J Soils Sediments (2014) 14:99–109
DOI 10.1007/s11368-013-0799-7

SOILS, SEC 2 • GLOBAL CHANGE, ENVIRON RISK ASSESS, SUSTAINABLE LAND USE • REVIEW ARTICLE

Responses of soil respiration and its components to drought stress

**Yanfen Wang · Yanbin Hao · Xiao Yong Cui ·
Haitao Zhao · Chengyuan Xu · Xiaoqi Zhou ·
Zhihong Xu**

Received: 11 July 2013 / Accepted: 21 October 2013 / Published online: 6 November 2013

Abstract

Purpose Climate change is likely to increase both intensity and frequency of drought stress. The responses of soil respiration (R_s) and its components (root respiration, R_r; mycorrhizal respiration, R_m; and heterotrophic respiration, R_h) to drought stress can be different. This work aims to review the recent and current literature about the variations in R_s during the period of drought stress, to explore potential coupling processes and mechanisms between R_s and driving factors in the context of global climate change.

Results and discussion The sensitivity of soil respiration and its components to drought stress depended on the ecosystems and seasonality. Drought stress depressed R_s in mesic and xeric ecosystems, while it stimulated R_s in hydric ecosystems. The reductions in supply and availability of substrate decreased both auto- and heterotrophic respirations, leading to the temporal decoupling of root and mycorrhizal respiration from canopy photosynthesis as well as C allocation. Drought stress also reduced the diffusion of soluble C substrate, and activities of extracellular enzymes, consequently, limited microbial activity and reduced soil organic matter decomposition. Drought stress altered Q_{10} values and broke the coupling between temperature and soil respiration. Under drought stress conditions, R_m is generally less sensitive to temperature than R_r and R_h. Elevated CO_2 concentration alleviated the negative effect of drought stress on soil respiration, principally due to the promotion of plant C assimilation subsequently, which increased substrate supply for respiration in both roots and soil microorganisms. Additionally, rewetting stimulated soil respiration dramatically in most cases, except for soil that experienced extreme drought stress periods. The legacy of drought stress can also regulate the response of soil respiration rate to rewetting events in terrestrial ecosystems through changing abiotic drivers and microbial community structure.

Conclusions and perspectives There is increasing evidence that drought stress can result in the decoupling of the above- and belowground processes, which are associated with soil respiration. However, studies on the variation in rates of soil respiration and its components under different intensities and frequencies of drought stress over the ecosystems should be reinforced. Meanwhile, molecular phylogenetics and functional genomics should be applied to link microbial ecology to the process of R_s. In addition, we should quantify the relationship between soil respiration and global change parameters (such as warming and elevated [CO_2]) under drought stress. Models simulating the rates of soil respiration and its components under global climate change and drought stress should also be developed.

Keywords Drought stress · Global climate change · Heterotrophic respiration · Mycorrhizal respiration · Root respiration

1 Introduction

Water is the most important matter for plant growth and productivity development for terrestrial ecosystems in the world (Prasolova et al. 2000, 2001; Xu and Chen 2006; Xu

---

Responsible editor: Hailong Wang

Y. Wang · Y. Hao (✉) · X. Y. Cui
College of Life Sciences, University Chinese Academy of Sciences,
Beijing 100049, China
e-mail: ybhao@ucas.ac.cn

Y. Hao
e-mail: ybhao2012@gmail.com

C. Xu · X. Zhou · Z. Xu
Environmental Futures Centre and School of Bimolecular and
Physical Sciences, Griffith University, Nathan, Brisbane 4111,
Australia

H. Zhao
College of Environmental Science and Engineering, Yangzhou
University, Yangzhou 225127, China

et al. 2000). Therefore, water availability and drought stress are intimately linked with the terrestrial carbon (C) cycling (van der Molen et al. 2011). Global climate change is likely to increase drought stress in many terrestrial ecosystems, which could alter the global patterns of organic matter production and decomposition (Feyen and Dankers 2009; Xu et al. 2009). Drought stress is expected to influence the C cycling more strongly in the future (Knorr et al. 2007). Ecosystem respiration is one of the largest gross fluxes in the global C cycle and integrates quite different processes of plant and microbial functions (Trumbore 2006; Casals et al. 2011). Soil CO_2 emission, combined plant–root (R_r), and heterotrophic (R_h) and mycorrhizal respiration (R_m) exceed anthropogenic CO_2 emissions by about 10 times (Hanson et al. 2000; Kuzyakov 2006). Because auto- and heterotrophic activity belowground is largely controlled by substrate availability, soil respiration is strongly linked to plant metabolism, photosynthesis, microbes, extracellular enzymes, and litterfall (Ryan and Law 2005). Therefore, the coupling of the biological processes of above- and belowground regulates the response of R_s to drought stress.

Climate-change scenarios indicate that many areas of the world will have much variation in precipitation patterns, with more frequent extreme rainfall events and longer drought stress periods for tropical and subtropical regions (Alley 2007; Allan and Soden 2008). Recently, many experiments have focused on the research meteorological drought stress affecting the soil CO_2 emission across the different biomes. These studies suggested that drought stress could alter the relationship between soil CO_2 efflux and its (environmental and biological) driving factors (Lavigen et al. 2004; Ruehr et al. 2009; van der Molen et al. 2011; Walter et al. 2011; Ford et al. 2012; Selsted et al. 2012; Signarbieux and Feller 2012). However, global climate models predict increased temperatures, and CO_2 concentration would interact with changes in precipitation patterns to affect R_s. In humid environments, increased temperatures may enhance R_s by stimulating microbial activity, whereas in dry soils, they coincide with or even contribute to dryer conditions, resulting in an apparent negative R_s response to temperature (Wan et al. 2007). Elevated CO_2 concentration and extended drought stress showed a positive interaction, and elevated $[CO_2]$ can reduce the effect of drought stress on R_s. Thus, the questions are how drought stress is coupled with soil respiration and how increased temperature and CO_2 concentration regulate the relationship between drought stress and soil CO_2 efflux. Here, we review the state of understanding of the relationship between drought stress and the soil respiration, and make some suggestions for further study in the context of global climate change. The paper is organized around a few aspects relevant to drought stress and the soil respiration and its components (Fig. 1). These include the following: (1) How does drought stress directly and indirectly influence soil respiration-observed results? (2) What are the mechanisms for the responses of soil respiration to drought stress? (3) What is the effect of drought stress on soil respiration in the context of climate change?

2 How drought stress influence soil respiration-observed results

2.1 The direct effect of drought stress on soil respiration and its components

In this paper, the drought stress is defined as precipitation deficiency deviated from normal conditions with respect to a percentage of normal rainfall (Joos et al. 2009; Brilli et al. 2011; Signarbieux and Feller 2012) and a period of more than some particular number of days with precipitation less than some specified small amount (Walter et al. 2011; Bloor and Bardgett 2012). We reviewed the studies of effects of soil water availability on R_s, to which drought stress applied. According to C pools recognized as sources of CO_2 efflux, agents of CO_2 production, and locations of CO_2 production, Kuzyakov (2006) suggested that the five sources are the main contributors to total soil CO_2 efflux: (1) basal respiration derived from decomposition of soil organic matter (SOM), (2) priming effect induced microbial decomposition of SOM, (3) microbial decomposition of dead plant remains, (4) rhizomicrobial respiration produced by microbial decomposition of rhizodeposits of living roots, and (5) root respiration. Because it was difficult to identify the process of items 2–4, in this study, we partition R_s into autotrophic respiration (R_a) including root respiration (R_r) and mycorrhizal respiration (R_m) and heterotrophic respiration (R_h) including items 1–4.

