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Stable germination behavior but partly changing seed–seed interactions along a steep rainfall gradient

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Abstract

Germination marks a critical transition in plant life that is prone to high mortality. Strong selection pressure is therefore expected to finely tune it to environmental conditions. Our study on the common Mediterranean grass *Brachypodium hybridum* assessed whether germination behavior changes systematically along a steep natural rainfall gradient ranging from harsh desert to rather mild mesic-Mediterranean conditions. We specifically tested hypotheses that germination behavior confers greater risk-spreading in populations from drier, unpredictable environments, and that seeds from wetter populations are better competitors.

In 14 populations (spanning 114–954 mm annual rainfall) we assessed three alternative key parameters of germination in a greenhouse experiment: between-year dormancy, days to emergence within a season, and temporal spread. Addition of neighbor seeds accounted for competition as another crucial environmental factor. In six of the 14 populations, we also compared seeds originating from corresponding north (more mesic) and south (more arid) exposed hill slopes to test whether germination patterns along the large-scale rainfall gradient are paralleled at this smaller scale.

B. hybridum exhibited generally high germination fractions and rapid emergence with very little temporal spread, indicating overall little risk-spreading germination. Surprisingly, none of the three parameters changed systematically with increasing aridity, neither at large scale along the rainfall gradient nor at small scale between north and south exposures. Neighbor seeds, however, mildly suppressed germination. Germination of neighbor seeds, in turn, was more strongly suppressed by *B. hybridum* seeds from drier populations, and this effect was stronger for forb than for grass neighbor species.

Our results provide strong evidence that increased risk-spreading germination is not a universal, essential strategy to persist in increasingly dry, unpredictable environments. They also highlight that competition with neighbors occurs even at the earliest plant life stage. Since neighbor effects were species-specific, competition among seeds can affect community composition at later plant stages.

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Keywords: Aridity gradient; Bet-hedging germination; *Brachypodium hybridum*; Density dependence; Dormancy; Emergence time; Risk spreading; Seed competition; Slope exposure; Temporal spread

Introduction

Germination marks the critical transition from the highly resistant seed stage of a plant to its vulnerable seedling stage

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that is prone to high mortality. Plants suffer similar if not higher mortality rates within the first week after emergence as do established tree saplings within three years (Moles & Westoby 2004; Moles & Westoby 2006) and as annual plants after establishment until reproduction (Metz et al. 2010). Strong selection is therefore expected to finely tune germination to environmental conditions, making germination a potential key trait for plant adaptation to local environments (Donohue, Rubio de Casas, Burghardt, Kovach, & Willis 2010).

Germination behavior may comprise alternative key aspects. One is between-year seed dormancy ('dormancy' hereafter), denoting that a fraction of viable seeds does not germinate in the first year(s) despite favorable conditions (Cohen 1966; Childs, Metcalf, & Rees 2010; Lampei, Metz, & Tielbörger 2017). It spreads offspring emergence in time to safeguard against poor reproduction in single years, thereby providing a risk-spreading (bet-hedging) strategy. The classic example is annual plants in dryland ecosystems where rainfall varies unpredictably across years. The costs of higher seed mortality during prolonged periods in the soil and of lower short-term fitness in favorable years are then compensated by reduced fitness variation and increased geometric mean fitness across years (Cohen 1966; Childs et al. 2010; Simons 2011). An alternative yet rarely investigated aspect of bet-hedging germination is adjusting the time to emergence *within* single years (Simons 2014; Gremer, Kimball, & Venable 2016). Several studies demonstrated that rapid emergence at the beginning of the growing season is favored because early emergers gain a head start over later seedlings, allowing them to attain greater final biomass and fecundity (Verdú & Traveset 2005; Mercer, Alexander, & Snow 2011; Cogoni, Fenu, & Bacchetta 2013). The inherent risk, however, of emerging early is high mortality from unpredictable early season hazards, e.g. sudden drought spells after initial rain events. Strong selection against early emergence may thus be apparent only in particular years and hence underrepresented in empirical studies (Donohue et al. 2010). Reducing this risk by adjusting the time to emergence can then be either conservative or diversifying (Philippi & Seger 1989; Childs et al. 2010; Simons 2011). With the conservative strategy, parental plants *delay* germination of their seeds within the season at the cost of lower final fecundity (Childs et al. 2010; Simons 2011; Gremer et al. 2016). With the diversifying strategy, parents *spread* seedling emergence over a greater period within a season so that some seeds will bet on the benefits of early emergence while later emergers play it safe and hedge against the risk of early mortality (Childs et al. 2010; Simons 2014). Increased bet-hedging germination may thus result from higher dormancy, delayed emergence within a season and greater within-season temporal spread.

The general long-term fitness benefits of dormancy and within-season temporal spread of emergence were convincingly demonstrated within an annual plant community from the Sonoran desert (Gremer & Venable 2014; Gremer et al. 2016). Controversial, however, remained the model predic-

tion that plants invest more in bet-hedging germination in drier, more variable environments (Cohen 1966; Childs et al. 2010). Empirical intraspecific tests along aridity gradients for the predicted shift of germination yielded quite heterogeneous patterns and were largely restricted to dormancy (summarized in Cochrane, Yates, Hoyle, & Nicotra 2015). This is unfortunate because one bet-hedging trait may compensate for another (Venable & Brown 1988; Simons 2014) so that a missing shift in dormancy may veil a shift in within-season emergence timing, and vice versa. Moreover, most existing dormancy studies included only 3–4 populations per species, so that (missing) general trends are difficult to separate from stochastic trait divergence between single populations (Kurze, Bareither, & Metz 2017). This strongly calls for studies that include larger numbers of populations across rainfall gradients to provide rigorous tests of Cohen's (1966) prediction, and for studies that quantify not only dormancy but also within-season emergence timing to account for alternative strategies of bet-hedging germination.

Rainfall gradients are not only governed by increasing aridity and rainfall unpredictability but also by changing competition regimes. Competition is more intense in rainier, more productive sites, both among annual plants (Schiffers & Tielbörger 2006; Liancourt & Tielbörger 2009) and between annuals and neighboring shrubs (Metz & Tielbörger 2016). Consistent with that trend, species often show marked intraspecific clines in various traits among populations to adapt locally to higher competition in wetter sites and to drought stress in arid sites (e.g. Del Pozo, Ovalle, Aronson, & Avendaño 2002; Liancourt & Tielbörger 2009; Kurze et al. 2017). It is unknown though whether these intraspecific adaptations comprise already the earliest life stage: emerging seedlings. There is convincing evidence that seeds sense each other and that seed–seed interactions can substantially alter germination behavior. For example, the presence of neighboring seeds can shift time to emergence by several days – in line with the idea that early emergers gain a competitive edge over co-emerging seedlings (Tielbörger & Prasse 2009; Orrock & Christopher 2010; Fenesi, Albert, & Ruprecht 2014; Houseman & Mahoney 2015). Moreover, germination fractions were often reduced under high seed densities (Tielbörger & Prasse 2009; Fenesi et al. 2014; Renne et al. 2014); but controversy remained whether this should be interpreted as adaptive competition avoidance or simply follows from neighbors suppressing other seedlings from germinating. These seed–seed interactions were generally highly species-specific and may therefore affect community composition at later plant stages. For example, it was proposed that weaker competitors such as early successional or small-seeded species are more strongly affected by neighbor seeds (Tielbörger & Prasse 2009; Renne et al. 2014). Interestingly, along the same line of thought one might expect differentiation *within* a species: populations from wetter, more competitive environments may be less suppressed by neighboring seeds than those from arid, less competitive envi-

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