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Research article

Variation in reproduction and growth in declining Scots pine populations

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ABSTRACT

Disentangling how variation in reproduction and growth is linked in plants across different ecological scales, and how allocation rules change in response to stress are fundamental aspects of life history theory. Although it is known that reproductive allocation is an allometric process and that environmental conditions can influence demographic traits, patterns of variation in vegetative and reproductive functions across and within individuals of tree species suffering drought-induced decline have rarely been documented. In this study we use Scots pine (*Pinus sylvestris* L.) as a model species to explore patterns of variation in cone production and growth in two declining populations at the southern edge of its distribution. A Bayesian approach was used to assess how these demographic traits vary as a function of drought effects and competition and covary across different ecological scales. The allometric trajectories relating tree size with cone production and growth differed along gradients of drought impacts and biotic interactions. Although reproduction and growth increased with tree size, cone production reached a maximum at intermediate sized trees and stabilized or decreased at larger sizes. Drought stress effects (defoliation at the tree level and overall decline at the plot level) and competition for resources reduced cone production and growth. Our results also showed differential effects of defoliation on cone production depending on tree size, with stronger effects on larger individuals. After accounting for these effects, much of the variation of demographic traits and correlations among them occurred at small ecological scales across individuals (i.e. within plots) and within individuals across years. This resulted in covariations between demographic traits among nearby individuals and within individuals through time, suggesting a consistent advantage in resource acquisition of some individuals within plots, and trade-offs between growth and cone production within trees across years. In conclusion, this study reports that drought-induced forest decline is associated with lower growth and cone production in Scots pine, which could contribute to explain the long-term impacts of drought in southern populations of this species and, in particular, its low regeneration capacity after severe drought.

Introduction

Disentangling how variation in reproduction and growth is linked in plants is a fundamental aspect of life history theory (Bonser and Aarssen, 2009). This topic deserves special attention for trees because of their long lifespans and the fact that their fecundity often increases continuously with increasing size, inducing a compromise in resource distribution between current reproduction and other functions such as growth or maintenance (Petit and Hampe, 2006). Therefore, trees may show differential allocation strategies and face trade-offs between reproduction and growth, suggesting ecological or physiological conflicts between these functions (Harper, 1977; El Kassaby and Barclay, 1992; Silvertown and Dodd, 1999; Climent et al., 2008). At the same time, the reproductive output is extremely variable both within and between individuals or populations due to factors operating at different ecological scales, including: fluctuations in climatic conditions (Knops et al., 2007), biotic interactions and disturbance effects (Haymes and Fox, 2012), individual size or population size class distributions (Bazzaz et al., 2000), availability of stored resources (Yasumura, 2006) and/or intra-individual variability (Sánchez-Humanes et al., 2010).

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Reproductive allocation in plants is mainly an allometric process, i.e. it changes with size and, consequently, characterizing size-dependent allocation is a first step in understanding between-plant reproductive behavior and life-history strategies (Niklas and Enquist, 2003). If allocation is size-dependent, an environmental factor that influences growth (i.e. changes in size) will also affect reproduction, and this effect should be accounted for when comparing plants under different environmental conditions (Weiner et al., 2009). According to this allometric perspective, only a change in the allometric trajectory between size and reproductive output through an environmental gradient can be interpreted as a differential response in terms of reproductive allocation (Weiner, 2004).

How variation of demographic traits is distributed across different ecological scales and how it is linked with environmental conditions is of major concern for global change ecology, since the future dynamics of populations will depend on the current demographic variation and processes related to such patterns. It is well known that resource availability affects individual performance. In the face of stressful conditions, reproductive reduction and failure are frequent (García et al., 2000; Zlotin and Parmeter, 2008) and growth is largely restricted (Aber et al., 2001; Adams and Kolb, 2005). Thus, variation in the environmental conditions in space can determine a complex pattern of resource allocation to reproduction and growth among individuals, and resource fluctuations through time can exacerbate trade-offs between the two functions. For instance, plant populations may show different strategies of resource allocation between reproduction and growth according to the strength of environmental stress (Guo et al., 2012).

At the intra-individual level, trees match their reproductive output to the fluctuations of resource availability, particularly in marginal environments where reproduction and growth are constrained by climate (Despland and Houle, 1997). However, it has been suggested that resource matching may not be enough to explain the outcome of reproduction or masting events, which might be under some selective pressure and, therefore, would come at a cost to other functions such as growth (Monks and Kelly, 2006). Disentangling the origin of putative trade-offs is complex because reproduction and growth can be influenced independently and in different ways by the availability of resources, by physiological constraints due to resource limitation and by adaptation to long-term local environmental conditions (Barringer et al., 2012).

