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REVIEW

Soil microbial community responses to heat wave components: drought and high temperature

Annette Bérard^{1,2,*}, Meriem Ben Sassi^{1,2}, Aurore Kaisermann³, Pierre Renault^{1,2}

¹INRA, UMR1114 EMMAH, 84914 Avignon, France

²UAPV, UMR1114 EMMAH, 84914 Avignon, France

³INRA, Centre de Bordeaux Aquitaine, 71 avenue Edouard Bourleaux CS 20032, 33 882 Villenave d'Ornon, France

ABSTRACT: Heat waves, defined as events associating high temperatures with severe drought, are expected to become increasingly recurrent. Research has focused heavily on the impacts of drought and temperature increase on soil functioning and microbial diversity, but little attention has been paid to soil microbial community responses to combined heat–drought stresses. Heat waves, which combine heat and drought stresses, may induce different microbial responses to those observed in studies focusing on heat or drought alone. Microbial recovery strategies to withstand heat–drought conditions, along with patterns of microbial functional redundancy and complex interactions with the soil physical–chemical–biological interface may have marked effects on soil ecosystem functioning, particularly in agroecosystems through the rhizosphere. To better understand how heat waves affect soil ecosystem functioning, we advocate the development of mechanistic approaches integrating individual to community level and biophysicochemical studies on the indirect effects of combined heat–drought stresses in microbial communities, observed through soil environment parameters in experimental and field studies. The challenge will be to define trait-based functional indicators of the microbial community response to heat waves, particularly the potential interrelatedness between the traits responsible for tolerance to drought and heat.

KEY WORDS: Heat wave · Drought · High temperature · Soil microbial communities · Cellular mechanisms · Soil physical–chemical properties · Microbial stability · Plant–microbe interaction

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1. INTRODUCTION

Climate change is already producing negative effects on crop production (IPCC 2014a) and is very likely set to intensify (IPCC 2013). There is growing evidence that change in climatic mean conditions will bring an increase in the frequency and intensity of extreme climate events (Planton et al. 2008, IPCC 2012, 2013), particularly in the Mediterranean context (Gibelin & Déqué 2003, IPCC 2014a,b, Swain et al. 2014). Among these extreme events, heat waves[#] (terms with an asterisk are defined in the Glossary), defined as prolonged period events associating severe drought and high temperature, may be more important drivers of ecosystem functions than changes

in climatic mean conditions (Heisler & Weltzin 2006). Better understanding of the consequences of heat waves on ecosystem functioning is therefore crucial in order to adopt the best ecosystem conservation strategies, particularly for agroecosystems that provide many essential services to human well-being (Millennium Ecosystem Assessment 2005).

Soil is a complex heterogeneous dynamic system that governs plant productivity and health (Nannipieri et al. 2003, Chakraborty et al. 2012). Soil microbial communities are central to nutrient cycling (Reynolds et al. 2003), and their activity is a key driver of plant community composition and productivity (Wardle et al. 2004). Recent reviews highlight how biodiversity is pivotal to soil functioning (Pul-

*Corresponding author: annette.berard@paca.inra.fr

leman et al. 2012, Thiele-Bruhn et al. 2012), and researchers are beginning to unravel the processes that determine the rate at which microbial services are ensured (Balser et al. 2006). However, there is still a knowledge gap on the impacts of climate change on microbial communities and their activity (Allison & Martiny 2008, Bell et al. 2009), particularly in the rhizosphere[#] environment (Philippot et al. 2013).

The last few decades have seen a plethora of studies dealing with effects of drought with high temperature on soil microbial physiology, biomass, community composition, diversity and activity (i.e. Potts 1994, Jensen et al. 2003, Hamdi et al. 2011). There are exhaustive reviews covering drought impacts on soil respiration (Manzoni et al. 2012) and drought impacts (Billi & Potts 2002, Vriezen et al. 2007) and temperature impacts (Schumann 2009) on prokaryote physiology for medicine, agriculture and the food industry (Garcia 2011). However, there is no synthesis of recent knowledge on the effects of extreme global change factors associated with both drought and high temperature on soil microbial communities and the implications for soil ecosystem function.

Drought with high temperature could have additive, synergetic, or contradictory effects on microbial communities, but few studies have addressed both stresses combined, and very few field studies have attempted to capture a natural record heat wave event (Acosta-Martinez et al. 2014a,b), despite the fact that both stresses co-occur during heat waves (Yuste et al. 2007, Bérard et al. 2011, Wang et al. 2014a). The study of microbiology is still quite separated from that of microbial ecology, yet microbial community responses to these stresses can only be properly understood by factoring in the cellular-level mechanisms involved. Indeed, drought with high temperature affects microbial communities in a very direct way by changing microorganism physiology. Microorganisms use various physiological strategies to survive a climatic stress, and some populations thrive while others die (Schimel et al. 2007, Allison & Martiny 2008), leading to a shift in microbial community composition (Acosta-Martinez et al. 2014a,b). On the other hand, drought with high temperature also induces changes in soil physical–chemical characteristics (Makino et al. 2000, Davidson & Janssens 2006). The net result is that extreme climate events can also indirectly change microbial communities through changes in microbial habitats (Parker & Schimel 2011, Navarro-García et al. 2012).

The objective of this paper is to provide an overview the impacts of severe drought associated with high temperature on soil microbes, from the cellular to ecosystem level (Fig. 1). The term ‘severe drought’ means soil with a gravimetric water content of <2–5% (corresponding to 10 to 15 MPa depending on soil characteristics), as seen in field observations by Acosta Martinez et al. (2014a,b) during the Texas heat wave of 2011 and in experimental studies by Bérard et al. (2011) and Fierer et al. (2003) on Mediterranean soils. The term ‘high temperature’ means a temperature higher than 45°C at the soil surface (5 cm depth), as seen in field observations by Acosta Martinez et al. (2014a,b) during the Texas heat wave of 2011, and in experimental studies by Bérard et al. (2011) and Hamdi et al. (2011) on Mediterranean soils. We first focus on (1) the direct responses to these stresses in microbial cells, then on (2) the indirect effects on microbial cells via changes in soil physical–chemical characteristics. We then move on to discuss the potential ecological consequences of these extreme climate events on (3) microbial community stability and (4) soil ecosystem functions by looking at the consequences for plant–microbe interactions. We round up by suggesting several lines of enquiry to guide future research on heat wave impacts in temperate agroecosystems (Fig. 1).

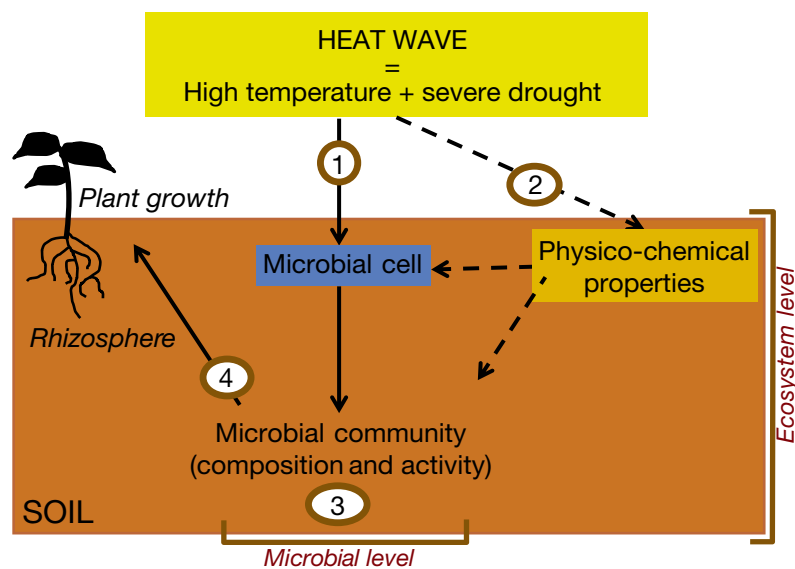


Fig. 1. Conceptual framework schematizing the impacts of severe drought plus high temperature on soil microbes from cellular level to ecosystem level. Heat waves induce (1) direct responses in microbial cells (solid arrows) but also (2) indirect effects through changes in soil physical and chemical characteristics (dashed arrows). (3) Microbial community composition and activity are shaped by the stability of microbial populations to these stresses, with (4) potential consequences for ecosystem functioning, particularly plant–microbe interactions and carbon cycling (*italics*)

2. DIRECT EFFECTS OF HEAT WAVES ON MICROBIAL CELLS

Microbes live in close contact with water via their semi-permeable cell walls. During drought events, loss of intracellular water may damage cell integrity and ultimately prove lethal to the cells (Billi & Potts 2002). Moreover, most microorganisms can only tolerate temperatures under 40°C, yet this threshold is exceeded in the first few centimeters of topsoil during heat waves (Acosta Martinez et al. 2014a,b). Nevertheless, some microbes living in extreme environments can survive and stay active under extreme desiccation and very high temperatures (Billi & Potts 2002, Norris et al. 2002). The following sections describe the stresses that the microbial cells are exposed to and the coping strategies they have developed.

