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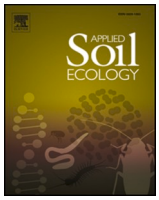

Short communication

Root hydraulic redistribution underlies the insensitivity of soil respiration to combined heat and drought

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ABSTRACT

The release of CO_2 from the soil into the atmosphere, due to soil respiration, is a major, yet poorly understood flux that regulates the terrestrial carbon balance. In particular, the apparent insensitivity of soil respiration to emerging combined extreme events of heatwave and drought makes terrestrial ecosystems likely to shift from being carbon sinks to sources. Limited understanding of the interactions underlying this response represents one of the key sources of uncertainty in forecasts of atmospheric CO_2. Here, we explore plant–microbe–soil interactions under heat and drought using a millifluidic setup that enables direct observations of hydration and oxygen content (the primary factors controlling soil respiration) in the root zone. Our observations reveal movement of water between soil regions *via* roots (termed root hydraulic redistribution), creating soil respiration hotspots and becoming a carbon source under combined heat and drought.

1. Introduction

After photosynthetic carbon uptake, CO_2 flux from the soil into the atmosphere represents the second largest carbon flux in terrestrial ecosystems, accounting for 60–90% of total ecosystem respiration (Longdoz et al., 2000). The potential of soils to increase in importance as a source of atmospheric CO_2, together with changing patterns in plant photosynthetic carbon uptake capacity in a warming climate (Humphrey et al., 2018), has motivated the development of diverse approaches to measure and model CO_2 fluxes from ecosystems under current and projected extreme climate conditions (Kuzyakov, 2006). Mounting evidence suggests negative effects of global warming on the carbon uptake capacity of plants (Le Quéré et al., 2018) and on the soil microbial community (Bérard et al., 2015). However, much less is known about how climate extremes combining drought and heat events, also called heatwaves (a prolonged period [>7 days] of combined drought and high temperature – sustained higher temperatures than the usual for the season; IPCC, 2007), will affect plant–microbes–soil interactions controlling respiratory release of carbon from soil, and hence the terrestrial carbon balance (Miralles et al., 2018; Zhou et al., 2019).

Limits to our understanding of the mechanisms underlying the sensitivity of soil respiration to individual or combined climate extremes represent one of the key sources of uncertainty in quantifying the terrestrial carbon balance and in predicting future shifts in the global climate (Reichstein et al., 2013). Recent syntheses of data from field observations of ecosystem-level primary production and respiration (von Buttlar et al., 2018) reveal that combined heat and drought events, rather than extremes in single factors, result in the strongest reductions in the capacity of an ecosystem to act as a carbon sink. This is crucial, given that numerous studies forecast an increase in combined heat and drought events across the globe (Zscheischler and Seneviratne, 2017; Zscheischler et al., 2018; Zhou et al., 2019). There is thus an urgent need to untangle the mechanisms governing the response to combined extreme events, to feed into models to assess whether terrestrial systems will transform from carbon sinks to sources in the face of global environmental change (Green et al., 2019).

Evidence suggests that soil respiration fluxes remain relatively unaffected under short-term episodes (on timescales of 1–3 weeks) of combined heat and drought. In contrast, photosynthetic carbon fluxes respond negatively, thereby accounting for the strongest reduction in the potential of terrestrial systems to act as a carbon sink (von Buttlar et al., 2018). A conventional interpretation attributes the initial insensitivity of soil respiration to the interplay of decreasing soil moisture and increasing temperature, considering the response as if these extremes

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occurred in succession rather than in combination. However, experimental and *in-situ* measurements of soil respiration under controlled conditions of soil moisture and temperature suggest that soil respiration dynamics are governed primarily by variation in soil moisture (*i.e.*, independently of temperature variation) under combined heat and drought (Zhang et al., 2015; Carey et al., 2016). We would thus expect soil respiration to decline with decreasing soil moisture. Under combined dry and hot soil conditions, where soil respiration dynamics are dominated by soil moisture variation (Fig. 1), we therefore hypothesize that there must be a supplementary water transfer mechanism compensating for the reduced water available to the rhizosphere microbiome, thereby accounting for the observed insensitivity of soil respiration to short-term combined heat and drought.

To test our hypothesis, we conducted a laboratory experiment to explore plant–soil–microbe interactions under combined heat and drought and focus on hidden belowground mechanisms controlling soil moisture redistribution, primarily driven by plant responses to the combined extremes. In particular, we explore the plant water saving effect (Fatichi et al., 2016) and the associated passive movement of soil water *via* plant roots (termed root hydraulic redistribution) (Richards and Caldwell, 1987; Feddes et al., 2001; Neumann and Cardon, 2012; Prieto et al., 2012), which may stimulate decomposition (Aanderud and Richards, 2009) and ultimately regulates rhizosphere respiration as the major source of the total soil CO_2 efflux, *i.e.*, regulates the soil carbon balance (Bond-Lamberty et al., 2018).

