

Review

Drought and ecosystem carbon cycling

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ABSTRACT

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.

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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 CO₂ 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 CO₂ 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

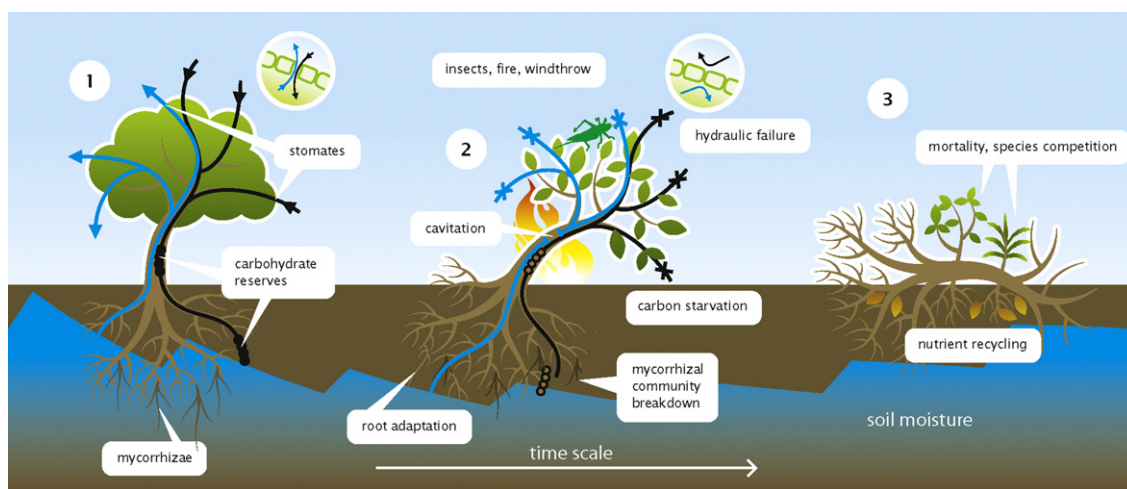


Fig. 1. Schematic illustration of the interaction of drought and the carbon cycle, before, during and after a period of intense moisture stress, and the time scales involved in the response. In situation (1) soil moisture is sufficient, and the flows of water and carbon are correlated through stomatal 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).

organic carbon compounds produced by photosynthesis, and likely to a lesser extent by the soil moisture effect on microbial activity. This explains the tendency for joint reductions in GPP and TER (Law, 2005; Ryan and Law, 2005). The absolute short-term reduction in GPP tends to be larger than in TER. Hence droughts generally turn ecosystems towards a source of CO₂ to the atmosphere.

The degree to which GPP is reduced depends on the *physiological response* to limited plant available water (Meir et al., 2009; Meir and Woodward, 2010) and on *structural changes* in the vegetation during the drought: *physiological responses* of the vegetation to drought include reductions in enzymatic activities as well as stomatal closure to prevent water loss. The latter has been shown both at leaf level (Lawlor, 1995) and at ecosystem level (Amthor and Baldocchi, 2001; Reichstein et al., 2003, 2002). Two contrasting strategies for water use have been hypothesized, although in reality these likely represent points on a continuum (Tardieu and Simonneau, 1998): isohydric species decrease stomatal conductance to prevent leaf water potential from reducing below a critical level, while anisohydric species are able to exert little or no stomatal control in response to drought. Because stomatal closure also reduces CO₂ diffusion into the leaf (Leuning, 1990) isohydric species experience a larger short-term reduction in GPP than anisohydric species. The longer-term consequences of these strategies are discussed in a later section.