2.1. Effects of drought with high temperature on microbial cells

Dehydration damages nucleic acids (Asada et al. 1979, Dose et al. 1991) via chemical modifications (alkylation or oxidation), cross-linking, or base removal such as depurination (Potts 1994, 1999). The increase in DNA strand breaks when microorganisms suffer long-term exposure to extreme dryness may be a general phenomenon (Dose et al. 1991, Mattimore & Battista 1996). Dehydration also induces conformational protein changes and restricts enzyme efficiency, resulting in changes in electron transport chains that lead to an accumulation of free radicals (Vriezen et al. 2007). The accumulation of free radicals during dehydration is thought to induce protein denaturation and lipid peroxidation and ultimately lead to cell lysis (Potts 1994). At the cell membrane level, if phospholipid bilayers are stripped of their hydration shell, van der Waal's interactions are increased between adjacent lipids, which increases their phase-transition temperature (T_m) and the transition to gel phase at environmentally relevant temperatures. Membranes with a higher T_m will pass to the gel phase and separate from those with a lower T_m , resulting in protein aggregation (Potts 1999, Billi & Potts 2002). During the rehydration process, if the T_m of the desiccated membrane is above ambient temperature (which may occur even in the post-heat wave period), this membrane leakage is lethal to the cell (Potts 2001).

Temperature rise changes gene expression patterns. For example, Schumann (2009) described 5 different types of high-temperature nucleic acid responses: (1) bent DNA, (2) supercoiling of DNA,

(3) chemical modification of DNA, (4) DNA-binding transcription factors and (5) secondary structures of mRNA. Moreover, temperature rise can also induce protein conformational changes, and high temperature affects the membrane characteristics of microorganisms through phospholipid fatty acid composition changes (Russell et al. 1995).

2.2. Cellular strategies to cope with these stresses

Microorganisms can employ a variety of physiological acclimation mechanisms that allow them to survive and remain active when exposed to environmental stress (Potts 1999, Schimel et al. 2007). The majority of these mechanisms protect their structures and organelles, but DNA repair pathways also come into play (Dose et al. 1991).

When exposed to high temperature, microorganisms can synthesize a small subset of proteins called heat-shock proteins (HSPs) (Parsell & Lindquist 1993, Hecker et al. 1996, Feder & Hofmann 1999). HSPs recognize and bind to other proteins if they are in non-native conformations (Feder & Hofmann 1999) and thus either degrade or reactivate them (Parsell & Lindquist 1993, Hecker et al. 1996). There are 2 main groups of HSPs (Hecker et al. 1996): (1) intra-cellular chaperones, which prevent misfolding and unwanted protein aggregation, and, once the stress is released, renature the proteins and renew their biological activity and (2) ATP-dependent proteases, which are involved in the degradation of denatured proteins. Schumann (2009) reviewed the thermotactic responses in bacteria and suggested that a larger temperature increment leads to stronger upregulation of heat-shock genes. Moreover, under drought challenge, some bacteria could store high quantities of ribosomes allowing them to respond with rapid protein synthesis when the stress is released (Placella et al. 2012). Microorganisms also effectuate membrane composition changes to maintain key properties such as a particular state of fluidity (Russell 2002), such as by modifying the composition of the lipid fatty acid component (Kieft et al. 1994, Russell et al. 1995), which is partially attributed to rapid physiological cell adjustments (Mrozik et al. 2004, Kakumanu et al. 2013).

To reduce water cellular potential and prevent membrane and protein damage during soil drying, microorganisms synthesize intracellular osmolytes (Dose et al. 2001, Billi & Potts 2002, Schimel et al. 2007, Zhang & Van 2012). It has been reported that the accumulation of compatible solutes not only allows cells to withstand a given osmolality but also increases the

thermotolerance of enzymes and inhibits the thermal denaturation of proteins (Conlin & Nelson 2007). More specifically, the carbohydrate trehalose can directly interact with the polar headgroups of membrane phospholipids to help maintain membrane integrity (see Welsh 2000 for a review). These solutes accumulate heavily in the cytoplasm and provide substantial intracellular stocks of carbon and/or nitrogen. Fungi accumulate polyols such as glycerol, erythritol, mannitol and trehalose (Witteveen & Visser 1995), whereas bacteria accumulate mainly K⁺ and proline, glycine betaine and trehalose (Kempf & Bremer 1998, Zhang & Van 2012). This ability to synthesize osmolytes can be an inductive property (for most Gram-negative [G⁻] bacteria), lending acclimation strategies, or a constitutive property (Gram-positive [G⁺] bacteria and fungi), lending inherent resistance (Schimel et al. 2007). However, observations of osmolyte accumulation are mainly based on nutrient-rich laboratory-culture conditions, and some field studies, especially in edaphic conditions, provide conflicting evidence (Bérard et al. 2011, Kakumanu et al. 2013, Warren 2014). In soil (nutrient-limited conditions), the production of intracellular osmolytes could be too costly (Kakumanu et al. 2013), and other strategies of coping with desiccation stress could be more widely used depending on the type of soil ecosystem involved (Warren 2014).

Indeed, other mechanisms also explain soil microbial responses to desiccation, such as increased efficiency of resource use and re-allocation within microbial cells (Tiemann & Billings 2011), as well as the production of extracellular polymeric substances (EPS). At the cellular level, EPS may prevent membrane fusion and help maintain a low T_m (see Section 2.1) in desiccated cells (Hill et al. 1997).

Lastly, sporulation and dormancy are also important strategies used by a variety of organisms to overcome unfavorable environmental conditions (Bär et al. 2002, Lennon & Jones 2011). These strategies mark the ultimate form of growth control and cell cycle regulation during stress (Kültz 2005), and are illustrated in the spore-forming *Bacilli* (Dose et al. 2001), the akinetes developed by cyanobacteria (Billi & Potts 2002), the conidia developed by fungi (Dose et al. 2001) and the formation of vegetative survival states (Potts 1994) (Fig. 2).

Given that DNA codes all these cellular responses and that gene expression is largely regulated in the cell, microbial ecology should profit from focusing on specific genes and associated metabolomes linked to these stress responses. We suggest that future research could focus on identifying genes linked to re-

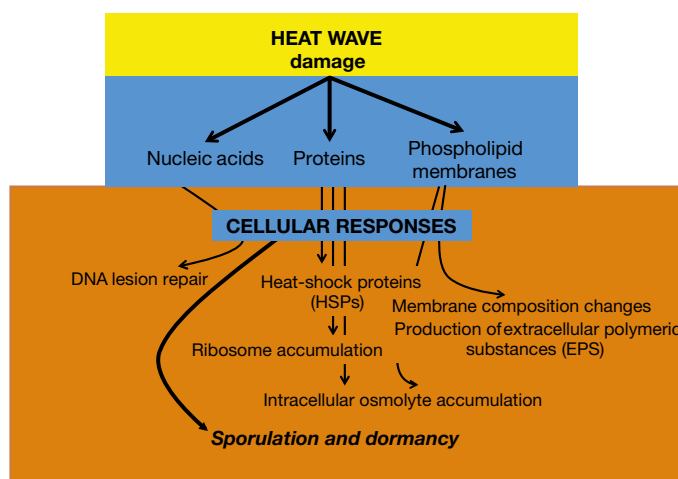


Fig. 2. Microbial cellular responses to heat and drought damages

sponses to these stresses at the community level in order to quantify potential resistance, as suggested by Lennon & Jones (2011) in the general case of dormancy.

Moreover, Lankadurai et al. (2013) recently highlighted how metabolomics approaches offer potential for studying organism responses to environmental stress and could be used to study the dynamics of extracellular osmolytes.