2. Materials and methods

2.1. Rhizotron and environmental chamber

Partitioning of the measured soil CO_2 efflux between sources has proved to be notoriously difficult (Kuzyakov, 2006), but O_2 measurements can be used to estimate the soil respiration flux in well-drained and non-carbonated soils (*e.g.*, Angert et al., 2015). For this purpose, we developed an experimental setup consisting of a rhizotron fabricated in plexiglass (3 mm thick) with internal dimensions 147 mm × 97 mm × 6 mm. This *quasi*-2D design was a compromise between providing good growing conditions for the plants and optimal visualization conditions for imaging. A removable front panel facilitated the filling of the rhizotron with soil. The rhizotron was closed at the bottom, except for a sealable valve connected to a Mariotte's bottle to control the water level within it. From one side, a CCD camera (Sony ICX834, Ximea GmbH, Münster, Germany) – providing images of 4244 × 2832 pixels, 1 pixel = 34 µm – was used to optically map root growth and soil water dynamics. From the other side, a 2D contactless read-out system, *i.e.*, a planar optode, was used to chemically map the oxygen distribution resulting from soil respiration. The optode consisted of a CCD camera (VisiSens™ TD, PreSens GmbH, Regensburg, Germany) – providing images of 1292 × 964 pixels, 1 pixel = 88 µm, with three channels in the red, green and blue (RGB) – and an O_2-sensitive foil (SF RPSu4, PreSens GmbH, Regensburg, Germany) mounted on the inside wall of the rhizotron. To prevent light interference with root growth and microbial function, images from both sides of the rhizotron were acquired in a dark chamber with only the aboveground plant parts exposed to light (Fig. S1, Supporting Information). Independent light sources (LEDs), white and pure color (single-analyte), were used for the optical and chemical imaging, respectively. Light sources were switched on for 5 s at the imaging frequency, with a 10 s time lag between them to avoid interference in acquisition. This short light exposition of the sensor foil also prevents its photobleaching (Schopf et al., 2015).

The equipment was installed within an environmental chamber with dimensions 1000 mm × 1300 mm × 700 mm (height × width × depth). The chamber itself was made of 10 mm plexiglass and PVC. The front panel contained an opening of 700 mm × 500 mm to allow experimental access. The environmental chamber allowed control of the temperature using a heater and a dual-relay thermostat, and the ambient CO_2 concentration by imposing a partial pressure of this gas by means of a pressure controller (OB1 MK3+, ELVEFLOW, Paris, France). The interior of the chamber included two grow lamps (20 W, Hgrope) to simulate day–night light cycles, and an infrared camera (ICI 9320 P-series, Infrared Cameras Inc., Texas, United States) with a noise equivalent temperature difference of 20 m°K to image leaf surface temperature (T_{leaf}) and its response to stressors (*i.e.*, combined heat and drought) at moderate resolution (320 × 240 pixels; 1 pixel = 630 µm). Plant leaf area was defined using color identification techniques (Wang et al., 2010). Within the chamber, ambient temperature (T_{env}), relative humidity and CO_2 concentration were also monitored (CL 11, Rotronic AG, Bassersdorf, Switzerland). Temperature difference (ΔT) between the leaf surface and its surrounding environment was used as a sensitive proxy for apparent stomatal opening or closure (Dhillon et al., 2014). The chamber was covered with an opaque black fabric to prevent penetration of external light (Fig. S1, Supporting Information).

2.2. Soil oxygen sensing

Oxygen optode images were analysed using an in-house Matlab script. A Gaussian filter ($\sigma = 2$) was applied to the raw RGB images, which were then split into red, green and blue channels. O_2 optodes contain two dyes: a sensitive dye emitting red (R) fluorescence dynamically quenched by oxygen, and a reference dye emitting constant green (G) fluorescence. O_2 concentrations are estimated based on Fluorescence Ratiometric Imaging (FRIM) using the Stern-Volmer relationship, in which the ratio of the oxygen sensitive dye (red channel) to the reference dye (green channel) serves as an explanatory variable.

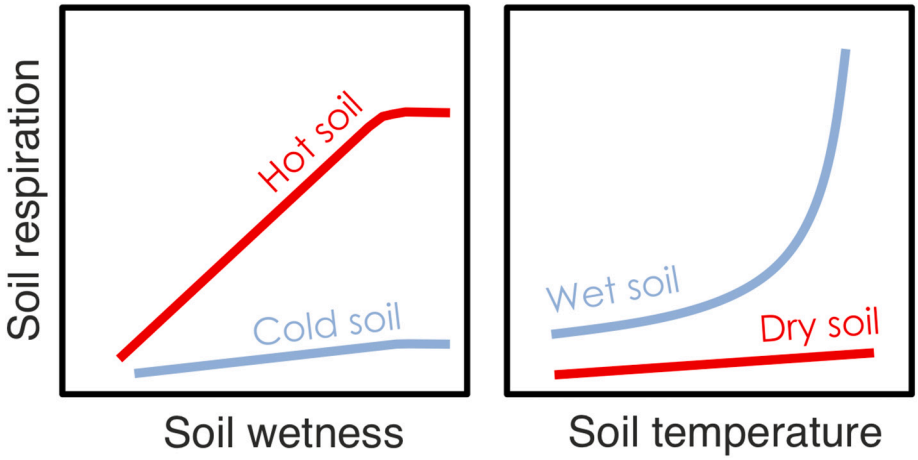

Fig. 1. Conceptual illustration of the response of soil respiration to soil wetness (typically below the "optimal" soil wetness that maximizes microbial activity; Skopp et al., 1990; Franzluebbers, 1999; Schjonning et al., 2003) and soil temperature. Under combined hot and dry soil conditions (red curves), the dynamics of soil respiration are primarily governed by soil hydration state, resulting in an expected linear relationship between soil respiration and soil wetness under hot conditions. Contrary to this, field observations suggest that soil respiration is initially insensitive to combined extremes of temperature and drought. In our experiments, we thus explore the soil-hydration-related mechanism(s) that may account for this apparent insensitivity. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Since changes in optical properties due to root growth and bacterial activity prevented the acquisition of reliable calibration images, we instead calculated the change in oxygen levels *via* a two-point calibration. For this, we took the maximum R/G ratio (1.1) during the experiments as anoxic condition, and the minimum R/G ratio (0.3) from the rhizotron filled only with water well-equilibrated with O_2 (no soil) as oxygenated condition (*e.g.*, Borer et al., 2020). The entire rhizotron, and isolated water clusters and roots (six different locations) selected as control regions, were used to assess the temporal dynamics of O_2 in the soil. O_2 measurements were expressed as the percentage of O_2 saturation in freshwater at atmospheric equilibrium (% atm. sat.) (*e.g.*, Lenzewski et al., 2018) and as actual concentration (mg/L). Note that due to the large difference in O_2 solubility between water and air, this technique also allows to infer soil water dynamics, including root exudation and hydraulic redistribution.

