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Review

Drought and ecosystem carbon cycling

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A B S T R A C T

Drought as an intermittent disturbance of the water cycle interacts with the carbon cycle differently than the 'gradual' climate change. During drought plants respond physiologically and structurally to prevent excessive water loss according to species-specific water use strategies. This has consequences for carbon uptake by photosynthesis and release by total ecosystem respiration. After a drought the disturbances in the reservoirs of moisture, organic matter and nutrients in the soil and carbohydrates in plants lead to longer-term effects in plant carbon cycling, and potentially mortality. Direct and carry-over effects, mortality and consequently species competition in response to drought are strongly related to the survival strategies of species. Here we review the state of the art of the understanding of the relation between soil moisture drought and the interactions with the carbon cycle of the terrestrial ecosystems. We argue that plant strategies must be given an adequate role in global vegetation models if the effects of drought on the carbon cycle are to be described in a way that justifies the interacting processes.

Contents

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1. Introduction

Water is essential for life on Earth. Water – and drought – are therefore intimately linked with the terrestrial carbon cycle. Recent notable droughts occurred in Central/SW Asia (1998–2003), Western North America (1999–2007), Australia (2002–2003), Europe (2003) and Amazonia (2005) (Cook et al., 2004; Thomas et al., 2009; Trenberth et al., 2007). Droughts impact a broad range of climates and ecosystems, on a regional to sub-continental scale. The geographic area affected by droughts globally has increased strongly in the last four decades (Dai et al., 2004). Although there are considerable uncertainties in climate model predictions, a majority of the IPCC-AR4 future climate projections indicate that more frequent and intense droughts are expected, in particular at the mid-latitudes and over Africa, Australia and Latin America (Bates et al., 2008; Meehl et al., 2007). Intermittent droughts impacting productive regions can cause abnormally high atmospheric CO_2 growth rates (Knorr et al., 2007), and therefore droughts are expected to impact the carbon cycle more strongly in the future. In this study we focus on the relation between soil moisture drought and the carbon cycle of terrestrial ecosystems, characterized by the severity, duration and frequency of the drought, and its impact on the exchanges of carbon among vegetation, soils and the atmosphere. This focus complements other specific interests in droughts, such as meteorological drought (precipitation), hydrological drought (run-off, water levels), ecological drought (ecosystem functioning), agricultural drought (yield reduction) and socioeconomic drought (Bates et al., 2008; Dai et al., 2004; Heim, 2002). We review the state of understanding of the relation between drought and the ecosystem carbon cycle, and identify knowledge gaps. We complement analysis of the short-term responses in photosynthesis and respiration, by looking at the more complex and uncertain long-term implications of drought on ecophysiology and ecosystem dynamics. The paper is organized around four aspects relevant to drought and the ecosystem carbon cycle (Fig. 1):

1) Direct effects of drought on gross primary production, total ecosystem respiration and net ecosystem exchange;
2) carry-over effects of droughts;
3) drought-induced vegetation mortality;
4) species competition and drought.

This paper is written from the perspective that these aspects are highly interconnected through a series of species-specific survival strategies ranging over short and long time scales. We argue that this interconnection of short and long-term processes is essential to develop a comprehensive view of the relation between drought and the carbon cycle of terrestrial ecosystems. Dynamic vegetation models currently consider broad plant functional types, and one of the emerging gaps is that they cannot account for species-specific drought survival strategies, which determine the response of the ecosystem carbon cycle.

2. Direct effects of drought on GPP, TER and NEE

Drought affects the terrestrial carbon balance by modifying both the rates of carbon uptake by photosynthesis (GPP) and release by total ecosystem respiration (TER), and the coupling between them (Meir et al., 2008). We call these direct effects, because the changes occur largely during the course of droughts (Fig. 1, left). Carbon uptake and release are non-linear functions of, among others, water availability and temperature. Using CO_2 flux measurements collected in a global network (Baldocchi et al., 2001), it was shown that the majority of sites experience reductions in both GPP and TER during drought (Baldocchi, 2008; Bonal et al., 2008; Ciais et al., 2005; Granier et al., 2007; Reichstein et al., 2007b; Schwalm et al., 2010). Because autotrophic respiration (foliage, stems, roots) accounts for ~60% of TER (Janssens et al., 2001; Law et al., 1999, 2001), and field experiments indicate a strong correlation between root respiration and recent carbon assimilation (Irvine et al., 2005), short-term variations in TER are largely determined by the supply of labile

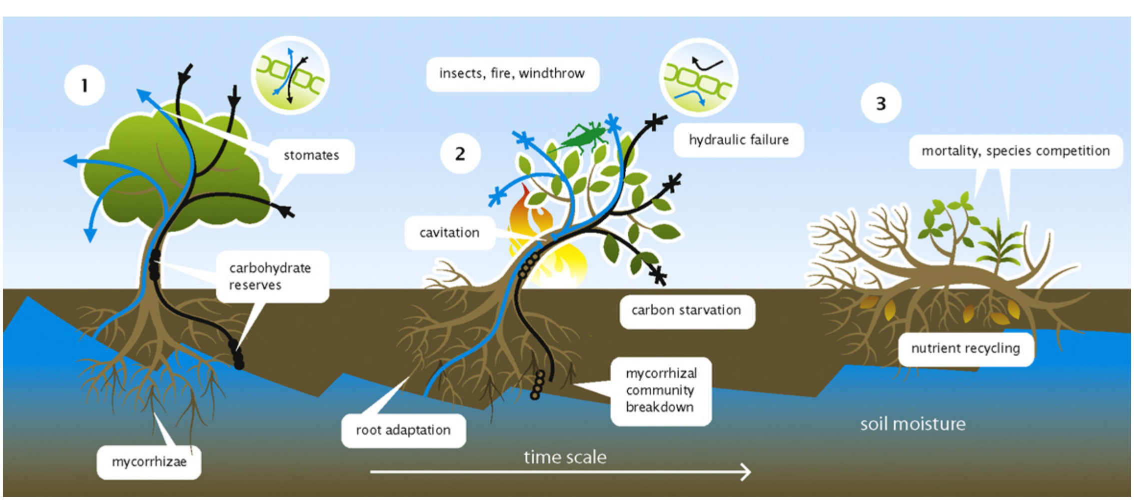

Fig. 1. Schematic illustration of the interaction of drought and the carbon cycle, before, during and after a period of intense moisture stress, and the time scales involved in the response. In situation (1) soil moisture is sufficient, and the flows of water and carbon are correlated through stomatal conductance (Section 2). In situation (2) a severe drought occurs, resulting in cavitation and/or carbon starvation, followed by increased vulnerability to other disturbances such as insects, fire and wind throw (Section 3). In situation (3) selective mortality and regrowth occurs, coherent with species' strategy (Sections 4 and 5).