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Manipulative experiments demonstrate how long-term soil moisture changes alter controls of plant water use

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ABSTRACT

Tree transpiration depends on biotic and abiotic factors that might change in the future, including precipitation and soil moisture status. Although short-term sap flux responses to soil moisture and evaporative demand have been the subject of attention before, the relative sensitivity of sap flux to these two factors under long-term changes in soil moisture conditions has rarely been determined experimentally. We tested how long-term artificial change in soil moisture affects the sensitivity of tree-level sap flux to daily atmospheric vapor pressure deficit (*VPD*) and soil moisture variations, and the generality of these effects across forest types and environments using four manipulative sites in mature forests. Exposure to relatively long-term (two to six years) soil moisture reduction decreases tree sap flux sensitivity to daily *VPD* and relative extractable water (*REW*) variations, leading to lower sap flux even under high soil moisture and optimal *VPD*. Inversely, trees subjected to long-term irrigation showed a significant increase in their sensitivity to daily *VPD* and *REW*, but only at the most water-limited site. The ratio between the relative change in soil moisture manipulation and the relative change in sap flux sensitivity to *VPD* and *REW* variations was similar across sites suggesting common adjustment mechanisms to long-term soil moisture status across environments for evergreen tree species. Overall, our results show that long-term changes in soil water availability, and subsequent adjustments to these novel conditions, could play a critical and increasingly important role in controlling forest water use in the future.

1. Introduction

Recent work has shown that plant transpiration could account for up to 90% of terrestrial evapotranspiration (Jasechko et al., 2013), making vegetation a dominant force in the global water cycle. Transpiration from forest ecosystems alone contributes between 50% and 70% to terrestrial evapotranspiration (Schlesinger and Jasechko, 2014). Climate-related shifts in forest transpiration could thus have large impacts on the global water cycle including modification in precipitation, groundwater recharge, renewable fresh water, increasing soil erosion, and feedbacks on (micro) climate. Average temperature at the world's surface has been steadily rising since the mid–50 s (IPCC, 2014). Warmer air increases vapor pressure deficit (*VPD*) and induces higher evaporation from land surfaces including transpiration from plants (Hardwick et al., 2010). Simultaneously, the risk for severe and extended droughts is increasing (Williams et al., 2013; Cook et al., 2015; Roderick et al., 2015).

At hourly to daily scales, tree-level sap flux primarily results from the driving force for transpiration (radiation, *VPD* and wind), and hydraulic and stomatal conductance of the trees (Oren et al., 1999).

Abbreviations: F_D, mean daily sap flux density ($g\,m^{-2}\,s^{-1}$; *LAI*, leaf area index ($m^2\,m^{-2}$); *REW*, relative extractable water (unitless); *VPD*, vapor pressure deficit (kPa)

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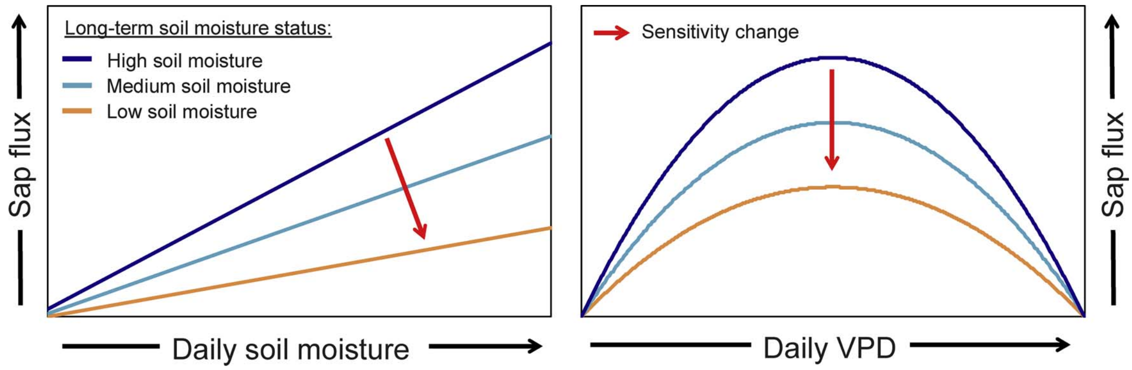