2.3. Experimental protocol

Bell pepper (*Capsicum annuum* L.) was used as the model plant and grown in a mixture of soil and peat (40% silty loam –which mineralogy is mainly silicate– and organic matter). The rhizotron was filled (while held horizontally to avoid layering) with a single plant (two replicates) and soil rich in organic matter (porosity of 0.8 and bulk density of 0.27 g/cm^3). The high porosity and low bulk density facilitated the visualization of the roots and processes around them, ensuring there was not oxygen limitation (by diffusion). Under such conditions, the CO_2 efflux is expected to be equal to the O_2 influx, and can thus be estimated from measurements of O_2 concentration (*e.g.*, Angert et al., 2015). After the rhizotron was placed into the environmental chamber, it was sealed during the experiment. The total duration of the experiment was nine days, with a progressive water shortage during this period (*i.e.*, no new water inputs), and having within the chamber a mean diurnal temperature of 28 °C, a mean nocturnal temperature of 26 °C, a relative humidity of 30%, and an ambient CO_2 concentration of 415 ppm. Note that for example in the mid/north of Europe, the mean temperature in summer season is 23 °C and the relative humidity >50%. Further, a universal decline in the temperature sensitivity of respiration at soil temperatures >25 °C has been observed (Carey et al., 2016), and a vapor pressure deficit is expected for increasing in Europe during 21st century (Zhou et al., 2019). A photoperiod of 12 h (06:00–18:00 h) was imposed from day one to six (0–144 h), while constant light was imposed from day seven to nine (144–216 h). The rhizotron was initially saturated in water, with saturation performed from below using the valve in the base. Water saturated conditions were maintained from day one to three (0–72 h). This period is used as control for each experiment. Subsequently, the rhizotron was partially desaturated until the end of the experiment and isolated from the Mariotte's bottle, although the deepest roots still had access to water. The plant was exposed to various stress factors including high temperature, water shortage and constant light, which forced the hydraulic redistribution as a consequence. We note that the limited ability of the bell pepper to export photosynthate out of its leaves when exposed to constant long photoperiod (Demers and Gosselin, 2002) contributes to mimic the plant response to heat stress (*i.e.*, a condition of high vapor pressure deficit) combined with water shortage. Optical images, oxygen optode images and thermal images of the plant were acquired almost simultaneously every 10 min (with 10 s lag to avoid interference of imaging and their respective light sources; see above).

3. Results

3.1. Stomatal response to stressors

Leaf temperature is a powerful indicator to track stomatal conductance, which causes changes in transpirational cooling. Drought is known to reduce stomatal conductance. We evaluated this