Drought is a common stress factor in Mediterranean ecosystems and several recent studies have reported drought-induced forest decline in terms of tree mortality, canopy defoliation (Lloret et al., 2004; Galiano et al., 2010; Carnicer et al., 2011; Di Filippo et al., 2012), reductions of growth rates (Gómez-Aparicio et al., 2011; Linares and Camarero, 2012; Sánchez-Salguero et al., 2012; Martínez-Vilalta et al., 2012), and reproduction restriction or failure (Mutke et al., 2005; Espelta et al., 2008; Pérez-Ramos et al., 2010; Sánchez-Humanes and Espelta, 2011). Physiological stress may lead to long-term effects and slow recovery of surviving individuals after severe drought episodes (Galiano et al., 2011). This delayed drought effects may be also linked to resource allocation to different functions, arising from differential responses and trade-offs between reproduction and growth across and within individuals.

Patterns of variation of reproduction and growth across and within individuals of long-lived tree species after suffering drought-induced decline have rarely been documented. In this study we use Scots pine (*Pinus sylvestris* L.), a widely distributed temperate tree, as a model species to explore patterns and dynamics of reproduction and growth in two populations located at the southern edge of its distribution and suffering from drought-induced decline. Four main hypotheses are addressed: (1) Growth and cone production are size-dependent and this allometric relationship differs depending on drought impacts and biotic interactions, so that drought stress and competition for resources reduce cone production and growth at a given tree size; (2) Growth and cone production are correlated positively across individuals, suggesting that some tress have a consistent advantage in terms of resource acquisition; (3) Growth and cone production are also linked within individuals across years, but in this case reflecting a trade-off between these two functions; and (4) This latter trade-off is steeper when trees suffer higher defoliation, reflecting lower overall availability of resources.

Materials and methods

Study area

The study was carried out in Catalonia (NE Iberian Peninsula; Fig. 1a) where Scots pine is the second most abundant tree species, covering 219,754 ha (18.4% of the total forested area, Gracia et al., 2000-2004). It occupies large areas in the Pyrenees and some residual locations in the center and south of the region (Fig. 1b). The species is present from 200 to 2100 m a.s.l., but it is mainly distributed between 800 and 1600 m a.s.l. Throughout the species distribution area, annual precipitation ranges from 520 to 1330 mm and average annual temperature between 3.6 and 14.3 °C.

Two Scots pine populations were selected (Fig. 1b), one located in the center of the region (Prades) and another one in the Central Pyrenees (Arcalís). The climate in Prades is characterized by an annual mean temperature of 11.6 °C and an annual mean precipitation of 699 mm, while Arcalís has an annual mean temperature of 9.6 °C and an annual mean precipitation around 922 mm (mean values for the plots surveyed in each population [see bellow]; data obtained from the Digital Climatic Atlas of Catalonia, Ninyerola et al., 2000). These two populations were selected because drought-induced forest decline has been observed in the recent decades: starting in the 1990s in Prades (Martínez-Vilalta and Piñol, 2002; Poyatos et al., 2013) and in more recently Arcalís (Galiano et al., 2010; see also Hereş et al. (2012)). Other tree species (mainly *Quercus* species) appear in the understory in both populations, and forest management has been minimal for the last decades in the two cases. Previous studies have reported that current patterns of Scots pine decline are the result of interactions between forest structural attributes and local site conditions that modulate forest responses to environmental stress (Galiano et al., 2010; Vilà-Cabrera et al., 2013).

Field sampling

During 2007 and 2008, 30 circular plots were established along an altitudinal gradient at each of the two studied Scots pine populations (Galiano et al., 2010; Vilà-Cabrera et al., 2013). Plot size in Arcalís was 314 m^2 (10 m radius) while in Prades was 491 m^2 (12.5 m radius). Within each plot, all adult Scots pines (diameter at breast height [dbh] ≥ 5 cm) were mapped, measured for dbh, censused for mortality and their percentage of green needles was estimated relative to a healthy canopy of a similar sized tree in the same population. During spring 2009, 2010 and 2011 we monitored the percentage of green needles and the number of mature cones (with binoculars) in the canopy of each individual in 54 plots (27 plots at each population). During spring 2011 a hand increment borer (5 mm diameter; Suunto,Vantaa, Finland) was used to obtain a sample core to the pith at 1.35 m above the ground and perpendicular to the slope from 5 to 7 trees per plot in each population. These trees were selected at random within each plot ensuring that dbh