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Scale dependent responses of pine reproductive traits to experimental and natural precipitation gradients

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ABSTRACT

Drought considerably affects physiological and biochemical processes in trees and thus also reproduction. However, little is known about shifts in reproductive strategies in relation to changes in water availability.

We investigated cone and seed traits as well as needle and twig growth traits in pine trees along a natural precipitation gradient (290 mm–750 mm) and in a long-term irrigation experiment to understand reproductive responses to water availability. Combining multiple traits, we found that cone trait richness and divergence were positively correlated with water availability. This suggests drought-induced environmental filtering resulting in a reduced set of cone trait combinations. In contrast, seed trait diversity indices were negatively correlated with water availability, suggesting that pine trees tend to maximize seed trait dissimilarity in multiple dimensions to efficiently utilize scarce resources. Trade-offs between reproduction and vegetative growth were observed along the transect but not in the irrigation experiment, which may be a result of different drought severity between the two study regions.

Our results highlight the importance of considering a broad aridity gradient and different spatial-temporal scales when studying plant reproductive responses to precipitation change. Furthermore, the present study indicates that quantifying complementary components of trait diversity allows to interpret ecologically complex changes in trait distribution in multiple dimensions.

1. Introduction

Global precipitation patterns have exhibited apparent changes in the last century in both temporal and spatial scales (Stocker, 2014) and are expected to be further modified. Such changes will affect soil water availability and will also modify intensity and frequency of drought events (O'Brien et al., 2017a). Substantial evidence has revealed the impacts of changes in water availability on the physiological and biochemical processes in trees (Li et al., 2008a,b; Zhu et al., 2012; Li et al., 2013; Wagg et al., 2017). In this context, exploring how reproductive strategies of plants, particularly of long-living tree species, respond to changes in precipitation regime has become a hot topic of current ecological studies (Mutke et al., 2005; Way et al., 2010). Pine species are highly suitable to study this issue, given their wide geographical distribution, as well as their ability to adapt to different environmental conditions (Leslie et al., 2012).

Traits of single individuals determine their fitness (Violle et al., 2007; Siefert et al., 2015) by affecting responses to the environment and ecological interactions (Bolnick et al., 2011; Violle et al., 2012; Kraft et al., 2014). Phenotypic plasticity of functional traits, both in morphology and in physiology, is increasingly considered to be a crucial strategy for tree species to respond rapidly to altered environmental conditions (O'Brien et al., 2017b), and to be also of importance for evolution on longer time scales (Sultan, 2000). However, large parts of

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current research on trait plasticity are concentrated on vegetative organs, including shifts in needle area and longevity (Oleksyn et al., 2003), changes in branch traits (Adams et al., 2015), as well as adjustments in stem and fine root growth (Brunner et al., 2009; Eilmann et al., 2009; Wang et al., 2017). Little information is available on the intraspecific variability in reproductive traits and phenology of trees in relation to intra and inter-annual mean precipitation changes (Volis and Bohrer, 2013; Ayari and Khouja, 2014). This has so far limited a comprehensive understanding of tree eco-physiological responses to environmental changes such as altered water availability, particularly considering that reproduction is directly related to plant fitness, population dynamics and community structure (Thomas, 2011).

Most of the few studies dealing with intraspecific variability of reproductive traits focused on overall cone and seed yield per tree rather than on the variability of single cones and seeds within individual trees, which however can even exceed mean differences among trees (Mutke et al., 2005). In addition, functional traits generally do not vary independently but rather co-vary, and plants tend to adopt certain trait combinations (trait syndromes) to maximize their performance. It is thus crucial to consider variability of multiple traits simultaneously to quantify functional changes. To this end, trait diversity indices specifically designed for the use of individual-level trait data have been recently developed (Fontana et al., 2016). Trait richness (the amount of trait space covered by individuals of a population) and trait divergence (a measure of dispersion of individuals around the centroid of trait distribution) potentially reflect environmental filtering, because they are sensitive to losses of trait combinations represented in a certain population (Cornwell et al., 2006; Mouillot et al., 2013; Fontana et al., 2016). Trait evenness quantifies the regularity in trait distribution and thus is supposed to respond mainly to biotic interactions (e.g. competition), which are arguably more intense under limited resources, and to detect niche partitioning (Fontana et al., 2018).

Female cones and seeds are two structures with different reproductive functions in conifers, and cone and seed morphological traits are positively correlated with each other (Leslie et al., 2017). Moreover, seed size is closely linked with plant life history, which usually involves a trade-off between seed quality and quantity (Smith and Fretwell, 1974). This pattern has been widely confirmed at the interspecific level, where few but bigger seeds are commonly produced by species living in unfavorable environmental conditions (Leishman et al., 2000; Pluess et al., 2005). However, patterns of intraspecific seed variation within or across populations in response to altered water availability have so far received little attention and the same is true for cone traits.

