Rhizodeposition under drought and consequences for soil communities and ecosystem resilience

Catherine Preece[1,2] and Josep Peñuelas[1,2]

1 – CREAF, Cerdanyola del Vallès, Catalonia, E-08193 Spain.

2 – CSIC, Global Ecology Unit, CREAF-CSIC-UAB, Cerdanyola del Vallès, Catalonia, E-08193 Spain

Corresponding author: catherine.preece09@gmail.com, (+34) 935814677.

Abstract

Background

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

Scope

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

Conclusions

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

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

Introduction

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

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

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

Rhizodeposition - an important plant-soil linkage

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

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

It may initially seem like a bad strategy for plants to lose carbon through their roots. However, rhizodeposition may be advantageous for plants, as it can increase the uptake of nutrients from the rhizosphere (Jones et al. 2004). One main way this occurs is through stimulation of soil microorganisms, which tend to be carbon-limited. Therefore the addition of an easily accessible C source into the soil (from the rhizodeposits) leads to increased activity of soil microbes and increased decomposition of soil organic matter (SOM). A review of the importance of rhizodeposition for carbon turnover found that a high proportion of rhizodeposits are bioavailable, as microorganisms rapidly respire 64-86% of these substances (Hütsch et al. 2002). This well-documented phenomenon is called the “priming effect” (Kuzyakov and Domanski 2000), and one way that this has been demonstrated is by greater soil microbial activity (i.e. CO_2 efflux) in soils that have plants growing in them compared with bare soils (Dijkstra and Cheng 2007).

The priming effect may be particularly significant in soils of low nutrient availability, where increased microbial activity and higher production of extracellular enzymes can enable the release of nutrients previously retained in the SOM, for use by microbes and plants (Dijkstra et al. 2013). For example, in nitrogen-limited soils, the priming effect can lead to increased availability in soil N, as shown by an experiment which added glucose (to represent root exudates) to soil and found increased activity of proteases and total soluble N (Asmar et al. 1994). In a field situation, rhizodeposition of carbon from temperate forest tree species was shown to stimulate soil N cycling, via an increase in extracellular enzymes (Brzostek et al. 2013). Similarly, increased exudation due to elevated CO_2 and temperature was shown to increase N cycling (via enhanced microbial activity) in low N soils in experiments with *Pinus taeda* and *Picea asperata* (Phillips et al. 2011; Yin et al. 2014). The links between roots, rhizodeposition, soil organic matter and microbial communities are summarised in Figure 1.

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

Besides the significant input of carbon into the soil, rhizodeposition can have impacts on soil structure in a number of different ways. For example, rhizodeposits can increase soil aggregate stability through the release of polysaccharides and proteins that have binding properties (Bardgett et al. 2014; Bronick and Lal 2005; Gregory 2006; Morel et al. 1991; Traore et al. 2000). This can have further impacts on the susceptibility of the soil to water run-off and erosion, which is increased in areas of low soil aggregate stability (Barthès and Roose 2002). During drying-rewetting cycles, addition of polygalacturonic acid, a root mucilage analogue, increased water repellency of soils leading to greater stability of the soil structure (Czarnes et al. 2000). Mucilage can also contain phospholipid surfactants (such as phosphatidylcholines) that can reduce soil water surface tension (Read et al. 2003). Micro-engineering of soil pores by microorganisms and plant roots, has been visualised using synchotron-radiation microtomography (three-dimensional reconstruction), showing changes towards a soil structure that is more porous, aggregated and ordered (Feeney et al. 2006). Soil microbial communities may be altered by such changes in the physical properties of the soil, but also directly due to the potential occurrence of antimicrobial compounds within rhizodeposits. The presence of such compounds is presumed to help protect the rhizosphere from attack by pathogens (Bais et al. 2006; Sobolev et al. 2006; Walker et al. 2003b).

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

Challenges in measuring drought impacts on rhizodeposition

Drought may impact rhizodeposition by changing the amount or composition of rhizodeposits, both of which may then affect microbial communities. There is still a relatively limited literature on how water stress impacts rhizodeposition, and it is difficult to assess, as there is no standardised drought treatment. This means that the duration of water stress differs for each study, as does the reduction in water, and the evaporative demand. Other challenges arise due to the differing methods used to measure rhizodeposition.

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

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

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

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

Data analysis of current literature

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

These effect sizes are shown for rhizodeposition (amount of organic carbon) per individual (or plot, in one case) (Fig. 2) and per gram of plant biomass (Fig. 3). For this second measurement total plant biomass was used where possible, but in two cases only shoot mass was directly measured. In the first instance, root biomass was estimated to be 25% of total biomass, and total biomass was back-calculated (Henry et al. 2007), but for the second study rhizodeposition was calculated per gram of shoot biomass (Somasundaram et al. 2009) and this is indicated on Table 1 and Figure 3. The use of effect sizes allows us to compare all types of study, but it is possible that drought effects on root: shoot ratios could alter results slightly for those calculating rhizodeposition relative to shoot mass. Positive values of the effect size indicate that the drought treatment increased rhizodeposition. The mean effect size was calculated and the 95 % confidence intervals around this mean were estimated using bootstrapping (1000 iterations). If these confidence intervals did not overlap with zero, the mean effect size was considered significant ($P < 0.05$) (Trap et al. 2015).

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

Variable responses of rhizodeposition to drought

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

Most studies in this review demonstrate a decrease in plant biomass under water stress, which whilst not a surprising finding (Brunner et al. 2015), does emphasise the importance of this measurement when attempting to determine the mechanisms behind any physiological changes in rhizodeposition. Therefore the ability to conserve biomass (especially roots) may be one of the most important factors for maintenance of rhizodeposition under water stress. Indeed, in studies that found evidence of a decrease in rhizodeposition per individual, a corresponding decrease in biomass was overwhelmingly suggested as the explanation, and when accounted for, the effect often disappeared. This is an important consideration when determining the effects on soils and their communities, and a change in plant biomass, specifically root biomass, offers a compelling and simple explanation for finding lower total rhizodeposition (per individual) under drought. In fact, it has been suggested that plants may have little control over regulation of rhizodeposition, overall and during abiotic stress such as drought (Jones et al. 2004). The significance of plant biomass on rhizodeposition has been previously demonstrated, for example, differences in rhizosphere priming effects of soybean (*Glycine max*) and sunflower (*Helianthus anuus*) on decomposition of SOM in two soil types (an organically farmed soil and an annual grassland) were predominantly explained by differences in plant biomass (Dijkstra et al. 2006). We recommend that future studies on rhizodeposition aim to measure both root and shoot biomass. While it may be presumed that root biomass will better correlate with rhizodeposition, there is not enough data to be sure of this. Also, changes in rhizodeposition patterns may likely occur before a change in overall plant biomass, so biomass should not be used as a replacement for measuring rhizodeposition directly.

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

A second explanation for signs of increased rhizodeposition under drought is that the water stress induces higher root mortality and lower cell membrane integrity, leading to increased leakage of solutes which are a source of carbon and cannot be easily distinguished from increased rhizodeposition of carbon (Henry et al. 2007). This could in fact be an explanation for the discrepancy between mucilage production and overall carbon release mentioned previously (Somasundaram et al. 2009). Similarly, damaged roots may have less reabsorption of rhizodeposits, further increasing the amount of carbon that is measured (Henry et al. 2007). Therefore, higher measurements of released C may be observed as a general response to stress, at least in the short term. However, over longer periods measured C would likely decrease unless roots were able to recover. Clearly, it is important for future studies to differentiate between these two conflicting explanations as the first (up-regulation) indicates tolerance and high likelihood of recovery and the second (root damage and death) indicates susceptibility and lower likelihood of recovery. Additionally, during a single drought event, increased carbon inputs may initially be due to up-regulation and later because of root damage.