Further research on cellular and molecular responses to drought and high temperature could be applied to help develop biomarkers for studying the consequences of heat wave exposure and stress on soil microbes, as already practiced for chemical stresses (Xuan et al. 2012), such as targeting genes involved in osmolyte and EPS synthesis (Bezzate et al. 2000, Cytryn et al. 2007, Yoshimura et al. 2007) or metabolomics studies on osmolytes (Lankadurai et al. 2013, Warren 2014).

2.3. Pitfalls to estimates of the combined effect of heat and drought?

In reality, soil systems are often subjected to combined abiotic stresses, especially drought and heat stresses that co-occur in heat waves (Mittler 2006). There are few studies describing microbial responses to combined heat and drought stresses, but reviewing examples with other combined stresses can help pose early hypotheses on the potential impacts of combined heat and drought on soil microbes. Stressors do share similarities, and a wide variety of stresses (from desiccation to irradiation, heat, chemical stresses) induce oxidative damage in microbial cells (Potts 2001). Examples of similarities among stressors include the

same DNA lesion induced by both desiccation and radiation stresses (Chanal et al. 2006) and the correlation between bacterial cell resistances to ionizing radiation and dehydration (Mattimore & Battista 1996, Rokitko et al. 2003). Moreover, as suggested in Section 2.2, DNA damage repair, HSP synthesis, physiological adjustments of membrane lipid composition, and sporulation and dormancy strategies are common cellular responses employed by microbes to cope with high temperature, drought and other physical stresses. In a heat wave context, combined drought and heat stresses may result in an addition of effects. However, stresses may not always have additive effects. A review by Roelofs et al. (2008) on transcriptomics studies concludes that, while gene expression profiles induced by different stress factors involve overlap (common environmental stress responses), they can also involve synergy (combined exposure 'turning on' genes not induced by single-stress exposure) or antagonism (one stress factor repressing genes induced by another factor), as already shown for plants (Mittler 2006). Interestingly, Sharma & Kaur (2009) observed the specific induction of a protein in wheat seedlings under combined drought and heat shock that was not activated under drought or heat shock stress alone. Consequently, the co-occurrence of drought and heat stress may induce new types of responses that would not have been induced by each stress applied individually, but there are still too few studies on soil microbial cells under combined drought and heat stress to confirm this hypothesis.

Stress-hardening (increased tolerance to a stress after preconditioning at low doses of that stress) and cross-tolerance (increased tolerance to one stress after preconditioning by another) can happen at the cellular level (Kültz 2005). For example, desiccated bacterial cells showed higher levels of survival after thermal shock than non-desiccated cells (Sartori et al. 2010). As reviewed by Welsh (2000) (see Section 2.2), the in-cell accumulation of compatible solutes may be a protective response induced by a first drought stress increasing microbial tolerance to other environmental stresses like heat. The alternative role of the osmoregulator trehalose cited in Section 2.2 is a good illustration of how osmotic or drought stress may induce cellular cross-protection of microbes to heat. Consequently, in soil microbes, a preliminary stress such as drought may induce cell cross-protection to a subsequent stress such as heat (Macario et al. 1999). Different heat wave scenarios (drought first or heat stress first) could thus have different consequences in terms of microbial responses to the stresses.

Direct impacts of heat and drought involve several mechanisms of microbial response to cellular damage. The degree of specificity of these mechanisms may have consequences on soil microbial responses to heat wave events depending on heat wave scenario. Moreover, these responses may also be dependent on soil physicochemical context, as discussed below.

3. INDIRECT EFFECTS OF HEAT WAVES ON MICROORGANISMS MEDIATED BY A CHANGE IN SOIL PHYSICAL-CHEMICAL PROPERTIES

Water is the operational matrix of active microbes, even if they only form a thin film covering soil particles. The characteristics of microbial habitats are determined by several abiotic properties, such as temperature, pH, salt and osmotic balance, soil nutrients, oxygen and redox potential. The arrangement of soil particles defines the pore space through which air and water pass (Voroney 2007). Inside this matrix, moisture determines soil physical connectivity and is one of the key factors controlling spatial heterogeneity in abiotic factors (Ettema & Wardle 2002). Soil thus features a huge variety of microsites that offer ecological niches more or less suitable for microbial growth, activity and survival. Consequently, different pore sizes provide stratified habitats to which different microbial populations could be adapted (Ruamps et al. 2011). Water movements under fluctuating environmental conditions drive fast spatial and temporal dynamics of microsite characteristics (Paul & Clark 2007) and thus determine which of these niches are potential for or realized by microorganisms (Wang & Or 2013). The impacts of heat waves on soil microorganisms depend on the soil properties involved, but as heat wave events can also change soil properties, they indirectly affect soil microbial community composition as well (Fig. 3).

3.1. Effects of drought with high temperature on the soil chemical environment of microorganisms

When soil water content decreases, the pores within solid matrices drain and the water films coating soil particle surfaces become thinner, ultimately become discontinuous with more severe drought (Stark & Firestone 1995). This alteration of conducting liquid pathways decreases solute diffusion rates while increasing soil aeration (Or et al. 2007b). Microbes live in low-Reynolds-number environments, meaning that compound movement is driven by dif-

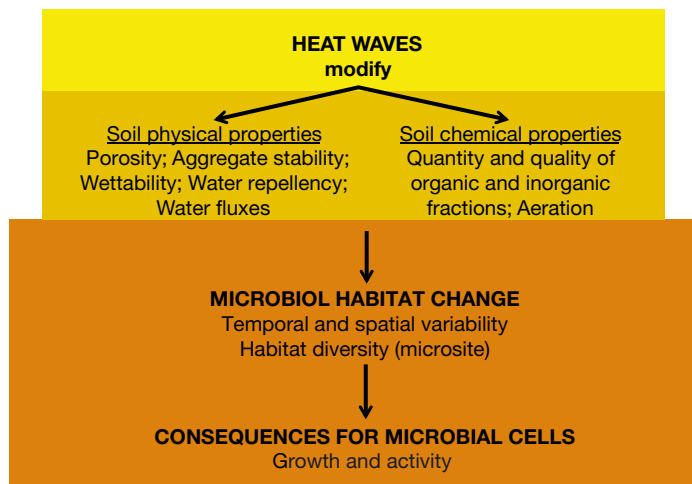


Fig. 3. Indirect effects of heat and drought on soil microbial habitat through changes in soil physical and chemical properties

fusion (Kirchman 2013). When nutrient and exoenzyme diffusion is restricted, nutrient availability to microorganisms is altered (Jensen et al. 2003, Manzoni et al. 2012, Henry 2013), leading to starvation (Lundquist et al. 1999, Bär et al. 2002). In microbial cells, starvation can induce dormancy (Hobbie & Hobbie 2013), which favors protection from subsequent stresses like high temperature. In the context of heat waves, better soil aeration with drought has been proven to increase organic matter decomposition. This is fairly intuitive for anoxic soils like peatland where drought lifts the oxygen limitation (Laiho 2006), but it also holds true in drier climates for micropores, which are normally in anoxic conditions. As oxygen diffusion in both air and water also increases with temperature (Agren & Wetterstedt 2007), heat waves could create a synergy that accelerates the decomposition of old and previously protected organic matter.

Better aeration might also change the redox state of soils and, consequently, the chemical form of the constituent elements. Some ions could be soluble or insoluble forms, and thus more or less bioavailable. In addition, pH depends on water content; thus, as the soil solution becomes more concentrated, it could expose microorganisms to osmotic stress (see Section 2.4; Chowdhury et al. 2011a, Bertram et al. 2012). Research tends to focus on ammonia versus ammonium transformation, as they have multiple implications for climate-driven changes in ecosystem function (Robertson & Groffman 2007). Novem Auyeung et al. (2013) highlighted that both warming and drought decrease the temperature sensitivity of

nitrogen transformation, but that this decrease is dependent on the combination of both. Drought has also been shown to change exchangeable forms of various elements, such as Mn, Co, Cd, As, Al, Zn and Cu (Makino et al. 1997, 2000, Ross et al. 2001, Sardans & Peñuelas 2007, Ben Sassi 2012). Some of these elements are known to be co-factors required for cellular functions (e.g. Tebo et al. 2005), so their increased availability could improve microbial growth and activity (Ross et al. 2001, Watanabe et al. 2012). In contrast, an increase in certain metals could add potential ecotoxicological stress, with negative implications for microbial growth (Kunito et al. 1999, Rajapaksha et al. 2004, Bérard et al. 2014). Theories like the Arrhenius equation suggest that the rate of chemical reactions will increase with heat, but it is still not clear how this combines with moisture for inorganic elements.

