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Time variable hydraulic parameters improve the performance of a mechanistic stand transpiration model. A case study of Mediterranean Scots pine sap flow data assimilation

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ABSTRACT

Tree transpiration is regulated by short-term physiological adjustments and long-term shifts in hydraulic architecture in response to fluctuating evaporative demand and water supply. Despite the tight interdependence of plant water loss and carbon uptake and its crucial implications for plant growth and survival under drought conditions, the underlying mechanisms remain incompletely represented in most state-of-the-art mechanistic models. Important process information is resolved in tree transpiration (sap flow) data, which are the measurable outcome of water transport through the soil-plant-atmosphere continuum under variable environmental conditions. Here, we assimilated sap flow data measured in two Scots pine stands from climatically contrasting sites – one of which experiencing a strong drought during the study period – in NE Spain into a process-based ecophysiological model (SPA) using the Ensemble Kalman Filter (EnKF) in order to: (1) distinguish differences in hydraulic characteristics between sites and between healthy and defoliated individuals within a site; (2) identify possible structural model deficiencies, particularly regarding temporal changes in plant hydraulic conductance which the model assumes constant; and (3) derive implications for gross photosynthesis and carbon cycling. In terms of stomatal control, the assimilation of sap flow data into SPA showed a more conservative water use under dry conditions. Time-varying plant conductivity substantially improved model performance under severe drought, while seasonally varying capacitance and stomatal efficiency only resulted in marginal improvements. Not accounting for this seasonal variability would translate into a 30–60% overestimation of modelled GPP during drought. Our results suggest that an explicit representation of mechanisms leading to temporal changes in hydraulic conductivity (i.e., xylem embolism) is required for models to reproduce tree functioning under extreme drought.

1. Introduction

In order to model the water and carbon balance of a forest ecosystem and predict its response to environmental changes, tree transpiration needs to be simulated as a function of ambient conditions (van der Molen et al., 2011). On a global scale, plant transpiration considerably influences climate through the release of latent heat and water vapour (Alton et al., 2009; Bodin et al., 2013). Transpiration is embedded within and controlled by a soil-plant-atmosphere continuum, which can be conceptualized as a series of hydraulic resistances. The flow of water between any two locations of this system is proportional to the hydraulic conductivity and the water potential gradient linking them (Tyree and Zimmermann, 2002). For some tree species, reductions in soil hydraulic conductivity are sufficient to explain transpiration decline during drought (Duursma et al., 2008; Fisher et al., 2007). However, the different components of the plant hydraulic system

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can also change during drought as a result of varying stomatal conductance, xylem embolism, and the regulation of leaf and root area (Chaves et al., 2003; Maseda and Fernández, 2006). Moreover, plants adopt various strategies to cope with short- and long-term effects of drought conditions, and can be broadly categorized along a continuum from drought avoiders (isohydric behaviour) to drought tolerators (anisohydric behaviour, Tardieu and Simonneau, 1998).

During the last decade, the understanding of mechanisms affecting water and carbon cycling during drought improved considerably. However, predictions of post-drought behaviour for months and years to follow are still highly uncertain (van der Molen et al., 2011) and large uncertainties remain in the understanding and modelling of species-specific responses to drought, including drought-induced mortality (McDowell et al., 2013). Important knowledge gaps exist, for instance, on the interactions between leaf microclimate, leaf water potential, and stomatal regulation of transpiration (Meinzer et al., 2009; Misson et al., 2004), on the role of light intensity (Pieruschka et al., 2010) and quality (Sellin et al., 2011), or on the mechanisms behind the seasonal variation of key hydraulic traits (Franks et al., 2007; Martínez-Vilalta et al., 2007).

These unknown processes are not represented within state-of-the-art ecosystem transpiration models. Consequently, missing mechanisms are partly compensated for when model parameters are calibrated using observational constraints (i.e., model structural deficiencies are "absorbed" by parameter calibration). Even though such a calibrated model might be able to reliably reproduce the measured data, the true causes of model-data discrepancy have not been addressed, limiting the predictive ability of the model. Today, a wealth of temporally highly resolved tree sap flow data is being collected and readily available. These data are of particular interest to modellers, as they bear the potential for extraction of information on important hydraulic mechanisms which current models fail to simulate.

