GfÖ
GfÖ Ecological Society of Germany, Austria and Switzerland
Basic and Applied Ecology 21 (2017) 13–22
Basic and Applied Ecology
www.elsevier.com/locate/baae

Seed bank, seed size and dispersal in moisture gradients of temporary pools in Southern France

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Received 23 January 2017; accepted 19 June 2017
Available online 27 June 2017

Abstract

Plants reduce risk of extinction due to unpredictable rainfall by soil seed banks, dispersal or large seeds. However, seed size also increases independently in dry habitats, and since seed size is in a trade-off with seed number, size of seed banks is expected to increase in moister habitats. Therefore, we wanted to test if seed abundance in soil increases in wet habitats, if seed size increases in dry habitats, and if spread of seeds along the gradient is higher for plants of intermediate habitats in local moisture gradients.

We studied 15 temporary pools in three biogeographically separated wetlands in Southern France. For each pool we studied five different moisture levels, totalling 75 local plant communities. We quantified soil seed bank by the seedling emergence method, seed size and an index of spatial spread of seeds in the soil for every species. We also quantified water levels for each plot.

We found increasing abundance of seeds in the soil with increasing water levels but lower seed size and higher spread at intermediate water levels. When we controlled for niche position, we found no trade-off between seed size, spread and abundance in the soil seed bank.

Type and importance of risk reduction strategies thus appeared to be strongly driven by the plant species' moisture niche and the spatial arrangement of water levels.

Keywords: Bet hedging; Vernal pool; Mediterranean; Risk reduction; Hydrological niche

Introduction

Climate change decreases rainfall predictablility and hence changes distribution of plants (Hooftman, Edwards, & Bullock 2016). Drought and frost contribute to local extinctions (Harrison 2000; Inouye 2000). Plants reduce these risks, by evolving soil seed banks and seed dispersal. Both multiply the opportunities for germination and thus ensure the long-term persistence of plant populations (Childs, Metcalf, & Rees 2010; Cohen 1966; Philippi & Seger 1989). Theoretical models and field data sustain the role of seed banks and dispersal for persistence in homogenous habitats (Bulmer 1984; Cohen 1966; Rees 1994; Tielbörger & Valleriani 2005; Venable & Brown 1988). These model assumptions contrast with the reality in many terrestrial ecosystems, which show small-scale gradients of soil moisture and hydrological niches, a gradient that has been shown to be a main fac-

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http://dx.doi.org/10.1016/j.baae.2017.06.003
1439-1791/

tor for co-existence in plant communities (Silvertown 2004; Silvertown, Araya, & Gowing 2015). A trade-off between water use efficiency and relative growth rate seems to drive niche partitioning along the hydrological gradient (Angert, Huxman, Chesson, & Venable 2009; Silvertown et al. 2015). Niche partitioning and risk-reduction are both important mechanisms for persistence, but we still do not know how niche partitioning relates to risk-reduction (Simons 2011). This is important because most plants grow separately in local gradients (e.g. García-Baquero, Silvertown, Gowing, & Valle 2015) and perceive varying risk levels according to their niche boundaries.

Soil seed banks reduce risks when rainfall is unpredictable (Cohen 1966) and this strategy can result in high abundance of seeds in the soil (Volis & Bohrer 2013). For deserts, one single global variance in rainfall is sufficient to model evolution of soil seed banks (Clauss & Venable 2000; Venable 2007). However, in small-scale gradients of moisture, the response of plants to rainfall variability is less synchronous (García-Baquero et al. 2015; Tielbörger & Petru 2008). In this case of uncorrelated local variances, when adjacent patches are different, seed dispersal is the optimal risk-reduction trait (Nathan & Muller-Landau 2000; Siewert & Tielbörger 2010; Snyder 2006; Venable & Brown 1988). This suggests a shift of seed dispersal distances and seed bank abundances in moisture gradients, which has never been detected yet. Large seeds increase survival of seedlings under drought (Baker 1972; Daws, Crabtree, Dalling, Mullins, & Burslem 2008; Leishman & Westoby 1994) and hence decrease the risk of extinction of a plant species. Soil seed banks may thus be negatively correlated with seed size and positively correlated with moisture. Since seed size is in a well-known trade-off with seed number (Moles & Westoby 2006), large seeds have lower abundance in the soil and limited dispersal (Bruun & Poschlod 2006; Saatkamp, Affre, Dutoit, & Poschlod 2009). Moreover, large seeds have been suggested a risk-reduction trait because they store resources to survive adverse times (Cohen 1966; Leishman & Westoby 1994; Philippi & Seger 1989; Siewert & Tielbörger 2010). Models revealed a negative correlation between seed size, seed banks and seed dispersal for locally homogenous habitats (Cohen & Levin 1987; Venable & Brown 1988). Altogether, large seed size should be associated with dry habitats and trade-off with soil seed bank abundance and seed dispersal in the moister habitats.