Heat waves may also increase microbial activities by changing nutrient availability. The drying and especially the wetting of dry soil can lead to increased organic matter (OM) availability through biological or physical processes, and thus concomitant increases in microbial activity (Birch 1958, Navarro-García et al. 2012). The physical changes involved are described in Section 3.2, and the biological processes involved, including the release of osmolytes and cell lysis, are described in Section 2. Another potential mechanism may be that the exoenzymes secreted by soil microorganisms are active in microsites during drought, but the substrates produced remain unavailable to microorganisms until wetting makes them bioavailable (Miller et al. 2005, Lawrence et al. 2009, Navarro-García et al. 2012, Acosta Martinez et al. 2014a). In addition, the 'quality' of the OM may increase, and it may become more easily degradable (high turnover rate), thus providing new nutrient niches for microbes (Zhang et al. 2010). Heat waves could amplify this increased decomposition, since temperature also controls substrate bioavailability (Dalias et al. 2001a,b, Davidson & Janssens 2006, Hamdi et al. 2011), promotes the desorption of high-affinity soil OM-minerals (Conant et al. 2011) and could kinetically stimulate the use of labile C by microorganisms (Hamdi et al. 2013). However, there is no clear consensus on the sensitivity of stable and labile fractions of OM to temperature (Davidson & Janssens 2006), and OM turnover could be governed more by accessibility than quality (Dungait et al. 2012). While the OM quality is probably related to different microbial populations, the response of decomposition rates to simultaneous changes in temperature and moisture is complex

(Sierra et al. 2015) and could additionally depend on adaptation of the microbial community either after metabolic adjustment to the stress (Allison et al. 2010) or with initial conditions (Blankinship et al. 2011).

3.2. Effects of drought with high temperature on the soil physical environment of microorganisms

Physical soil properties such as porosity, wettability and water holding capacity could change with extreme climate events, thus changing the physical habitats of microorganisms. These physical processes could be important in driving microbial respiration responses to drought (Navarro-García et al. 2012). The effects of drought on soil structure are modulated through processes that increase and decrease aggregation (Denef et al. 2001). The major aggregate-destroying processes that occur when dry soil is rewetted are shrinkage, slaking and swelling, whereas OM stabilizes the aggregates against these processes by increasing cohesion and decreasing the wetting rate (Sullivan 1990, Chenu et al. 2000). Their relative importance, i.e. aggregate stability[#], depends on key soil characteristics, including pore size distribution (macropore-rich soils being more vulnerable) and quantity and quality of cohesive and hydrophobic substances (Haynes & Swift 1990, Denef et al. 2001, Peng et al. 2007). As aggregate stability is dependent on the intensity of previous wet–dry events, the more intense droughts predicted in the near future could possibly increase these actions (Peng et al. 2007). The modification of soil structure affects soil water movement by altering the soil's net hydraulic properties (Alaoui et al. 2011) and water retention capacity (Rawls et al. 1991) but also its thermal conductivity (Usowicz et al. 2013), pointing to an additional impact of heat waves.

Another possible alteration concerns soil wettability[#]. Goebel et al. (2011) highlighted that soil water repellency, which reduces water infiltration capacity, could increase with the repeated wet–dry cycles due to the increase in repeated wet–dry cycles in combination with extreme temperature. This may promote the creation of preferential flow paths and the subsequent heterogenic penetration of water, and loss of water holding capacity may intensify the effects of climatic drought (Zhang et al. 2007, Goebel et al. 2011). However, during the slower increase in water potential due to water repellency, microorganisms could also have more time to adjust their cellular potential, which could result in a different overall

microbial community response. Here again, the concomitant increase in temperature with drought could have synergistic effects on these processes: water repellency could prove more severe with higher temperatures due to variations in surface tension and soil–water contact angle (Dekker et al. 1998), making water retention temperature dependent (Bachmann et al. 2002). Moreover, this temperature dependence of water retention could increase with increasing dryness due to the loss of water film thickness on the mineral surface, inducing higher interactions (adsorptive forces) between water and minerals than between pure water molecules in dry conditions (Schneider & Goss 2011).

3.3. Microorganisms that modify or counterbalance their physical and chemical environment in response to stresses: EPS production at biofilm scale

Various microbial biofilm environments, such as aquatic periphytons and biological soil crusts, are known to be favorable to microbial communities, protecting them against extreme environmental and other disturbances (for review, see Zaady et al. 2000, Serra & Guasch 2009, Flemming & Wingender 2010). In extreme environment settings, microbial production of EPS plays a key role not just at the cellular but also the environmental level (Rossi et al. 2012). Here, EPS protects not only the cell but also the local edaphic environment in which the cell is embedded and connected through a biofilm matrix, which is tightly related to EPS characteristics.

Indeed, biological soil crust formation, soil stabilization and water retention in these desert surface soil microecosystems submitted to drought, erosion, irradiation and high temperatures are all dependent on EPS production (Zaady et al. 2000, Wu et al. 2010, Fischer et al. 2012). EPS (predominantly polysaccharides but also proteins, enzymes, DNA and lipids; Flemming & Wingender 2010) synthesized by microorganisms (archaea, bacteria, fungi and algae) forms protective coatings for the embedded colonies (Roberson & Firestone 1992, Orell et al. 2013), and the EPS layer creates a micro-habitat with specific physical–chemical characteristics (Roberson & Firestone 1992, Chenu 1995, Chenu & Roberson 1996, Fischer et al. 2013, Rosenzweig et al. 2012). EPS attracts and absorbs water from the environment (Potts 2001), sequesters nutrients (Mager & Thomas 2011), maintains transport properties in soil, influences soil water repellency and wettability (for re-

view, see Or et al. 2007a, Schaumann et al. 2007), and increases soil aggregate stability (Sandhya et al. 2009). This means that EPS could induce 'hydraulic decoupling' during rapid drying–wetting events, thus protecting in-soil biofilm-embedded microorganisms (Flemming & Wingender 2010). The ability to produce biofilm and EPS provides benefits to EPS-producer microbes in these moisture fluctuation contexts (Allison & Prosser 1991). Lennon et al. (2012) recently derived niche parameters from physiological response curves that quantified microbial respiration for a diverse collection of soil bacteria and fungi along a soil moisture gradient, and found that biofilm-producing strains had drier moisture optima and wider niche breadths.

Spohn & Rillig (2012) investigated the effects of drought and temperature on the ability of a fungus to influence soil water repellency. They suggested that the hydrophobic proteins excreted by the fungi during drought change their secondary structure at high temperature, increasing soil water repellency. However, this kind of study covering both temperature and drought stresses remains rare, and more research is needed to understand the impact of temperature and drought on soil microbes through interactions between their coping strategy and soil physicochemical parameters.

Clearly, there is a need to develop tools able to gauge heat wave impacts on soil microbes through edaphic physicochemical parameters. Reapplying developments in physics and biochemistry technologies to soil could bring new insight on these impacts. Examples include stable isotope techniques to study biogeochemical cycles in the context of heat wave events (Unger et al. 2010, Blazewicz et al. 2014) or tomography techniques to understand the interactions between soil pore connectivity and microbial activity influenced by hydration cycles (Crawford et al. 2012). Given the position of soil EPS at the soil–microbial interface and their specific hydrological characteristics, soil EPS analysis could be a good candidate for this kind of indicator (Chenu & Robertson 1996, Redmile Gordon et al. 2014).

4. STABILITY OF SOIL MICROBIAL COMMUNITIES EXPOSED TO HEAT WAVE EVENTS

All the effects on microbial cells presented in Sections 2 and 3 can potentially modify soil microbial community composition and activity. As microbial communities are drivers of ecological processes, we

need to understand how climate change will affect them. Ecologists use the concept of stability[#] (resistance and resilience) to describe the effects of drought with high temperature events on microbial communities. A more stable microbial community could reflect a higher ability to perform functions (Griffiths & Philippot 2012, see Section 5). Therefore, one way to forecast ecosystem functioning under climate change is to look at the resistance[#] and resilience[#] of microbial communities during heat wave events (Seybold et al. 1999, Griffiths & Philippot 2012, Shade et al. 2012, Tardy et al. 2014) (Fig. 4).