Components of soil respiration followed the different seasonal trends but all were affected by drought stress (Rey et al. 2002; Risk et al. 2012). It is stated that drought stress can reduce R_s ratio in the mesic and xeric ecosystems (Borken et al. 2006; Joos et al. 2009) (Fig. 2a), while it can stimulate R_s in the hydric ecosystem (Savage and Davidson 2001; Knorr et al. 2007; Sowerby et al. 2008) (Fig. 2b). For example, soil respiration may decline by 25–50% in response to modest water stress (minimum Ψ_s of −0.6 to −0.2 MPa) in a balsam fir ecosystem (Lavigen et al. 2004). The degree of R_s reduced depends on community composition (Talmon et al. 2011; Breulmann et al. 2012), species richness (Correâ Dias et al. 2010), and the intensity and frequency of drought stress.

Since components of soil respiration have the potential to respond quite differently to climatological controls, microbial community composition, and climate change, the impacts of drought stress on R_r, R_h, and R_m are distinctive in different ecosystems (Fig. 2). The autotrophic component of soil CO_2 efflux is dominant and mainly from maintenance respiration of root, whereas the heterotrophic respiration derived from microbial respiration is minimized or even ceased during the drought stress period (Casals et al. 2011; Bulter et al. 2012).

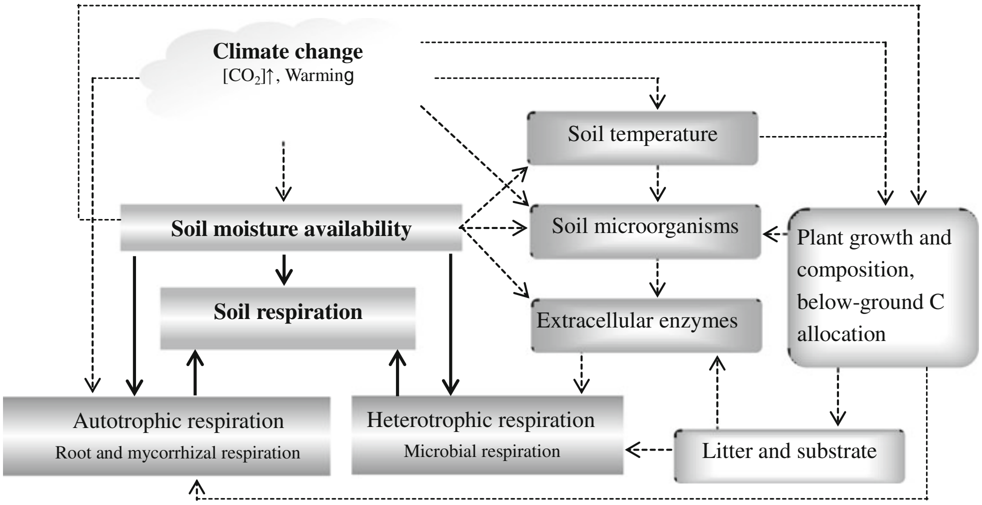

Fig. 1 Conceptual framework outlining the distinctions among direct effects of soil water availability (SWA) on soil respiration in situ under climate change conditions (*solid line*), the effects of SWA on soil respiration that occur via changes in microbial activity, community composition and extracellular enzymes dynamics and the indirect effects of climate on soil microorganisms (*dotted lines*), and shifts in relationship between the aboveground and belowground processes. The interaction of global change drivers (atmospheric N deposition, elevated atmospheric CO$_2$, and warming) and SWA affects indirectly on the soil respiration

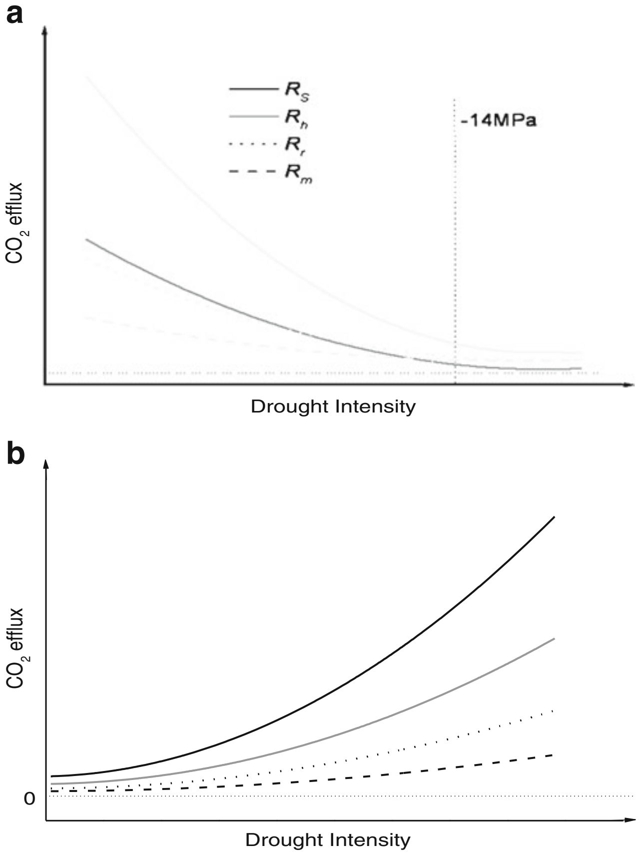

Fig. 2 Hypothetical variation in soil respiration (R_s) and its components (root respiration, R_r; mycorrhizal respiration, R_m; and heterotrophic respiration, R_h along drought stress gradients in **a** mesic and xeric ecosystem and **b** a hydric ecosystem. The *vertically dashed lines* in the *top panel* means the R_h approximate 0 when $\Psi_s \approx -14$ MPa

Overall, R_h is more sensitive to drought stress than R_a (Fig. 2a). At the initial stage of drought stress, R_h begins to decline at the upper soil layers, whereas R_r remains stable and thus increases its relative contribution to total soil efflux (Unger et al. 2010). However, an extreme drought stress causes greater reductions in the heterotrophic component of soil respiration compared with the rhizospheric component (Scott-Denton et al. 2006). Some studies suggested that the microbial respiration is more strongly affected than root respiration by intensive and long-term drought stress events(Scott-Denton et al. 2006; Williams 2007; Suseela et al. 2012), while other researchers found that root respiration was more sensitive than microbial respiration to water stress (Lavigen et al. 2004; Carbone et al. 2011). The reasons for these conflicting experimental results may contribute to that were run at the different ecosystems and different temporal measuring scale. Because a thinner film of water coats the soil particles, diffusion of labile substrates is slowed and the activity of exoenzymes needed for the decomposition of organic matter in drier soils is reduced (Suseela et al. 2012). Therefore, the mycorrhizal respiration rate decreases during a period of drought stress and is more sensitive to drought stress than R_h (Fenn et al. 2010). In hydric ecosystems, R_s has been observed to increase as water tables drop and peat begins to dry out (Brown 1998; Alm et al. 1999; Aurela et al. 2001). Drying raised air-filled porosity in the soil and increase R_h by stimulating the microbial activity. However, root associated respiration (R_a) was concentrated in the uppermost peat layer and was insensitive to drought stress compared to R_h (Knorr et al. 2008) (Fig. 2b).