Variation in plant reproduction in response to environmental changes involves a range of physiological processes, such as resource allocation among different functions or organs (Obeso, 2002; Thomas, 2011; Deyn, 2017). Under limited resources availability, increased resource investment in reproduction (i.e. reproductive allocation) may entail decreased allocation to vegetative tissues and functions, leading to trade-offs between reproduction and vegetative growth, as defined by the 'resource switching hypothesis' by Monks and Kelly (2006). However, this kind of correlation does not seem to be universal. For example, Despland and Houle (1997) found that changes in both reproduction and vegetative growth of *Pinus banksiana* in Subarctic Quebec simply matched variations in resource availability without any apparent trade-off, following the 'resource matching hypothesis' (Kelly, 1994). Which of these two hypotheses is applicable in a specific situation may depend on the spatial-temporal scale of analysis (Barringer et al., 2013; Vilà-Cabrera et al., 2014), type and range of stress gradients, ontogenetic stages (Genet et al., 2009) and hierarchical levels studied (Obeso, 2002), as well as underlying mechanisms (e.g. acclimation *vs*. adaptation). Despite recent efforts, our understanding on how resource allocation between reproductive and vegetative growth responds to changing water availability is still limited. Moreover, given the multi-year duration of the reproductive cycle of pine trees, it is necessary to study reproductive allocation across years (Pérez-Ramos et al., 2010).

To our knowledge, few studies have simultaneously combined natural transect and manipulation experiment to explore the functional response of trees to environmental changes. In this study, we investigated the reproductive (seeds and cones) and vegetative traits (needles and shoots) of pine trees in relation to water availability along a natural precipitation gradient and in a controlled long-term irrigation (i.e. precipitation manipulation) experiment. Our experimental design allows us to explore the pine reproductive strategies at different scales in the context of global precipitation changes. Such scales not only involve different time spans of pine trees exposed to drought, but also encompass a steep gradient of drought severity. We expected acclimation responses of reproductive traits (or phenotypic plasticity) of *Pinus sylvestris* L. to short-term changes in water availability in the irrigation experiment, and adaptive responses of *P. sylvestris* var. *mongolica* Litvinov to long-term persistence of the species along the natural precipitation gradient. By using *P. sylvestris* var. *mongolica* along the natural gradient and *P. sylvestris* in the irrigation experiment we assumed that observed patterns can be attributed to different underlying mechanisms rather than to the autoecology of trees (very similar in this case). We investigated the relationships between vegetative growth and reproduction, and calculated diversity indices of reproductive traits, to test the hypotheses that (I) trade-offs exist between seed size and number, as well as between reproduction and vegetative growth, (II) the strength of these trade-offs is inversely proportional to water availability, and (III) decreasing water availability causes lower trait richness and divergence (environmental filtering) but higher trait evenness (niche partitioning).

2. Material and methods

2.1. Transect study: study area, aridity gradient, sampling and measurements

The research was carried out in six *P. sylvestris* var. *mongolica* plantations with an age between 35–50 years along a 1200 km transect in Northeastern China (Fig. S1). In the six *P. sylvestris* var. *mongolica* plantations, all trees developed from seeds collected from the same natural *P. sylvestris* var. *mongolica* population in Honghuaerji (HHEJ) (47°35–48°36′N, 118°58–120°32′E), Hulunbeier/China, and were planted to prevent soil erosion (Zhu et al., 2003). They had a Sokal (1958)'s genetic simple matching (SM) coefficient of 86% (Fig. S2). Along the transect, mean annual temperature (MAT) ranges from 4.7 °C to 6.8 °C, with a tendency for slightly higher values in the West. The transect is characterized by a steep climate gradient with increasing aridity from East to West: mean annual precipitation (MAP) dramatically decreases from 748 mm (East) to 284 mm (West), while mean annual potential evapotranspiration (PET) sharply increases from 1206 mm (East) to 2300 mm (West). In addition, soils also show variability along the transect. The two easternmost sites (QD and BL) are located in the mountain areas of Jilin Province, where soils are silty and relatively nutrient-rich, with a thick organic layer. The other four sites (FJ, ZG, NM and WL) are distributed in the Keerqin sandlands, where soils are sandy, nutrient-poor, loosely structured and susceptible to wind erosion (Fig. S1, Table S1).

To describe the water availability of each site along the transect, we calculated the aridity index according to Delgado-Baquerizo et al. (2013):

$$Aridity \quad index = 1 - MAP/PET \tag{1}$$

Where *MAP* represents the mean annual precipitation, *PET* represents the potential evapotranspiration. From West to East along the transect, *aridity index* declines from 0.88 to 0.38 (Table S1), indicating a decrease of aridity, due to increasing water availability. The climate data used in this experiment was obtained from the closest meteorological stations