To discuss disturbance, it is first necessary to define a basal level of stability. Kaisermann et al. (2015) observed a rapid succession of fungal populations in a non-extreme range of change in soil moisture, suggesting that fungal communities are adapted to normal moisture variations via high plasticity, whereas the lack of change in bacterial community composition in the same environmental conditions showed that stability is a more 'static' feature of bacterial composition. Bacterial and fungal communities can thus present different basal levels of stability, pointing to different drought-response mechanisms. This reinforces the need to understand why some microbial communities are lastingly changed by severe drought (Bérard et al. 2011).

4.1. Resistance to heat wave disturbance: variability in sensitivity of species and microbial groups, and consequences for microbial community composition

It has recently been suggested that the ability to adapt to different soil water potentials may be conserved at the phylum level (Lennon et al. 2012, Barnard et al. 2013). For example, fungi are thought (with some exceptions, e.g. Denef et al. 2001, Williams 2007) to be more adapted to low soil moisture conditions than bacteria (Beare et al. 1992, Jensen et al. 2003, Yuste et al. 2011). This difference in adaptation is linked to particular fungal traits[#], for example their hyphae making them less dependent on water-driven transport processes than bacteria when diffusivity is low (Griffin 1981, Poll et al. 2006). Consequently, drought events may increase fungal dominance in the microbial community (Ross & Sparling 1993, Joergensen et al. 1995, Bapiri et al. 2010, Barnard et al. 2013, Zeglin et al. 2013). Within the bacteria group, Gram-positive bacteria are thought to be better adapted to high water potential (Rokitko et al. 2003) than to Gram-negative bacteria, as they

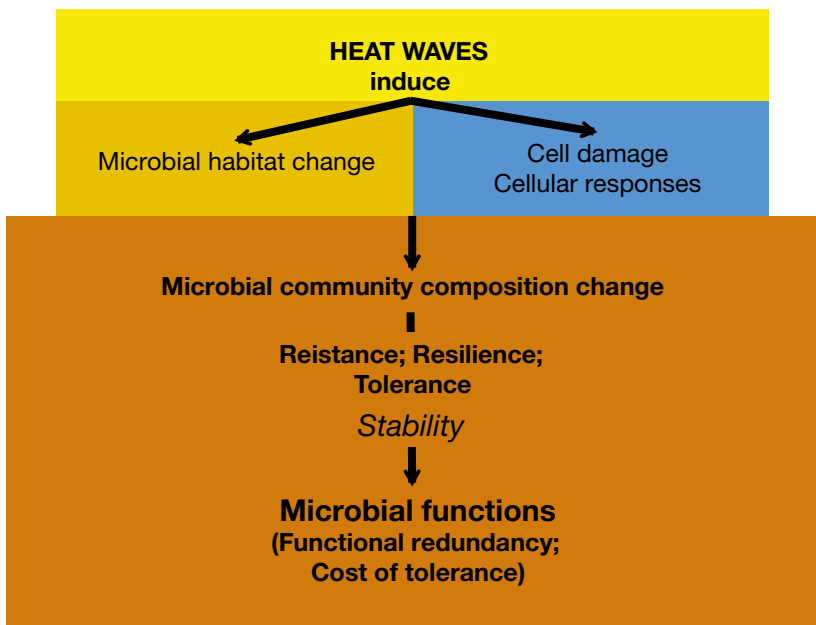


Fig. 4. Soil microbial habitat change and microbial cellular damage and responses to heat and drought lead to soil microbial community changes that involve phenomena such as resistance, tolerance and resilience. In functional terms, these microbial stability characteristics are visible in functional redundancy and cost of tolerance

have conserved biological traits like thick and rigid cell walls, high osmoregulatory abilities, oligotrophic[#] behavior (Kempf & Bremer 1998, Uhlirova et al. 2005, Hamer et al. 2007, Schimel et al. 2007) and spore-forming ability (Potts 1994). Drought could therefore favor Gram-positive bacteria at the expense of Gram-negative bacteria (Nazih et al. 2001, Uhlirova et al. 2005, Fierer et al. 2007, Schimel et al. 2007, Castro et al. 2010). De Vries & Shade (2013) applied these findings and proposed Gram-positive-to-Gram-negative and fungi-to-bacteria ratios as global indicators of community resistance to drought. The Gram-positive-to-Gram-negative ratio was recently applied in a field study on a natural record heat wave-drought (Acosta-Martinez et al. 2014b). Fungi are globally more sensitive to high temperatures than bacteria (Bollen 1969, Pietikäinen et al. 2005, Riah-Anglet et al. 2014). Heat tolerance is also species specific, and attempts have been made to classify the thermo-resistance of fungi (Jesenská et al. 1993) and bacteria (Schumann 2009). Cellular HSP production may be one biological trait favoring heat resistance differences between species (Feder & Hofmann 1999).

Very few studies separate the individual effects of drought and heat during a heat-drought disturbance (Ben Sassi 2012). Early research suggested that temperature has stronger effects on soil microbial community structure than drought effects (Bell et al.

2009) and this was later confirmed *in situ* by Acosta-Martinez et al. (2014b) who compared microbial community structures of agricultural soils during a natural heat wave event and 8 months after this extreme event. The heat wave event was found to have a higher impact on fungal diversity than bacterial diversity. Moreover, inside the bacterial community, they observed higher abundance of *Bacteroidetes* during the heat-wave event. Interestingly; this phylum showed resistance to heat in an experiment (28 d at 50°C) performed by Riah-Anglet et al. (2014).

The Actinobacteria group offers a perfect illustration of why it is so important to factor in both disturbances concurrently, as this Gram-positive group is known to be highly tolerant to desiccation (Uhlirova et al. 2005, LeBlanc et al. 2008, Barnard et al. 2013, Bouskill et al. 2013), yet it also appears sensitive to osmotic shock at rewetting (Williams 2007) and displays contrasting responses to high temperatures (Klamer & Bååth 1998, Riah-Anglet et al. 2014). Actinobacteria were observed in higher abundance during, compared to after, the heat-drought event studied by Acosta-Martinez et al. (2014b).

4.2. Stability of microbial communities after heat-drought events, influence of environmental parameters

The resilience of microbial community composition after heat-drought disturbance can be partial or complete and take more or less time (Bérard et al. 2011, Chowdhury et al. 2011b). Bear in mind that both the duration of the recovery experiment and method of resilience measurement can shape conclusions on resilience (Deng 2012). Both strength and duration of disturbance affect soil microbial responses (Unger et al. 2010, Shade et al. 2012). For example, increasing drought severity decreases respiration (Abera et al. 2012) and some soil enzyme activities (Sardans & Peñuelas 2005). Higher temperatures also lead to higher rates of change in both the phospholipid-derived fatty acid pattern and bacterial activity compared with lower temperatures (Pettersson & Bååth 2003). Looking at stress duration, 2 wk droughts in birch litter reduced microbial biomass and activity

more strongly than shorter droughts (Schimel et al. 1999). A long-term (14 yr) field study by Zeglin et al. (2013) highlighted a key role of dry period duration between rainfall events on soil microbial respiration and biomass, and this role was further confirmed in an experimental study performed by Barnard et al. (2015) on soil microbial responses to wet-up after a severe drying period. Bérard et al. (2011) also observed that the resilience of microbial parameters (microbial biomass, community structure and catabolic functions) is inversely related to duration of disturbance. No microbial resilience was observed after a 21 d heat–drought disturbance, whereas microbial resilience had been observed in 7 d disturbed soils. It was thus suggested that above a critical threshold of heat wave duration, the soil microbial communities may have undergone a drastic biomass kill-off (Banning & Murphy 2008) along with restructuring associated with a shift in physiological traits.

r-strategic[#] microbes may be favored among the microbial community after the end of the heat-wave (Fierer et al. 2007). This is the case for *Proteobacteria* that have the ability to grow fast, and were suggested to be favored after severe drought (Thomson et al. 2010, Barnard et al. 2013). Moreover, in *Proteobacteria*, speed of response after wetting may be class level-dependent (Placella et al. 2012). Interestingly, *Proteobacteria* gained abundance in soils during the natural heat–drought observed by Acosta-Martinez et al. (2014b) and in microcosms submitted to heat–drought in Bérard et al.'s (2011) experiment.