Structural changes in the vegetation in response to drought may also cause reductions in GPP. These changes include reductions in leaf area due to early leaf senescence, and leaf shed or the arrest of leaf expansion as observed in some conifers (Fisher et al., 2007), and the alteration of leaf angle distribution within the canopy (Kull et al., 1999). Some tree species have shown large dynamic responses of fine roots, which may effectively increase specific root length and area, increasing the potential for water and nutrient uptake with minimal carbon investment (Katterer et al., 1995; Metcalfe et al., 2008; Schymanski et al., 2008; Singh and Srivastava, 1985). However, not all species show such a dynamical root response (Mainiero and Kazda, 2006). Root adaptation varies among species, soil types and climate conditions (Ostle et al., 2009) as a function of (1) the mechanisms of root adaptation that apply in time and space (e.g. through changes in root – shoot ratio, root volume – surface area ratio and vertical distribution) including the costs and benefits of adaptation; (2) the relationship between vertical profiles in root density and conductivity, soil physical properties and water uptake; and (3) the processes controlling the spatial variability in hydraulic redistribution over the root zone. Understanding of root distribution and adaptation is largely based on observations at the scale of single experimental sites while the variability across sites and species is not well sampled. This hinders applying this understanding at larger scales, such as those used in global vegetation or climate models.

Total ecosystem respiration encompasses autotrophic maintenance and growth respiration (“within plants”) and heterotrophic terms (“within soils”), associated with decomposition of pools of varying turnover times (e.g. leaves, woody tissue, roots, coarse woody debris, soil organic matter). Soil respiration (autotrophic root and heterotrophic respiration combined) may contribute up to 70% of TER and is tightly linked to GPP on annual time scales (Irvine et al., 2008; Law, 2005; Ryan and Law, 2005). Labile soil carbon pools generally reach new equilibrium pool sizes quickly after changes in the environmental conditions, so that the amount of labile soil carbon affected during the drought depends on the pool size. In contrast, stable pools take longer to reach a new equilibrium, so that the amount of stable soil carbon affected during the drought depends on the change in decomposition rate and the duration of the drought. The decomposition rates of soil carbon pools of different stability are functions of temperature, available water, chemical composition, microbial community composition, priming

(stable organic matter made available for decomposition by emission of labile compounds from roots) and acclimation (Burton et al., 2008; Davidson and Janssens, 2006; Fang et al., 2005; Fontaine et al., 2007; Knorr et al., 2005; Ostle et al., 2009; Smith et al., 2008) and it remains challenging to propose functional descriptions applicable on broad time and space scales (Bond-Lamberty and Thomson, 2010; Migliavacca et al., 2011).

With rising atmospheric CO₂ concentrations due to anthropogenic emissions, more CO₂ would diffuse into the plant stomates under unchanged stomatal conductance. Plants may respond to this CO₂ fertilization by reducing the stomatal conductance (Field et al., 1995; Katul et al., 2010), or even reducing the number of stomates per unit leaf area (Kouwenberg et al., 2003; Woodward, 1987). As a consequence, the transpirational water loss would decline (Sellers et al., 1996) or the plants may increase leaf area (Woodward, 1990). This implies that soil water may be used more efficiently, and that soil moisture may decline slower in future periods of lack of precipitation (Betts et al., 2007; Gedney et al., 2006; Volk et al., 2000). In practice, the response to this CO₂ fertilization needs better quantification (Rammig et al., 2010) and it is observed to vary widely across plant species (Konrad et al., 2008).

As an example of the direct effects of droughts, the anomaly of net ecosystem exchange (NEE = GPP – TER) during the well-studied record 2003 European summer drought and heatwave was estimated to be $+270 \pm 140 \text{ TgCyr}^{-1}$ (range -20 and $+500 \text{ TgCyr}^{-1}$, positive numbers indicate carbon sources to the atmosphere) (Ciais et al., 2005; Peters et al., 2010; Reichstein et al., 2007a; Smith et al., in press; van der Werf et al., 2009; Vetter et al., 2008) relative to multi-year average NEE estimates ranging from $-165 \pm 437 \text{ TgCyr}^{-1}$ (Peters et al., 2010) to $-274 \pm 163 \text{ TgCyr}^{-1}$ (Schulze et al., 2009). The short-term effects of the 2003 European drought thus appear large for the continental carbon balance, even though there remains discussion on whether the effect was due to the simultaneously occurring heat and moisture stress.