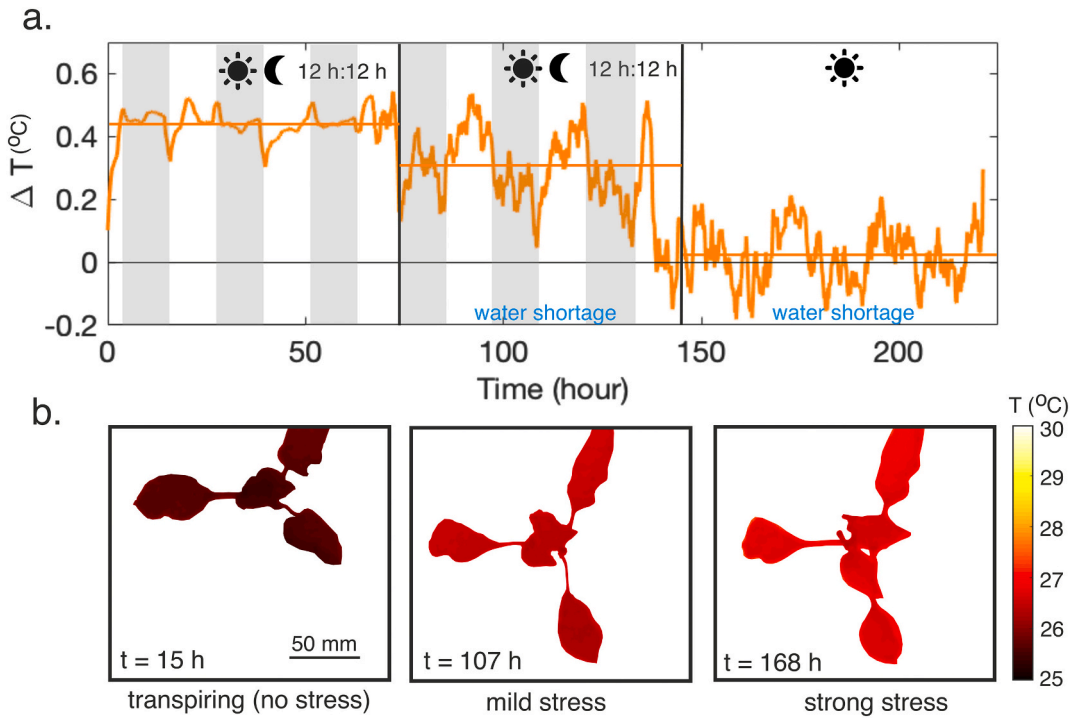

Fig. 2. a. Temporal evolution of the temperature difference, $\Delta T = T_{env} - T_{leaf}$, between the temperature of the environment (T_{env}) and the average leaf surface temperature (T_{leaf}) determined by infrared thermography. Day–night light cycles of 12 h (06:00–18:00 h) were imposed for the period 0–144 h (nights shadowed in gray color), and constant light for 144–216 h. Soil was saturated in water the period 0–72 h, then desaturated and naturally dried by evaporation and transpiration (72–216 h). b. Thermal images of *Capsicum annuum* plants under three different stress conditions: 0–72 h, water saturation and 12 h light cycle; 72–144 h, water shortage and 12 h light cycle; and 144–216 h, water shortage and constant light. An increase in leaf surface temperature (*i.e.*, a reduced difference with the ambient temperature) is observed as drought is imposed.

interdependency by tracking the temporal evolution of ΔT determined by infrared thermography (Fig. 2). Under water-saturated conditions (0–72 h), there was a lower temperature of the leaf compared to its environment, suggesting evaporative cooling caused by plant transpiration, with a $\Delta T \approx 0.5$ °C. This difference decreased slightly during the night because of temporary stomatal closure. Under drought (72–144 h), the cooling effect decreased, indicating that partial stomatal closure led to a lower transpiration rate, having a $\Delta T \approx 0.3$ °C, with larger fluctuations. Water shortage and constant light (144–216 h), mimicking combined water and heat stress, reduced ΔT to nearly zero, indicating that it induced more severe stomatal closure and a reduction of transpiration to nearly zero (*e.g.*, Isoda, 2010; Martynenko et al., 2016; Page et al., 2018).

3.2. Spatial distribution of O_2 and hydraulic redistribution

Under almost fully water-saturated conditions in the soil, the limited oxygen supply and the consumption by microorganisms in the rich nutrient environment reduced the dissolved oxygen concentration. Water desaturation of the rhizotron started after 72 h (Fig. 3a), and continued to the end of the experiment by the combined action of evaporation and transpiration (root water uptake). Water clusters that form under drying conditions increase the water–gas interfacial area, which enhances gas diffusion and exchange with the atmosphere (*e.g.*, Or et al., 2007). The high porosity and low density of the substrate used as soil reduces the water retention capacity, thereby facilitating oxygenation (Noguera et al., 2003) (Fig. S2, Supporting Information). Despite soil microorganisms remaining active during the drying period and continuing to consume dissolved oxygen, the enhanced oxygen supply resulted in a significant increase in oxygen saturation within water clusters (Fig. 3b).

We observed that roots released water into dry soil regions, *i.e.*, root hydraulic redistribution, when the plant was under stress and transpiring at a reduced or zero rate (Fig. 3c; Video S1, Supporting Information). In these experiments, root hydraulic redistribution was monitored through the oxygen concentration signature. The water redistributed by the roots mainly remains surrounding them and so is not expected to be subjected to limitation of oxygen diffusion from the surrounding air in the soil. Nevertheless, a temporal decrease of dissolved oxygen in the release water by roots was observed.

3.3. Temporal dynamics of O_2 and CO_2 efflux

We used the temporal dynamics of O_2 concentration to determine the effect of hydraulic redistribution by roots on soil CO_2 efflux under extreme environmental conditions. Measures of the temporal evolution of dissolved oxygen within permanently wetted water clusters show an increase in oxygen concentration (by 0.3 mg/L in 72 h) during the desaturation process (Fig. 4a), and similarly for the average oxygenation of the entire rhizotron (Fig. 4b). In contrast, during hydraulic redistribution, the opposite trend is seen in measures of individual locations, including roots, and of the entire rhizotron (Fig. 4c and d), although the changes are of a smaller extent (a reduction of 0.05 mg/L in 72 h) and with greater variability (expressed as a standard deviation among locations and for the two replicates).

4. Discussion

Stomata determine the flux of CO_2 into the leaf, water loss through transpiration, and ultimately maintain plant hydration, leaf temperature and photosynthetic rates (Jones, 2013). Internal and external environmental signaling causes changes in guard cell turgor (Roelfsema and Hedrich, 2005), driving the behavior of stomatal conductance (Matthews and Lawson, 2019). Increasing light and ambient temperature or a reduction of CO_2 and vapor pressure deficit, for example, trigger stomatal opening, while reduced light, extreme low and high temperatures, high ambient CO_2, high vapor pressure deficit or low soil water availability cause stomatal closure. Therefore, exposure to light and drought normally induce opposite stomatal responses. While light stimulates the opening of stomata to promote photosynthetic CO_2 uptake, drought stimulates stomatal closure to reduce transpirational water loss. In our experiments, as in nature under combined extreme events (Zhou et al., 2019), light and drought stress coincide during the day and plants must make a trade off (Roelfsema and Hedrich, 2005). Although previous studies indicate that root hydraulic redistribution enhances plant photosynthesis (Lee et al., 2005) and survival (Prieto et al., 2011), and therefore increasing ecosystem carbon uptake, our thermal images indicate that the model plants were transpiring progressively less through the experiment, which can be induced by the closing of the stomata under the imposed drought and light conditions (given bell pepper's photosynthesis limitation when exposed to constant long