Although drought and heat–drought can decrease soil microbial diversity (Rokitko et al. 2003, Acosta-Martinez et al. 2014b), physical–chemical habitat diversity and connectivity (depending on water content), short-term temporal variation in soil characteristics can increase microbial diversity (Section 3, Fig. 3; Young et al. 2008, Carson et al. 2010). Different taxa with different moisture optima may be able to coexist by partitioning the soil moisture niche axis (Lennon et al. 2012, Wang & Or 2013), which would favor microbial diversity and whole-community stability (Griffiths et al. 2000, Proulx et al. 2010, Tardy et al. 2014). Moreover, microorganisms recolonizing from favorable to more impacted zones of the soil could facilitate soil activity recovery after heat–drought disturbance. Microbial colonization of soil occurs via bacterial transport through water flow, bacterial motility and bacterial growth (Wertz et al. 2007), and moisture is a factor of spatial interaction (and isolation) between soil microbes (Treves et al. 2003). In addition to those cited so far (Sections 3.1 and 4.1), motility (Turnbull et al. 2001) is another bio-

logical trait that confers advantages for microbial recovery in soil environments previously disturbed by dry–heat events. Interestingly, EPS can facilitate motility (Hu et al. 2012). Moreover, as stated in Section 2.2, sporulation and dormancy are strategies used by a variety of organisms to cope with unfavorable environmental conditions. Through this lens, spores, akinetes, conidia and dormant cells could be seen as members of a soil ‘microbial seedbank’ shaping community diversity and recovery (Jones & Lennon 2010, Lennon & Jones 2011) in soils submitted to extreme climate events. Norris et al.'s (2002) study at a geothermal site suggests that thermophiles are probably distributed throughout the observed soil temperature gradient and that they likely subsist in a dormancy state in low-temperature environments, ‘awaiting’ favorable conditions (in this case high temperature) for growth. These observations are an example of the ‘misplaced microorganisms’ theory described by Lennon & Jones (2011).

As suggested earlier, functional trait[#] approaches would be a valuable complement to community structure studies in order to inform on community stability in ecosystems impacted by disturbances (Lennon & Jones 2011, Lennon et al. 2012, Barnard et al. 2013, De Vries & Shade 2013, Krause et al. 2014). These traits may differ between resistance and resilience, suggesting that initial resistance to stress is not predictive of resilience over time (Kuan et al. 2006, Banning & Murphy 2008, Bérard et al. 2012). For example, K-strategy[#], hypha production, thick cell walls, sporulation ability, EPS synthesis and constitutive osmolytes are resistance traits to desiccation and heat, whereas, r-strategy[#] resuscitation and colonization strategies, sporulation (as a dispersal mechanism) and EPS synthesis are resilience traits. This again is illustrated by Actinobacteria which were observed to be resistant to drought, heat and heat–drought (e.g. Barnard et al. 2013, Acosta-Martinez et al. 2014b, Riah-Anglet et al. 2014) but showed a low post-heat–drought recovery after rewetting and temperature reduction (Bérard et al. 2011). As resistance and resilience traits can differ between drought events, high temperature events and heat wave disturbances, we need to further characterize the links between specific biological traits and these climatic disturbances in order to determine reliable microbiological trait indicators of stability to heat–drought. Mouillot et al. (2013) proposed a theoretical framework based on the definition of ‘functional space’ in which species are positioned according to their functional trait metrics. It would be interesting to apply this approach to soil microbial

communities impacted by concomitant drought and heat in the context of heat waves. Another challenge for research is to pinpoint and connect microbiological trait indicators of stability to heat waves (especially the possible interrelatedness between traits responsible for drought and heat tolerance) with the presence and expression of genes specifically involved in resistance and resilience to this kind of disturbance and with microbial structure and diversity (De Vries & Shade 2013, Krause et al. 2014). Recent high-throughput molecular analysis techniques like pyrosequencing (Barnard et al. 2013, Acosta-Martinez et al. 2014b), stable isotope probing (e.g. Blazewicz et al. 2014, who quantified microbial population dynamics with H_2^{18}O) and metatranscriptomics (Carvalhais et al. 2012) would facilitate the effort to establish such connections. For example, studies by Yoshimura et al. (2007) on a cyanobacterial strain suggest that a gene involved in the synthesis of EPS could be a key regulator of desiccation tolerance.

Resistance and resilience depend on habitat history (Zelles et al. 1991, Feder & Hofmann 1999, Banning & Murphy 2008). We saw in Section 2 that stress-hardening and cross-tolerance can happen at the cellular level (Kültz 2005). Moreover, in a comparative strain study, Lennon et al. (2012) suggested that microorganisms living in dry soil environments should also be adapted to moisture regime variations in these dry soils, whereas microorganisms from stable mesic environments would be less adapted to moisture variation. At the community level, resistance and resilience to additional stressors may depend on species tolerance being positively correlated, which Vinebrooke et al. (2004) termed 'positive species co-tolerance'. Initial exposure to a stressor combined with positive species co-tolerance should reduce the impacts of other stressors, which Vinebrooke et al. (2004) termed 'stress-induced community tolerance'. This concept has been extensively developed for chemical stressors (where it is termed 'pollution-induced community tolerance', e.g. Bérard et al. 2014), but remains under-explored for physical stressors like temperature (Ranneklev & Bååth 2001). In the context of soil microbial communities regularly submitted to drought, studies show a lower impact of additional drought stress, probably due to a pre-selection by drying–rewetting stresses (Fierer et al. 2003, Williams 2007, Bouskill et al. 2013, Zeglin et al. 2013, Wang et al. 2014b). An *in situ* study by Norris et al. (2002) performed on sudden temperature shift changes linked to underlying geothermal activity found that microbial communities are selected for by localized thermal activity. Bérard et al. (2012)

reported that soil microbial communities previously submitted to 75 d severe drought are more tolerant to a subsequent heat–drought disturbance than non-preconditioned controls. This higher tolerance could reflect drought-induced community tolerance to subsequent drought, as suggested by the authors, but also cellular cross-tolerance between drought and heat. Recovery depends not only on type of disturbance, but also on soil physicochemical characteristics (see Section 3.1). Soil microbial biomass recovery after air-drying may depend on soil OM content, but with contrasting conclusions (De Nobili et al. 2006, Hamer et al. 2007, Kaisermann et al. 2013), suggesting that post-disturbance recovery is context dependent and influenced by multiple environmental factors (Deng 2012). For example, Bárcenas Moreno et al. (2011) showed that low-pH humus soils favored fungal re-colonization after a heating event, whereas high-pH calcareous soil with lower carbon content favored bacterial re-colonization.

Finally, both abiotic parameters and changes in microbial community structure induced by soil environmental history (anthropological, geographic and meteorological pressures; e.g. Grüter et al. 2006, De Vries et al. 2012) may further impact microbial response to climatic events (Evans & Wallenstein 2012), with different responses between soils from different latitudes and different land soil management histories (Makino et al. 1997, Jensen et al. 2003, De Vries et al. 2012, Kaisermann et al. 2013, Riah-Anglet et al. 2014).

5. CONSEQUENCES OF HEAT WAVES FOR MICROBIAL FUNCTIONS

Soil ecosystem functioning can be considered as a network of ecological interactions (Zhou et al. 2010), especially in soil microbial activity 'hotspots' like the rhizosphere that engage processes operating at different spatial and temporal scales (Chakraborty et al. 2012). Changes in soil conditions, especially severe drought with high temperatures, are expected to affect microbial functions in terms of CO_2 emissions, OM degradation, nutrient cycling and mobilization or carbon sequestration (e.g. Jensen et al. 2003, Reynolds et al. 2003, Sardans & Peñuelas 2005, Bell et al. 2009, Unger et al. 2010, Hamdi et al. 2011, Zeglin et al. 2013, Acosta-Martinez et al. 2014a, Mills et al. 2014,). Here, we focus on the ecological mechanisms underpinning these changes in microbial function and the consequences for plant–microbe interactions (Fig. 4).

5.1. Functional performance in response to drought and heat stress

Microbial community composition and species interactions are key drivers of ecosystem functioning (Bell et al. 2005). Heat–drought disturbance-induced change in microbial composition can potentially affect soil functions and thus the services delivered (Waldrop et al. 2000, Strickland et al. 2009). On this point, studies by Acosta-Martinez et al. (2014a,b) have brought precious cues and clues on the links connecting the bacterial and fungal assemblages involved in biogeochemical cycling in heat wave-impacted agroecosystems.

