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Effects of stand composition and tree size on resistance and resilience to drought in sessile oak and Scots pine

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ABSTRACT

The IPCC previsions for the upcoming decades include an increase in frequency and intensity of drought events in several regions worldwide, including Northern Europe. Drought significantly affects forest ecosystems through decreased productivity, increased vulnerability to biotic disturbances and increased subsequent mortality. How forest ecosystems maintain resistance and resilience to drought events are important questions. Our study aimed to assess whether species mixture or an individual tree size within a stand alters a given tree's resilience and resistance to drought. A retrospective study of tree-ring widths allowed us to calculate resistance, resilience and recovery indices for five recent drought events: 1976, the 1990–1992 period, 2003, 2006 and 2010. These drought events were selected based on the SPEI (Standardized Precipitation Evapotranspiration Index) drought index. Our study sample consisted of 108 individual sessile oak (*Quercus petraea* (Matt.)) or Scots pine (*Pinus sylvestris* L.) trees sampled in 2012 and 2013 (Orleans forest, central France) in pure and mixed stands, divided into three diameter classes corresponding to three sizes: large, medium and small trees. Scots pine performed better than sessile oak during the 1990–1992 and 2010 droughts while the contrary was observed for the 2003 and 2006 droughts. They performed equally in 1976. We suggest that the differing sensitivity of the two species to spring and summer drought explained this result. In our study, stand composition had no effect on resilience or resistance for either species. The size effect in oaks was unclear as small oaks displayed either a better performance or a worse performance than large oaks. Small pines displayed better resistance and resilience than pines of a larger size. This work stressed the importance of taking into account stand composition and trees size as well as soil and climatic conditions for each drought events to achieve a better understanding of the diversity of responses to climatic variations among forest ecosystems.

1. Introduction

In the recent decades, the long term increase in temperature and changes in precipitation patterns (IPCC, 2013) accompanied by an increase in the frequency and intensity of extreme climatic events such as droughts (Smith, 2011) have been the object of several studies. The events are major disturbances, both ecologically and socially. The intense 1976 and 2003 droughts in Europe marked people's minds, and foresters were no exception. They were the first to witness forest decline and tree mortality following these droughts. The ability of forest ecosystems to face such climate changes and extreme events has become a major question for the scientific community. There is a large number of studies addressing this question (Bréda et al., 2006; Allen et al., 2010; Lloret et al., 2012). At the ecosystem level, the composition (Smith, 2011; Cavin et al., 2013), structure and distribution of forests as well as the water, carbon and nutrient cycles are expected to be modified in the context of climate change (Bréda et al., 2006; Galiano et al., 2011; Cheaib et al., 2012). Impacts on tree growth and wood production are becoming significant with increasing forest decline and mortality in some parts of Europe, especially in Mediterranean environments (Martinez-Vilalta and Piñol, 2002; Vacchiano et al., 2012; Vilà-Cabrera et al., 2013).

To assess ecosystem stability or species response, three basic aspects can be considered: resistance, recovery and resilience (Grimm and Wissel, 1997). Resistance is the capacity of an ecosystem, species or individual to remain basically unchanged when it is subjected to a disturbance. Recovery is the capacity to regain growth or any other characteristic negatively affected after a disturbance. Resilience is the ability to recover pre-disturbance structures and functions after a disturbance. In the perspective of climate change, these three aspects are essential to conserving ecosystems and their functions, or at a smaller scale, species and even individuals.

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Ecosystems involve several levels of complexity and diversity. Many studies have examined the benefits of mixed forests (Forrester et al., 2006; Kelty, 2006). Interest in mixed stands is inspired by observations of increased biodiversity in the ecosystem (Felton et al., 2010), better resistance to some biotic disturbances (Jactel and Brockerhoff, 2007; Perot et al., 2013) and an increase in productivity in most cases when compared to monoculture stands (Knoke et al., 2008; Vallet and Perot, 2011; Toïgo et al., in press). Despite an increasing number of studies relative to mixed stands, we still know little about their functioning compared with pure stands. Niche complementarity, which enables a better use of the available resources – including water, is a common hypothesis to explain increased productivity in mixtures (Lebourgeois et al., 2013). Therefore, studying the potential consequences of climate change – induced modifications in water availability on mixed and monoculture stands is crucial. Two hypotheses could be made for the response of mixed stands to drought. Firstly, mixed stands could improve individual tree species' performance during drought; a species might be mixed with another species which does not occupy the same water reserves. This would lead to a release of intraspecific competition combined with the possibility of facilitation alleviating drought stress through a partitioning of the water reserves between the species (Lebourgeois et al., 2013; Pretzsch et al., 2013). The involved species would be expected to benefit from this interaction. Secondly and reversely, mixed stands could decrease individual species' performance during drought as it has been observed depending on the tree species and soil conditions. This would result in an increased interspecific competition during drought stress (Jucker et al., 2014). The involved species or the least competitive species would then suffer from mixing during water shortage periods, affecting tree growth and functions such as photosynthesis, transpiration or sap flow (Grossiord et al., 2014).