Data assimilation (DA) methodology, applying the Ensemble Kalman Filter (EnKF) among others, has shown to be a useful technique for model state and/or parameter estimation in various disciplines of the geosciences. Early efforts were made in the fields of hydrology, oceanography, or meteorology (see review in Evensen (2009)). More recently, eddy covariance (EC) flux data were used to constrain ecosystem carbon (C) mass balance models using diverse DA techniques (e.g. Chen et al., 2008; Mo et al., 2008; Reichstein et al., 2003; Richardson et al., 2010; Sus et al., 2013; Williams et al., 2005; Wu et al., 2012). Posterior (i.e. after DA) temporal parameter variability within some of these carbon models was interpreted either as ecosystem functional change (Rowland et al., 2013; Wu et al., 2012) or, more commonly, as a result of model structural deficiencies. These results show that temporally highly resolved carbon flux data bear important model constraints. However, the models applied for parameter estimation showed different degrees of structural completeness and, consequently, the discussion of model results is confined to attributing parameter temporal variability to *known* sources of model deficiency. If we intend to use measurements within a DA scheme for the identification of currently *unknown* sources of model deficiency or even of processes hitherto unknown to ecophysiologists, models need to reflect the state-of-the-art of process understanding of the scientific community. Without a doubt, uncertainties in observations, model drivers, and representation of known processes will exist and influence parameter adjustment. However, the discussion of model results could then go further and associate parameter variability to unexplained ecosystem responses under given climatic constraints. Such a study will allow researchers to formulate more robust hypotheses about ecosystem functioning, which then can be used to guide further field studies and model development.

In contrast to EC carbon flux data, studies that have applied sap flow DA to constrain hydraulic parameters of forest transpiration models are rare (see Reichstein et al. (2003) as an exception). Sap flow data are likely to contain important process information on plant hydraulics, as they are the measurable outcome of water transport through the soil-plant-atmosphere continuum in response to environmental conditions. Accordingly, these data provide temporally highly resolved (sub-hourly) constraints on associated key parameters within models. Sap flow data are more useful for this purpose than latent energy flux data from EC, as the EC data include poorly quantified evaporation terms not connected with plant processes. With this study, we aim for highlighting the potential of sap flow data for assimilation into models, followed by an ecophysiological interpretation of parameter variability, and an analysis of hypotheses on plant hydraulic behaviour. This study can thus be regarded as a detailed manuscript of sap flow DA methodology.

We assimilated sap flow data from two Scots pine (*Pinus sylvestris* L.) stands with contrasting water availability (mesic: Vallcebre, xeric: Prades) into a process-based ecophysiological ecosystem model (SPA, Williams et al., 1996, 2001b). In contrast to the mesic Vallcebre site, Prades is located at the southern dry limit of Scots pine distribution, and drought-induced tree defoliation and mortality events have been reported previously (Martínez-Vilalta and Piñol, 2002; Poyatos et al., 2013). As the SPA model contains an advanced process representation of forest transpiration (Bodin et al., 2013; Misson et al., 2004), it is especially suitable for improving our understanding of ecosystem hydraulic functioning through confronting the model with the observed data.

The SPA model assumes an isohydric stomatal behaviour (Fisher et al., 2006), as has been repeatedly showed for Scots pine (Irvine et al., 1998; Poyatos et al., 2013). However, the basic model structure is mechanistically incomplete by not representing drought-induced damage of the hydraulic water pathway (although see Williams et al. (2001a) for alternate structures). Applying a sequential DA technique (EnKF), we constrained key hydraulic and structural parameters (aboveground plant conductance, stomatal efficiency, plant capacitance, root to leaf mass ratio) and further analyzed apparent patterns of their seasonal variability. We conducted the assimilation experiments with both synthetic (i.e. model generated) and measured sap flow data in order to estimate the applicability of the DA methodology. Our results are complementary to field site experiments by providing independent insights into stand-scale plant hydraulics, which bear further implications on water use efficiency and hydraulic limitations on carbon assimilation.

We pursued the following key research questions and hypotheses: (1) Are there between-site differences in hydraulic parameters, both in terms of magnitude and seasonality? We expect only minor parameter seasonality at the wetter Vallcebre site and larger values of water storage capacity, plant hydraulic conductance, and stomatal conductance than at Prades. (2) According to recent observations (Poyatos et al., 2013), we expect maximum plant hydraulic conductance per unit of leaf area to be higher but more sensitive to drought in defoliated (DF) than in non-defoliated (NDF) trees at the xeric Prades site. (3) We further hypothesize that a measured decrease in tree transpiration during extreme drought is accompanied by (partial) embolism of the hydraulic pathway, which is not fully accounted by reductions in stomatal conductance. We thus expect that a temporal decline in plant hydraulic conductance significantly improves model goodness-of-fit at Prades. (4) For the same reason, at the Prades site the posterior model will show considerable reductions in gross primary productivity (GPP) compared to a standard model run with temporally constant parameters, with important implications for the local carbon balance.