Allison & Martiny (2008) proposed a conceptual model of how disturbance may or may not change ecosystem processes via microbial functions. Their model is based on levels and patterns of functional redundancy[#], i.e. the ability of one microbial taxon to carry out a process at the same rate as another under the same environmental conditions. For instance, among the many microbes responsible for litter and OM breakdown, there are also taxonomic groups like Gram-positive bacteria and fungi that are also drought tolerant (De Vries & Shade 2013). This means that decomposition processes could remain resilient to drought stress despite drought stress-induced changes in microbial community structure (Section 4) (Manzoni et al. 2012). However, resilience is not always observed after extreme heat–drought events. Bacteria and fungi differ in terms of ecological processes (Strickland & Rousk 2010) and heat and drought sensitivity (Kaisermann et al. 2015), so, even for a general process like decomposition, functional redundancy may prove impossible to maintain, which would have knock-on effects on C cycling (Wang et al. 2014b). This was illustrated by Ben Sassi et al. (2012) who showed that fungal substrate-induced respiration (measured using the FungiResp method that gives extra data on the fungal component of microbial substrate-induced respiration) is highly impacted by both heat and heat–drought disturbances, whereas whole-community microbial substrate-induced respiration is less impacted.

Even in theoretically drought-resistant fungal communities, it has been shown that water-stress and heat sensitivity may be dependent on functional species traits. As a rule, responses to drought, heat and post-drought rewetting differ between xerophilic and wood-decaying species (Manzoni et al. 2012) and between saprophytic and pathogenic species (Bollen 1969), as well as between copiotrophic[#] and oligotrophic microbes (characterized by their differences in

substrate affinities; Fierer et al. 2007). Furthermore, specialized functions prove less stable to disturbances than broad-scale functions in response to changes in microbial diversity or microbial community structure (Fetzer et al. 1993, Stark & Firestone 1995, Griffiths et al. 2000, Deng 2012). Indeed, many of these specialized organisms, such as nitrifiers, sulfur oxidizers and CH₄ oxidizers, are drought-sensitive Gram-negative taxa (Stark & Firestone 1995, Schimel et al. 2007). Chaer et al. (2009) showed how ‘narrow-niche’ cellulase and laccase activities are less resilient to heat shock than ‘broad-scale’ protease, lipase and esterase activities, and suggested that this reduced resilience of laccase and cellulase activities in soils is probably the result of relatively limited diversity in the microorganisms capable of producing these enzymes and inhibited or killed by the heat disturbances.

In short, microbial functions could be achieved by microbial taxa that share phylogenetic similarity (inducing ‘functional redundancy’), but stability to extreme events conferred through physiological traits and microbial strategy responses to heat–drought disturbances could also be related to the phylogenetic level. Functional redundancy (and thus soil microbial function) may therefore depend on whether phylogenetic similarity is or is not related to taxa traits and heat–drought responses. To conclude, these microbiological trait indicators of stability to heat–drought need to be compared and connected to functional trait indicators of microbial soil functioning in order to better understand the impacts of heat waves on soil ecosystem functions and better inform agrosystem managers. This leads to the following section on the cost of tolerance.

5.2. The cost of tolerance

There may be fitness costs to microbial acquisition of tolerance to stress, i.e. greater energy demand by microorganisms in order to cope with the disturbance-induced stress (Shade et al. 2012), resulting in a lesser ability to cope with other environmental changes (Tlili et al. 2011) and/or less functional microbial competence and growth (Bérard et al. 2014). For example, Lennon et al. (2012) observed that strains adapted to drought by producing biofilms have a long lag phase to growth, suggesting that the energy required to produce EPS slowed growth (Or et al. 2007a). Geisel et al. (2011) proposed a microbial resting growth strategy model taking into account trade-offs between stress resistance and maximum growth after the disturbance, and providing in-

formation on the ecological consequences of stress-resistance versus growth constraints. This 'cost of tolerance' applied at the community level may refer to the energy budget and the reduction of global genetic variation in the community selected by the disturbance (Bérard et al. 2014), with subsequent consequences for ecosystem functions.

5.3. Consequences for plant–microbe interactions

Perhaps the most important soil microbial role in ecosystem functioning, especially in agrosystems, is its contribution to plant diversity and productivity (see Van der Heijden et al. 2008 for review). Inversely, plants are known to directly or indirectly control and mediate multitrophic interactions in soil, notably the microbial loop (Chakraborty et al. 2012, Bakker et al. 2014, Chaparro et al. 2014), and plant community composition could induce differences in resistance and resilience of microbial biomass and catabolic activities to a wetting–drying disturbance (Orwin & Wardle 2005). De Vries & Shade (2013) recently hypothesized that the microbial community structure resilience to global change disturbances increases with greater resource availability via C inputs by plants, which probably stimulate EPS production and biofilm development (Nunan et al. 2003, Redmile-Gordon et al. 2014).

Water stress changes a plant's rhizodeposition (i.e. the quantity and composition of root exudates) and nutrient allocation (Lynch & Whipps 1990, Henry et al. 2007, Mahieu et al. 2009) depending on physiological plant type (C4 vs. C3 plants; Zhou et al. 2012) and plant development (Chaparro et al. 2014), and these changes in carbon compound exudation may then affect microbial community dynamics and functions (Nazih et al. 2001, Sanaullah et al. 2011). Furthermore, plants may respond differently to combined heat–drought stress than to each stressor separately (Mittler 2006), adding complex reactions and retroactions into the rhizospheric ecosystem impacted by extreme climate events like heat waves.

Rhizomicrobial (mycorrhizal and rhizobial) communities are enrolled in diverse mutualistic associations with plants (Brundrett 2009, Franche et al. 2009). In drought, rhizomicrobial communities may protect host plants against adverse impacts via a combination of nutritional, physical and cellular effects (reviewed in Compant et al. 2010). Plant growth-promoting microorganisms (PGPM[#]) are known to be drought stress-tolerant, and recent studies demonstrate their capacity to sustain plant development under drought

stress, with help from the drought-stressed plant itself via its root exudates (e.g. Marasco et al. 2013, Coleman-Derr & Tringe 2014). Moreover, the 'habitat-specific symbionts' concept posits that plants will tend to increase their stress tolerance via co-evolution between plant and fungi under stressful environmental conditions (Rodriguez et al. 2008). Márquez et al. (2007) gave a nice example of multitrophic interactions protecting plants against climate stress in their study on a virus-infected endophytic fungus conferring plant heat tolerance. Fungal isolates without the virus were unable to confer plant heat tolerance, whereas heat tolerance was restored after the virus was reintroduced to the endophyte, letting plants grow at soil temperatures up to 50°C. These examples highlight rhizomicrobial communities and rhizospheric soil as a potentially useful tool for climate change mitigation in the wider context of increasingly drought–heat-impacted agriculture (East 2013, Coleman-Derr & Tringe 2014).

The rhizosphere is a place where soil aggregates are more stable, and where bulk density, porosity and water and nutrient transfers are modified with respect to the bulk soil (Whalley et al. 2005, Hinsinger et al. 2009), partially due to EPS production by roots and microorganisms (Chenu 1995, Fischer et al. 2013, Wu et al. 2013, Redmile-Gordon 2014). In turn, the specific physical–chemical conditions of the rhizosphere could induce specific patterns of microorganism and plant behavior to stresses. Insight into these rhizospheric interactions between local hydric soil properties and microbial behavior in response to drought could yield a better understanding of how agro-ecosystems function and how they need to be managed in a changing climate.

In situ non-invasive techniques, such as the new method of soil zymography that maps the distribution of enzyme activity in soil (Spohn et al. 2013)—especially coupled with imaging tools such as optodes (Blossfeld et al. 2013, Spohn & Kuzyakov 2013), stable isotope techniques (e.g. Griffiths et al. 2006 studying the microbial turnover of plant exudates when ¹³CO₂ is delivered to plants) and the physico-chemical soil parameter measures mentioned in Section 3—could add valuable knowledge to how heat wave events impact plant–microbe interactions in the rhizosphere environment.

6. CONCLUSIONS

This review suggests that heat waves, defined as drought co-occurring with high-temperature events,

may induce different responses to those observed in studies focusing on only one stressor alone, due to overlap, synergy, antagonism and co-tolerance effects on soil microorganisms. To withstand these conditions, microorganisms mobilize recovery strategies, ranging from the individual up to the colony, and community level responses at a microniche scale that have consequences on ecosystem stability in terms of recovery trajectories and cost of tolerance. In short, these microbial recovery strategies, along with patterns of microbial functional redundancy and complex interplay with the soil chemical and biological environment, may have major impacts on soil ecosystem functions, particularly in agroecosystems through the rhizosphere.