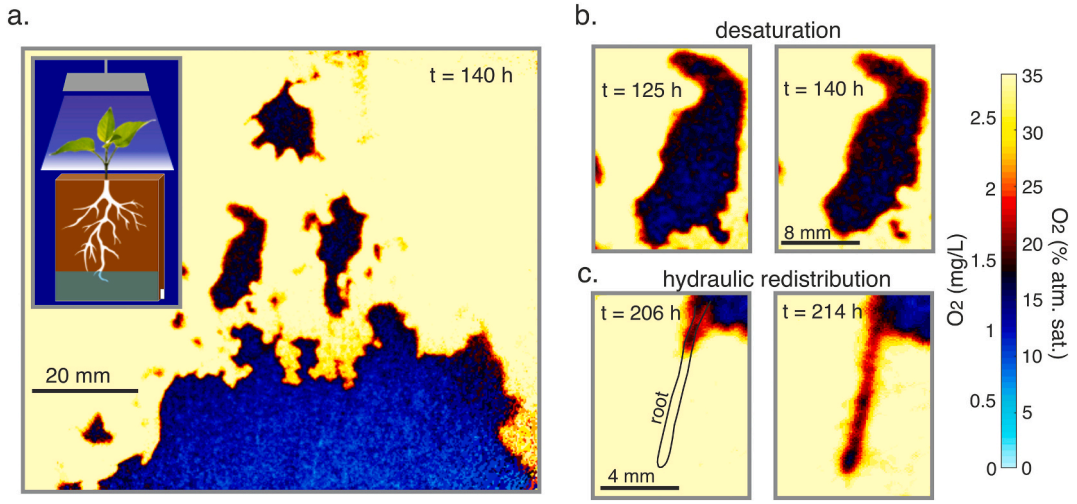

Fig. 3. a. O_2 concentration field (color scale) in the rhizotron under partially saturated conditions ($t = 140$ h). Water clusters in the root zone (in dark blue) can be recognized by their oxygen concentration lower than the surrounding air within the soil. b. Water cluster oxygenation during the soil drying process. For the selected water cluster (of relatively constant volume between $t = 125$ h and 140 h), both the boundary and the interior show an enrichment in oxygen with time. c. Root hydraulic redistribution (for an optically selected developed root) between $t = 206$ h and 214 h. After water is released by the root, a temporal decrease of dissolved oxygen in the immediate proximity of the root is observed. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

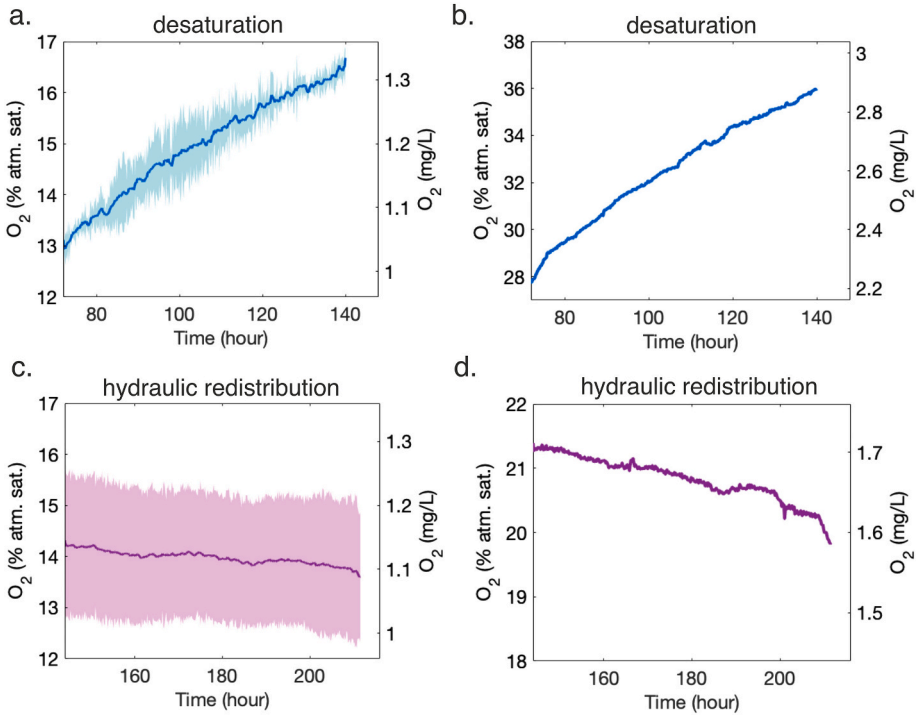

Fig. 4. a. Temporal dynamics of O_2 concentration during soil drying. Values were computed from six permanently wetted locations (water clusters) and for two replicates. An increase in O_2 (blue curve) is observed between 72 and 144 h, with relatively little variability between observation points (plotted as standard deviation, light blue shaded region). b. Average O_2 concentration during soil drying, computed for the entire rhizotron in two replicates. c. Temporal dynamics of O_2 concentration during hydraulic redistribution. Measures were taken from six locations, including roots, in two replicates. A decrease in O_2 (purple curve) is observed, with large variability (standard deviation, light pink shaded region). d. Average O_2 concentration during hydraulic redistribution, computed for the entire rhizotron in two replicates. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

photoperiod, see above in the Experimental protocol section). The observed stomatal closure is theoretically accompanied by a strong decline in carbon assimilation by photosynthesis. Note that a reduction in carbon assimilation can additionally be caused by biochemical and photochemical limitations (Costa et al., 2013). Therefore, we expect a reduction of belowground carbon allocation, in the form of sugars and other metabolites like amino acids and organic acids, available to the rhizomicrobial community *via* root exudation (Badri and Vivanco, 2009; Canarini et al., 2019).