It is important to note that these NEE anomaly estimates result from top to down observation methods (e.g. eddy covariance, inverse modeling, satellite-derived remote sensing) and dynamic vegetation models (DVM's), none of which account for any species or soil specific response. Instead, they describe the response of the ‘average’ ecosystem to drought. Ecosystems, however, may be composed of species with contrasting short-term responses to drought (Breshears et al., 2009), implying that some species are more affected than average, and some less. This introduces species-specific non-linearities into the ecosystem response, which become even more apparent when considering carry-over effects.

3. Carry-over effects of drought

‘Carry-over effects’ of drought on ecosystems refer to ecological processes concerning forms of soil and plant ‘memory’, such as the fill level of storage reservoirs. Through such reservoirs, droughts still affect ecosystem carbon dynamics after the initial response of GPP and TER has ended. Carry-over effects can occur when the response time of the reservoir is longer than the duration of the drought. The response time of the carry-over effect typically corresponds to the mean turnover time of the reservoir, i.e. the ratio of reservoir size and refreshment rate. We examine carry-over effects in the reservoirs of soil moisture, nutrients in litter and soil organic matter, carbohydrate reserves in the plants, and fuel for fires (Fig. 1, middle). Because the turnover times of the relevant reservoirs vary, processes such as GPP, TER and evapotranspiration – which depend on multiple reservoirs – may yield chaotic responses, and in the longer-term may even cause the system to have multiple equilibrium states (Allen et al., 2010; Schimel et al., 2005).

Recovery of depleted soil moisture after the drought, e.g. during the next wet season, largely determines the carry-over effects of drought on the vegetation. In this perspective, a carry-over effect occurs when soil moisture was incompletely replenished in the season before or after the drought. Depletion of soil moisture storage may affect plant available water and non-structural carbohydrates, as well as soil organic matter decomposition and nitrogen mineralisation (Arnone et al., 2008). The frequency of droughts, the soil characteristics and the variability of precipitation intensity and frequency affect the soil moisture replenishment as well as leakage and run-off (Knapp et al., 2008). Carry-over effects of incomplete soil moisture replenishment have been shown to last up to 2 years, and increase the direct NEE anomaly by 40% (Arnone et al., 2008; Schimel et al., 2005).

During droughts reduced decomposition rates and initially increased litterfall (Brando et al., 2008) may cause an abnormal accumulation of soil organic matter (SOM). During prolonged drought litterfall may eventually decline due to the reduced GPP. When, after the drought conditions for microbial activity become more favorable, the accumulated SOM may cause a pulse in SOM decomposition (Law, 2005; Ryan and Law, 2005). There are indications that the species distribution in ecosystems influences litter quality, the composition of soil biota and the turnover of SOM (Wardle et al., 2004). The nitrogen mineralisation associated with lagging decomposition will favour plant growth after the drought (Schimel et al., 2005; Sokolov et al., 2008; Tilman et al., 2000). The response time of SOM appears slower (~10 years) than for mineral nitrogen (~2 years), because the latter is associated with faster processes such as nutrient uptake and leaching (Schimel et al., 2005).

The direct effect of reduced GPP during drought has a carry-over effect on carbohydrate reserves, which has important implications for the resilience of plants (McDowell and Sevanto, 2010; Sala et al., 2010). Insufficient carbohydrate reserves will limit full leaf area production and growth the years following the drought (Breda et al., 2006). Such delayed effects may explain small tree ring width during several years following a severe drought as evidenced by dendrochronological studies (Drobyshev et al., 2007a). The carbohydrate reserves in leaves may change more slowly in evergreen than in deciduous species, because of the longer retention time of evergreen leaves (Schimel et al., 2005), although evergreens tend to shed more leaves in response to drought, or needles do not fully extend that year.

Depleted carbohydrate reserves and reduced carbon allocation to defense compounds can progressively reduce the plant resilience to new disturbances such as attacks of insects or pathogens, frost or another drought (Allen et al., 2010; Lloret et al., 2005; Waring, 1987; Waring and Pitman, 1985). A possible mechanistic pathway to explain drought impact on plant resilience is the emissions of specific gasses by drought-affected trees which may inadvertently alert insects to their increased vulnerability (McDowell et al., 2008; Staudt and Lhoutellier, 2007). The attracted insects may inoculate the vulnerable trees with diseases (Ayres and Lombardero, 2000; McDowell et al., 2008). Such insect attacks may last several years and have a large impact on the carbon balance at the decadal time scale (Clark et al., 2009; Kurz et al., 2008).

