



## Interspecific competition influences the response of oak transpiration to increasing drought stress in a mixed Mediterranean forest



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### ABSTRACT

Increasingly severe droughts are expected to negatively impact forest functioning in the future, especially in the Mediterranean region. Favoring mixed species stands has been advocated as a compromise between wood production and biodiversity conservation, but whether such management practices would allow forest ecosystems to acclimate to future climate conditions remains to be addressed. We tested whether the transpiration of *Quercus cerris* (Qc) and *Quercus petraea* (Qp) during droughts differ when they grow in pure or mixed forests. We measured sap flux density ( $F_D$ ) and leaf carbon isotope composition ( $\delta^{13}C$ ), as a proxy for intrinsic water use efficiency ( $WUE_{int}$ ), in pure and mixed Qc and/or Qp forest plots in Italy during the summer 2012. Qc and Qp showed a drop in  $F_D$  of 41% and 52% respectively during the summer drought independently of the mixtures, but with different seasonal trends. Qp transpiration response to soil drought did not differ between pure and mixed plots. In contrast, Qc transpiration was reduced by 56% in mixed plots at the maximum of the drought and only by 31% in the pure plot. Furthermore, we observed higher  $WUE_{int}$  for Qc in the mixed plot and no change for Qp, supporting the higher water stress intensity in the mixed plot for Qc. Our study illustrated the negative impact of Qp on Qc when these species compete for water resources. We suggest that managing for mixed stands in the Mediterranean region might, in some cases, increase the detrimental effect of drought on species functioning.

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### 1. Introduction

Both fundamental and applied questions are emerging about potential changes in the functioning of European forest ecosystems in regions subjected to severe climatic changes. Scenarios predict a global increase in the frequency and intensity of atmospheric and soil drought during the growing season throughout Europe (IPCC, 2007) and whether today's forest ecosystems will acclimate and survive in the upcoming decades remains to be seen. The Mediter-

anean zone will be one of the regions most affected during the next decades, with a considerable reduction in rainfall during the growing season accompanied by more frequent and more intense heat-waves (Giorgi, 2006; Somot et al., 2008). Ecological stability and productivity of Mediterranean forests is particularly sensitive to climatic conditions (Scarascia-Mugnozza et al., 2000). In this context, forest management practices adapted to future climatic change must be implemented (Fabbio et al., 2003). Specifically, these practices should be able to counteract the likely decrease in productivity and increase of catastrophic events such as fires and pests outbreaks so that acceptable levels of goods and services can continue to be provided.

Mixed forests have been advocated as a potential compromise between high wood production and biodiversity conservation (Kelty, 2006) and seem to be an interesting management option to help forest ecosystems acclimate to future climatic conditions. The two mechanisms underlying the positive effects of biodiversity on ecosystem services in mixed forests are: complementarity of resource use arising from facilitation and/or niche stratification

**Abbreviations:**  $F_D$ , sap flux density ( $L\ dm^{-2}\ h^{-1}$ );  $F_{D\ Mean}$ , mean daily sap flux density ( $L\ dm^{-2}\ h^{-1}$ );  $F_{D\ Mean-S}$ , mean daily sap flux density standardized by potential evapotranspiration ( $L\ dm^{-2}\ h^{-1}\ mm^{-1}$ );  $PET$ , daily potential evapotranspiration (mm); Qc, *Quercus cerris* L.; Qp, *Quercus petraea* (Matt) Liebl; REW, relative extractable water (unitless); VPD, vapor pressure deficit (kPa);  $WUE_{int}$ , intrinsic water use efficiency ( $\mu mol^{-1}\ mol^{-1}$ );  $\delta^{13}C$ , leaf carbon isotope composition (‰).

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between species with different functional traits, and selection effects explained by a higher probability of including one or several highly productive species in more diverse stands (Loreau and Hector, 2001). Positive effects of biodiversity on productivity in mixed Mediterranean forests have already been demonstrated (i.e. Vilà et al., 2007); however, species interactions in mixed forests may also strongly influence other ecosystem functions, particularly related to water use under soil water deficit conditions, though studies to date are lacking for these ecosystems.

The influence of tree species diversity on ecosystem transpiration has already been observed (Forrester et al., 2010; Gebauer et al., 2012; Grossiord et al., 2013; Kunert et al., 2012). In tropical and temperate tree plantations, higher water use seems to be triggered by a complementary behavior between the interacting species through differential canopy and/or root stratification in mixed and pure stands (Forrester et al., 2010; Kunert et al., 2012). Conversely, in a mature temperate forest and a boreal tree plantation, higher transpiration of mixed-species stands was due to the presence of a species with particularly high water use per canopy projection area (Gebauer et al., 2012; Grossiord et al., 2013). Including species with high transpiration rates in mixed species stands subjected to periods of reduced precipitation may therefore exhaust soil water reserves earlier during drought as compared to pure stands. In addition, soil water limiting conditions may have negative consequences on species survival, ecosystem productivity and ecosystem resistance to soil drought.

