



Forward modeling of tree-ring width improves simulation of forest growth responses to drought



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ABSTRACT

Drought is a key factor affecting forest ecosystem processes at different spatio-temporal scales. For accurately modeling tree functioning – and thus for producing reliable simulations of forest dynamics – the consideration of the variability in the timing and extent of drought effects on tree growth is essential, particularly in strongly seasonal climates such as in the Mediterranean area. Yet, most dynamic vegetation models (DVMs) do not include this intra-annual variability of drought effects on tree growth. We present a novel approach for linking tree-ring data to drought simulations in DVMs. A modified forward model of tree-ring width (VS-Lite) was used to estimate seasonal- and site-specific growth responses to drought of Scots pine (*Pinus sylvestris* L.), which were subsequently implemented in the DVM ForClim. Ring-width data from sixteen sites along a moisture gradient from Central Spain to the Swiss Alps, including the dry inner Alpine valleys, were used to calibrate the forward ring-width model, and inventory data from managed Scots pine stands were used to evaluate ForClim performance. The modified VS-Lite accurately estimated the year-to-year variability in ring-width indices and produced realistic intra-annual growth responses to soil drought, showing a stronger relationship between growth and drought in spring than in the other seasons and thus capturing the strategy of Scots pine to cope with drought. The ForClim version including seasonal variability in growth responses to drought showed improved predictions of stand basal area and stem number, indicating the need to consider intra-annual differences in climate–growth relationships in DVMs when simulating forest dynamics. Forward modeling of ring-width growth may be a powerful tool to calibrate growth functions in DVMs that aim to simulate forest properties in across multiple environments at large spatial scales.

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1. Introduction

Drought is one of the main drivers of forest dynamics. It impacts a variety of plant physiological processes (Ryan, 2011) and modifies the structure, functioning and vitality of individual trees at both the short and the long term (Breda et al., 2006). The carbon budget of trees is highly sensitive to drought via stomatal closure which impacts photosynthesis, but also via limitations on secondary growth (i.e., wood formation; McDowell et al., 2010; Müller et al., 2011; Palacio et al., 2014). Intense drought may also induce xylem embolism, changes in carbon allocation, and an increased risk from abiotic and biotic disturbance agents (e.g., fungal pathogens, insects, frost events; cf. Camarero et al., 2015; Sangüesa-Barreda et al., 2015). Moreover, drought can induce changes in tree regeneration rates, and mortality of individual trees in case of extreme and/or recurring events (McDowell et al., 2008).

Although the global drought has shown little change during the last decades (Sheffield et al., 2012), many regions have experienced increases in drought intensity and frequency with negative consequences on forest ecosystems (Allen et al., 2010; Anderegg et al., 2013; Bigler et al., 2006). Frequency and intensity of drought events are expected to continue intensifying in the future (Cook et al., 2014; Dai, 2013), and hence there is a strong need for better understanding tree responses to drought (Allen et al., 2015).

Xylem growth is among the main and first processes impacted by drought (see Palacio et al., 2014) and it can be reduced for several years after a severe drought event (i.e., legacy effects; cf. Anderegg et al., 2015). First, xylogenesis requires certain ranges of temperatures and soil moisture to allow for cell division (Mooney and Dunn, 1970), and it stops when water potential is too low. As a consequence, a bimodal growth pattern is observed for several species growing under continental Mediterranean climates (Camarero et al., 2010; Gutierrez et al., 2011; Primicia et al., 2013), experiencing double winter–summer stress (Mitrakos, 1980). Second, xylem growth is indirectly affected by drought through the reduction in photosynthetic rates caused by stomatal closure,

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reducing the amount of carbohydrates available for building new cells (Palacio et al., 2014; Zweifel et al., 2006). The intra-annual variation of cambial and photosynthetic activity depends strongly on the species, which have evolved to use different strategies for facing drought (Lévesque et al., 2014; Zweifel et al., 2009). For example, isohydric species are able to maintain high mid-day leaf water potential by reducing their crown-level stomatal conductance with the decrease in soil water availability (McDowell et al., 2008). Contrarily, anisohydric species tend to keep their stomata open during drought to maximize carbon assimilation which leads to more negative leaf water potentials (Tardieu and Simonneau, 1998). Moreover, the intra-specific differences in growth responses to dry conditions observed between provenances and populations (Herrero et al., 2013; Martín et al., 2010; Sánchez-Salguero et al., 2015) demonstrate the importance of site-specific adaptations to drought.