Another level of complexity in forest ecosystems lies in the existence of varying individual tree size within a stand. The majority of studies conducted on the impact of drought on forest stands focus on dominant trees, i.e. the largest in diameter with generally more developed crowns and root systems. It is possible to hierarchically organize the trees in an even-aged stand according to their diameter, reflecting differences between individual tree functional statutes within an even-aged stand (Dhôte, 1994). This hierarchy implies a differential availability of resources such as water (Dawson, 1996), nutrients and light (Dhôte, 1994). It also affects the intensity of competition between individuals. Population hierarchy can consequently play an important role in an individual's responses to climatic and biological disturbances (Pichler and Oberhuber, 2007; Martín-Benito et al., 2008; Mérian and Lebourgeois, 2011; Zang et al., 2012). It is important to incorporate both stand composition (pure or mixed stands) and individual tree size in the stand as explanatory variables when studying tree species response to abiotic disturbances such as drought in order to assess the risks associated with climate change and to propose adapted forest management strategies.

We studied the effects of tree size and stand composition on resistance and resilience to drought in terms of radial growth for two species: a deciduous broadleaved species; sessile oak (*Quercus petraea* Matt.) and a conifer needled species; Scots pine (*Pinus sylvestris* L.). These two tree species have very different characteristics, suggesting they may have different responses to drought (Bréda et al., 2006; Eilmann et al., 2006; Bréda and Badeau, 2008; Michelot et al., 2012a), and are widespread throughout European forests in both pure and mixed stands. Sessile oak is a mesophilic species with a deep root system which prefers semi-shady environments well adapted to occasional droughts. During periods of water deficit, leaf water potential is reduced, potentially leading to xylem cavitation. The large vessels in oak earlywood are very sensitive to winter embolism (Tyree and Cochard, 1996) and water circulation must be restored each spring by the formation of at least one new tangential row of large vessels. Sessile oak is common in Western Europe and is the most widespread species in French forests (National Forest Inventory data). Scots pine is a light-demanding evergreen species. Its root system is more superficial than most broadleaved species but it does develop a strong first pivot and lateral roots. Water potential in the needles is maintained above a threshold level thanks to stomatal closure during periods of water deficit which minimizes the risk of xylem cavitation. Scots pine can stop its radial growth entirely when conditions are too harsh possibly leading to missing tree rings. Its drought tolerance as defined by Niinemets and Valladares (2006) is slightly higher than sessile oak. It is widely distributed throughout temperate and boreal Europe and is common in French forests and around the Mediterranean basin. Both species are present in pure or mixed stands at our study site in the Orléans National Forest in central France.

Radial growth is sensitive to biotic and abiotic disturbances (Lebourgeois et al., 2010; Olivar et al., 2012; Wiley et al., 2013; Palacio et al., 2014). It can be used for past climatic reconstructions or for retrospective analysis of tree performance during past known disturbances (Speer, 2010). We thus used radial growth to evaluate how individual trees responded to past climatic severe events such as drought using indices of resistance, recovery and resilience. We selected five drought events between 1970 and 2013 based on the SPEI (Standardized Precipitation Evapotranspiration Index), a drought index defined by Vicente-Serrano et al. (2010). We sought to answer the following three questions:

1. Do sessile oak and Scots pine respond differently to past drought events?
2. Does stand composition (mixed stand *versus* pure stand) improve or deteriorate individual tree's radial growth during drought events?
3. Does tree status represented by tree size affect individual tree's response to drought?

2. Material and methods

2.1. Study site and species

The study site is located in the center of France, in the Orléans National Forest (France, 48°00′ N, 2°09′ E) which extends over 35,000 hectares and is managed by the National Forest Office. Elevation ranges from 107 m to 174 m a.s.l. Throughout the forest the soil is relatively poor and acidic with a sandy clay-loam texture (Table 1), and is classified as a planosol (IUSS Working Group, 2014). Superimposed layers of clay and sand lead to a temporary perched water table in winter, but the low soil water storage capacity reduces available water for plants in summer. The area has a temperate continental climate with an oceanic influence (mean minimum temperature of 0.7 °C in February; mean maximum temperature of 25 °C in July). The mean annual rainfall is 740 mm (1969–2013 data from the weather station at Nogent-sur-Vernisson, France).

The species studied were sessile oak *Quercus petraea* (Matt.) and Scots pine *Pinus sylvestris* L., managed in pure or mixed stands.

2.2. Sampling design

Nine plots were selected on three sites in even-aged stands (50–80 years old) as part of the Oak Pine Tree Mixture Experiment (OPTMix) (Korboulewsky et al., 2013). Each site has one plot of pure sessile oak, one plot of pure Scots pine and one plot with a mixture of the two species. All plots have similar soil conditions,