Drought-affected ecosystems have a higher risk of fires, because dry wood and litter burn more easily (Aragao et al., 2007; van der Werf et al., 2008), and litter accumulates during the drought. Carry-over effects such as defoliation after insect attacks and diseases induced by drought also carry over the risk of wildfires to subsequent years. Thus disturbances are not mutually independent, and droughts may invoke favorable conditions for other disturbances such as insects, diseases, fire and wind throw (Meigs et al., 2009). Plants living on the fringes of their geographic distribution where climate is favorable for growth (i.e. in ecotones) may be more vulnerable to direct and carry-over effects of drought (Allen et al.,

2010). Depletion of one or more of these carry-over reservoirs may eventually lead to mortality (Drobyshev et al., 2007b; McDowell et al., 2008).

4. Drought-induced vegetation mortality

Drought-induced mortality may affect the carbon budget of ecosystems very strongly (Fig. 1, middle to right) (Delbart et al., 2010; McDowell et al., 2010). Despite its key role in determining the medium-term carbon budget, understanding of how droughts kill trees is surprisingly limited (Adams et al., 2009; McDowell and Sevanto, 2010; Phillips et al., 2009; Sala et al., 2010; van Mantgem et al., 2009). The representation in current vegetation models tends to be very crude, with assumed constant mortality rates (Allen et al., 2010), unless climate-induced disturbances are explicitly accounted for. Mortality may be considered as the result of excessive depletion of the reservoirs of plant available water, nutrients, carbohydrate reserves and resilience. A useful framework to address this gap in understanding on the causes of tree mortality has been formulated in the recent literature by three hypotheses (Breda et al., 2006; McDowell et al., 2008; Tardieu and Simonneau, 1998): hydraulic failure due to cavitation, carbon starvation, and interaction with mycorrhizae. With these hypotheses we focus on mortality due to water or carbohydrate limitation, as the most direct consequences of drought, and not on other potential causes, such as wind throw.

Hydraulic failure due to cavitation occurs when the demand for water by the canopy exceeds the supply, and air is aspirated into the xylem, resulting in a large decrease in hydraulic conductivity (Breda et al., 2006; McDowell et al., 2008). During severe droughts cavitation may increase to the point of hydraulic failure, resulting in desiccation and death. There is evidence that cavitation is more likely in anisohydric species (Maherali et al., 2006), which exert little or no stomatal control to prevent water loss, thus sustaining photosynthesis during drought. This implies a trade-off between fast growth and the risk of cavitation. Young trees are more vulnerable to cavitation, because they have less water storage in their stems, they are exposed to more extreme micro-climates and because their root system is less developed (Beedlow et al., 2007; Schwarz et al., 2004; Wharton et al., 2009).

Carbon starvation has been hypothesized to occur when photosynthesis is strongly reduced, and autotrophic respiration exceeds the rate of photosynthesis over an extended period of time, so that the plant runs out of carbohydrate reserves and is no longer capable of maintaining a basic metabolism. Whether carbon starvation-mediated mortality actually occurs, and thus the precise mechanisms causing it, particularly the role of inhibition of carbohydrate transport under water stress, are currently debated (McDowell and Sevanto, 2010; Sala et al., 2010). Clearly the plants' strategy for building water and carbohydrate reserves has consequences for the risk of carbon starvation. Carbon starvation is theoretically more likely in isohydric plants, which exert strong stomatal control to prevent water loss at the cost of substantial declines in photosynthesis.

