Assessing drought-driven mortality trees with physiological process-based models

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ABSTRACT

(1) This study describes how physiological process-based models can be used to assess the mortality risk of forest trees under global change. (2) Using the CASTANEA model, we simulated the development over time of tree functioning with different ontogenetic and phenotypic characteristics (age, diameter, Leaf Area Index, leaf traits) and growing in different site conditions (elevation, soil water content). Based on this set of simulations, we determined the carbon and hydraulic physiological thresholds associated with tree mortality that best reproduce the observed mortality rate. (3) We tested this methodology on a long-lasting and patchy drought-induced mortality event of silver fir (*Abies alba* Mill.) in South-Eastern France. (4) We found that tree mortality was not caused by a massive summer xylem embolism, but rather by depletion in carbon reserves probably associated with bark beetle attacks. Simulation outputs also revealed that trees with high diameter and Leaf Area Index and growing on shallower soils were more prone to die. (5) This study highlighted that physiological process-based models can be of high interest to determine the factors predisposing and inducing tree death.

1. Introduction

The anthropogenic influence on the earth's climate will be substantial by end of this century (Vitousek et al., 1997). The extreme scenario predicts up to a six degrees increase in southern Europe during the summer months combined with a 25% decrease in precipitation (IPCC, 2014). Such scenario would correspond to an upward shift of climatic niches of almost 1000 m along elevation gradients and would strongly affect tree species vegetation belts (Randin et al., 2009). In fact, many of the trees alive today will probably experience drought and temperature levels outside the range to which they are adapted (Allen et al., 2015). Trees are keystone species in many terrestrial ecosystems, and the legacy of tree mortality on forest dynamics, structure and functions can persist for a long time (e.g., Goetz et al., 2012). Consequently, it is important to correctly understand the ecological mechanisms leading to tree mortality and project the future mortality risk under climate change (e.g., Breshears et al., 2005; Adams et al., 2009; Trumbore et al., 2015).

Although a variety of stress and disturbances may predispose and trigger tree mortality (e.g., shading, wind-throws, wildfires, pests, frosts, or floodings), drought-induced mortality represents one major cause of the recent widespread increases in number of tree mortality events (Allen et al., 2010; Allen et al., 2015; Hartmann, 2015). Mortality caused by drought is also expected to increase in the future due to the projected rise in temperature and decrease in precipitation in certain regions (IPCC, 2014; Allen et al., 2015; Anderegg et al., 2012). As drought can occur at various spatial and temporal (i.e., duration and frequency) scales with different severities, and interact with many other mortality agents, it is important to better understand the complexity of the drought-induced mortality process. Moreover, drought increases the vulnerability of forest stands to fire (Westerling et al., 2006; Brando et al., 2014) and reduces the resistance of trees to pest attacks, especially from bark beetles (Netherer et al., 2015). Despite the recent wealth of ecophysiological research on this process (e.g., McDowell et al., 2011), the physiological mechanisms leading to tree mortality, when drought increases in intensity and duration, i.e. carbon starvation or hydraulic failure, are still under debate (e.g., Hartmann, 2015). A decrease in soil water content and/or an increase in air vapour pressure deficit increase the tension in the soil-to-leaf water continuum, that potentially leads to xylem embolism (i.e., the formation of vapour cavities in the xylem caus-

ing water column breakage; Tyree and Ewers, 1991). Trees can prevent this functional damage by closing their stomata in the early stages of drought to limit water losses (Tyree and Sperry, 1988), but to the detriment of carbon uptake. For these reasons, during a long-lasting drought, these trees face a sort of cornelian dilemma to die either by xylem embolism and/or by carbon starvation (McDowell et al., 2008).

On one hand, the risk of xylem embolism might be important for many tree species as the hydraulic safety margin, i.e., the difference between minimal leaf water potential and xylem potential leading to cavitation, is low for many species across biomes (Choat et al., 2012). However, embolism leads to tree death only when xylem conductivity loss is above 80–90% for angiosperms (Urli et al., 2013) and 50% for gymnosperms (Brodribb and Cochard, 2009). These values are quite high because trees can recover their conductivity thanks to their potential capacity to refill embolized xylem conduits (mainly for angiosperms; Choat et al., 2012), and by building new xylem tissues through primary and secondary growth (Brodribb et al., 2010).