The responses of components of soil respiration to drought stress intensity are different. Suseela et al. (2012) found R_h

decreased sharply when volumetric soil moisture dropped below 15% or exceeded 26%, but R_h increased more gradually when soil moisture rose from the lower threshold. In mineral soil, microbial respiration is near zero when $\Psi_s \approx -14$ MPa (Manzoni et al. 2012). The responses of R_r, R_m, and R_h to the time of drought stress and duration are inconsistent (Lavigen et al. 2004; Carbone et al. 2011; Gomez-Casanovas et al. 2012). Therefore, it is urgent to quantify the variation in rates of soil respiration and its components under different intensity and frequency of drought stress in different terrestrial ecosystems. In addition, the effect of drought stress, especially extreme drought stress, on soil respiration can persist for 1–9 years. However, recent studies have always focused on 1–3 years. Therefore, long-term and continuous measurements are also necessary.

2.2 Drought stress indirect affects through the coupling of temperature and soil respiration

Respiration of both microbial communities and plant roots can be sensitive to variations in soil temperature. The sensitivity of soil respiration to soil water content and soil temperature may be a function of the proportions of auto- and heterotrophic components of soil respiration at any given time (Gomez-Casanovas et al. 2012). Exponential relationships, especially the Q_{10}—the increase in respiration rates with a 10 °C increase in temperature—have been commonly used to estimate R_s rates with the temperature (Epron et al. 1999; Buchmann 2000; Rey et al. 2002). The coupling of temperature and soil respiration would be broken by drought stress since drought stress reduced the diffusion of soluble C substrate and the extracellular enzymes, consequently, limited the microbial activity (Manzoni et al. 2012). Soil–water deficit substantially reduced R_s sensitivity to temperature, resulting in a lower Q_{10} (Sampson et al. 2007; Jassal et al. 2008; Manzoni et al. 2012; Rey et al. 2002). The responses of temperature sensitivity of its components of soil respiration to drought stress are different, depending on the specific controlling factors. R_r is largely associated with the physiological response of root to drought stress. The seasonal variation in root growth with temperature may explain the difference of Q_{10} of R_r (Boone et al. 1998; Rey et al. 2002). The growth and death of roots are very sensitive to drought stress, depending on plant functional types. C_4 plants required the lower root biomass than C_3 plants under the same water stress and have lower Q_{10} of root-respiration as well than C_3 during drought stress periods (Zhou et al. 2012). Moisture limitation can suppress microbial activity regardless of temperature, which should decrease the temperature sensitivity of R_h (Davidson and Janssens 2006). The influence of drought stress on response of R_h to temperature depends on seasonal dynamics and soil properties (Craine and Gelderman 2011).The sensitivity to temperature of R_m under drought stress conditions is not as significant as those of R_r and R_h. The variation in Q_{10} of R_m depends on the presence of mycorrhizal and rhizospheric respiration sources, as well as on plant development (Moyano et al. 2007; Fenn et al. 2010).

3 What are the mechanisms for the responses of soil respiration to drought stress?

3.1 Direct effect of drought stress through soil microorganisms and extracellular enzymes on soil respiration

Soil organic matter decomposition ultimately contributes very significantly to soil CO_2 efflux and thus to global CO_2 emissions (Bond-Lamberty et al. 2004). The role of microbial population in how SOM decomposition responds to drought stress with different intensities and durations could be of paramount importance. The relative contributions of the microbial functional groups, such as fungi and bacteria, to SOM decomposition are different, and these groups directly influence terrestrial C cycling. The factors controlling ecological aspects of the soil microbial community directly limit the SOM decomposition. Drought stress not only limits physiological performance, diffusion of microbes, and the diffusion of nutrients to microbes in the soil pore space but also submits the microbial community to an important adaptive force. Furthermore, the limited substrate supply under drought stress reduces the activity of microbes and diminishes R_s (Bardgett et al. 2005; Suseela et al. 2012). Apart from the effect of drought stress on R_s through limiting microbial activity, the change of microbial community composition also may influence R_s. The response of R_h to water availability change depends on the relative importance of fungi in the decomposer community. As the soil dries, conditions shift from favorable to soil fauna and bacteria to more favorable to fungi and actinomycetes (Freckman 1986), and the microbial community structure may become dominated by drought stress-tolerant species (Williams and Hallsworth 2009; Wallenstein and HE 2011; Manzoni et al. 2012). Shifting from microbial communities to fungal dominant communities improves the C stability of the physical environment and generates a more protected and stable C (Bardgett et al. 2005; Manzoni et al. 2012). Alternatively, Chowdhury et al. (2011) found that drought stress did not significantly affect the microbial community abundance (bacteria and fungi), suggesting that large differences in soil respiration were due to modulation of the activity per cell. In addition, mobility of microbes can be limited by drought stress due to the lack of soil water. The SOM decomposition rate of mineral soils containing the bulk of organic matter is limited by microbes' ability to access due to drought stress (John et al. 2005).

Extracellular enzymes are the "proximate agents of organic matter decomposition," and its activity is generally used to infer shifts in microbial demand for C (Henry 2012). Microbial extracellular enzyme production is related to microbial activity as well as soil physico-chemical properties (Sowerby et al. 2005). While an ecosystem encounters drought stress, two steps are required for microbes to process the material wrapped by a thinner film of water coats—first a physical step of aggregate disruption, and then possibly a second step in which exoenzymes break up the polymers (Navarro-García et al. 2011). Thus, the slowed diffusion of labile substrates and the reducing activity of extracellular enzymes would limit the decomposition of SOM. During the period of drought stress, the activity of enzymes associated with C cycling, such as xylanse, β-cellobiosidase, and β-glucosidase, would reduce and thus slow the decomposition of litters (Kardol et al. 2010; Sanaullah et al. 2011). Drought stress also may affect the production of extracellular polymeric materials, which bridge between microbes and their substrates. It allows microbes to survive in dry soils and can either promote (Chenu and Roberson 1996) or constrain C diffusion to microbes (Holden et al. 1997). The activity of enzymes under drought stress conditions is also affected by plant successional stages in which the composition and activity of microbial communities change and evolve as a consequence of changes in the physico-chemical status of soils. Less enzyme activities and soil respiration reduction were observed in soils with mature plant covered than in degraded soils under drought stress (Fioretto et al. 2009). However, Freeman et al. (1996) found the elevated enzyme activities without an associated increase in microbial respiratory activity in a peatland ecosystem, suggesting that drought stress conditions influence peatland mineralization rates through a direct stimulation of existing enzymes, rather than through a generalized stimulation of microbial metabolism. Although these studies of in situ microbial communities can partially account for the mechanisms in physiological and community ecology of soil respiration under drought stress, molecular phylogenetics and functional genomics should be applied to link microbial ecology to the process of R_s. Combinations of new molecular methodology and genomics may link microbial phylogeny with function in R_s studies and provide significant insights into plant–microbe interactions in the R_s.

3.2 The regulation of plant growth and composition and belowground C allocation to soil respiration under drought stress

Seasonal variations in soil respiration and its auto- and heterotrophic components have often been accounted for by changes in soil temperature and moisture (Davidson and Holbrook 2009; Phillips et al. 2011; Taneva and Gonzalez-Meler 2011). However, evidence from recent studies suggested that recent and current plant photosynthesis influences soil respiration and its components at different time scales in both forests and grasslands (Rey et al. 2002; Ruehr et al. 2009; Flanagan 2009; Fenn et al. 2010; Kuzyakov and Gavrichkova 2010; Moyano et al. 2012). Because the responses of the components of soil respiration to photosynthesis are different, the effect of drought stress on soil respiration through reduced plant growth, productivity and variation in vegetation composition would be distinctive. The response of R_m to photosynthetic activity is more sensitive than R_r and R_h (Moyano et al. 2007). Photosynthesis supplies C substrate for root metabolism and growth, and a decrease in substrate supply can decrease R_r within days (Bowling et al. 2002; Bardgett et al. 2005; Ruehr et al. 2009). Under drought stress condition, low-productivity grassland ecosystem has lower decomposition rate of root litters, influencing the microbial communities, as well as the ratio between fungal and bacterial biomass and patterns of soil enzyme activity (Breulmann et al. 2012). During drought stress periods, photosynthesis declines and stored nonstructural carbohydrates are used to maintain living tissues so that R_r is temporarily decoupled from the canopy photosynthesis (Högberg et al. 2001).