The presence of mycorrhizal communities (fungi which live in symbiosis with roots) may reduce drought-induced mortality for trees. The symbiosis of trees and mycorrhizae (roots supply labile carbohydrates to the mycorrhizae in exchange for improved water and nutrient uptake) is particularly beneficial for the trees under drought conditions (Egerton-Warburton et al., 2007; Querejeta et al., 2007). There are indications that larger mycorrhizal communities facilitate increased drought survival rates of trees, because of the enhanced capacity to take up water and nutrients (Allen, 2007; Wardle et al., 2004), and the consequent ability to ward off diseases (Swaty et al., 2004). Indications that drought impacts the

mycorrhizal communities are mixed (Gehring and Whitham, 1995; Nilsen et al., 1998; Querejeta et al., 2007; Runion et al., 1997; Swaty et al., 1998). Research on the relation of mycorrhizae and roots is still largely focused on the molecular level, while the precise role of mycorrhizae in plant water uptake during drought still remains unexplored.

Irrespective of the mechanisms of mortality, in two long-term precipitation throughfall exclusion experiment in East Amazonia the tree mortality rate was observed to increase by as much as 2–5 times (from ca. 1% yr⁻¹ to 2–5% yr⁻¹) (Brando et al., 2008; da Costa et al., 2010; Nepstad et al., 2007; Phillips et al., 2009), while increases in mortality were also observed across the Amazon basin during the 2005 natural drought (Phillips et al., 2010). During this marked Amazonian drought in 2005, an estimated 1.2–1.6 PgC of dead biomass was created by increased mortality (Phillips et al., 2009). These reports provide congruent evidence from both experimental and observational studies that drought can cause a large disruption of within-ecosystem carbon fluxes (Meir and Woodward, 2010). But the implications of a pulse of dead biomass production for the long-term net C exchange remain uncertain. After tree death, stemwood decomposition can occur over decades (Baker et al., 2007), which implies long-term carry-over effects (Kurz et al., 2008). It is unclear how much of the decomposed carbon is released to the atmosphere and at what rate, and how much returns to the soil where it would decompose more slowly depending on the stability of the carbon stock (Trumbore and Czimczik, 2008). It is also unknown whether mortality due to drought is superimposed on the normal mortality rate, or whether drought kills trees that were already marginal so that the drought merely changes the time of death, resulting in lower mortality rates in the years after the drought, although there is recent evidence suggesting that drought mortality is additional to normal mortality rates (Phillips et al., 2010). In addition, increased mortality may lead to enhanced carbon uptake in consecutive years by 'pioneer' species, partly offsetting the committed carbon loss.

5. Species competition and drought

Droughts, carry-over effects, and particularly mortality are expected to alter species competition (Fig. 1, right). As discussed above, there are various species-specific strategies for coping with drought, with advantages for drought resilient species. Changes in the species and age composition of ecosystems are relevant for the actual carbon content, the maximum carbon content at maturity, as well as the carbon residence time. The success rate of a particular species strategy depends on the duration and severity of the drought, e.g. the isohydric strategy may be more advantageous for short and severe droughts, whereas the anisohydric strategy may be more successful for long droughts. For instance during the 2003 drought in western Europe, beech and (surprisingly) broadleaved Mediterranean trees appeared to be more sensitive to drought than conifers (Granier et al., 2007). In the case of tropical rainforest, a 7-year partial rainfall exclusion experiment in eastern Amazonia demonstrated very clear taxonomic differences in vulnerability to drought-induced mortality, showing, for example that species from the X genus tend to be more vulnerable than those from Y (da Costa et al., 2010). Further, but more generally, droughts may favour invasive species if they are more drought tolerant than the endemic species, or 'reset' the ecosystem, by wiping out the ecosystem history and forcing new succession. However, existing knowledge is largely very limited to individual species at the site level (Adams et al., 2009; Breshears et al., 2009; da Costa et al., 2010; McDowell et al., 2008; Narasimhan and Srinivasan, 2005). Based upon the observed long-term coexistence of species with contrasting short-term drought survival strategies we spec-

ulate that unsuccessful short-term strategies are compensated by advantages in other strategies, e.g. successful regeneration or fast growth. A framework for species competition in vegetation models accounting for species strategies is unfortunately lacking at present.