On the other hand, the carbon starvation hypothesis is above all a theoretical consideration coming from the acquired knowledge of plant functioning (Hartmann, 2015). During a drought event, plants stop their growth before closing their stomata that paradoxically increases carbon storage and non-structural carbohydrate (NSC) concentration (Sevanto et al., 2014). Then, the reduction in Gross Primary Production (carbon uptake) due to stomata closure is stronger than the decrease in respiration and becomes not sufficient to fulfil carbon requirements for respiration, defences and reproduction leading to a decline in NSC content (McDowell et al., 2008; Sala et al., 2010). But the rhythm of these declines depends on the overall carbon economy of the plant, and the hypothetical threshold of NSC below which death occurs remains difficult to determine (McDowell et al., 2013). Indeed, plants can acclimatize their carbon economy to recurrent droughts through many mechanisms by reducing the respiratory costs or increasing the water use efficiency, e.g., via a decrease in leaf area, an increase in the thickness of leaves, or an increase in root growth (Martin-StPaul et al., 2013). In addition, the presence of pests can modify carbon allocation within a tree and often induces tree death before it reaches a threshold below which no NSC can be mobilised anymore (Herms and Mattson, 1992). For all these reasons, observations and experiments have often failed to confirm the role of carbon starvation, when observing on-going diebacks (Gruber et al., 2012; Hartmann 2015). It is unlikely that we could discover a universal NSC threshold value that could be applied across species and across a variety of ecological situations that would mimic the thresholds obtained on the percentage of conductivity loss. However, it may be possible to approximate such a NSC threshold in specific case studies, for instance through the use of physiological process-based models (e.g., McDowell et al., 2013).

model CASTANEA on a silver fir (*Abies alba* Mill.) drought-induced mortality event that occurred on Mont Ventoux, south-eastern France (Cailleret et al., 2013).

2. Materiel and methods

2.1. CASTANEA model

CASTANEA is a generic process-based model used to simulate carbon and water fluxes and tree growth in forest ecosystems (Dufrêne et al., 2005). The canopy is divided into five layers of leaves, while branches, stem, coarse and fine roots, and NSC compartments compose the rest of the tree. Photosynthesis is hourly estimated for each canopy layer using the Farquhar et al. (1980) model analytically coupled to the stomatal conductance model proposed by Ball et al. (1987) that linearly relate stomata conductance to the product of photosynthesis and relative humidity. Maintenance and growth respiration are respectively estimated proportional to the nitrogen content of the considered organs (Ryan, 1991) and from growth increment combined with a construction cost specific to the type of tissue (De Vries et al., 1974). Transpiration is also hourly calculated using the Monteith (1965) equations. The dynamics of soil water content (WC; in mm) is estimated daily using a three-layers bucket model. Soil drought drives stomata closure via a linear decrease in the Ball et al. (1987) slope, when relative soil water content is under 40% of field capacity (Sala and Tenhunen, 1996; Granier et al., 2000). More details are available in Dufrêne et al. (2005).

The model was originally developed and validated from organ to stand scales for *Fagus sylvatica* L. (Davi et al., 2005), but was also successfully applied to *Pinus sylvestris* L., *Pinus pinaster* Aiton, *Quercus ilex* L., *Quercus robur* L and *Picea abies* Karst (Davi et al., 2006b; Delpierre et al., 2012). For this study, CASTANEA was parameterized for *Abies alba* Mill. using data from the literature and *in situ* measurements (Table 1 and Table s1). We used the leaf phenology module developed for *Picea abies* Karst (Delpierre et al., 2012), while the phenology of wood growth was simulated with the same forcing model than for leaves, but with distinct parameters ($F_{critWood}$ Stop in Table 1).

Soil water potential (Ψ_{soil} in MPa) was calculated from daily soil water content (Campbell, 1974), and leaf water potential (Ψ_{leaf}) was estimated hourly from simulated transpiration (TR in mmol m^{-2} leaf s^{-1}) using one resistance ($R_{soil-leaf}$ in MPa.m^{-2} s^{-1} kg^{-1}) and one capacitance (Cap$_{soil-leaf}$ in kg m^{-2} Mpa^{-1}) along the soil-to-leaves hydraulic pathway following the model used in Loustau et al. (1998; see eq. 1). The resistance ($R_{soil-leaf}$) was assessed using sapflow measurements and midday and predawn water potentials measured in 2009 in Ventoux.

$$\Psi_{leaf}(t+1) = \Psi_{soil}(t+1) - \frac{TR}{3600} \times R_{soil-leaf} + \left(\begin{array}{c} \Psi_{leaf}(t) \\ -\Psi_{soil}(t+1) + TR \times R_{soil-leaf} \end{array} \right) \times \exp\left(\frac{3600}{R_{soil-leaf} \times Cap_{soil-leaf}} \right) \qquad (1)$$

The objectives of the present paper were to show how physiological process-based models (PBMs) that explicitly simulate water and carbon pools and fluxes in trees can help (1) to determine which process (i.e., carbon starvation or hydraulic failure) is the most involved in a given drought-induced mortality event, (2) to estimate physiological thresholds using an inverse modelling approach by comparing simulated and observed mortality rates in different environmental and biotic conditions, and (3) to hierarchize the environmental and ontogenic processes that predispose tree to death. We tested this overall approach with the process-based

In the carbon allocation sub-model (Davi et al., 2009), the allocation coefficients between compartments were estimated daily depending on the sink force and the phenology constraints. During winter, carbon was only distributed to reserves and fine roots. After the initiation of budburst, carbon was first used for the development of leaves and fine roots, and then for wood growth (stem and coarse roots). The fine roots sink was calculated in order to sustain a constant ratio between fine roots and leaves, while the leaf sink was forced by phenology. Considering that tissue formation is one of the first physiological processes inhibited by drought (Körner, 2015), we also added a direct effect of Ψ_{soil} on wood growth that