Apart from the reduced coupling between canopy photosynthesis and the belowground process, the life types of plants, vegetation cover, and structure and community composition also influence the response of soil respiration to drought stress. Soil respiration rate decreases from wet to dry seasons in the shallow-rooted ecosystem, whereas deep-rooted forests maintain substantial soil respiration during the dry seasons (Davidson et al. 2000). Talmon et al. (2011) suggested that drought stress decreased the rates of soil respiration not only by lowering biological activity but also by drastically reducing shrub cover and in heterogeneous ecosystems, such as Mediterranean and deserts shrublands. Thus, there would be a major impact on R_s by feedbacks through change in vegetation structure. Long-term drought stress may affect soil respiration by altering the community composition, particularly the presence of legume species, which affect soil organic C (SOC) dynamics and below-ground microbial processes, especially via roots. However, the regulating role of plant diversity in the response of R_s to drought stress is still poorly understood. In general, higher plant diversity with higher productivity may partly counteract the impact of drought stress (Craine et al. 2001). The reduction of the N concentration of organic matter in more diverse plant community may negatively affect both R_a and R_h (Correâ Dias et al. 2010). Therefore, how changes in plant community diversity can affect soil respiration needs to be studied. In addition, drought stress also has effects on soil respiration through feedback influence of soil nitrogen (N) pools since the microbial processes that regulate soil N availability are sensitive to short-term variations in soil moisture. The increased duration and intensity of drought stress are usually linked to decreasing N mineralization and inorganic N fluxes (Borken and Matzner 2009).

In general, drought stress leads to an increase in C allocation to roots, although the magnitude and duration of drought stress responses differ among the studies (Gilgen and Buchmann 2009; St. Clair et al. 2009; Jentsch et al. 2011). However, some studies found that drought stress may decrease C flow (that is, C assimilate by photosynthesis, and carbon input into soil by litter and root excretion, and decomposed by microbes) from the roots to the soil compartments. Symbiotic fungi and many free-living microorganisms depend on the C transfers from roots, and microbial CO_2 production is consequently reduced (Palta and Gregory 1997; Gorissen et al. 2004). In addition, about half of the soil CO_2 efflux is thought to originate from recent (i.e., several days old) photosynthates (Högberg et al. 2008) and is rapidly transferred specifically to mycorrhizal fungi and other decomposers. However, drought stress decreases C assimilation and increases the residence time of recently assimilated C in leaf biomass, and thereby prolonging the time course of the recent C allocation from the plants to the soil (Högberg et al. 2008; Ruehr et al. 2009). Therefore, R_s probably have a temporary decoupling with C allocation under drought stress conditions.

3.3 Substrate supply and litters affect soil respiration

Microbial-mediated decomposition of SOM ultimately makes a considerable contribution to soil respiration, which is typically the main source of CO_2 arising from terrestrial ecosystems (Yuste et al. 2011). The effect of drought stress on the rates of SOM respiration and the sensitivity to temperature has been discussed above. Here, we focus on the issue about how drought stress indirectly influences soil respiration through shaping the supply and availability of substrate. Although drought stress can alter R_r because of reduced photosynthates supply (Domec and Gartner 2003; Carbone et al. 2011; Gomez-Casanovas et al. 2012), it is not known to what extent this substrate for microbial respiration is derived from younger soil organic C, such as dead and/or older labile SOC free from the physical breakup of soil aggregates. In general, with water contents between desiccation stress (usually <-1.5 MPa matric potential) and field capacity (about -0.1 MPa matric potential), variation in drought stress is thought to affect microbial respiration primarily through reducing the diffusion of organic solutes (Grant and Rochette 1994; Sowerby et al. 2005; Davidson and Janssens 2006). As substrate availability largely depends on soil water content, this would explain why drought stress dampened the increase in respiration at higher temperatures. In the case of microbial respiration, substrate levels decreased during the drought stress periods as litters from the plants declined. The much weaker response or more resistance to drought stress of rhizospheric respiration is also likely related to their dependence on substrate supply. Among components of R_s, the mostly affected one by substrate supply under drought stress conditions is R_m, which exhibited a strong relationship with the photosynthetic activity of the previous day (Bardgett et al. 2005; Ryan and Law 2005; Unger et al. 2010, 2012; Heinemeyer et al. 2012).

Litter decomposition not only supplied the substrates for microbial activity but also emitted CO_2 to the atmosphere. Drought stress slowed leaf litter C and N decomposition by more than 50% compared to regular weather conditions, mainly by strongly decreasing the decomposition rate constants and also depending on litter quality (Sanaullah et al. 2012). The CO_2 derived from the litter decomposition and contributed approximately 3–4% of the total CO_2 efflux during drought stress periods may decline by 74%, indicating that drought stress would have a stronger effect on the CO_2 release from litter than on the belowground-derived CO_2 efflux (i.e., SOM and root respiration) (Joos et al. 2009; van Straaten et al. 2010). Theis et al. (2007) found in an alpine grassland that during the drought stress period the CO_2 efflux from litters and top soil horizons were close to zero due to the desiccation of these layers. Soil respiration was obviously originating from the deeper soil horizons with different temperature and moisture regimes. However, recent radiocarbon data suggested that respiration of young C substrates, such as those respired by living roots, would be less affected by drought stress than the microbial decomposition of older substrates in the litter layer in the forests (Borken et al. 2006) and grassland ecosystems (Xiang et al. 2008). In addition, plant litter quality also controls litter decomposition, apart from water availability. How the influence of the interaction of drought stress and quality on plant litter decomposition contributes to the R_s is not well known. During the period of drought stress, some fluctuations in soil respiration occurred independently of microbial growth and abiotic interactions, such as desorption in combination with solvation status and conformational changes of enzymes (Alarcón-Gutiérrez et al. 2010).

4 Effect of drought stress on soil respiration in the context of climate change

4.1 The effect of the interaction of elevated temperature, CO_2 concentration, and drought stress on soil respiration

Soil respiration and gross primary productivity (GPP) are the most important flux between the atmosphere and terrestrial ecosystems in terms of C quantities (Schimel 1995; Schlesinger and Andrews 2000). Much evidence suggested that temperature (Davidson and Janssens 2006; Aanderud et al. 2013), soil water content (Davidson et al. 1998; Metcalfe et al. 2011), and GPP (Davidson and Holbrook 2009; Janssene et al. 2001; Martin et al. 2012) are three common drivers for respiration. As atmospheric [CO_2] continues to rise due to fossil fuel combustion and land use change, global mean surface temperature is projected to concurrently increase by 1.1–6.4 °C towards the end of this century (Solomon et al. 2007). Increased temperature may directly accelerate R_h and R_a by stimulating the activities of soil microbes and plant roots (Rustad et al. 2001; Melillo et al. 2002) and indirectly stimulate R_h by stimulating N mineralization, primary production, litter production, and therefore substrate and N availability (Stromgren and Linder 2002; Pendall et al. 2004). Recent model simulation suggested the magnified R_a responses to temperature increasing with the depressed R_h responses across the whole range of soil temperature anomaly (0–8 °C) under extended drought stress conditions (Shen et al. 2009). In general, under drought stress, warming can cause further drying of the ecosystem and hence act to further reduce R_s (Selsted et al. 2012). However, the study manipulated on a temperate spruce suggested that R_h and R_a were affected to the same extent by soil drought stress and warming, and if summer drought stress become more server in the future, warming reduced C loses will likely to offset by reduced soil efflux during summer drought stress (Schindlbacher et al. 2012).