6. Discussion and conclusions

6.1. State of the art and emerging gaps

Our level of understanding of drought impacts on the carbon cycle has improved spectacularly over the last decade for the period during a drought, but large uncertainties still remain for the months to years after a drought (Fig. 1). The factors responsible for the difference are primarily the measurability of long-term effects, and the level of integration of available ecological observations from long-term monitoring sites or manipulative experiments into vegetation models. The effects of short-term processes impacting on GPP, TER, evapotranspiration and stomatal control are relatively easily observable with ecophysiological measurement techniques and eddy covariance. A large 'climate-space' spanning observation network of more than 250 sites (FLUXNET (Baldocchi et al., 2001)) exists, with an ever increasing length of observation period. The resulting data and process understanding from this wealth of new information is not yet fully used in DVM's and diagnostic models but model parameterizations could be upgraded within a few years, thanks to new model-data fusion and parameter inversion techniques (Fox et al., 2009).

By contrast, many of the longer-term processes, or their effects, such as mortality, insect attacks, and nutrient recycling, suffer from a lack of (planned) observations. Current understanding is based on sparse and scattered in situ data, where complementary measurement approaches are often lacking. The increasing knowledge of mortality benefits from emergent observation networks such as ENFIN (2010) and RAINFOR (2010). The sporadic carbon emissions from fires are a notable exception from the idea that understanding declines with time scale.

We identify the following major gaps between relevant processes, observations and current model formulations (Fig. 1):

- 1) Understanding of the functional relationships between soil organic matter decomposition, temperature, available water, chemical composition, microbial composition, priming and acclimation is not sufficiently far advanced; the relationships between root distribution, root adaptation, soil characteristics and vegetation water uptake are uncertain; the short-term strategies of individual species to cope with drought, and their effects on GPP and TER are not represented in most DVM's.
- 2) Experimental data of carbohydrate and nutrient reservoir dynamics in soil and vegetation and their relationships with plant resilience are scarce; the reservoirs of carbohydrates, and their physiologic importance, are not explicitly described in DVM's.
- 3) The precise mechanisms causing mortality are still debated, and how they vary among species and ecosystems is poorly known; threshold levels of plant available water and carbohydrate reserves leading to cavitation or possible carbon starvation and variation among species are unknown; the fate of carbon in dead biomass is uncertain considering the fractionation and stability of decomposed carbon; it is unknown to what extent the drought-induced mortality rates are superimposed on the normal mortality rates.
- 4) It is largely unknown how species competition and changes in ecosystem composition during and after droughts leads to

changes in actual carbon content, maximal carbon content at ecosystem maturity and ecosystem carbon turnover times.

These gaps have in common that the main mechanistic pathways of drought response (e.g. root adaptation, WUE, carbon allocation, and reproduction strategies) are relatively well characterized at the species level. The understanding emerges that ecosystems are composed of coexisting species with contrasting strategies and that these strategies determine the species' response to drought on short and longer time scales. The net ecosystem response may thus depend on the species composition of the ecosystem, with differences in species performance and tolerance potentially leading to substantial quantitative differences in ecosystem function, for example as shown by Fisher et al. (2010) for NPP. Knowledge about species and their strategies is nevertheless scarce and scattered. Similarly, the main functional relationships between the decomposition rate of SOM and environmental factors are known, but the relationships are often specific for particular combinations of soil type, quality of SOM due to differences in plant species, and climate zones.

We argue that understanding the interactions between drought and the carbon cycle of terrestrial ecosystems may be improved through better observation and modeling of, on the one hand, species and soil specific drought responses and, on the other hand, the net response of ecosystems over longer time periods, to include carry-over effects. To strengthen the first approach, observation techniques for roots, soil moisture, soil carbon content and stability, and plant strategies are urgently needed on species scales to ecosystem scales. To strengthen the second approach, it must be realized that ecosystems are often composed of species with contrasting strategies, so that the net ecosystem response may be the difference between larger opposite species responses.

Knowledge of the ecosystem carbon cycle and interactions with climate is integrated in dynamic vegetation models, with the aim to test hypotheses, understand interrelationships and to forecast future behavior. The next section is focused on what is needed to make DVM's better-suited for describing drought – carbon cycle interactions.