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

Amongst the studies that measured rhizodeposition using pulse-labelling with ^{13}C or ^{14}C (which comprised the majority of studies), rhizodeposition per gram of plant decreased as the intensity of drought increased (linear model, effect size of rhizodeposition ~ drought intensity, $F_{1,7} = 5.757$, $P = 0.048$). This indicates that carbon inputs may be augmented under low to moderate water stress, but this becomes less likely under more extreme and prolonged water stress, perhaps after a threshold level of water stress has been reached. Similar patterns have been shown with other root responses to drought, for example fine root length and the live-to-dead ratio of fine roots were shown to increase under moderate drought, but then decrease with further water stress in beech saplings (*Fagus sylvatica*) (Zang et al. 2014). It has been suggested that fine root production may initially compensate for root mortality, but that root growth stops in extreme drought conditions (Brunner et al. 2015; Gaul et al. 2008), and this level of drought may be when the soil water matrix potentials approaches −0.12 MPa (Gaul et al. 2008). This definition of extreme drought is used later when considering the interactions between rhizodeposition and microorganisms under different drought regimes (Fig. 4).

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

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

There may be changes in composition of rhizodeposits in response to drought. *Brassica napus* seedlings grown in an axenic system with 24 hours of water stress showed a shift in the composition of soluble organic carbon towards a lower proportion of amino acids (7% in droughted plants compared to 28% in controls) and exuded more sterols per root dry mass and a higher number of types of polar lipids (Svenningsson et al. 1990). Crested wheatgrass (*Agropyrum cristatum*) undergoing a 35 day drought treatment in axenic conditions had increased levels of succinic acid in the rhizodeposits (Henry et al. 2007), and amongst two varieties of maize (*Zea mays*) grown in hydroponics, water stress induced by exposure to a polyethylene glycol (PEG) solution for 24 hours led to an increase in the amount of organic acids in rhizodeposits, and in the more drought tolerant variety there was found to be higher concentrations of proteases and catalases (Song et al. 2012).

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

Effects of rhizodeposits on microorganisms

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

Rhizodeposition effects on soils can be studied in the field by trenching (cutting the roots from a channel of soil around the base of a tree) and girdling (removing a strip of bark from the entire circumference of the trunk, disrupting phloem transport). In general, rhizodeposition increases microbial biomass due to the additional inputs of carbon into the soil (Paterson 2003). Such experiments have consistently shown positive correlations between the amount of rhizodeposition (often shown by total organic carbon in the soil) and microbial biomass (Dannenmann et al. 2009; Zeller et al. 2008) and soil respiration (Högberg et al. 2001; Subke et al. 2004). Positive correlations between root mass or activity and soil microbial biomass have also been shown in studies on forest die-back which compare living and dead trees (Xiong et al. 2011), and in studies comparing soil containing living roots with bare soil (Loeppmann et al. 2016) and comparisons of rhizosphere soil with bulk soil (Finzi et al. 2015).

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

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

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

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

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

Role of plant-soil microbe interactions in ecosystem resilience

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

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

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

In addition to effects of microbes on plants, changes in the amount or composition of rhizodeposits by water-stressed plants may affect soil microbial community composition through recruitment or population increases of microorganisms that are drought tolerant. There is evidence of changes in rhizodeposits leading to changes in soil communities (Bakker et al. 2013; Bulgarelli et al. 2013). For example, experimental application of different glucose substrates to microcosms altered the soil bacteria community composition (Eilers et al. 2010). In light of our observation that plants are able to respond to moderate drought by increasing relative levels of rhizodeposition (per gram of root biomass), high resistance of soil communities may be linked to the presence of plants with this capacity. For example, there may be fewer negative effects for the soil microorganisms under plants that can maintain or up-regulate rhizodeposition, as the relative increase in C inputs may offset any decrease in living root biomass. Conversely for plant species that cannot increase rhizodeposition in response to drought, changes in soil microbial communities may be more likely to occur. In Figure 4 we summarise the direct and indirect (via rhizodeposition) effects of moderate and extreme drought on microbial communities, and how this may impact ecosystem resistance and resilience.

Conclusions

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

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

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

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

Acknowledgements

This research was supported by the European FP7 S-Clima project PIEF-GA-2013-626234, the European Research Council Synergy grant ERC-2013-726 SyG-610028 IMBALANCE-P, the Spanish Government project CGL2013-48074-P and the Catalan Government project SGR 2014- 274.

Figures

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

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

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

Fig. 4 Schematic diagram showing how interactions between rhizodeposition and the microbial community affect ecosystem resistance and resilience under moderate and extreme drought. Extreme drought refers to water stress leading to large-scale root mortality without replacement from new root growth. Under moderate drought there are more likely to be positive relationships (+) between drought, rhizodeposition, microbial community. Under more extreme droughts, relationships may be more variable and less predictable (+/-) but positive relationships are unlikely to be maintained over prolonged periods of time.

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

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

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

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

References

Allison SD, Martiny JBH (2008) Resistance, resilience, and redundancy in microbial communities. Proceedings of the National Academy of Sciences 105: 11512-11519. doi: 10.1073/pnas.0801925105.

Asmar F, Eiland F, Nielsen NE (1994) Effect of extracellular-enzyme activities on solubilization rate of soil organic nitrogen. Biol Fertil Soils 17: 32-38. doi: 10.1007/bf00418669.

Averill C, Waring BG, Hawkes CV (2016) Historical precipitation predictably alters the shape and magnitude of microbial functional response to soil moisture. Glob Change Biol 22: 1957-1964. doi: 10.1111/gcb.13219.

Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM (2006) The role of root exudates in rhizosphere interations with plants and other organisms. Annual Review of Plant Biology.

Bakker PA, Berendsen RL, Doornbos RF, Wintermans PC, Pieterse CM (2013) The rhizosphere revisited: root microbiomics. Frontiers in plant science 4.

Baptist F, Aranjuelo I, Legay N, Lopez-Sangil L, Molero G, Rovira P, Nogues S (2015) Rhizodeposition of organic carbon by plants with contrasting traits for resource acquisition: responses to different fertility regimes. Plant Soil 394: 391-406. doi: 10.1007/s11104-015-2531-4.

Bardgett RD, Manning P, Morrien E, De Vries FT (2013) Hierarchical responses of plant-soil interactions to climate change: consequences for the global carbon cycle. J Ecol 101: 334-343. doi: 10.1111/1365-2745.12043.

Bardgett RD, Mommer L, De Vries FT (2014) Going underground: root traits as drivers of ecosystem processes. Trends in Ecology & Evolution 29: 692–699. doi: http://dx.doi.org/10.1016/j.tree.2014.10.006.

Barthès B, Roose E (2002) Aggregate stability as an indicator of soil susceptibility to runoff and erosion; validation at several levels. CATENA 47: 133-149. doi: http://dx.doi.org/10.1016/S0341-8162(01)00180-1.

Belimov AA, Dodd IC, Hontzeas N, Theobald JC, Safronova VI, Davies WJ (2009) Rhizosphere bacteria containing 1-aminocyclopropane-1-carboxylate deaminase increase yield of plants grown in drying soil via both local and systemic hormone signalling. New Phytol 181: 413-423. doi: 10.1111/j.1469-8137.2008.02657.x.