Elevated CO_2 often accelerates R_s and R_a through direct stimulation on photosynthetic activity (Nowak et al. 2004; Sarah Bachman et al. 2010), root growth, litter production, and rhizospheric deposition (Zak et al. 2000; Norby and Luo 2004) or indirect impacts on litter chemistry, and microbial community composition (Pendall et al. 2004; Wan et al. 2007; Pregitzer et al. 2008) and enzyme activity (Kandeler et al. 2006). Importantly, an elevated CO_2 environment may also increase plant water use efficiency and thus soil water contents due to the reduction in stomatal conductance and alleviate the impact of drought stress (Dermody et al. 2007; Leuzinger and Körner 2010). Elevated CO_2 may reduce the impact of summer drought stress on R_s, depending on seasonal variation (Selsted et al. 2012). However, the studies about interactive effects of multiple factors on R_s and its components under the scenarios of upcoming drought stress are lacking, especially the studies about underlying mechanisms. Therefore, furthermore work is needed to establish the comprehensive research and evaluate the integrated impact of multiple factors on soil respiration under drought stress in different ecosystems.

4.2 The impact of drought stress legacy on soil respiration

The legacy of drought stress can regulate the responses of soil respiration rates to rewetting events in terrestrial ecosystems through changes in abiotic drivers and in microbial community structure (Gordon et al. 2008; Bapiri et al. 2010; Evans and Wallenstein 2012; Göransson et al. 2013). Upon rewetting dry soils, within minutes, the respiration rates increase to a magnitude of 10–20-fold that in the continually moist soil. Wood et al. (2001) attributed this drastic response of R_s during rewetting to the stress response of microbes to suddenly increase in moisture and soil water potential: Microbes must expend energy to regulate osmotic pressure to their microenvironment and release solutes before osmotic pressure bursts cells. However, after reaching peak respiration rates, the respiration rate in continuous moist soils then remain at rates higher than those in the drought stress-treated soils (Göransson et al. 2013). The soil respiration rates would change less in response to dry-rewetting pulses in the experienced extreme drought stress patterns, due to the adaptation of soil microbial communities, than those that experienced ambient rainfall events (Evans and Wallenstein 2012). However, these studies was operated generally with a coupled field-laboratory experiment and persisted in short term. It is unknown how the drought stress history with long-term modifications of the timing and intensity of drought stress events affect soil respiration after rewetting events through altering microbial community composition and function. We also do not understand whether microbial adaptation to precipitation regimes can affect soil respiration. In general, long-term or severe drought stress may cause the extensive root mortality. Root mortality reduces mycorrhizal fungal abundance by severing their access to root C (Högberg et al. 2001; Landesman and Dighton 2011) and the quantity of root exudates (Clarholm 1981), which can suppress microbial growth following rainfall, resulting in declines of R_h. However, we have no direct evidence to prove that root respiration will change less in the experienced drought stress in response to rewetting events than that experienced ambient rainfall events. During the peak drought stress, the plants with mycorrhizas had greatest resistance to drought stress (Davies et al. 1993; Hughes et al. 2008). Therefore, we assume that the soil respiration with mycorrhizas will change less in the experienced drought stress in response to rewetting events than that experienced ambient rainfall events.

5 Conclusions

There are a lot of evidence that drought stress, characterized by the severity, duration, and frequency, are expected to influence the C cycling more strongly in the future. Soil respiration is one of the most important biological processes in C cycling. Drought stress reduces rates of soil respiration in mesic and xeric ecosystems through decoupling between the above- and belowground processes and increases soil respiration in hydric ecosystem through stimulating soil microbial activity. However, intensity and frequency, duration of drought stress impacts on the soil respiration are not well understood, particularly in terms of the synergetic controlling of driver factors. In addition, how the responses of R_r, R_m, and R_h to drought stress are also not well understood, due to the difficulty of partitioning the components of soil respiration. Therefore, further work should focus on how the responses of soil respiration and its components to different drought stress scenarios and how the controlling factors of soil respiration function on the same temporal scale. The next challenge is to establish the relationship between soil respiration and global change parameters (such as warming and elevated [CO_2] under drought stress. It is worth pointing out that the models of simulating the rates of soil respiration and its components under global climate change and drought stress should be developed.

Acknowledgments Financial support was provided by the National Natural Sciences Foundation (NSFC) (number 31170459, 11079053, and 31300417), the Strategic Priority Research Program—Climate Change: Carbon Budget and Relevant Issues of the Chinese Academy of Sciences (grant no. XDA05050402), the National Key Basic Research Program (NKBRP) (number 2010CB833501), and the Knowledge Innovation Program of the Chinese Academy of Sciences (number KSCX2-EW-J-29).

References

Aanderud ZT, Jones SE, Schoolmaster DR, Fierer N, Lennon JT (2013) Sensitivity of soil respiration and microbial communities to altered snowfall. Soil Biol Biochem 57:217–227

Alarcón-Gutiérrez E, Floch C, Ziarelli F, Augur C, Criquet S (2010) Dryingerewetting cycles and γ-irradiation effec ts on enzy me activities of distinct layers from a *Quercus ilex L.* litter. Soil Biol Biochem 42:283–290

Allan RP, Soden BJ (2008) Atmospheric warming and the amplification of precipitation extremes. Science 321:1481–1484

Alley Rea (2007) Climate change 2007. The physical science basis. Summary for policymakers. Fourth Assessment Report of Working Group I, IPCC, Geneva

Alm J, Schulman L, Walden J, Nykanen H (1999) Carbon balance of a boreal bog during a year with an exceptionally dry summer. Ecology 80:161–174

Aurela M, Laurila T, Tuovinen J (2001) Seasonal CO2 balances of a subarctic mire. J Geophys Res 106:1623–1637

Bapiri A, Bååth E, Rousk J (2010) Drying-rewetting cycles affect fungal and bacterial growth differently in an arable soil. Microb Ecol 60: 419–428

Bardgett RD, Bowman WD, Kaufmann R, Schmidt SK (2005) A temporal approach to linking aboveground and belowground ecology. Trends Ecol Evol 20:634–641

Bloor JMG, Bardgett RD (2012) Stability of above-ground and below-ground processes to extreme drought in model grassland ecosystems: Interactions with plant species diversity and soil nitrogen availability. Perspect Plant Ecol 14:193–204

Bond-Lamberty B, Wang CK, Gower ST (2004) A global relationship between the heterotrophic and autotrophic components of soil respiration? Glob Change Biol 10:1756–1766

Boone RD, Nadelhoffer KJ, Canary JD, Kaye JP (1998) Roots exert a strong inuenceon the temperature sensitivity of soil respiration. Nature 36:570–572

Borken W, Matzner E (2009) Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. Glob Change Biol 15: 808–824

Borken W, Savage K, Davidson EA (2006) Effects of experimental drought on soil respiration and radiocarbon efflux from a temperate forest soil. Glob Change Biol 12:177–193