It cannot be discerned whether there is a single type of root hydraulic redistribution at work, or a combination of several types (*e.g.*, hydraulic lift from deeper soil, lateral distribution among roots, or direct tissue dehydration; Nadezhdina et al., 2010; Prieto et al., 2012). However, while respiration by roots and mycorrhizae accounts for a significant fraction of soil respiration, our results suggest that aerobic respiration was strongly stimulated by root hydraulic redistribution (root-induced respiration). A controversy exists about root exudation under global warming scenarios. While some works indicate an increase in root exudation in droughts (*e.g.*, Karst et al., 2017; Preece et al., 2018; Jakoby et al., 2020), recent studies demonstrate that root exudation can be reduced up to ~50%, however, exudation of carbohydrates and cations (such as K^+ and Na^+) under stress conditions still occurs (Calvo et al., 2019). Therefore, our observation of oxygen consumption producing an anoxic wetted region around roots indicates CO_2 production due to root and microbial respiration. The region around roots is likely to be critical in governing soil respiration under combined extremes, because the compounds released by plant roots make them a hotspot for microbial density and activity (Scharf et al., 2016; Poole, 2017; Canarini et al., 2019). Between these compounds, mucilage plays a key role in the root-soil water transfer. During drying, mucilage keeps the rhizosphere wet and conductive, but on drying it turns hydrophobic, limiting root water uptake. The use of rhizoligands (additives) has been proposed in agriculture to improve plant adaptation to drought (Ahmed et al., 2018). In summary, although under drought conditions soil CO_2 efflux rates may be reduced (*e.g.*, Burri et al., 2014), this root-assisted mechanism mitigating local drought may account for the observed insensitivity of soil CO_2 efflux to combined extremes (*e.g.*, Cardon et al., 2013; Zhou et al., 2019). This behavior reduces the short-term coupling of above- and below-ground processes.

Follow up research is recommended to replace assumptions we had to make here. The soil was encapsulated by two plexiglass walls and all the components involved were at the same temperature, differing from a natural soil. Nevertheless, this setting provides reliable insight on the root hydraulic redistribution pattern and dynamics. More elaborated setups are needed to confirm findings in natural soils. For example, the inclusion of other analytes such as pH measured from the optode and zymography measurements would provide information on physico-chemical properties and microbial activity, respectively. While in our study, only one example soil type was used, we also suggest to evaluate the consistency of results for different soil types according to its properties (*e.g.*, texture, mineral composition, or microbial composition) and in different plant species/functional types. This also concerns the diversity of experiments, *e.g.*, soil water saturation or temperature regimes at the beginning of the experiments, since this likely will impact microbial activity and thus oxygen distribution patterns.

5. Conclusions

Our experimental observations of plant–microbe–soil interactions suggest that plant roots are responsible for hydraulic redistribution of water between soil regions. This transfer mechanism provides water and nutrients for microorganisms and thereby maintains their functioning under extreme environmental conditions with overall reduced soil moisture (Domec et al., 2010; Fu et al., 2018). This root-assisted water transport mechanism and associated support of microbial activity can potentially account for the global observations of insensitivity of soil respiration (at short-term, 1–3 weeks) to combined water and heat stress (von Buttlar et al., 2018). This is a fundamental component of the ecosystem response to combined climatic extremes, which when combined with the reduction in photosynthetic carbon flux, results in a strong reduction in the potential of terrestrial systems to act as a carbon sink. We suggest additional work to improve our understanding of root-mediated control mechanisms on soil water and biogeochemical fluxes under extreme conditions. Nonetheless, our laboratory results already provide new insights into concealed mechanisms that are neither accounted for by large-scale Earth system models nor readily quantified

by field observations (*e.g.*, Classen et al., 2015; Anderegg and Venturas, 2020).