Benizri E, Nguyen C, Piutti S, Slezack-Deschaumes S, Philippot L (2007) Additions of maize root mucilage to soil changed the structure of the bacterial community. Soil Biology and Biochemistry 39: 1230-1233. doi: http://dx.doi.org/10.1016/j.soilbio.2006.12.026.

Berg G, Smalla K (2009) Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. Fems Microbiology Ecology 68: 1-13. doi: 10.1111/j.1574-6941.2009.00654.x.

Blum A (1989) Osmotic adjustment and growth of barley genotypes under drought stress. Crop Science 29: 230-233.

Boer Wd, Folman LB, Summerbell RC, Boddy L (2005) Living in a fungal world: impact of fungi on soil bacterial niche development. FEMS Microbiology Reviews 29: 795-811. doi: 10.1016/j.femsre.2004.11.005.

Bota J, Medrano H, Flexas J (2004) Is photosynthesis limited by decreased Rubisco activity and RuBP content under progressive water stress? New Phytol 162: 671-681. doi: 10.1111/j.1469-8137.2004.01056.x.

Broeckling CD, Broz AK, Bergelson J, Manter DK, Vivanco JM (2008) Root exudates regulate soil fungal community composition and diversity. Applied and environmental microbiology 74: 738-744. doi: 10.1128/aem.02188-07.

Bronick CJ, Lal R (2005) Soil structure and management: a review. Geoderma 124: 3-22. doi: 10.1016/j.geoderma.2004.03.005.

Brunner I, Herzog C, Dawes MA, Arend M, Sperisen C (2015) How tree roots respond to drought. Frontiers in Plant Science 6: 547. doi: 10.3389/fpls.2015.00547.

Brzostek ER, Greco A, Drake JE, Finzi AC (2013) Root carbon inputs to the rhizosphere stimulate extracellular enzyme activity and increase nitrogen availability in temperate forest soils. Biogeochemistry 115: 65-76. doi: 10.1007/s10533-012-9818-9.

Bulgarelli D, Schlaeppi K, Spaepen S, van Themaat EVL, Schulze-Lefert P (2013) Structure and functions of the bacterial microbiota of plants. Annual Review of Plant Biology 64: 807-838. doi: 10.1146/annurev-arplant-050312-120106.

Canarini A, Dijkstra FA (2015) Dry-rewetting cycles regulate wheat carbon rhizodeposition, stabilization and nitrogen cycling. Soil Biology and Biochemistry 81: 195-203. doi: http://dx.doi.org/10.1016/j.soilbio.2014.11.014.

Carvalhais LC, Dennis PG, Fedoseyenko D, Hajirezaei M-R, Borriss R, von Wirén N (2011) Root exudation of sugars, amino acids, and organic acids by maize as affected by nitrogen, phosphorus, potassium, and iron deficiency. Journal of Plant Nutrition and Soil Science 174: 3-11. doi: 10.1002/jpln.201000085.

Chaves MM (1991) Effects of water deficits on carbon assimilation. J Exp Bot 42: 1-16. doi: 10.1093/jxb/42.1.1.

Chaves MM, Maroco J, #227, P. o, Pereira J, #227, S. o (2003) Understanding plant responses to drought — from genes to the whole plant. Funct Plant Biol 30: 239-264. doi: http://dx.doi.org/10.1071/FP02076.

Chaves MM, Oliveira MM (2004) Mechanisms underlying plant resilience to water deficits: prospects for water-saving agriculture. J Exp Bot 55: 2365-2384. doi: 10.1093/jxb/erh269.

Cheng W, Gershenson A (2007) Carbon fluxes in the rhizosphere. The rhizosphere: An ecological perspective.

Clark JS, Campbell JH, Grizzle H, Acosta-Martinez V, Zak JC (2009) Soil microbial community response to drought and precipitation variability in the Chihuahuan Desert. Microb Ecol 57: 248-260. doi: 10.1007/s00248-008-9475-7.

Cruz-Martinez K, Suttle KB, Brodie EL, Power ME, Andersen GL, Banfield JF (2009) Despite strong seasonal responses, soil microbial consortia are more resilient to long-term changes in rainfall than overlying grassland. ISME J 3: 738-744. doi: http://www.nature.com/ismej/journal/v3/n6/suppinfo/ismej200916s1.html.

Curiel Yuste J, Fernandez-Gonzalez AJ, Fernandez-Lopez M, Ogaya R, Penuelas J, Sardans J, Lloret F (2014) Strong functional stability of soil microbial communities under semiarid Mediterranean conditions and subjected to long-term shifts in baseline precipitation. Soil Biol Biochem 69: 223-233. doi: 10.1016/j.soilbio.2013.10.045.

Czarnes S, Hallett PD, Bengough AG, Young IM (2000) Root- and microbial-derived mucilages affect soil structure and water transport. European Journal of Soil Science 51: 435-443. doi: 10.1046/j.1365-2389.2000.00327.x.

Dai A (2011) Drought under global warming: a review. Wiley Interdisciplinary Reviews: Climate Change 2: 45-65. doi: 10.1002/wcc.81.

Dannenmann M, Simon J, Gasche R, Holst J, Naumann PS, Kögel-Knabner I, Knicker H, Mayer H, Schloter M, Pena R, Polle A, Rennenberg H, Papen H (2009) Tree

girdling provides insight on the role of labile carbon in nitrogen partitioning between soil microorganisms and adult European beech. Soil Biology and Biochemistry 41: 1622-1631. doi: http://dx.doi.org/10.1016/j.soilbio.2009.04.024.
Delgado-Baquerizo M, Maestre FT, Reich PB, Jeffries TC, Gaitan JJ, Encinar D, Berdugo M, Campbell CD, Singh BK (2016) Microbial diversity drives multifunctionality in terrestrial ecosystems. Nat Commun 7. doi: 10.1038/ncomms10541.
Dennis PG, Miller AJ, Hirsch PR (2010) Are root exudates more important than other sources of rhizodeposits in structuring rhizosphere bacterial communities? FEMS Microbiology Ecology 72: 313-327. doi: 10.1111/j.1574-6941.2010.00860.x.
Dijkstra FA, Carrillo Y, Pendall E, Morgan JA (2013) Rhizosphere priming: a nutrient perspective. Front Microbiol 4: 8. doi: 10.3389/fmicb.2013.00216.
Dijkstra FA, Cheng W, Johnson DW (2006) Plant biomass influences rhizosphere priming effects on soil organic matter decomposition in two differently managed soils. Soil Biology and Biochemistry 38: 2519-2526. doi: http://dx.doi.org/10.1016/j.soilbio.2006.02.020.
Dijkstra FA, Cheng WX (2007) Moisture modulates rhizosphere effects on C decomposition in two different soil types. Soil Biol Biochem 39: 2264-2274. doi: 10.1016/j.soilbio.2007.03.026.
Ehrenfeld JG, Ravit B, Elgersma K (2005) Feedback in the plant-soil system. Annual Review of Environment and Resources 30: 75-115. doi: 10.1146/annurev.energy.30.050504.144212.
Eilers KG, Lauber CL, Knight R, Fierer N (2010) Shifts in bacterial community structure associated with inputs of low molecular weight carbon compounds to soil. Soil Biology and Biochemistry 42: 896-903. doi: http://dx.doi.org/10.1016/j.soilbio.2010.02.003.
Evans SE, Wallenstein MD (2012) Soil microbial community response to drying and rewetting stress: does historical precipitation regime matter? Biogeochemistry 109: 101-116. doi: 10.1007/s10533-011-9638-3.
Feeney DS, Crawford JW, Daniell T, Hallett PD, Nunan N, Ritz K, Rivers M, Young IM (2006) Three-dimensional microorganization of the soil–root–microbe system. Microbial Ecology 52: 151-158.
Field CB, Barros VR, Mach KJ, Mastrandrea MD, Aalst Mv, Adger WN, Arent DJ, Barnett J, Betts R, Bilir TE, Birkmann J, Carmin J, Chadee DD, Challinor AJ, Chatterjee M, Cramer W, Davidson DJ, Estrada YO, Gattuso JP, Hijioka Y, Hoegh-Guldberg O, Huang HQ, Insarov GE, Jones RN, Kovats RS, Lankao PR, Larsen JN, Losada IJ, Marengo JA, McLean RF, Mearns LO, Mechler R, Morton JF, Niang I, Oki T, Olwoch JM, Opondo M, Poloczanska ES, Pörtner HO, Redsteer MH, Reisinger A, Revi A, Schmidt DN, Shaw MR, Solecki W, Stone DA, Stone JMR, Strzepek KM, Suarez AG, Tschakert P, Valentini R, Vicuña S, Villamizar A, Vincent KE, Warren R, White LL, Wilbanks TJ, Wong PP, Yohe GW (2014) Technical Summary. In: CB Field, VR Barros, DJ Dokken, KJ Mach, MD Mastrandrea, TE Bilir, M Chatterjee, KL Ebi, YO Estrada, RC Genova, B Girma, ES Kissel, AN Levy, S MacCracken, PR Mastrandrea, LL White (eds) Climate Change 2014: Impacts, Adaptation, and Vulnerability Part A: Global and Sectoral Aspects Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on

Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
Fierer N, Bradford MA, Jackson RB (2007) Toward an ecological classification of soil bacteria. Ecology 88: 1354-1364.
Fierer N, Schimel JP, Holden PA (2003) Influence of drying-rewetting frequency on soil bacterial community structure. Microb Ecol 45: 63-71. doi: 10.1007/s00248-002-1007-2.
Finzi AC, Abramoff RZ, Spiller KS, Brzostek ER, Darby BA, Kramer MA, Phillips RP (2015) Rhizosphere processes are quantitatively important components of terrestrial carbon and nutrient cycles. Glob Change Biol 21: 2082-2094. doi: 10.1111/gcb.12816.
Flexas J, Bota J, Loreto F, Cornic G, Sharkey TD (2004) Diffusive and metabolic limitations to photosynthesis under drought and salinity in C3 plants. Plant Biology 6: 269-279. doi: 10.1055/s-2004-820867.
Fuchslueger L, Bahn M, Fritz K, Hasibeder R, Richter A (2014) Experimental drought reduces the transfer of recently fixed plant carbon to soil microbes and alters the bacterial community composition in a mountain meadow. New Phytol 201: 916-927. doi: 10.1111/nph.12569.
Gargallo-Garriga A, Sardans J, Pérez-Trujillo M, Rivas-Ubach A, Oravec M, Vecerova K, Urban O, Jentsch A, Kreyling J, Beierkuhnlein C, Parella T, Peñuelas J (2014) Opposite metabolic responses of shoots and roots to drought. Scientific Reports 4: 6829. doi: 10.1038/srep06829
http://www.nature.com/articles/srep06829#supplementary-information.
Gaul D, Hertel D, Borken W, Matzner E, Leuschner C (2008) Effects of experimental drought on the fine root system of mature Norway spruce. For Ecol Manage 256: 1151-1159. doi: http://dx.doi.org/10.1016/j.foreco.2008.06.016.
Glick BR, Todorovic B, Czarny J, Cheng Z, Duan J, McConkey B (2007) Promotion of plant growth by bacterial ACC deaminase. Critical Reviews in Plant Sciences 26: 227-242. doi: 10.1080/07352680701572966.
Gorissen A, Tietema A, Joosten NN, Estiarte M, Peñuelas J, Sowerby A, Emmett BA, Beier C (2004) Climate change affects carbon allocation to the soil in shrublands. Ecosystems 7: 650-661. doi: 10.1007/s10021-004-0218-4.
Grassi G, Magnani F (2005) Stomatal, mesophyll conductance and biochemical limitations to photosynthesis as affected by drought and leaf ontogeny in ash and oak trees. Plant, Cell & Environment 28: 834-849. doi: 10.1111/j.1365-3040.2005.01333.x.
Gregory PJ (2006) Roots, rhizosphere and soil: the route to a better understanding of soil science? European Journal of Soil Science 57: 2-12. doi: 10.1111/j.1365-2389.2005.00778.x.
Griffiths BS, Philippot L (2013) Insights into the resistance and resilience of the soil microbial community. FEMS Microbiology Reviews 37: 112-129. doi: 10.1111/j.1574-6976.2012.00343.x.
Griffiths BS, Ritz K, Ebblewhite N, Dobson G (1999) Soil microbial community structure: Effects of substrate loading rates. Soil Biol Biochem 31: 145-153.
Guggenberger G, Frey SD, Six J, Paustian K, Elliott ET (1999) Bacterial and fungal cell-wall residues in conventional and no-tillage agroecosystems. Soil Sci Soc Am J 63: 1188-1198. doi: 10.2136/sssaj1999.6351188x.
Haichar FeZ, Marol C, Berge O, Rangel-Castro JI, Prosser JI, Balesdent J, Heulin T, Achouak W (2008) Plant host habitat and root exudates shape soil bacterial