This paper presents a field study on the impact of soil water deficit on the tree-level transpiration of two oak species (*Quercus cerris* L., turkey oak, Qc, and *Quercus petraea* (Matt) Liebl., sessile oak, Qp) growing in pure or mixed conditions in Tuscany in central Italy. We tested whether the transpiration response of these species to severe soil water depletion would differ in pure and mixed plots. We also analyzed whether these differences were related to differing intrinsic water use efficiencies ( $WUE_{int}$ ). We hypothesized that mixing the two oak species would lead to a better utilization of available resources during a summer drought and that, consequently, transpiration rates would decrease less than in the pure plots. Indeed, these two oak species are known to have different water use strategies (Tognetti et al., 1996) and to differ in their rooting systems (Nardini and Tyree, 1999). Turkey oak is considered to be highly opportunistic for water uptake and keeps stomata open during summer drought periods, whereas sessile oak has a more conservative strategy of controlling transpiration earlier during drought.

## 2. Materials and methods

### 2.1. Site description

The study was conducted in a thermophilous deciduous forest situated in south-central Tuscany in the natural forest of Alto Merse, Italy (43.08°N, 11.19°E). One pure plot of turkey oak (*Q. cerris* L., Qc), one of sessile oak (*Q. petraea* (Matt) Liebl., Qp) and one mixed plot with both oaks (Qc/Qp) were selected. The 30 m × 30 m plots were no more than 2 km from one another and are included in the exploratory platform of the FP7- FunDivEUROPE project ("Functional Significance of Forest Biodiversity in Europe") (Baeten et al., in press). They are situated on Cambisol soils (World Reference Base for Soil Resources, FAO classification) above quartzite and anagenite bedrock and were selected to maximize soil type homogeneity and reduce as much as possible differences in diameter distribution, basal area, tree height, tree density, or canopy structure. The plots were composed of 50- to 60-year-old trees at altitudes ranging from 250 to 450 m a.s.l. The past management of all plots is coppice with standards and the last cut was about 20 years ago. Mean annual rainfall in the region is

950 mm, occurring mainly during the winter, and mean annual temperature is around 13.5 °C. Detailed plot characteristics are presented in Table 1.

### 2.2. Drought intensity

In order to characterize the drought intensity experienced by the study trees, we estimated the daily relative extractable water in the soil over the whole root zone ( $REW$ , unitless) in each plot over 2012.  $REW$  is defined as the ratio between available soil water and maximum extractable water. It varies between 1.0 (field capacity) and 0.0 (permanent wilting point). When  $REW$  is higher than 0.4, soil water conditions are non-limiting for transpiration of a large range of tree species and stomatal conductance mainly depends on air vapor pressure deficit, irradiance and forest phenology (Granier et al., 1999). When  $REW$  is below 0.4, the resulting soil water shortage induces a drop in stomatal conductance and thus in leaf gas exchange, causing most tree species to cease radial growth (Granier et al., 1999). In order to simulate  $REW$  at a daily time-scale, we ran the BILJOU water balance model (Granier et al., 1999) with measurements of daily climate conditions (rainfall, global radiation, air temperature and humidity, wind speed) from a nearby meteorological station in Pentolina (43.12°N, 11.10°E, 414 m a.s.l.), 1 km from the study plots. This generic model calculates the different water fluxes at daily time-scale in the ecosystem: tree transpiration, understory evapotranspiration, rainfall interception and drainage. These fluxes are dependent on plant area index and evaporative demand, i.e. the potential evapotranspiration, calculated using the Penman equation ( $PET$ , mm). The difference between rainfall and evapotranspiration fluxes refills the soil reservoir, whereas excess of water is drained out. All the functions implemented in the model were calibrated using various field experiments in different forests, climate conditions, and soil types. In order to parameterize the model to our study site, the plant area index ( $PAI$ ,  $m^2 m^{-2}$ ) of each selected plot was measured in September 2012. We used a LAI 2000 Plant Canopy Analyzer (PCA, LI-COR, Lincoln, NE, USA) to measure  $PAI$  at five locations in each plot and then calculated plot average (Table 1). Maximum extractable water (i.e. the water holding capacity) in this soil type was assumed to be 140 mm (Badeau V, pers. comm.). Sensitivity tests using lower (100 mm) and higher (160 mm) water holding capacities did not change the seasonal patterns of  $REW$  (data not shown).

### 2.3. Tree transpiration

We followed the thermal dissipation method described by Granier (1985) to measure volumetric sap flux density ( $F_D$ ,  $L dm^{-2} h^{-1}$ ) in the three selected plots at four periods in the 2012 growing season (P1 = June, P2 = July, P3 = August, and P4 = September). In the pure plots, five trees were equipped with sapflow sensors; in the mixed plot, five trees per species were equipped with sapflow sensors, for a total of 20 trees (Table 2). This number of replicates was considered representative of the response of single tree species to soil drought and it is currently used in the literature on tree-level transpiration research. All sapflow sensors were installed on the North faced side of trees in order to reduce the effect of direct sunshine that can be responsible of thermal gradients that would alter measurements. Each sensor was supplied with a power of 0.2 W.

Studied trees were randomly selected among the dominant and co-dominant tree classes (canopy stage) for each species in each plot. These classes were defined according to the diameter of the trees in each plot and an index of light interception (Dawkins index) that was visually assigned for each tree. Together, the dominant and co-dominant classes represented 86%, 93% and 80% of the sapwood area in the Qc, Qp and Qc/Qp plots, respectively. Measurements were restricted to trees of the dominant and

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