Bowling DR, McDowell NG, Bond BJ, Law BE, Ehleringer JR (2002) ^{13}C content of ecosystem respiration is linked to precipitation and vapor pressure deficit. Oecologia 131:113–124

Breulmann M, Schulz E, Weißhuhn K, Buscot F (2012) Impact of the plant community composition on labile soil organic carbon, soil microbial activity and community structure in semi-natural grassland ecosystems of different productivity. Plant Soil 352:253–265

Brilli F, Hörtnagl L, Hammerle A, Haslwanter A (2011) Leaf and ecosystem response to soil water availability in mountain grasslands. Agric For Meteorol 151:1731–1740

Brown DA (1998) Gas production from an ombrotrophic bog-effect of climate change on microbial ecology. Climate Change 40:277–284

Buchmann N (2000) Biotic and abiotic factors regulating soil respiration rates in Picea abies stands. Soil Biol Biochem 32:1625–1635

Bulter A, Meir P, Saiz G, Marachipes L, Marimon BS, Grace J (2012) Annual variation in soil respiration and its component parts in two structurally contrasting woody savannas in Central Brazil. Plant soil 352:129–142

Carbone MS, Still CJ, Ambrose AR, Dawson TE, Williams AP, Boot CM, Schaeffer SM, Schimel JP (2011) Seasonal and episodic moisture controls on plant and microbial contributions to soil respiration. Oecologia 167:265–278

Casals P, Lopez-Sangil L, Carrara A, Gimeno C, Nogués S (2011) Autotrophic and heterotrophic contributions to short-term soil CO_2 efflux following simulated summer precipitation pulses in a Mediterranean dehesa. Glob Biogeochem Cy 25:GB3012. doi:10.1029/2010GB003973

Chenu C, Roberson EB (1996) Diffusion of glucose in microbial extracellular polysaccha-ride as affected by water potential. Soil Biol Biochem 28:877–884

Chowdhury N, Burns RG, Marschner P (2011) Recovery of soil respiration after drying. Plant Soil 348:269–279

Clarholm M (1981) Protozoa grazing of bacteria in soil-impact and importance. Microb Ecol 7:343–350

Correâ Dias AT, van Ruijven J, Berendse F (2010) Plant species richness regulates soil respiration through changes in productivity. Oecologia 163:805–813

Craine JM, Gelderman TM (2011) Soil moisture controls on temperature sensitivity of soil organic carbon decomposition for a mesic grassland. Soil Biol Biochem 43:455–457

Craine JM, Wedin DA, Reich PB (2001) The response of soil CO_2 flux to changes in atmospheric CO_2, nitrogen supply and plant diversity. Glob Change Biol 7:947–953

Davidson EA, Holbrook NM (2009) Is temporal variation of soil respiration linked to the phenology of photosynthesis? Springer, New York

Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440:165–173

Davidson EA, Belk E, Boone RD (1998) Soil water content and temperature as independent or confounded factors controlling soil respiration in a temprate mixed hardwood forest. Glob Change Biol 4:217–227

Davidson EA, Verchot L, Catttanio JH, Ackerman IL, Carvalho JEM (2000) Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. Biogeochemistry 48:53–69

Davies FT, Potter JJ, Linderman RG (1993) Mycorrhiza and repeated drought exposure affect drought resistance and extraradical hyphae development of pepper plants independent of plant size and nutrient content. J Plant Physiol 139:289–294

Dermody O, Weltzin JF, Engel EC (2007) How do elevated [CO_2], warming, and reduced precipitation interact to affect soil moisture and LAI in an old field eco-system? Plant Soil 301:255–266

Domec JC, Gartner BL (2003) Relationship between growth rates and xylem hydraulic characteristics in young, mature and old-growth ponderosa pine trees. Plant Cell Environ 26:471–483

Epron D, Farque L, Lucot E (1999) Soil CO_2 efflux in a beech forest: dependence on soil temperature and soil water content. Ann For Sci 56:221–226

Evans SE, Wallenstein MD (2012) Soil microbial community response to drying and rewetting stress: does historical precipitation regime matter? Biogeochemistry 109:101–116

Fenn KM, Malhi Y, Morecroft MD (2010) Soil CO_2 efflux in a temperate deciduous forest: environmental drivers and component contributions. Soil Biol Biochem 42:1685–1693

Feyen L, Dankers R (2009) Impact of global warming on streamflow drought in Europe. J Geophys Res: Atmospheres 114:1–14

Fioretto A, Pellegrino SP, Ferrigno A (2009) Microbial activities in soils of a Mediterranean ecosystem in different successional stages. Soil Biol Biochem 41:2061–2608

Flanagan LB (2009) Phenology of plant production in the Northwestern Great Plains: relationships with carbon isotope discrimination, net ecosystem productivity and ecosystem respiration. phenology of ecosystem processes. Springer, Berlin, pp 169–185

Ford CR, McGee J, Scandellari F (2012) Long- and short-term precipitation effects on soil CO_2 efflux and total belowground carbon allocation. Agric For Meteorol 156:54–64

Freckman DW (1986) The ecology of dehydration in soil organisms. In: Leopold AC (ed) Membranes, metabolism, and dry organisms. Cornell University Press, Ithaca, pp 157–168

Freeman C, Liska G, Ostle NJ, Lock MA, Reynolds B, Hudson J (1996) Microbial activity and enzymic decomposition processes following peatland water table drawdown. Plant Soil 180:121–127

Gilgen AK, Buchmann N (2009) Response of temperate grasslands at different altitudes to simulated summer drought differed but scaled with annual precipitation. Biogeosciences 6:5217–5250

Gomez-Casanovas N, Matamala R, Cook DR, Gonzalez-Meler MA (2012) Net ecosystem exchange modifies the relationship between the autotrophic and heterotrophic components of soil respiration with abiotic factors in prairie grasslands. Glob Change Biol 18: 2532–2545

Göransson H, Godbold DL, David L, Jones DL, Jousk J, Caldwell BA (2013) Bacterial growth and respiration responses upon rewetting dry forest soils: impact of drought-legacy. Soil Biol Biochem 57: 477–486

Gordon H, Haygarth PM, Bardgett RD (2008) Drying and rewetting effects on soil microbial community composition and nutrient leaching. Soil Biol Biochem 40:302–311

Gorissen A, Tietema A, Joosten NN (2004) Climate change affects carbon allocation to the soil in shrublands. Ecosystems 7:650–661

Grant RF, Rochette P (1994) Soil microbial respiration at different water potentials and temperatures: theory and math-ematical modeling. Soil Sci Soc Am J 58:1681–1690

Hanson PJ, Edwards NT, Garten CT, Andrews JA (2000) Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry 48:115–146

Heinemeyer A, Wilkinson M, Vargas R, Subke JA, Casella E, Morison JIL, Ineson P (2012) Exploring the "overflow tap" theory: linking forest soil CO_2 fluxes and individual mycorrhizosphere components to photosynthesis. Biogeosciences 9:79–95

Henry HAL (2012) Soil extracellular enzyme dynamics in a changing climate. Soil Biol Biochem 47:53–59

Högberg P, Nordgren A, Buchmann N, Taylor AFS, Ekblad A, Hogberg MN (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411:789–792

Högberg P, Högberg MN, Göttlicher SG, Betson NR, Keel SG, Metcalfe DB, Campbell C, Schindlbacher A, Hurry V, Lundmark T (2008) High temporal resolution tracing of photosynthate carbon from the tree canopy to forest soil microorganisms. New Phytol 177:220–228

