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Evapotranspiration deficit controls net primary production and growth of silver fir: Implications for Circum-Mediterranean forests under forecasted warmer and drier conditions

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ABSTRACT

Warming-induced drought stress has been hypothesized as a major driver of forest net primary production (NPP) reduction, but we lack reliable field data to assess if higher temperatures lead to forest NPP reduction, particularly in humid sites and at basin to landscape spatial scales. The use of a landscape approach would allow considering the feedbacks operating between climate, topography, soil vegetation and water resources. Here we follow that approach by simulating NPP using the regional hydro-ecologic simulation system (RHESSys) model and by comparing the results with radial growth data (tree-ring widths and intrinsic water-use efficiency – iWUE). We evaluate the relationships between climate, growth, NPP, atmospheric CO_2 concentrations (c_a) and iWUE in xeric and mesic silver fir forests subjected to contrasting water balances. The growth data successfully validated the 11-month NPP cumulated until spring. The main negative climatic driver of growth and NPP was the summer evapotranspiration deficit, which shows a negative association with tree-ring width indices. Sensitivity analyses indicate that rising c_a do not compensate the severe NPP reduction associated to warmer and drier conditions. The positive effect of rising c_a on NPP is mediated by climatic site conditions being detected only in mesic sites, whereas the negative effects of drought on NPP override any c_a-related enhancement of NPP in xeric sites. Future warmer and drier conditions causing a higher evaporative demand by the atmosphere could lead to a NPP decline in temperate conifer forests subjected to episodic droughts.

1. Introduction

Water deficit is likely to increase if climate warms and both drying and warming trends could lead to a reduction in net primary production (NPP) and growth of forests (Allen et al., 2010; Carnicer et al., 2011). Some studies already suggest that warming-related aridification trends are causing NPP reductions in forests subjected to contrasting water balances including semiarid (Breshears et al., 2005; Adams et al., 2009; Williams et al., 2013), boreal (Peng et al., 2011), temperate (van Mantgem and Stephenson, 2007) or tropical biomes (Phillips et al., 2010). However, there are still many research gaps on the roles played by rising temperatures and increased evapotranspiration levels on NPP and growth of forests under current and future climatic conditions.

Comparing NPP and growth responses to observed and forecasted climate and emission scenarios in sites with different water balances could aid to determine if temperature or precipitation are the major drivers of NPP and growth. Rising atmospheric CO_2 concentrations (c_a) may also affect NPP and growth by improving the intrinsic water-use efficiency (iWUE, i.e., ratio of net assimilation to stomatal conductance), but improved iWUE has not translated into enhanced growth neither in xeric nor in mesic sites (Peñuelas et al., 2011; Lévesque et al., 2014). So, the question remains open about which climatic factors and c_a levels would mainly drive NPP and growth.

The synergistic effects of warmer and drier conditions could also lead to reduction in NPP and growth across multiple spatial scales. Furthermore, a reduction in growth and NPP could lead to defoliation with cascading effects on hydrological processes at the basin and landscape levels (run-off, groundwater recharge, streamflow, etc.) (Guardiola-Claramonte et al., 2011; Anderegg et al., 2013). These complex feedbacks call for an integrated evaluation

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of landscape-level forest responses to climate warming including drought and related hydro-ecological processes. These assessments should consider nonlinear NPP and growth responses to future warmer and drier climatic conditions (Lloyd et al., 2013), including novel climatic or emission scenarios or unprecedented events (e.g., severe droughts).

In the Mediterranean Basin and also in Spain there is an increase in the frequency and severity of droughts (Hoerling et al., 2012). For instance, during the last 50 years there has been a persistent decrease of surface relative humidity of the growing season in mainland Spain associated with a marked warming trend, which caused increased atmospheric evaporative demand (Vicente-Serrano et al., 2014). Projections indicate an even higher warming trend and a decrease in precipitation across the Western Mediterranean Basin (Giorgi and Lionello, 2008).

Recent climate variability have caused widespread drought-linked reductions in NPP and growth of Circum-Mediterranean forests both in dry (Sarris et al., 2007; Vicente-Serrano et al., 2010a; Barbeta et al., 2013) and mesic sites (Jump et al., 2006; Linares and Camarero, 2012a,b). In Iberian pine forests warming-induced drought stress particularly affected growth and survival of those species with higher xylem vulnerability to cavitation (Sánchez-Salguero et al., 2012) or those populations living in the driest sites (Martínez-Vilalta and Piñol 2002; Martínez-Vilalta et al., 2008). However, other authors have noted either a remarkable capacity of tree populations from drought-prone areas to adapt to water shortage by changing growth dynamics and water use (Alla and Camarero, 2012; Granda et al., 2014) or a high sensitivity to dry periods in humid sites (Büntgen et al., 2013).