community structure. ISME J 2: 1221-1230. doi: http://www.nature.com/ismej/journal/v2/n12/suppinfo/ismej200880s1.html.
Hawkes CV, Keitt TH (2015) Resilience vs. historical contingency in microbial responses to environmental change. Ecol Lett 18: 612-625. doi: 10.1111/ele.12451.
Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis or response ratios in experimental ecology. Ecology 80: 1150-1156. doi: 10.1890/0012-9658(1999)080[1150:TMAORR]2.0.CO;2.
Henry A, Doucette W, Norton J, Bugbee B (2007) Changes in crested wheatgrass root exudation caused by flood, drought, and nutrient stress. Journal of Environmental Quality 36: 904-912. doi: 10.2134/jeq2006.0425sc.
Hoffland E, Van Den Boogaard R, Nelemans J, Findenegg G (1992) Biosynthesis and root exudation of citric and malic acids in phosphate-starved rape plants. New Phytol 122: 675-680. doi: 10.1111/j.1469-8137.1992.tb00096.x.
Högberg P, Nordgren A, Buchmann N, Taylor AFS, Ekblad A, Högberg MN, Nyberg G, Ottosson-Lofvenius M, Read DJ (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411: 789-792.
Holling CS (1973) Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4: 1-23. doi: doi:10.1146/annurev.es.04.110173.000245.
Hütsch BW, Augustin J, Merbach W (2002) Plant rhizodeposition: An important source for carbon turnover in soils. Journal of Plant Nutrition and Soil Science 165: 397-407.
Jaleel CA, Manivannan P, Wahid A, Farooq M, Al-Juburi HJ, Somasundaram R, Panneerselvam R (2009) Drought stress in plants: a review on morphological characteristics and pigments composition. Int J Agric Biol 11: 100-105.
Johnson JF, Allan DL, Vance CP (1994) Phosphorus Stress-Induced Proteoid Roots Show Altered Metabolism in Lupinus albus. Plant Physiol 104: 657-665. doi: 10.1104/pp.104.2.657.
Jones DL, Hodge A, Kuzyakov Y (2004) Plant and mycorrhizal regulation of rhizodeposition. New Phytol 163: 459-480. doi: 10.1111/j.1469-8137.2004.01130.x.
Jones DL, Nguyen C, Finlay RD (2009) Carbon flow in the rhizosphere: carbon trading at the soil–root interface. Plant Soil 321: 5-33. doi: 10.1007/s11104-009-9925-0.
Kuzyakov Y, Domanski G (2000) Carbon input by plants into the soil. Review. Journal of Plant Nutrition and Soil Science 163: 421-431. doi: 10.1002/1522-2624(200008)163:4<421::AID-JPLN421>3.0.CO;2-R.
Lal R (2009) Soil degradation as a reason for inadequate human nutrition. Food Sec 1: 45-57. doi: 10.1007/s12571-009-0009-z.
Lau JA, Lennon JT (2012) Rapid responses of soil microorganisms improve plant fitness in novel environments. Proceedings of the National Academy of Sciences 109: 14058-14062. doi: 10.1073/pnas.1202319109.
Li YP, Ye W, Wang M, Yan XD (2009) Climate change and drought: a risk assessment of crop-yield impacts. Clim Res 39: 31-46.
Lipton DS, Blanchar RW, Blevins DG (1987) Citrate, malate, and succinate concentration in exudates from P-sufficient and P-stressed *Medicago sativa* L. seedlings. Plant Physiol 85: 315-317. doi: 10.1104/pp.85.2.315.
Loeppmann S, Blagodatskaya E, Pausch J, Kuzyakov Y (2016) Substrate quality affects kinetics and catalytic efficiency of exo-enzymes in rhizosphere and

detritusphere. Soil Biol Biochem 92: 111-118. doi: 10.1016/j.soilbio.2015,09.020.
Marasco R, Rolli E, Ettoumi B, Vigani G, Mapelli F, Borin S, Abou-Hadid AF, El-Behairy UA, Sorlini C, Cherif A, Zocchi G, Daffonchio D (2012) A drought resistance-promoting microbiome is selected by root system under desert farming. PLoS One 7: e48479. doi: 10.1371/journal.pone.0048479.
Mayak S, Tirosh T, Glick BR (2004) Plant growth-promoting bacteria that confer resistance to water stress in tomatoes and peppers. Plant Sci 166: 525-530. doi: 10.1016/j.plantsci.2003.10.025.
McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG, Yepez EA (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytol 178: 719-739. doi: 10.1111/j.1469-8137.2008.02436.x.
Meharg AA (1994) A critical review of labelling techniques used to quantify rhizosphere carbon-flow. Plant Soil 166: 55-62. doi: 10.1007/BF02185481.
Mishra AK, Singh VP (2010) A review of drought concepts. Journal of Hydrology 391: 202-216. doi: http://dx.doi.org/10.1016/j.jhydrol.2010.07.012.
Mommer L, Padilla FM, Ruijven J, Caluwe H, Smit‐Tiekstra A, Berendse F, Kroon H (2015) Diversity effects on root length production and loss in an experimental grassland community. Functional Ecology 29: 1560-1568.
Morel JL, Habib L, Plantureux S, Guckert A (1991) Influence of maize root mucilage on soil aggregate stability. Plant Soil 136: 111-119. doi: 10.1007/bf02465226.
Neumann G, George T, Plassard C (2009) Strategies and methods for studying the rhizosphere—the plant science toolbox. Plant Soil 321: 431-456. doi: 10.1007/s11104-009-9953-9.
Neumann G, Römheld V (1999) Root excretion of carboxylic acids and protons in phosphorus-deficient plants. Plant Soil 211: 121-130. doi: 10.1023/A:1004380832118.
Neumann G, Römheld V (2007) The release of root exudates as affected by the plant physiological status. The Rhizosphere Biochemistry and Organic Substances at the Soil–Plant Interface. 2nd edn. CRC Press/Taylor and Francis, New York.
Nguyen C (2003) Rhizodeposition of organic C by plants: mechanisms and controls. Agronomie 23: 375-396.
Nielsen UN, Ayres E, Wall DH, Bardgett RD (2011) Soil biodiversity and carbon cycling: a review and synthesis of studies examining diversity–function relationships. European Journal of Soil Science 62: 105-116. doi: 10.1111/j.1365-2389.2010.01314.x.
Oburger E, Dell'mour M, Hann S, Wieshammer G, Puschenreiter M, Wenzel WW (2013) Evaluation of a novel tool for sampling root exudates from soil-grown plants compared to conventional techniques. Environmental and Experimental Botany 87: 235-247. doi: http://dx.doi.org/10.1016/j.envexpbot.2012.11.007.
Oburger E, Schmidt H (2016) New methods to unravel rhizosphere processes. Trends Plant Sci 21: 243-255. doi: http://dx.doi.org/10.1016/j.tplants.2015.12.005.
Palta JA, Gregory PJ (1997) Drought affects the fluxes of carbon to roots and soil in C-13 pulse-labelled plants of wheat. Soil Biol Biochem 29: 1395-1403. doi: 10.1016/s0038-0717(97)00050-3.
Paterson E (2003) Importance of rhizodeposition in the coupling of plant and microbial productivity. European Journal of Soil Science 54: 741-750. doi: 10.1046/j.1351-0754.2003.0557.x.

Paterson E, Gebbing T, Abel C, Sim A, Telfer G (2007) Rhizodeposition shapes rhizosphere microbial community structure in organic soil. New Phytol 173: 600-610. doi: 10.1111/j.1469-8137.2006.01931.x.

Penuelas J, Prieto P, Beier C, Cesaraccio C, de Angelis P, de Dato G, Emmett BA, Estiarte M, Garadnai J, Gorissen A, Lang EK, Kroel-Dulay G, Llorens L, Pellizzaro G, Riis-Nielsen T, Schmidt IK, Sirca C, Sowerby A, Spano D, Tietema A (2007) Response of plant species richness and primary productivity in shrublands along a north-south gradient in Europe to seven years of experimental warming and drought: reductions in primary productivity in the heat and drought year of 2003. Glob Change Biol 13: 2563-2581. doi: 10.1111/j.1365-2486.2007.01464.x.

Phillips DA, Fox TC, King MD, Bhuvaneswari TV, Teuber LR (2004) Microbial products trigger amino acid exudation from plant roots. Plant Physiol 136: 2887-2894. doi: 10.1104/pp.104.044222.

Phillips RP, Erlitz Y, Bier R, Bernhardt ES (2008) New approach for capturing soluble root exudates in forest soils. Functional Ecology 22: 990-999. doi: 10.1111/j.1365-2435.2008.01495.x.

Phillips RP, Finzi AC, Bernhardt ES (2011) Enhanced root exudation induces microbial feedbacks to N cycling in a pine forest under long-term CO2 fumigation. Ecol Lett 14: 187-194. doi: 10.1111/j.1461-0248.2010.01570.x.

Pimentel D (2006) Soil Erosion: A Food and Environmental Threat. Environ Dev Sustain 8: 119-137. doi: 10.1007/s10668-005-1262-8.