Holden PA, Hunt JR, Firestone MK (1997) Toluene diffusion and reaction in unsaturated *Pseudomonas putida* biofilms. Biotechnol Bioeng 56:656–670

Hughes JK, Hodge A, Fitter AH, Atkin OK (2008) Mycorrhizal respiration: implications for global scaling relationships. Trends Plant Sci 13:583–588

Janssene IA, Lankreuer H, Matteucci G (2001) Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Glob Change Biol 7:269–278

Jassal RS, Black TA, Novak MD, Gaumont-Guay D, Nesic Z (2008) Effect of soil water stress on soil respiration and its temperature sensitivity in an 18-year-old temperate Douglas-fir stand. Glob Change Biol 14:1305–1318

Jentsch A, Kreyling J, Elmer M (2011) Climate extremes initiate ecosystem-regulating functions while maintaining productivity. J Ecol 99:689–702

John B, Yamashita T, Ludwig B, Flessa H (2005) Storage of organic carbon in aggregate and density frac-tions of silty soils under different types of land use. Geoderma 128:63–79

Joos O, Heim HA, Gilgen AK, Schmidt MWI, Siegolf RTW, Buchmann N (2009) Summer drought reduces total and litter-derived soil CO_2 effluxes in temperate grassland-clues from a ^{13}C litter addition experiment. Biogeosciences 6:11005–11034

Kandeler E, Mosier AR, Morgan JA, Milchunas DG (2006) Response of soil microbial biomass and enzyme activ ities to the transient elevation of carbon dioxide in a semi-arid grassland. Soil Biol Biochem 38:2448–2460

Kardol P, Cregger MA, Campany CE, Classen AT (2010) Soil ecosystem functioning under climate change: plant species and community effects. Ecology 91:767–781

Knorr W, Gobron N, Scholze M, Kaminski T, Schnur R, Pinty B (2007) Impact of terrestrial biosphere carbon exchanges on the anomalous CO_2 increase in 2002–2003. Geophys Res Lett 34:L09703. doi:10.1029/2006GL029019

Knorr KH, Oosterwoud MR, Blodau C (2008) experimental drought alters rates of soil respiration and methanogenesis but not carbon exchange in soil of a temperate fen. Soil Biol Biochem 40:1781–1791

Kuzyakov Y (2006) Sources of CO_2 efflux from soil and review of partitioning methods. Soil Biol Biochem 38:425–448

Kuzyakov Y, Gavrichkova O (2010) Time lag between photosynthesis and carbon dioxide efflux from soil: a review of mechanisms and controls. Glob Change Biol 16:3386–3406

Landesman WJ, Dighton J (2011) Shifts in microbial biomass and the bacteria: fungi ratio occur under field conditions within 3 h after rainfall. Microb Ecol 62:228–236

Lavigen MB, Foster RJ, Goodine G (2004) Seasonal and annual changes in soil respiration in relation to soil temperature, water potential and trenching. Tree Physiol 24:415–424

Leuzinger S, Körner C (2010) Rainfall distribution is the main driver of runoff underfuture CO_2-concentration in a temperate deciduous forest. Glob Change Biol 16:246–254

Manzoni S, Schimel JP, Porporato A (2012) Responses of soil microbial communities to water stress: results from a meta-analysis. Ecology 93:930–938

Martin JG, Phillips CL, Schmidt A, Irvine J, Law BE (2012) High-frequency analysis of the complex linkage between soil CO_2 fluxes, photosynthesis and environmental variables. Tree Physiol 32:49–64

Melillo JM, Steudler PA, Aber JD (2002) Soil warming and carbon-cycle feedbacks to the climate system. Science 298:2173–2176

Metcalfe DB, Fisher RA, Wardle DA (2011) Plant communities as drivers of soil respiration: pathways, mechanisms, and significance for global change. Biogeosciences 8:2047–2061

Moyano F, Kutsch W, Schulze E (2007) Response of mycorrhizal, rhizosphere and soil basal respiration to temperature and photosynthesis in a barley field. Soil Biol Biochem 39:843–853

Moyano FE, Vasilyeva N, Bouckaert L, Cook F, Craine J, Curiel Yuste J, Don A, Epron D, Formanek P, Franzluebbers A, Ilstedt U, Kätterer T, Orchard V, Reichstein M, Rey A, Ruamps L, Subke JA, Thomsen

IK, Chenu C (2012) The moisture response of soil heterotrophic respiration: interaction with soil properties. Biogeosciences 9:1173–1182

Navarro-García F, Casermeiro ÁM, Schimel JP (2011) When structure means conservation: effect of aggregate structure in control-ling microbial responses to rewetting events. Soil Biol Biochem 44:1–8

Norby RJ, Luo Y (2004) Evaluating ecosystem responses to rising atmospheric CO_2 and global warming in a multi-factor world. New Phytol 162:281–293

Nowak RS, Ellsworth DS, Smith SD (2004) Functional responses of plants to elevated atmospheric CO_2—do photosynthetic and productivity data from FACE experi-ments support early predictions? New Phytol 162:253–280

Palta J, Gregory P (1997) Drought affects the fluxes of carbon to roots and soil in ^{13}C pulse-labelled plants of wheat. Soil Biol Biochem 19: 1395–1402

Pendall E, Bridgham S, Hanson PJ (2004) Below-ground process responses to elevated CO_2 and temperature: a discus-sion of observations, measurement methods, and models. New Phytol 162:311–322

Phillips CL, Nickerson N, Risk D, Bond BJ (2011) Interpreting diel hysteresis between soil respiration and temperature. Glob Change Biol 17:515–527

Prasolova NV, Xu ZH, Farquhar GD, Saffigna PG, Dieters MJ (2000) Variation in branchlet delta $\delta^{13}C$ in relation to branchlet nitrogen concentration and growth in 8-year-old hoop pine families (*araucaria cunninghamii*) in subtropical Australia. Tree Physiol 20: 1049–1055

Prasolova NV, Xu ZH, Farquhar GD, Saffigna PG, Dieters MJ (2001) Canopy carbon and oxygen isotope composition of 9-year-old hoop pine families in relation to seedling carbon isotope composition, growth, field growth performance, and canopy nitrogen concentration. Can Forest Res 31:673–681

Pregitzer KS, Burton AJ, King JS (2008) Soil respiration, root biomass, and root turnover following long - term exposure of northern forests to elevated atmospheric CO_2 and tropospheric O_3. New Phytol 180: 153–161

Rey A, Pegoraro E, Tedeschi V, De parri I (2002) Annual variation in soil respiration and its components in a coppice oak forest in central Italy. Glob Change Biol 8:851–866

Risk D, Nickerson N, Phillips CL (2012) Drought alters respired $\delta^{13}CO_2$ from autotrophic, but not heterotrophic soil respiration. Soil Biol Biochem 50:26–32

Ruehr NK, Offermann CA, Gessler A, Winkler JB, Ferrio JP, Buchmann N, Barnard RL (2009) Drought effects on allocation of recent carbon: from beech leaves to soil CO_2 efflux. New Phytol 184: 950–961

Rustad LE, Campbell JL, Marion GM (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126:543–562

Ryan MG, Law BE (2005) Interpreting, measuring, and modeling soil respiration. Biogeochemistry 73:3–27

Sampson DA, Janssens IA, Curiel Yuste J, Ceulemans R (2007) Basal rates of soil respiration are correlated with photosynthesis in a mixed temperate forest. Glob Change Biol 13:2008–2017

Sanaullah M, Blagodatskaya E, Chabbi A, Rumpel C, Kuzyakov Y (2011) Drought effects on microbial biomass and enzyme activities in the rhizosphere of grasses depend on plant community composition. Appl Soil Ecol 48:38–44