This intra-annual variability in growth response to drought is partially considered in some process-based dynamic vegetation models (DVMs) that simulate physiological mechanisms on an hourly or daily basis (Fontes et al., 2010). In most ‘mechanistic’ DVMs, however, the impact of drought on plant growth is not captured accurately because growth is assumed to be exclusively source-driven (i.e., simulated growth is limited only by carbon assimilation; cf. Fatichi et al., 2014; but see Davi et al., 2009; Schiestl-Aalto et al., 2015). In another class of DVMs, such as forest succession models (also called ‘patch’ or ‘gap’ models, cf. Bugmann, 2001), sink limitation is assumed to be the main process driving growth (Leuzinger et al., 2013), and water stress limitation is captured through an annual drought index calculated as an average over the growing season that reduces growth rates (Bugmann and Cramer, 1998; Pausas, 1999). In contrast to global DVMs, which typically are based on plant functional types rather than species (De Kauwe et al., 2015), forest succession models account for the inter-specific sensitivity to drought using species-specific parameters as a threshold of maximum drought tolerance. Nevertheless, they do not consider local adaptation to drought (i.e., intra-specific and intra-annual variability) and still are prone to considerable uncertainties regarding the drought tolerance parameters (e.g., Gutiérrez et al., 2016; Weber et al., 2008). In addition, the intra-annual growth pattern related to drought is not taken into account because in most models every month within the growing season has the same influence on the calculation of the annual drought index (Bugmann and Cramer, 1998).

In the studies that focused on improving and applying succession models in Mediterranean-type ecosystems, drought effects were modeled by increasing the temporal resolution of the water balance submodel to a daily time step (Fyllas and Troumbis, 2009; Pausas, 1998). This modification imposed limitations to the general applicability of the models, particularly due to constraints on deriving accurate local daily time series data of weather variables (in contrast to widely available monthly time-series). Thus, there is scope for improving the modeling of drought impacts on tree growth in forest succession models without a strong increase in model complexity. In addition, reliable forest models incorporating data related to species- and site-specific growth responses are essential for forecasting the effect of climate change on species composition, and for improving management and conservation practices (Fontes et al., 2010; Sánchez-Salguero et al., 2015).

Simulating the effects of drought more mechanistically remains a challenge, regardless of the type of model considered (e.g., Gustafson et al., 2015). In the case of forest succession models, it requires the determination of robust growth functions by means of high temporal and spatial (i.e., on different individuals/populations) resolution measurements of growth and climate for a long time period, followed by skillful model simplification to make the approach tractable in long-term simulations.

Tree-rings are a potentially powerful source of data, as they allow for the investigation of a large amount of samples with an individual and annual resolution. While ring-width data are often used to evaluate the performance of forest models (Li et al., 2014), they have been rather neglected in the calibration phase or for deriving new functions (but see Gea-Izquierdo et al., 2015; Guiot et al., 2014). Tree-rings have been used to derive empirical growth–mortality functions and to calibrate growth response to temperature in DVMs (Bircher et al., 2015; Rickebusch et al., 2007). However, ring-width data have never been employed for improving processes at the intra-annual scale in DVMs.

In the present study, we explore a novel approach to improve the simulation of drought effects on tree radial growth in a forest succession model while maintaining its structural simplicity. We define drought as insufficient soil water availability for tree growth, soil moisture being dependent on soil properties, precipitation and actual evapotranspiration. Specifically, we incorporate a forward modeling approach of tree-ring width, the Vaganov–Shashkin Lite model (VS-Lite, cf. Tolwinski-Ward et al., 2011) in the forest succession model ForClim (Bugmann, 1996) to determine seasonal growth responses to drought for Scots pine (*Pinus sylvestris* L.) in sixteen sites that cover most of the environmental conditions of the species in Europe. Scots pine is a keystone species in many forest ecosystems and has a high importance in terms of forest economics, habitat conservation and biodiversity (Matias and Jump, 2012). Being the most widespread conifer globally (Nikolov and Helmisaari, 1992), its geographical distribution extends from the northern boreal regions, where growth is limited by growing-season low temperatures, to the southern continental Mediterranean forests, where a combination of summer drought and high temperature is the main limiting factor (Matias and Jump, 2012). We (1) describe a methodology to consider the intra-annual variation in growth response to drought in forest succession models, and (2) investigate if intra-annual and site-specific growth strategies should be included in models that aim to forecast forest dynamics at large spatial scales.

2. Materials and methods

2.1. Calibration of the growth responses to drought

2.1.1. Study sites

We re-analyzed published tree-ring width datasets from 16 sites in different European biogeographical regions: the Iberian Central System, the Iberian Mountains, the northern, central and southern Alps, the Swiss Plateau, and the Jura Mountains (Fig. 1). Distributed across Switzerland, Spain, and northern Italy, these sites covered a wide climatic gradient in terms of temperature and precipitation (Table 1). The three Iberian sites were characterized by relatively high annual precipitation but dryer summer periods compared to the sites in the inner Alpine valleys (Fig. 1).

2.1.2. Ring-width datasets

For nine sites, ring-width data were obtained from Lévesque et al. (2014) and Martín-Benito et al. (2013) (see these two publications for details of the sampling methods) while data for the remaining seven sites were downloaded from the International Tree-Ring Data Bank (ITRDB, <http://www.ncdc.noaa.gov/paleo/treering.html>; last accessed on 11/08/2015; Table 1). Each dataset included between 15 and 48 trees. For each site we built a ring-width index chronology from individual raw ring-width series. First, individual series were detrended to remove non-climatic low-frequency variability (most likely due to tree aging and stand dynamics) using a spline function with a 50% variance cut-off equal to two-thirds of the series length, using the package *dplR*

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