Pinton R, Varanini Z, Nannipieri P (2007) The rhizosphere: biochemistry and organic substances at the soil-plant interface. CRC press.

Pollierer MM, Langel R, Körner C, Maraun M, Scheu S (2007) The underestimated importance of belowground carbon input for forest soil animal food webs. Ecol Lett 10: 729-736. doi: 10.1111/j.1461-0248.2007.01064.x.

Ravenek JM, Bessler H, Engels C, Scherer ‐ Lorenzen M, Gessler A, Gockele A, De Luca E, Temperton VM, Ebeling A, Roscher C (2014) Long ‐ term study of root biomass in a biodiversity experiment reveals shifts in diversity effects over time. Oikos 123: 1528-1536.

Read DB, Bengough AG, Gregory PJ, Crawford JW, Robinson D, Scrimgeour CM, Young IM, Zhang K, Zhang X (2003) Plant roots release phospholipid surfactants that modify the physical and chemical properties of soil. New Phytol 157: 315-326. doi: 10.1046/j.1469-8137.2003.00665.x.

Rolli E, Marasco R, Vigani G, Ettoumi B, Mapelli F, Deangelis ML, Gandolfi C, Casati E, Previtali F, Gerbino R, Pierotti Cei F, Borin S, Sorlini C, Zocchi G, Daffonchio D (2015) Improved plant resistance to drought is promoted by the root-associated microbiome as a water stress-dependent trait. Environmental Microbiology 17: 316-331. doi: 10.1111/1462-2920.12439.

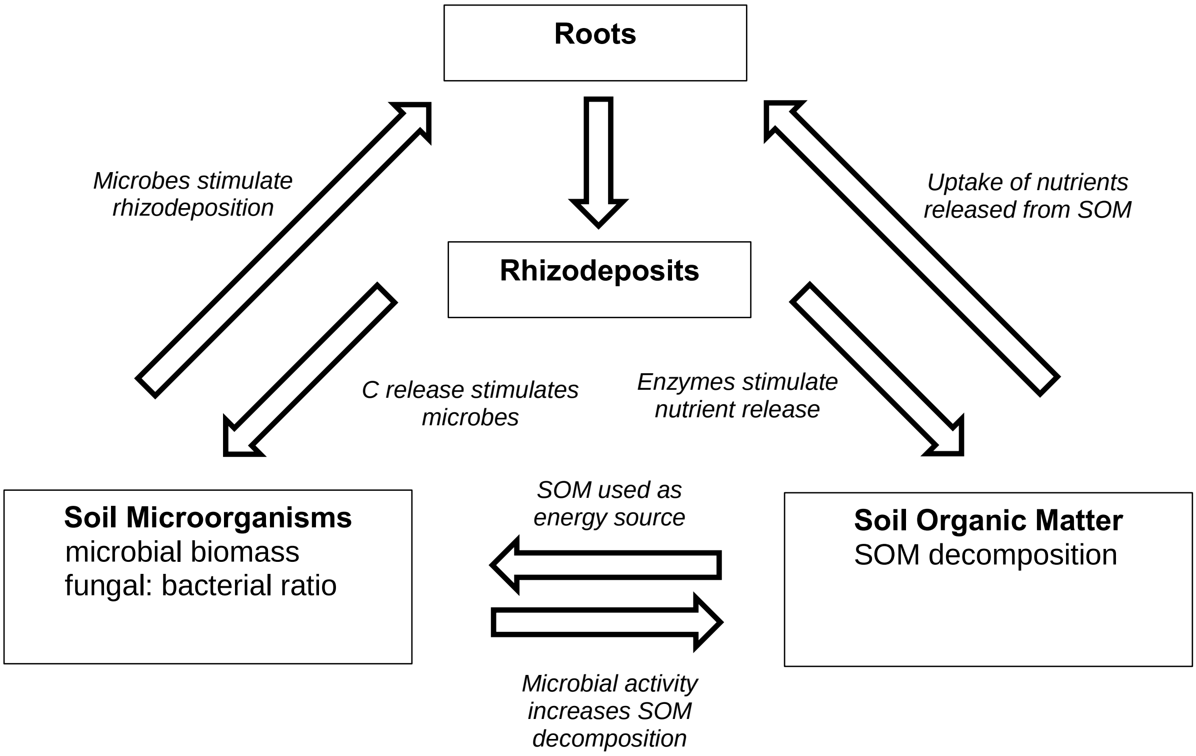
Ruf A, Kuzyakov Y, Lopatovskaya O (2006) Carbon fluxes in soil food webs of increasing complexity revealed by 14C labelling and 13C natural abundance. Soil Biology and Biochemistry 38: 2390-2400. doi: http://dx.doi.org/10.1016/j.soilbio.2006.03.008.

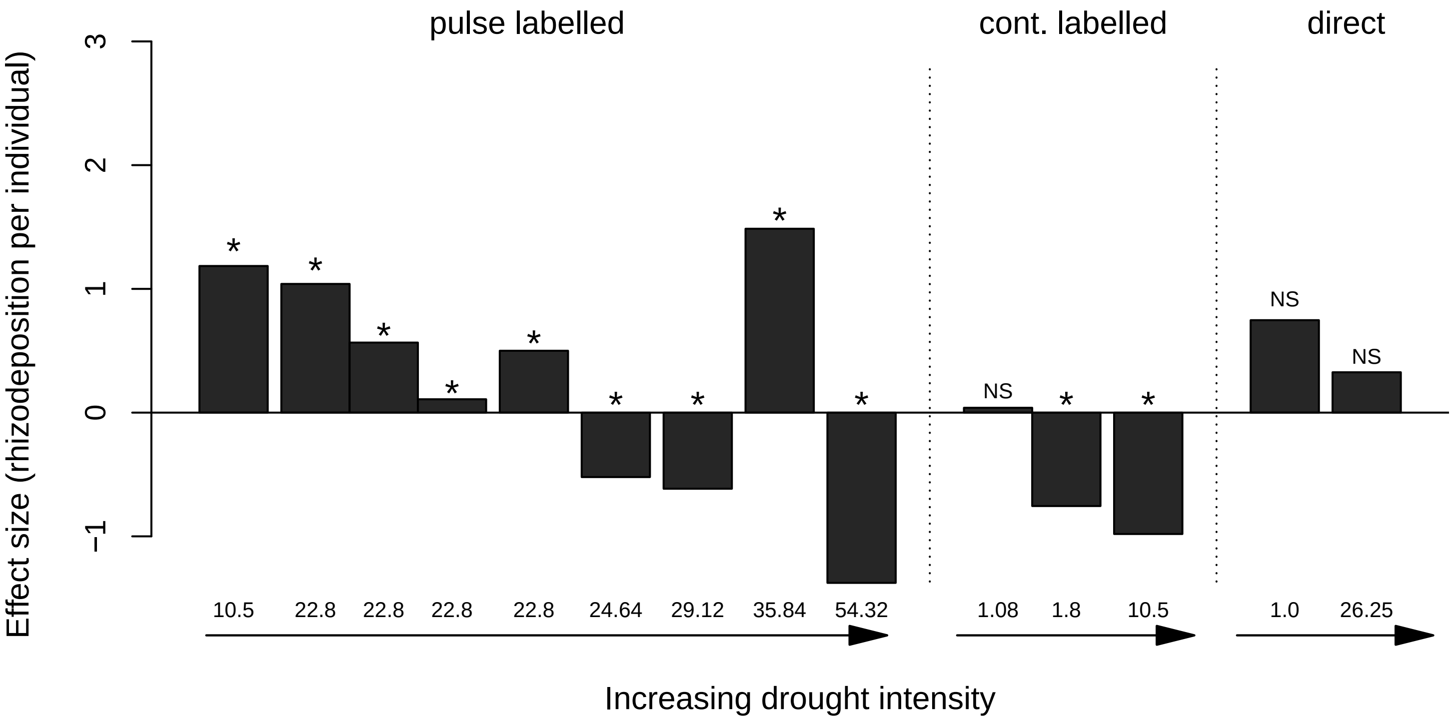
Sanaullah M, Chabbi A, Rumpel C, Kuzyakov Y (2012) Carbon allocation in grassland communities under drought stress followed by C-14 pulse labeling. Soil Biol Biochem 55: 132-139. doi: 10.1016/j.soilbio.2012.06.004.