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2021.104155.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Aanderud, Z.T., Richards, J.H., 2009. Hydraulic redistribution may stimulate decomposition. Biogeochem. 95 (2), 323–333.
Ahmed, M.A., Zarebanadkouki, M., Ahmadi, K., Kroener, E., Kostka, S., Kaestner, A., Carminati, A., 2018. Engineering rhizosphere hydraulics: pathways to improve plant adaptation to drought. Vadose Zone J. 17 (1), 1–12.
Anderegg, W.R., Venturas, M.D., 2020. Plant hydraulics play a critical role in earth system fluxes. New Phytol. 226, 1535–1538.
Angert, A., Yakir, D., Rodeghiero, M., Preisler, Y., Davidson, E.A., Weiner, T., 2015. Using O_2 to study the relationships between soil CO_2 efflux and soil respiration. Biogeosciences 12, 2089–2099.
Badri, D.V., Vivanco, J.M., 2009. Regulation and function of root exudates. Plant Cell Environ. 32, 666–681.
Bérard, A., Sassi, M.B., Kaisermann, A., Renault, P., 2015. Soil microbial community responses to heat wave components: drought and high temperature. Clim. Res. 66 (3), 243–264.
Bond-Lamberty, B., Bailey, V.L., Chen, M., Gough, C.M., Vargas, R., 2018. Globally rising soil heterotrophic respiration over recent decades. Nature 560 (7716), 80–83.
Borer, B., Jiménez-Martínez, J., Stocker, R., Or, D., 2020. Reduced gravity promotes bacterially mediated anoxic hotspots in unsaturated porous media. Sci. Rep. https://doi.org/10.1038/s41598-020-65362-w.
Burri, S., Sturm, P., Prechsl, U.E., Knohl, A., Buchmann, N., 2014. The impact of extreme summer drought on the short-term carbon coupling of photosynthesis to soil CO_2 efflux in a temperate grassland. Biogeosciences 11 (4), 961–975.
Calvo, O.C., Franzaring, J., Schmid, I., Fangmeier, A., 2019. Root exudation of carbohydrates and cations from barley in response to drought and elevated CO_2. Plant Soil 438 (1–2), 127–142.
Canarini, A., Kaiser, C., Merchant, A., Richter, A., Wanek, W., 2019. Root exudation of primary metabolites: mechanisms and their roles in plant responses to environmental stimuli. Front. Plant Sci. 10, 157. https://doi.org/10.3389/fpls.2019.00157.
Cardon, Z.G., Stark, J.M., Herron, P.M., Rasmussen, J.A., 2013. Sagebrush carrying out hydraulic lift enhances surface soil nitrogen cycling and nitrogen uptake into inflorescences. Proc. Natl. Acad. Sci. 110 (47), 18988–18993.
Carey, J.C., et al., 2016. Temperature response of soil respiration largely unaltered with experimental warming. Proc. Natl. Acad. Sci. 113 (48), 13797–13802.
Classen, A.T., Sundqvist, M.K., Henning, J.A., Newman, G.S., Moore, J.A.M., Cregger, M. A., Moorhead, L.C., Patterson, C.M., 2015. Direct and indirect effects of climate change on soil microbial and soil microbial-plant interactions: what lies ahead? Ecosphere 6 (8), 130. https://doi.org/10.1890/ES15-00217.1.
Costa, J.M., Grant, O.M., Chaves, M.M., 2013. Thermography to explore plant–environment interactions. J. Exp. Bot. 64 (13), 3937–3949.
Demers, D.A., Gosselin, A., 2002. Growing greenhouse tomato and sweet pepper under supplemental lighting: optimal photoperiod, negative effects of long photoperiod and their causes. Acta Hortic. 580, 83–88.
Dhillon, R., Udompetaikul, V., Rojo, F., Roach, J., Upadhyaya, S., Slaughter, D., Lampinen, B., Shackel, K., 2014. Detection of plant water stress using leaf temperature and microclimatic measurements in almond, walnut, and grape crops. T. ASABE 57 (1), 297–304.
Domec, J.C., King, J.S., Noormets, A., Treasure, E., Gavazzi, M.J., Sun, G., McNulty, S.G., 2010. Hydraulic redistribution of soil water by roots affects whole-stand evapotranspiration and net ecosystem carbon exchange. New Phytol 187 (1), 171–183.
Fatichi, S., Leuzinger, S., Paschalis, A., Langley, J.A., Barraclough, A.D., Hovenden, M.J., 2016 . Partitioning direct and indirect effects reveals the response of water-limited ecosystems to elevated CO_2. Proc. Natl. Acad. Sci. 113 (45), 12757–12762.
Feddes, R.A., Hoff, H., Bruen, M., Dawson, T., De Rosnay, P., Dirmeyer, P., Jackson, R.B., Kabat, P., Kleidon, A., Lilly, A., Pitman, A.J., 2001. Modeling root water uptake in hydrological and climate models. Bull. Am. Meteorol. Soc. 82 (12), 2797–2810.
Franzluebbers, A.J., 1999. Microbial activity in response to water-filled pore space of variably eroded southern Piedmont soils. Appl. Soil Ecol. 11 (1), 91–101.
Fu, C., Lee, X., Griffis, T.J., Wang, G., Wei, Z., 2018. Influences of root hydraulic redistribution on N_2O emissions at AmeriFlux sites. Geophys. Res. Lett. 45 (10), 5135–5143.
Green, J.K., Seneviratne, S.I., Berg, A.M., Findell, K.L., Hagemann, S., Lawrence, D.M., Gentine, P., 2019. Large influence of soil moisture on long-term terrestrial carbon uptake. Nature 565 (7740), 476.
Humphrey, V., Zscheischler, J., Ciais, P., Gudmundsson, L., Sitch, S., Seneviratne, S.I., 2018. Sensitivity of atmospheric CO_2 growth rate to observed changes in terrestrial water storage. Nature 560 (7720), 628–631.
IPCC (Intergovernmental Panel on Climate Change), 2007. 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 University Press, Cambridge.
Isoda, A., 2010. Effects of water stress on leaf temperature and chlorophyll fluorescence parameters in cotton and peanut. Plant Prod. Sci. 13 (3), 269–278.
Jakoby, G., Rog, I., Megidish, S., Klein, T., 2020. Enhanced root exudation of mature broadleaf and conifer trees in a Mediterranean forest during the dry season. Tree Physiol. 1–11.
Jones, H.G., 2013. Plants and microclimate: a quantitative approach to environmental plant physiology. Cambridge University Press, Cambridge.
Karst, J., Gaster, J., Wiley, E., Landhäusser, S.M., 2017. Stress differentially causes roots of tree seedlings to exude carbon. Tree Physiol. 37, 154–164.
Kuzyakov, Y., 2006. Sources of CO2 efflux from soil and review of partitioning methods. Soil Biol. Biochem. 38 (3), 425–448.
Le Quéré, C., Andrew, R.M., Friedlingstein, P., Sitch, S., Hauck, J., Pongratz, J., Pickers, P.A., Korsbakken, J.I., Peters, G.P., Canadell, J.G., Arneth, A., 2018. Global carbon budget 2018. Earth Syst. Sci. Data 10 (4), 2141–2194.
Lee, J.-E., Oliveira, R.S., Dawson, T.E., Fung, I., 2005. Root functioning modifies seasonal climate. Proc. Natl. Acad. Sci. 102, 17576–17581.
Lenzewski, N., Mueller, P., Meier, R.J., Liebsch, G., Jensen, K., Koop-Jakobsen, K., 2018. Dynamics of oxygen and carbon dioxide in rhizospheres of Lobelia dortmanna–a planar optode study of belowground gas exchange between plants and sediment. New Phytol. 218 (1), 131–141.
Longdoz, B., Yernaux, M., Aubinet, M., 2000. Soil CO_2 efflux measurements in a mixed forest: impact of chamber disturbances, spatial variability and seasonal evolution. Glob. Change Biol. 6, 907–917.
Martynenko, A., Shotton, K., Astatkie, T., Petrash, G., Fowler, C., Neily, W., Critchley, A. T., 2016. Thermal imaging of soybean response to drought stress: the effect of Ascophyllum nodosum seaweed extract. Springerplus 5 (1), 1–14.
Matthews, J.S.A., Lawson, T., 2019. Climate change and stomatal physiology. Annu. Plant Rev. Online 2, apr0667.
Miralles, D.G., Gentine, P., Seneviratne, S.I., Teuling, A.J., 2018. Land-atmospheric feedbacks during droughts and heatwaves: state of the science and current challenges. Ann. N. Y. Acad. Sci. https://doi.org/10.1111/nyas.13912.
Nadezhdina, N., David, T.S., David, J.S., Ferreira, M.I., Dohnal, M., Tesar, M., Gartner, K., Leitgeb, E., Nadezhdin, V., Cermak, J., Jimenez, M.S., Morales, D., 2010. Trees never rest: the multiple facets of hydraulic redistribution. Ecohydrology 3, 431–444.
Neumann, R.B., Cardon, Z.G., 2012. The magnitude of hydraulic redistribution by plant roots: a review and synthesis of empirical and modeling studies. New Phytol. 194 (2), 337–352.
Noguera, P., Abad, M., Puchades, R., Maquieira, A., Noguera, V., 2003. Influence of particle size on physical and chemical properties of coconut coir dust as container medium. Comm. Soil Sci. Plan. 34 (3–4), 593–605.
Or, D., Smets, B.F., Wraith, J.M., Dechesne, A., Friedman, S.P., 2007. Physical constraints affecting bacterial habitats and activity in unsaturated porous media–a review. Adv. Water Resour 30 (6-7), 1505–1527.
Page, G.F., Liénard, J.F., Pruett, M.J., Moffett, K.B., 2018. Spatiotemporal dynamics of leaf transpiration quantified with time-series thermal imaging. Agric. For. Meteorol. 256, 304–314.
Poole, P., 2017. Shining a light on the dark world of plant root–microbe interactions. Proc. Natl. Acad. Sci. 114 (17), 4281–4283.
Preece, C., Farré-Armengol, G., Llusià, J., Peñuelas, J., 2018. Thirsty tree roots exude more carbon. Tree Physiol. 38, 690–695.
Prieto, I., Padilla, F.M., Armas, C., Pugnaire, F.I., 2011. The role of hydraulic lift on seedling establishment under a nurse plant species in a semi-arid environment. Perspect. Plant Ecol. Evol. Syst. 13, 181–187.
Prieto, I., Armas, C., Pugnaire, F., 2012. Water release through plant roots: new insights into its consequences at the plant and ecosystem level. New Phytol. 193 (4), 830–841.
Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M.D., Seneviratne, S.I., Zscheischler, J., Beer, C., Buchmann, N., Frank, D.C., Papale, D., 2013. Climate extremes and the carbon cycle. Nature 500 (7462), 287–295.
Richards, J.H., Caldwell, M.M., 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by Artemisia tridentata roots. Oecologia 73 (4), 486–489.
Roelfsema, M.R.G., Hedrich, R., 2005. In the light of stomatal opening: new insights into 'the Watergate'. New Phytol. 167 (3), 665–691.
Scharf, B.E., Hynes, M.F., Alexandre, G.M., 2016. Chemotaxis signaling systems in model beneficial plant–bacteria associations. Plant Mol. Biol. 90 (6), 549–559.