Sanaullah M, Rumpel C, Charrier X, Chabbi A (2012) How does drought stress influence the decomposition of plant litter with contrasting quality in a grassland ecosystem? Plant Soil 352:277–288

Sarah Bachman S, Heisler-White JL, Pendall E, Williams DG (2010) Elevated carbon dioxide alters impacts of precipitation pulses on ecosystem photosynthesis and respiration in a semi-arid grassland. Oecologia 126:791–802

Savage KE, Davidson EA (2001) Interannual variation of soil respiration in two New England forests. Global Biogeochem Cy 15:337–350

Schimel DS (1995) Terrestrial ecosystems and the carbon cycle. Glob Change Biol 1:77–91

Schindlbacher A, Wunderlich S, Borken W (2012) Soil respiration under climate change: prolonged summer drought offsets soil warming effects. Glob Change Biol 18:2270–2279

Schlesinger WH, Andrews JA (2000) Soil respiration and the global carbon cycle. Biogeochemistry 48:7–20

Scott-Denton LE, Rosenstiel TN, Monson RK (2006) Differential controls by climate and substrate over the heterotrophic and rhizospheric components of soil respiration. Glob Change Biol 12:205–216

Selsted MB, Linden L, Ibrom A, Michelsen A, Larsen KS, Pedersen JK, Mikkelsen TN, Pilegaard K, Beier C, Ambus P (2012) Soil respiration is stimulated by elevated CO_2 and reduced by summer drought: three years of measurements in a multifactor ecosystem manipulation experiment in a temperate heathland (CLIMAITE). Glob Change Biol 18:1216–1230

Shen W, Reynolds JF, Hui D (2009) Responses of dryland soil respiration and soil carbon pool size to abrupt vs. gradual and individual vs. combined changes in soil temperature, precipitation, and atmospheric [CO_2]: a simulation analysis. Glob Change Biol 15:2274–2294

Signarbieux C, Feller U (2012) Effects of an extended drought period on physiological properties of grassland species in the field. J Plant Res 125:251–261

Solomon S, Qin D, Manning M (2007) Technical summary. In: Solomon S, Qin D, Manning M, Chen Z (eds) Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge/New York

Sowerby A, Emmett B, Beier C, Tietema A, Peñuelas J, Estiarte M, Van Meeteren MJM, Hughes S, Freeman C (2005) Microbial community changes in heathland soil communities along a geographical gradient: interaction with climate change manipulations. Soil Biol Biochem 37:1805–1813

Sowerby A, Emmett BA, Tietema A, Claus B (2008) Contrasting effects of repeated summer drought on soil carbon efflux in hydric and mesic heathland soils. Glob Change Biol 14:2388–2404

St. Clair SB, Sudderth EA, Castanha C, Torn MS, Ackerly DD (2009) Plant responsiveness to variation in precipitation and nitrogen is consistent across the compositional diversity of a California annual grassland. J Veg Sci 20:860–870

Stromgren M, Linder S (2002) Effects of nutrition and soil warming on stemwood production in a boreal Norway spruce stand. Glob Change Biol 8:1195–1204

Suseela V, Conant RT, Wallenstein MD, Dukes JS (2012) Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. Glob Change Biol 18:336–348

Talmon Y, Sternberg M, GrÜNzweig JM (2011) Impact of rainfall manipulations and biotic controls on soil respiration in Mediterranean and desert ecosystems along an aridity gradient. Glob Change Biol 17:1108–1118

Taneva L, Gonzalez-Meler MA (2011) Distinct patterns in the diurnal and seasonal variability in four components of soil respiration in a temperate forest under free-air CO_2 enrichment. Biogeosciences 8: 3077–3092

Theis DE, Jaggi M, Aschlimann D, Blum H, Frossard E, Siegwolf RTW (2007) Dynamics of soil organic matter turnover and soil respired CO_2 in a temperate grassland labelled with ^{13}C. Eur J Soil Sci 58: 1364–1372

Trumbore SE (2006) Carbon respired by terrestrial ecosystems—recent progress and challenges. Glob Change Biol 12:141–153

Unger S, Máguas C, Pereira JS, Aires LM, David TS, Werner C (2010) Disentangling drought-induced variation in ecosystem and soil respiration using stable carbon isotopes. Oecologia 163:1043–1057

Unger S, Máguas C, Pereira JS, David TS, Werner C, Luc A (2012) Interpreting post-drought rewetting effects on soil and ecosystem carbon dynamics in a Mediterranean oak savannah. Agric For Meteorol 154:9–18

van der Molen MK, Dolman AJ, Ciais P, Eglin T (2011) Drought and ecosystem carbon cycling. Agric For Meteorol 151:765–763

van Straaten O, Veldkamp E, Kohler M, Anas I (2010) Spatial and temporal effects of drought on soil CO_2 efflux in a cacao agroforestry system in Sulawesi, Indonesia. Biogeosciences 7:1223–1235

Wallenstein M, HE K (2011) A trait-based framework for predicting when and where microbial adaptation to climate change will affect ecosystem functioning. Biogeochemistry 109:35–47

Walter J, Nagy L, Hein R (2011) Do plants remember drought? Hints towards a drought-memory in grasses. Environ Exp Bot 71:24–40

Wan S, Norby RJ, Ledford J, Weltzin JF (2007) Responses of soil respiration to ele-vated CO_2, air warming, and changing soil water availability in a model old - field grassland. Glob Change Biol 13:2411–2424

Williams MA (2007) Response of microbial communities to water stress in irrigated and drought-prone tallgrass prairie soils. Soil Biol Biochem 39:2750–2757

Williams JP, Hallsworth JE (2009) Limits of life in hostile environments: no barriers to biosphere function? Environ Microbiol 11:3292–3308

Wood JM, Bremer E, Csonka LN, Kraemer R, Poolman B, van der HT, Smith LT (2001) Osmosensing and osmo-regulatory compatible solute accumulation by bacteria. Comp Biochem Physiol A 130:437–460

Xiang S, Doyle A, Holden PA, Schimel JP (2008) Drying and rewetting effects on C and N mineralization and microbial activity in surface and subsurface California grassland soils. Soil Biol Biochem 40: 2281–2289

Xu ZH, Chen CR (2006) Fingerprinting global climate change and forest management within rhizosphere carbon and nutrient cycling processes. Environ Sci Pollut Res 13:293–298

Xu ZH, Saffigna PG, Farquhar GD, Simpson JA, Haines RJ (2000) Carbon isotope discrimination and oxygen isotope composition in clones of the F1 hybrid between slash pine and Caribbean pine in relation to tree growth, water-use efficiency and foliar nutrient concentration. Tree Physiol 20:1209–1218

Xu ZH, Chen CR, He JZ, Liu JX (2009) Trend and challenges in soil research 2009: linking global climate change to local long-term forest productivity. J Soils Sediments 9:83–88

Yuste JC, PeÑUelas J, Estiarte M, Garcia-Mas J, Mattana S, Ogaya R, Pujol M, Sardans J (2011) Drought-resistant fungi control soil organic matter decomposition and its response to temperature. Glob Change Biol 17:1475–1486

Zak DR, Pregitzer KS, King JS (2000) Elevated atmospheric CO_2, fine roots and the response of soil microorganisms: a review and hypothesis. New Phytol 147:201–222

Zhou X, Fei S, Sherry R, Luo Y (2012) Root biomass dynamics under experimental warming and doubled precipitation in a tallgrass prairie. Ecosystems 15:542–554