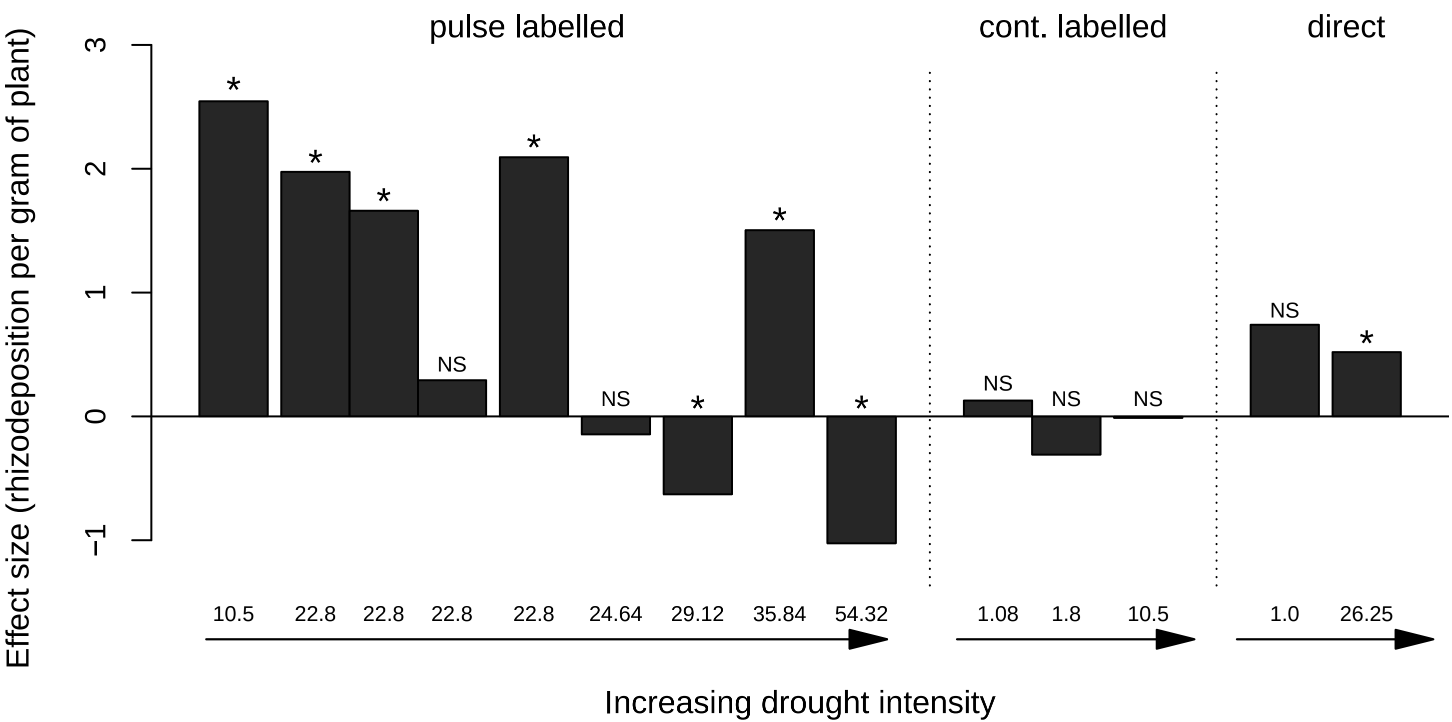
Scheunemann N, Digel C, Scheu S, Butenschoen O (2015) Roots rather than shoot residues drive soil arthropod communities of arable fields. Oecologia 179: 1135-1145. doi: 10.1007/s00442-015-3415-2.