Schjonning, P., Thomsen, I.K., Moldrup, P., Christensen, B.T., 2003. Linking soil microbial activity to water- and air-phase contents and diffusivities. Soil Sci. Soc. Am. J. 67, 156–165.
Schopf, A., Boehler, C., Asplund, M., 2015. Optical pH surveillance in a microfluidic system for cell culture. In: PreSens Application Note.
Skopp, J., Jawson, M.D., Doran, J.W., 1990. Steady-state aerobic microbial activity as a function of soil-water content. Soil Sci. Soc. Am. J. 54, 1619–1625.
von Buttlar, J., et al., 2018. Impacts of droughts and extreme temperature events on gross primary production and ecosystem respiration: a systematic assessment across ecosystems and climate zones. Biogeosciences 15, 1293–1318.
Wang, X., Yang, W., Wheaton, A., Cooley, N., Moran, B., 2010. Automated canopy temperature estimation via infrared thermography: a first step towards automated plant water stress monitoring. Comput. Electron. Agric. 73 (1), 74–83.
Zhang, Z.S., Dong, X.J., Xu, B.X., Chen, Y.L., Zhao, Y., Gao, Y.H., Hu, Y.G., Huang, L., 2015. Soil respiration sensitivities to water and temperature in a revegetated desert. J. Geophys. Res. Biogeosci. 120 (4), 773–787.
Zhou, S., Zhang, Y., Williams, A.P., Gentine, P., 2019. Projected increases in intensity, frequency, and terrestrial carbon costs of compound drought and aridity events. Sci. Adv. 5 (1), eaau5740.
Zscheischler, J., Seneviratne, S.I., 2017. Dependence of drivers affects risks associated with compound events. Sci. Adv. 3 (6), e1700263.
Zscheischler, J., Westra, S., Van Den Hurk, B.J., Seneviratne, S.I., Ward, P.J., Pitman, A., AghaKouchak, A., Bresch, D.N., Leonard, M., Wahl, T., Zhang, X., 2018. Future climate risk from compound events. Nat. Clim. Chang. 8 (6), 469–477.