Fig. 1. Hypothetical relationships between sap flux and daily soil moisture or vapor pressure deficit (*VPD*) variation under different long-term soil moisture conditions (high, medium and low soil moisture). The red arrow indicates changes in sap flux sensitivity to soil moisture and *VPD* resulting from physiological and possible structural adjustments to soil moisture change (e.g. hydraulic resistance, stomatal density, synthesis of chemicals inducing stomatal closure, rooting depth). Because of adjustments to reduced soil moisture, trees would experience a decreased sensitivity to daily soil moisture and *VPD* variation inducing lower sap flux under both high and low soil moisture status, and lower maximum sap flux under optimal *VPD*. Sensitivity to soil moisture would thus be reflected through changes in the slope of the linear relationship between sap flux and soil moisture while changes in *VPD* sensitivity would be reflected in shifts of maximum sap flux at optimal *VPD* (location of the vertex of the curve). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Without stomatal control, tree-level transpiration increases progressively with rising *VPD* as a consequence of the atmosphere becoming less moisture saturated. As *VPD* increases, stomata respond via an exponential decrease in stomatal conductance (Lange et al., 1971; Monteith, 1995). Consequently, when high *VPD* is reached (≈2.5 kPa, species-specific), stomata start modulating the transpiration flux and thus tree-level transpiration starts dropping due to partial stomatal closure. Therefore, the response of tree-level transpiration to *VPD* can be expressed as a parabolic equation (Fig. 1) (Monteith, 1995). By closing their stomata to avoid critically high sap flux rates and impacts on embolism, trees can avoid excessive damages to their hydraulic system (Saliendra et al., 1995). At daily or longer time scales, tree-level sap flux regulation is also largely controlled by soil moisture variation. Tree responses to soil water availability are triggered by a chemical signal originating from the roots exposed to dry soil (see reviews by Davies and Zhang, 1991; Davies et al., 1994). Strong relationships have already been established between soil moisture (or water stress indexes) and tree-level sap flux enabling the incorporation of sap flux responses to short-term precipitation change in several climate-vegetation models so far (e.g. Sala and Tenhunen, 1996; Granier et al., 1999; Verhoef and Egea, 2014; De Cáceres et al., 2015).

Although rapid sap flux responses to soil moisture and evaporative demand have been the subject of attention before, the relative sensitivity of sap flux to these two factors under long-term precipitation and soil moisture change has rarely been determined experimentally (but see Grossiord et al., 2017). However, to maintain integrity of water resources, and improve global predictions it is essential to determine how these two drivers will influence forest transpiration in the long-term under projected climate. Plants are known to have a wide range of active adjustment strategies to deal with long-term exposure to changing soil moisture, including physiological and structural adjustments (Chaves et al., 2002) directly influencing sap flux regulation. Under drier soil conditions, plants often undergo adjustments that are directed toward a water saving strategy to limit excessive water loss (Ogaya and Peñuelas, 2003; Leuzinger et al., 2005; Brando et al., 2008). For instance, trees may produce conducting elements with reduced lumen diameters (Hacke et al., 2004; Fonti and Jansen, 2012; Grossiord et al., 2017), which can result in reduced sensitivity to short-term soil moisture variation (i.e. reduced sap flux under both high and low soil water availabilities because of higher flow resistance, Fig. 1). Long-term soil moisture reduction may also result in changes in stomata density (Luomala et al., 2005), or in the synthesis of chemical signals inducing stomatal closure (Bartlett et al., 2012; Meinzer et al., 2014), which can decrease the sensitivity of trees to evaporative demand and result in reduced sap flux, even under optimal *VPD* (≈1.5 kPa) (Fig. 1) (Grossiord et al., 2017).

Most of our knowledge on tree responses to climate variability is based on studies with potted plants or seedlings under common garden conditions, which may not represent the true responses of mature forests (Poorter et al., 2012; Rigling et al., 2013; Herzog et al., 2014). Manipulative field experiments on mature individuals are one way to decipher ecosystem sensitivity to possible precipitation change, but only a few experiments have been established in natural forests to date (Knapp et al., 2016). The lack of experiments in natural conditions is partially related to the obvious technical limitations and the financial costs associated with large-scale climate manipulation but also legal restrictions that can occur in natural areas (Kayler et al., 2015). Such experiments have however great value as, contrary to studies conducted along environmental gradients, they provide the ability to expose plants to environmental conditions they would not experience otherwise (i.e. broadening of environmental conditions), isolate mechanistic functions and identify threshold responses necessary for global predictions (Kayler et al., 2015; Estiarte et al., 2016; Knapp et al., 2016).

Here we tested how long-term (multi-year) artificial change in incoming precipitation (i.e. increasing or reducing long-term soil water availability) influences the sensitivity of tree sap flux to daily *VPD* and soil moisture variations, and the generality of these effects across four forest types and environments using four manipulative sites in natural and mature forests in the USA and Europe. We hypothesized that:

(1) changes in long-term soil moisture would modify the sap flux sensitivity of trees to environmental variability with trees subjected to reductions in soil water availability showing decreased sap flux sensitivity to soil moisture and VPD variation while trees exposed to increased soil moisture would show an enhanced sensitivity to the same factors, both because of long-term adjustments in their physiology and structure (Fig. 1),
(2) changes in sap flux sensitivity to soil moisture and VPD variation would vary across climatic and environmental conditions, and for various forest types as tree species have different inherent responses to climatic variations (e.g. iso- and anisohydric strategies) and have adapted to their local climate (e.g. long-term structural and physiological adjustments).

2. Materials and methods

2.1. Experimental sites

We used data collected from mature forest plots in four regions covering a large gradient of environmental and climatic conditions and