Such apparently contradictory findings can be resolved by upscaling physiological models of photosynthetic activity, growth or NPP (e.g., Sabaté et al., 2002) to a basin level thus integrating the complex interactions between climate, c_a, forests and soil hydrological processes (Tague and Band, 2004; Tague et al., 2009a,b). In this sense, hydro-ecological models considering tree processes as constrained by climate and water availability allow simulating forest responses (NPP, growth, carbon and water use) to observed and projected warming at basin to landscape scales (Morales et al., 2005; Medlyn et al., 2011). Here, we use a hydro-ecological model to understand the causes of the observed and simulated NPP and growth year-to-year variability of silver-fir (*Abies alba*) at a landscape level in the Spanish Pyrenees. Hydro-ecological simulations are validated using radial-growth data obtained in a dendrochronological network. Silver-fir growth decline in that area has been observed since the 1980s in the most xeric sites, being attributed to drought stress (Camarero et al., 2002; Linares and Camarero, 2012a). Different scenarios of emission of greenhouse gases (IPCC, 2007) indicate that forecasted regional warming may vary between +2.8 °C and +4 °C in the Pyrenees (López-Moreno et al., 2008). Further, warmer conditions and a reduction in soil water resources (López-Moreno et al., 2011; López-Moreno and Beniston, 2009) are expected to intensify in late summer, when silver-fir is particularly sensitive to dry conditions (Camarero et al., 2011; Pasho et al., 2011).

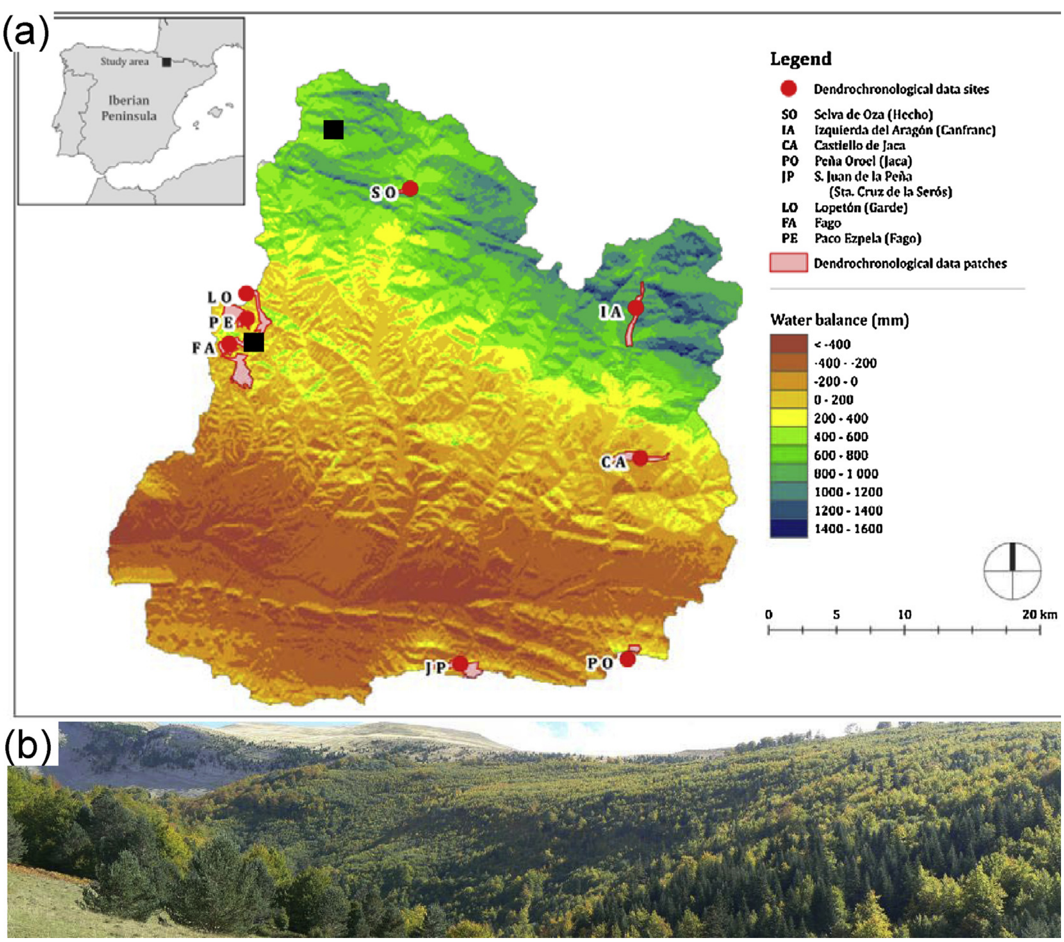

Fig. 1. Study area located in the Spanish Pyrenees (Aragón) (a) and view of a mixed silver-fir-beech forest (Las Eras) located near the upper black square on the map. The red symbols correspond to the eight silver fir forests with available tree-ring width series, while red polygons indicate the forest patches simulated by the model RHESSys. The black symbols show the two study forests were intrinsic water-use efficiency was also estimated. Note the sharp gradient of annual water balance indicated by the brown-to-blue scale corresponding to a shift from dry to wet conditions as elevation increases northwards.