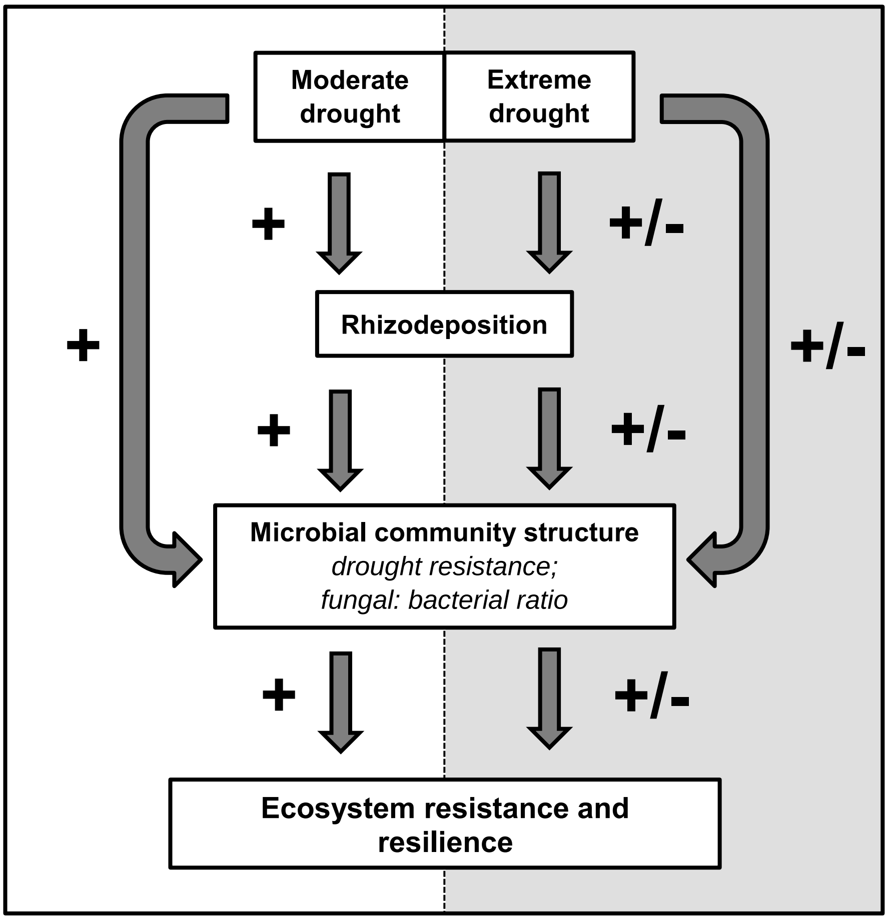
Schimel J, Balser TC, Wallenstein M (2007) Microbial stress-response physiology and its implications for ecosystem function. Ecology 88: 1386-1394. doi: 10.1890/06-0219.
Shade A, Peter H, Allison SD, Baho DL, Berga M, Bürgmann H, Huber DH, Langenheder S, Lennon JT, Martiny JB (2012) Fundamentals of microbial community resistance and resilience. Front Microbiol 3: 166-181. doi: 10.3389/fmicb.2012.00417.
Six J, Frey SD, Thiet RK, Batten KM (2006) Bacterial and Fungal Contributions to Carbon Sequestration in Agroecosystems. Soil Sci Soc Am J 70: 555-569. doi: 10.2136/sssaj2004.0347.
Sobolev VS, Potter TL, Horn BW (2006) Prenylated stilbenes from peanut root mucilage. Phytochemical Analysis 17: 312-322. doi: 10.1002/pca.920.
Somasundaram S, Rao TP, Tatsumi J, Iijima M (2009) Rhizodeposition of mucilage, root border cells, carbon and water under combined soil physical stresses in *Zea mays* L. Plant Prod Sci 12: 443-448.
Song FB, Han XY, Zhu XC, Herbert SJ (2012) Response to water stress of soil enzymes and root exudates from drought and non-drought tolerant corn hybrids at different growth stages. Can J Soil Sci 92: 501-507. doi: 10.4141/cjss2010-057.
Strickland MS, Rousk J (2010) Considering fungal:bacterial dominance in soils – Methods, controls, and ecosystem implications. Soil Biology and Biochemistry 42: 1385-1395. doi: http://dx.doi.org/10.1016/j.soilbio.2010.05.007.
Subke J-A, Hahn V, Battipaglia G, Linder S, Buchmann N, Cotrufo MF (2004) Feedback interactions between needle litter decomposition and rhizosphere activity. Oecologia 139: 551-559. doi: 10.1007/s00442-004-1540-4.
Svenningsson H, Sundin P, Liljenberg C (1990) Lipids, carbohydrates and amino acids exuded from the axenic roots of rape seedlings exposed to water-deficit stress. Plant, Cell & Environment 13: 155-162. doi: 10.1111/j.1365-3040.1990.tb01287.x.
Traore O, Groleau-Renaud V, Plantureux S, Tubeileh A, Boeuf-Tremblay V (2000) Effect of root mucilage and modelled root exudates on soil structure. European Journal of Soil Science 51: 575-581. doi: 10.1111/j.1365-2389.2000.00348.x.
Trap J, Bonkowski M, Plassard C, Villenave C, Blanchart E (2015) Ecological importance of soil bacterivores for ecosystem functions. Plant Soil 398: 1-24. doi: 10.1007/s11104-015-2671-6.
van Dam NM, Bouwmeester HJ (2016) Metabolomics in the rhizosphere: tapping into belowground chemical communication. Trends Plant Sci 21: 256-265. doi: http://dx.doi.org/10.1016/j.tplants.2016.01.008.
Van Der Heijden MGA, Bardgett RD, Van Straalen NM (2008) The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol Lett 11: 296-310. doi: 10.1111/j.1461-0248.2007.01139.x.
van der Putten WH, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T, Kardol P, Klironomos JN, Kulmatiski A, Schweitzer JA, Suding KN, Van de Voorde TFJ, Wardle DA (2013) Plant–soil feedbacks: the past, the present and future challenges. J Ecol 101: 265-276. doi: 10.1111/1365-2745.12054.
Vranova V, Rejsek K, Skene KR, Janous D, Formanek P (2013) Methods of collection of plant root exudates in relation to plant metabolism and purpose: A review. Journal of Plant Nutrition and Soil Science 176: 175-199. doi: 10.1002/jpln.201000360.
Walker TS, Bais HP, Grotewold E, Vivanco JM (2003a) Root exudation and rhizosphere biology. Plant Physiol 132: 44-51. doi: 10.1104/pp.102.019661.

Walker TS, Bais HP, Halligan KM, Stermitz FR, Vivanco JM (2003b) Metabolic profiling of root exudates of *Arabidopsis thaliana*. Journal of Agricultural and Food Chemistry 51: 2548-2554. doi: 10.1021/jf021166h.
Wardle DA, Bardgett RD, Klironomos JN, Setälä H, van der Putten WH, Wall DH (2004) Ecological linkages between aboveground and belowground biota. Science 304: 1629-1633. doi: 10.1126/science.1094875.
Watt M, Evans JR (1999) Proteoid Roots. Physiology and Development. Plant Physiol 121: 317-323. doi: 10.1104/pp.121.2.317.
Williams MA (2007) Response of microbial communities to water stress in irrigated and drought-prone tallgrass prairie soils. Soil Biology and Biochemistry 39: 2750-2757. doi: http://dx.doi.org/10.1016/j.soilbio.2007.05.025.
Xiong YM, D'Atri JJ, Fu SL, Xia HP, Seastedt TR (2011) Rapid soil organic matter loss from forest dieback in a subalpine coniferous ecosystem. Soil Biol Biochem 43: 2450-2456. doi: 10.1016/j.soilbio.2011.08.013.
Yin H, Wheeler E, Phillips RP (2014) Root-induced changes in nutrient cycling in forests depend on exudation rates. Soil Biology and Biochemistry 78: 213-221. doi: http://dx.doi.org/10.1016/j.soilbio.2014.07.022.
Zang U, Goisser M, Häberle K-H, Matyssek R, Matzner E, Borken W (2014) Effects of drought stress on photosynthesis, rhizosphere respiration, and fine-root characteristics of beech saplings: A rhizotron field study. Journal of Plant Nutrition and Soil Science 177: 168-177. doi: 10.1002/jpln.201300196.
Zeller B, Liu J, Buchmann N, Richter A (2008) Tree girdling increases soil N mineralisation in two spruce stands. Soil Biology and Biochemistry 40: 1155-1166. doi: http://dx.doi.org/10.1016/j.soilbio.2007.12.009.
Zhao MS, Running SW (2010) Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. Science 329: 940-943. doi: 10.1126/science.1192666.
Zhu B, Cheng WX (2013) Impacts of drying-wetting cycles on rhizosphere respiration and soil organic matter decomposition. Soil Biol Biochem 63: 89-96. doi: 10.1016/j.soilbio.2013.03.027.


Roots
Microbes stimulate rhizodeposition
Uptake of nutrients released from SOM
Rhizodeposits
C release stimulates microbes
Enzymes stimulate nutrient release
SOM used as energy source
Soil Microorganisms
microbial biomass
fungal: bacterial ratio
Soil Organic Matter
SOM decomposition
Microbial activity increases SOM decomposition


pulse labelled
cont. labelled
direct
Effect size (rhizodeposition per individual)
3
2
1
0
−1
*
*
*
*
*
*
*
*
*
NS
*
*
NS
NS
10.5
22.8
22.8
22.8
22.8
24.64
29.12
35.84
54.32
1.08
1.8
10.5
1.0
26.25
Increasing drought intensity


pulse labelled
cont. labelled
direct
Effect size (rhizodeposition per gram of plant)
3
2
1
0
−1
*
*
*
NS
*
NS
*
*
*
NS
NS
NS
NS
*
10.5
22.8
22.8
22.8
22.8
24.64
29.12
35.84
54.32
1.08
1.8
10.5
1.0
26.25
Increasing drought intensity



Moderate drought
Extreme drought
+
+/-
Rhizodeposition
+
+/-
+
+/-
Microbial community structure
drought resistance;
fungal: bacterial ratio
+
+/-
Ecosystem resistance and resilience

Electronic Supplementary Material

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