Key conclusions of this review are that there are still too few studies integrating both high-temperature and drought stresses on soil microbial communities and their functions to give a firm picture of the impacts of heat waves on land and in agroecosystems (Fig. 5). Moreover, we should consider *in situ* studies of extreme climatic events and their impacts on soil microbial communities (Acosta-Martinez et al. 2014a,b) and discuss the results obtained through models incorporating the impacts of drought and heat together (Rodrigo et al. 1997, Bauer et al. 2008, Lawrence et al. 2009). There is a clear need to develop studies providing data on redundancy in functional traits, co-tolerance and microbiological trait indicators of stability to drought and heat disturbances, both separately and together, and their connections to microbial phylogeny (Yuste et al. 2007, Allison & Martiny 2008, Geisel et al. 2011, Krause et al. 2014, Wang et al. 2014b). The advent of meta-omics offers elegant complementary tools for connecting stability to functions in the context of heat waves. As suggested by Shade et al. (2012), the challenge of meta-omics is to associate metagenomic (investigating the distribution of potential functional trait genes in the environment; Lennon & Jones 2011), metatranscriptomic (reflecting immediate regulatory responses to environmental changes; Carvalhais et al. 2012) and metabolomic (identifying metabolites released by microbes in response to environmental changes; Lankadurai et al. 2013) approaches that, in a single soil sample, can provide quantitative information on functions

shared across taxa from the same microbial community, identify the taxa expressing genes for those functions at a given point in time and determine the functional output from those transcripts in the context of environmental disturbances. This challenge also needs further investigation.

Another key conclusion is the need to develop interdisciplinary environmental studies on the indirect impacts of heat–drought on soil microbial communities via biophysicochemical parameters (Chenu & Roberson 1996, Young et al. 2008), especially in the rhizosphere (Wu et al. 2013).

Land-use agroecosystems may impact microbial community structure and dynamics via changes in soil environment (e.g. physicochemical characteristics) in ways that would then impact microbial stability to extreme climate events. There is a need to better understand the links between changes in microbial environment and community composition due to interactions between anthropological, geographical and meteorological factors. Here again, more experimental and field studies are needed to compare microbial community responses to extreme climate events in soils from different latitudes and different land soil management histories (Makino et al. 1997, Jensen et al. 2003, Luo et al. 2011, De Vries et al. 2012, Acosta-Martinez et al. 2014a,b).

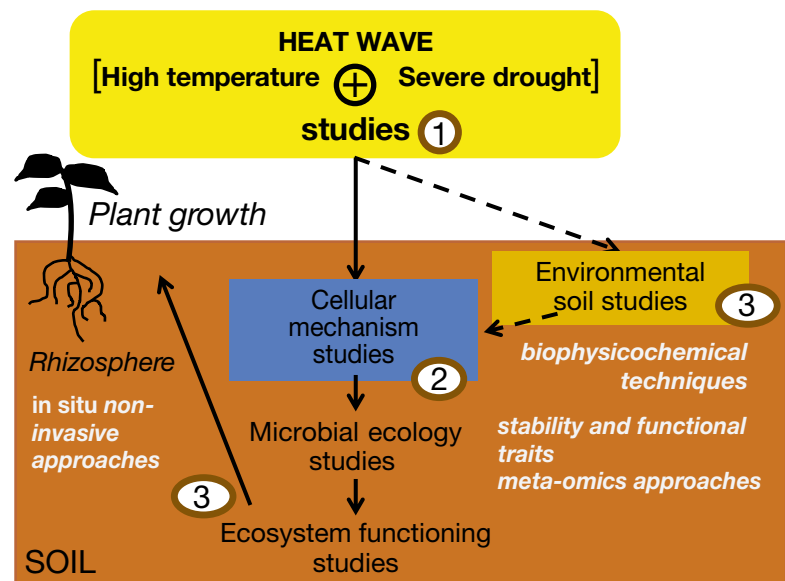


Fig. 5. Several lines of enquiry to guide future research in the context of temperate agroecosystems impacted by heat waves. More studies need to be performed on: (1) both stressors (heat and drought) simultaneously, (2) mechanistic frameworks to integrate individual-level to community-level responses via microbial traits and meta-omic approaches, (3) indirect impacts of heat–drought on microbial communities via soil biophysicochemical characterizations, with special focus on the rhizosphere. White lettering: examples of tools that could be mobilized to perform these studies

Anticipating this ideal interdisciplinary approach, spatial and temporal scales and heterogeneity emerge as central issues in soil ecosystems (Mills et al. 2014, Kuzyakov & Blagodatskaya 2015; see Sections 3.1 and 5.2 for examples), particularly in the context of extreme climate events where physical-chemical heterogeneity induced by interactions between soil characteristics and climate pressures may impact specialized ecological niches. The most pressing need is to further characterize the rhizosphere, and the physical, chemical, plant and microbial interactions it hosts (Hinsinger et al. 2009, Wu et al. 2013, Bakker et al. 2014, Coleman-Derr & Tringe 2014) before, during and after heat wave events. This is important in order to capture agronomic benefits in the context of global change.

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Glossary

(water) **aggregate stability**: The ability of soil aggregates to resist disintegration when disruptive forces associated with water are applied (Chenu et al. 2000).

copiotrophic behavior: see **r-strategists**. (From Fierer et al. 2007: 'Microbiologists are more likely to use the terms copiotroph and oligotroph to describe those microorganisms with ecological attributes typical of r- and K-strategists'.)

functional redundancy: The ability of one microbial taxon to carry out a process at the same rate as another under the same environmental conditions (Allison & Martiny 2008).

functional traits: Any trait directly influencing organismal performance (Mouillot et al. 2013). A trait is a phenotypic characteristic or attribute of an individual microbe that is affected by genotype and environment (De Vries & Shade 2013). In our conceptual framework, we distinguish functional traits by (1) the direct functional role that defines a microbe in terms of its ecological role (De Vries & Shade 2013), (2) microbiological trait indicators of stability to heat–drought disturbance that are physiological characteristics and (3) microbial life strategies involved in coping with this disturbance.

heat wave: A prolonged period (>7 d) of combined drought and high temperature. A heat wave is measured relative to the usual weather in the area and relative to normal temperatures and humidity for the season. This means that a heat wave corresponds to the occurrence of a temperature and humidity value above a threshold value near the upper end of the range of observed values for that variable in the area (IPCC 2007). This review deals with temperate and Mediterranean agricultural areas. As illustrative examples, 21 d was the actual duration of the 2003 European heat wave in the area of Avignon (France; Bérard et al. 2011), and 3 mo was the duration of the 2011

Texas (USA) heat wave in the Southern High Plains cotton-producing area (Acosta-Martinez et al. 2014a,b).

K-strategists: Organisms adapted to compete and survive when populations are near carrying capacity and resources are limited (Fierer et al. 2007).

oligotrophic behavior: see **K-strategists**

plant growth-promoting microorganisms: Plant-associated microbes that offer benefits to the host, improving nutrient uptake, preventing pathogen attack and increasing plant growth under adverse environmental conditions. In return, these microorganisms receive shelter from the surrounding environment and access to a carbon-rich food supply (Coleman-Derr & Tringe 2014).

r-strategists: Organisms adapted to maximize their intrinsic rate of growth when resources are abundant (Fierer et al. 2007).

resilience of microbial communities: The ability of microbial communities (structure or function) to recover after a disturbance, often reported as rate of return (Griffiths & Philippot 2012).

resistance of microbial communities: The ability of microbial communities (structure or function) to remain unchanged in response to a disturbance (Griffiths & Philippot 2012).

rhizosphere: The volume of soil around living roots that is influenced by root activity and exudation (Hinsinger et al. 2009).

soil wettability: In opposition to water repellency, soil wettability defines the ability of the soil to intake water (Chenu et al. 2000).

stability of microbial communities: The response of soil ecosystems to disturbance or environmental change in terms of the resistance and resilience of soil microorganisms to these environmental changes (Griffiths & Philippot 2012).

trait: A phenotypic characteristic or attribute of an individual microbe that is affected by genotype and environment (De Vries & Shade 2013).