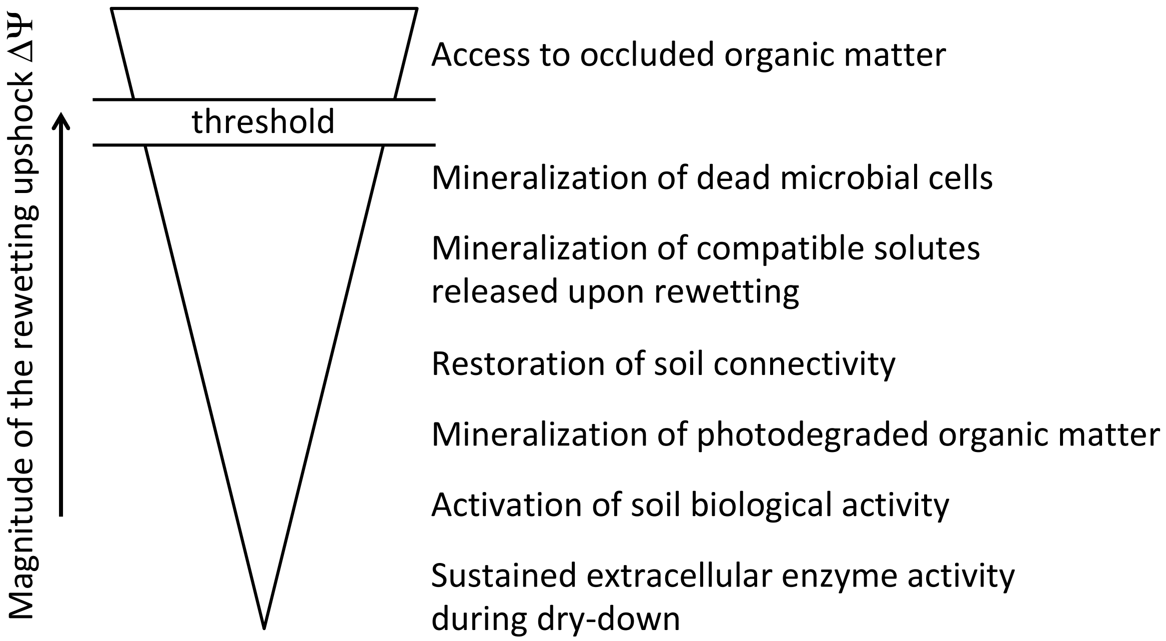
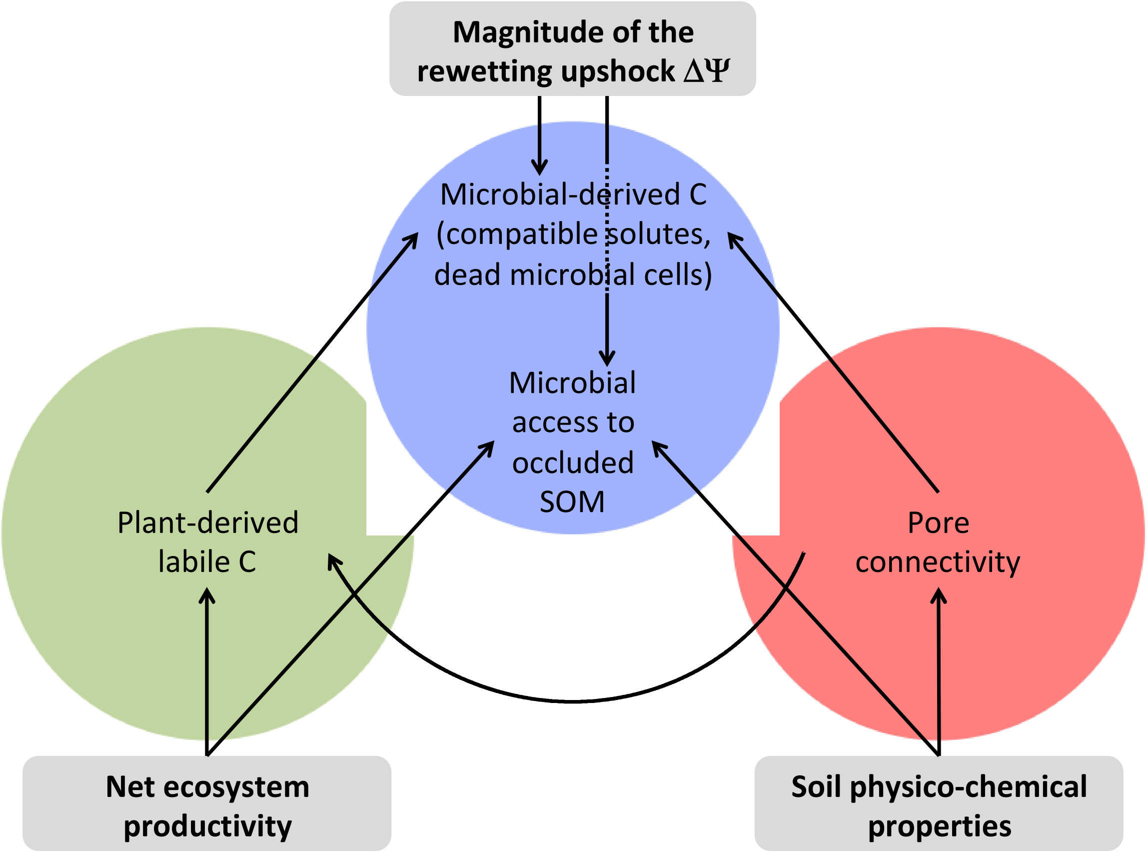

Magnitude of the rewetting upshock ΔΨ
threshold
Access to occluded organic matter
Mineralization of dead microbial cells
Mineralization of compatible solutes released upon rewetting
Restoration of soil connectivity
Mineralization of photodegraded organic matter
Activation of soil biological activity
Sustained extracellular enzyme activity during dry-down

Figure 2


Magnitude of the rewetting upshock ΔΨ
Microbial-derived C (compatible solutes, dead microbial cells)
Microbial access to occluded SOM
Plant-derived labile C
Pore connectivity
Net ecosystem productivity
Soil physico-chemical properties