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Seed mass and dormancy of annual plant populations and communities decreases with aridity and rainfall predictability

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Abstract

Several theoretical and empirical studies have examined the influence of environmental conditions on seed traits and germination strategies of annual species. A positive relationship between seed mass and dormancy has been described for annuals occupying climatically unpredictable ecosystems. Larger-seeded species tend to have higher seedling survival rates, while dormancy allows a bet-hedging strategy in unpredictable environments. Until now, these ideas have been addressed primarily for only one or a few focal species, without considering differences among populations and communities. The novelty of the present study lies in the population and community-level approach, where a comprehensive seed trait database including 158 annual species occurring along a gradient of rainfall variability and aridity in Israel was used to ask the following question: Does average seed mass and dormancy of annual populations and communities decrease with increasing aridity and rainfall unpredictability?

Soil seed bank samples were collected at the end of the summer drought, before the onset of the rains, from four plant communities. Germination was tested under irrigated conditions during three consecutive germination seasons to determine the overall seed germinability in each soil sample. Seed mass was obtained from newly produced seeds collected at the study sites in late spring. The community level results showed that, in contrast to common theoretical knowledge, seed mass and dormancy of the dominant annual species decreased with increasing aridity and rainfall variability. Accordingly, a negative correlation was found between seed mass and seed germination fractions. The present study demonstrates that an analysis of seed traits along climatic gradients is significantly improved by approaches that target both population and community levels simultaneously. A critical evaluation sheds new light upon the selective pressures that act on seed ecology of annuals along a climatic gradient and facilitates formulation of more mechanistic hypotheses about factors governing critical seed traits.

Zusammenfassung

Theoretische und empirische Studien haben sich mit dem Einfluss von Umweltbedingungen auf die Eigenschaften von Pflanzensamen und auf Keimungsstrategien annueller Arten befasst. In stochastischen Ökosystemen ist eine positive Korrelation zwischen Samenmasse und Dormanz für annuelle Pflanzen als typisch beschrieben worden. Arten mit grösseren Samen neigen dazu höhere Keimlingsüberlebensraten zu haben, während erhöhte Dormanz als Absicherungstrategie gegen unvorhersehbare Umweltbedingungen gedeuted wurde. Bis jetzt sind diese Ausagen ledigich für einzelne oder wenige Arten untersucht worden und Ansätze, die Unterschiede zwischen Populationen und Pflanzengemeinschaften berücksichtigen, fehlen weitaus.

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Die Neuheit der gegenwärtigen Untersuchung beruht auf der Fragestellung auf Populations- und Gemeinschaftsniveau. Eine umfassende Datenbank, welche die Sameneigenschaften von 158 Anuellen entlang eines Tockenheitsgradienten in Israel umfasst, wurde verwandt, um die folgende Frage zu untersuchen: Wie verhält sich die durchschnittliche Samenmasse und Dormanz in Bezug zu zunehmender Aridität und Niederschlagsvorhersehbarkeit?

In vier Pflanzengemeinschaften entlang des Gradienten wurden Samenbankproben am Ende der Sommertrockenheitsperiode vor den ersten Regenfällen genommen. Die Bodenproben wurden während drei aufeinanderfolgenden Wachstumsperioden bewässert, um Keimungsprozente aller Arten zu bestimmen. Samenfrishgewicht wurde anhand von in den Untersuchungsgebieten gesammelter Samen bestimmt.

Samenmasse und Dormanz nahmen auf Gemeinschaftsniveau mit zunehmender Aridität und Niederschlagsvorhersehbarkeit ab; ein Ergebnis, welches im Kontrast zu bestehender Theorie steht. Eine negative Korrelation zwischen Samenmasse und der prozentualen Keimungsrate wurde darüberhinus gefunden. Die vorliegende Untersuchung demonstriert, dass eine umfassende Analyse von Sameneigenschaften entlang eines klimatischen Gradienten sowohl auf Populations–als auch auf Gemeinschaftsniveau unternommen werden sollte. Eine kritische Bewertung des Selektionsdruckes auf die Samenökologie annueller Arten ist notwendig, um mechanistische Hypothesen bezüglich der Charaktereigenschaften von Pflanzesamen aufstellen zu können.

Keywords: Desert; Germination strategies; Mediterranean; Plant community; Seed bank; Seed size

Introduction

Soil seed banks play an important role in annual plant populations by buffering populations against temporal variation (Clauss & Venable 2000) and by avoiding the demographic effects of reproductive failure (Evans & Cabin 1995). Such seed banks contain dormant seeds that did not germinate even when placed under conditions that are generally suitable for germination (Philippi 1993).

Deserts and Mediterranean-type ecosystems are good examples of ecosystems where soil seed banks play an important role in preserving plant populations and communities. This is especially true for annuals, as their seeds are the only structure linking one year to the next (Pake & Venable 1996; Adondakis & Venable 2004). Delayed germination (a bet-hedging strategy) is, in theory, one of the most efficient adaptations for annuals inhabiting arid environments, which are typically characterized by highly variable and unpredictable climatic conditions (Philippi 1993). This adaptation buffers against reproductive failure by spreading seed germination over several years, reducing the variance in fitness across years, at the cost of reducing the (arithmetic) average fitness within each year (Philippi & Seger 1989; Philippi 1993). In more mesic and climatically predictable Mediterranean-type ecosystems, the formation of soil seed banks is also regarded as an adaptive response to disturbance and grazing (Holzapfel, Schmidt, & Shmida 1993; Sternberg, Gutman, Perevolotsky, & Kigel 2003; Osem, Perevoltsky, & Kigel 2006) and/or competition (Aikio, Ranta, Kaitala, & Lundberg 2002; Volis, Mendlinger, & Ward 2002).

Seed mass, which links plant regeneration, vegetative growth, and survival, is another key functional trait for coping with environmental stress. Larger-seeded species tend to have higher seedling survival rates (e.g. Westoby, Falster, Moles, Vesk, & Wright 2002) especially under dry conditions (e.g. Baker 1972) and are thus more common in such environments (Wright & Westoby 1999). Seedlings produced by larger seeds may be more capable of resisting environmental hazards due to larger reserves that can be exploited as a mechanism of drought resistance (Leishman & Westoby 1994).

Environmental gradients provide a useful framework for evaluating the relative importance of differential selective forces on adaptive traits (here: seed mass and dormancy) that maximize fitness among different species (Endler 1986). In the present study we used an aridity gradient as a framework for investigating the effects of climatic differences on adaptive variation in seed life traits in four annual plant communities. We focused on annual species as they encompass more than 80% of the species present in the soil seed banks at the study sites. The gradient ranges from arid desert to a mesic Mediterranean ecosystem and varies both in rainfall quantity and predictability. At the arid end of the precipitation gradient, rainfall events are highly unpredictable between years, while at the mesic end of the gradient climatic conditions are more favorable.

Previous studies have examined the influence of environmental conditions such as climatic variability and water availability on seed dormancy and seed size in annual plant species (Philippi 1993; Clauss & Venable 2000; Adondakis & Venable 2004). However, most studies have focused on only one or few focal species, without scaling up to the higher community level. We believe that scaling up from species and population level is needed in order to advance in understanding of, and ability to, predict community assembly (McGill, Enquist, Weiher, & Westoby 2006). By assembling a comprehensive database of seed life traits of the complete annual plant community, the present study combined novel population and community-level approaches. According to ecological theory, populations of annual species from climatically unpredictable arid and semiarid ecosystems should exhibit (1) lower germination rates (or a higher proportion