6.2. Plant strategies as the key component

Current state of the art DVM's using plant functional types (PFT's) tend to ignore population-level processes and are primarily structured to go straight from physiology to the grid-cell (Ostle et al., 2009). PFT's were originally designed to deal with the exchange of water, momentum and energy (Pitman and McAvaney, 2002). In more recent years, carbon and vegetation models have extended their area of application, without fundamentally (re)considering whether the current set of PFT's is the most appropriate to deal with the complexity of different response strategies of plant towards their environment.

In this study we argue that a model constructed around PFT's cannot possibly deal with the complexities of ecosystem drought response, particularly contrasting within-ecosystem water use strategies, related mortality, and regeneration. Even without being able estimate their impact on the carbon cycle, each of these processes seems to have a potential for large impact.

Model approaches built around plant strategies, however, may be in a better position to describe the water and carbon cycles in a process-oriented way. With respect to ecosystem carbon content and exchange, we suggest the following interlinked strategies are important:

1) strategy for light and energy use (light absorption, transpiration, photosynthesis);

- 2) strategy for water use efficiency (isohydric/anisohydric stomatal control, CO₂ response);
- 3) strategy for carbon allocation (carbohydrate reserves vs. fast growing);
- 4) strategy for root distribution (deep vs. shallow, growth rate, mycorrhizae);
- 5) strategy for dealing with fire (fire resisters, avoiders, invaders, endurers);
- 6) strategy for regeneration (seed dispersal, migration rates).

In plant strategy oriented models PFT's would be replaced by sets of plant strategical properties (PSP's), expressing the different strategical choices species may take. PSP's have a certain analogy with plant traits (cf. Reich et al., 1997; Wright et al., 2004), but where plant traits often describe physiological relationships at the leaf level, PSP's describe strategies at the species level. In the case of drought we suggest that sets of PSP's will drastically increase the DVM's capability to model the non-linearities associated with the response of the ecosystem carbon cycle to drought. To manage the computational efficiency of PSP oriented models, we need to know how few plant strategies are needed in the model to realistically simulate both the contrasting species response and the average response of ecosystems to drought. Positive results in the field of plant traits and initial attempts to implement species competition in DVM's (Bonan et al., 2002; Fisher et al., 2010; Moorcroft et al., 2001; Reich et al., 1997; Smith et al., 2001; Wright et al., 2004) suggest feasibility of the PSP approach.

The PSP approach may have a potential field of application in evaluating the likelihood of Amazon 'dieback', which has been forecast by various combinations of global climate models and (dynamic) vegetation models (Cook and Vizy, 2008; Cox et al., 2000; Huntingford et al., 2008; Li et al., 2006; Schaphoff et al., 2006) but for which, despite recent advances, there remain uncertainties relating to plant response as well as future climate (Galbraith et al., 2010; Meir and Woodward, 2010). Summarized, Amazon dieback has been predicted by some models as a result of a reduction in the recycling of moisture advected into South America coupled with substantially increased temperature. The reduction in recycling is modeled to be due to radiative forcing (global warming due to radiative forcing of enhanced CO₂ concentration causes a reduction in cloud cover and precipitation) and/or physiological forcing (enhanced CO₂ concentration leads to reduced stomatal conductance, and hence lower transpiration rates (Betts et al., 2007, 2004; Cox et al., 2004; White et al., 1999)). The model studies have in common that they use PFT's to represent vegetation, often not more than five different ones. These PFT's describe the average response of ecosystems to drought. Our study makes the point that the average ecosystem is composed of species with contrasting water use strategies and probably other linked physiological responses. Depending on the severity and duration of the drought, particular species may have higher or lower mortality responses (da Costa et al., 2010; Phillips et al., 2010) and we can also expect differences in physiological temperature optima and water acquisition strategies that may determine these mortality responses (Galbraith et al., 2010). Thus the limited evidence recently emerging is consistent with a logic suggesting that drought will cause shifts in ecosystem composition in favour of more drought tolerant species. PFT-oriented models can only make large shifts to completely different types of ecosystems (Kleidon et al., 2007). As a result, the 'average' Amazonian ecosystem represented by a PFT-based framework may be less drought resistant than a 'diverse' ecosystem composed of species with diverging water use strategies.

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