Beyond seed size, plants differ in adaptations to hydrology leading to varying water use efficiency, e.g. by C3, C4 and CAM phytosynthesis (Keeley 1998) and in this way enable temporarily coexisting guilds (Angert et al. 2009) or coexistance in spatially partitioned hydrological niches (Ellenberg 1953; García-Baquero et al. 2015; Silvertown et al. 2015). It has been shown that niche partitioning in local moisture gradients contributes importantly to plant diversity (Bauder 2000; Violle et al. 2010). We therefore expect that effects of moisture niches on risk-reduction traits are strongest for moisture gradients on short spatial scales and when moisture gradients interfere with the extent of seed dispersal such as in Mediterranean temporary pools (Deil 2005). Temporary pools are also subjected to strong year-to-year fluctuations in rainfall, increasing the importance of risk-reduction and they are notoriously rich in annual plants (Deil 2005). Interestingly, year-to-year changes in surface are unequal for wet and dry habitats in the hydrological gradient. In wet years, high and steep areas remain dry while many lower parts are flooded, whereas in dry years even the lowest points remain dry. This implies that the importance of global versus local temporal variance experienced by plants differs according to their moisture niche in our gradient, i.e. aquatic plants have no escape and build up highly abundant soil seed banks (Bauder 2005), whereas plants with intermediate moisture niches should show higher seed dispersal.

Building on this context, we tested the following hypotheses on risk-reduction traits and moisture niches. (1) Abundance of seeds in soil banks increases towards the wet end of the moisture gradient, which is particularly pronounced in aquatic plants. (2) Dispersal of seeds in local gradients is highest for species with intermediate moisture niches, resulting in a higher spread in the soil seed bank for intermediate species. (3) Seed size increases for species from dry habitats, reducing the effects of drought. (4) Seed dispersal, seed bank abundance and seed size may be negatively related, since they are alternative strategies of risk reduction.

We quantified abundance and dispersal of seeds in the soil bank as well as seed size for all vascular plant species in 15 Mediterranean temporary pools. We also quantified changes of water level over short distances, which are known to vary inter-annually with rainfall and to drive small-scale turnover in these plant communities (Brock 2011; Deil 2005; Rhazi, Grillas, Tan Ham, & El Khyari 2001).

Materials and methods

Study sites

We studied three temporary wetland areas in Southern France, Feuillane (43°28′14″N, 4°52′41″E), Evenos (43°12′40″N, 5°51′10″E) and Plaine des Maures (43°21′12″N, 6°26′06″E). At Feuillane, the mean annual temperature is 15.2 ± 0.68 °C and the mean annual rainfall is 455 ± 158 mm (2004–2013, Istres). This site has alluvial soils with temporary pools in winter.

Evenos has a mean annual temperature of 16.4 ± 0.47 °C and a mean annual rainfall of 585 ± 168 mm (2004–2013, Toulon). A layer of tertiary basalt is the substrate for temporary pools.

Plaine des Maures has a mean annual temperature of 15.4 ± 0.56 °C and a mean annual rainfall of 747 ± 299 mm (2004–2013, Le Luc). Permian sandstones form shallow soils and temporary streamlets and pools. This site is of prime interest for the conservation of temporary pools in Europe