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Correlates of inter-specific variation in germination response to water stress in a semi-arid savannah

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Abstract

Within arid plant communities species vary considerably in the ability to germinate under water stress. Attempts to correlate this variation with environmental gradients have remained largely inconclusive. Germinating only at high water potentials can be seen as a form of predictive germination. Predictive germination provides a fitness variance reducing mechanism and is therefore expected to show negative correlations with other variance reducing life-history attributes such as large seed size or dormancy. We predicted that differences in life-history attributes rather than edaphic gradients could explain the variation in germination responses to water stress found in arid plant communities. To test our hypothesis we determined the germination response of 28 species from the arid Kalahari savannah to a gradient of osmotic stress, expressed as the water potential needed to reduce germination by 50%. In addition, we determined the life-history variables seed mass and germination fraction and the habitat variables soil texture preference and association with acacias. The data were analysed using phylogenetically independent contrasts in a multiple regression model.

Contrary to our hypothesis we found no increase in the capacity to germinate under osmotic stress with increasing seed mass and an increase with increasing germination fraction. However, we also found no significant effect of the habitat variables. This result may be explained by variation in seedling drought tolerance. Drought tolerance will also have a variance-reducing effect and can be expected to trade-off with fractional germination. Our results suggest that in arid plant communities most variation in the capacity to germinate under water stress expresses different ways to make a living under similar conditions rather than adaptations to environmental gradients.

Zusammenfassung

Innerhalb arider Pflanzengesellschaften gibt es große zwischenartliche Unterschiede in der Fähigkeit unter Wasserstress zu keimen. Versuche, diese Variation mit Umweltgradienten zu korrelieren, bleiben meistens ergebnislos. Die Keimung nur bei hohen Wasserpotenzialen ist eine Art prädiktiver Keimung. Prädiktive Keimung ist ein Mechanismus zur Reduzierung der Varianz der Fitness, weshalb man eine negative Korrelation mit anderen Varianz-reduzierenden Life-history-Attributen wie große Samen oder Dormanz erwarten kann. Wir nehmen an dass statt edaphischer Gradienten unterschiedliche Life-history-Merkmale die Variation im Keimungsverhalten bei Wasserstress in ariden Pflanzengesellschaften bestimmen. Zur Überprufung unserer Hypothese bestimmten wir das Keimungsverhalten von 28 Arten der ariden Kalahari-Savanne auf einem Gradienten von osmotischem Stress, ausgedrückt als

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Wasserpotenzial, das die Keimung zu 50% reduziert. Dazu bestimmten wir die Life-history-Variablen Samenmasse und Keimungsfraktion und die Habitatvariablen Bodenkorngröße-Präferenz und Assoziation mit Akazien. Die Daten wurden unter Verwendung phylogenetisch unabhängiger Kontraste in einem Multiplen Regressions-Model analysiert. Im Gegensatz zu unserer Annahme fanden wir mit zunehmender Samenmasse keine Zunahme in der Fähigkeit unter Wasserstress zu keimen sowie mit zunehmender Keimungsfraktion eine Zunahme in der Fähigkeit unter Wasserstress zu keimen. Allerdings fanden wir auch keinen signifikanten Effekt der Habitatvariablen. Dieses Ergebnis könnte man durch die Variation in der Trockenheitstoleranz von Keimlingen erklären. Trockenheitstoleranz wird auch einen Varianz-reduzierenden Effekt haben, weshalb man einen trade-off mit der fraktionellen Keimung erwarten kann. Unsere Ergebnisse weisen darauf hin, dass innerhalb arider Pflanzengesellschaften der größte Teil der Variation in der Fähigkeit unter Wasserstress zu keimen unterschiedliche Lebensstrategien unter gleichen Umweltbedingungen ausdrückt als Anpassungen an Umweltgradienten.

Keywords: Dormancy; Drought tolerance; Facilitation; Nurse plants; PEG; Predictive germination; Seed mass; Soil moisture; Soil texture; Southern Kalahari

Introduction

Germination is a high-risk event in the life cycle of most plants (Harper, 1977). Mechanisms reducing the risks associated with germination can therefore be expected to be under strong selection pressure. Accordingly, plants have developed a wide array of predictive germination strategies where the response to specific environmental cues maximizes the probability that germination takes place at the optimal time for establishment (Baskin & Baskin, 1998). Drought is one of the major causes of seedling mortality (Moles & Westoby, 2004) and in arid environments soil moisture is likely to be one of the more important factors upon which predictive germination is based.

Numerous studies describe the response of one or a few species to a gradient of osmotic stress (see Baskin & Baskin, 1998, for an overview) and the results are usually interpreted in relation to habitat or climate. Yet the few studies that included a larger number of species within a community show that large inter-specific variation is found in the ability of different species to germinate under water stress. Attempts to correlate this variation with edaphic factors like soil type and moisture conditions (Briedé & McKell, 1992; Evans & Etherington, 1990; Schütz, Milberg, & Lamont, 2002; Sy, Grouzis, & Danthu, 2001; but see Allen, Meyer, & Khan, 2000), or climate (Köchy & Tielbörger, 2007) have been largely inconclusive.

We predict that differences in life-history attributes rather than the physical environment can explain the large variation in germination response to osmotic stress found within arid plant communities. Temporally variable environments may favour life-history traits that reduce fitness variance, such as increased seed size, dormancy and dispersal, and theory predicts that life-history attributes that reduce the impact of environmental variation on fitness will be negatively correlated (Rees, 1994; Venable & Brown, 1988). Predictive germination (i.e. germinating only at high water potentials) also provides a variance-reducing mechanism (Venable & Brown, 1988) and is therefore expected to show negative correlations with other variance-reducing life-history attributes.

Here we specifically address the effect of seed size and dormancy on predictive germination. Large seeds may buffer seedlings from some of the negative effects of drought (Leishman, Wright, Moles, & Westoby, 2000) and there is experimental evidence for the advantage of large seed size for establishment under low soil moisture conditions (Leishman & Westoby, 1994). Seed size is therefore expected to be positively correlated with the ability to germinate under osmotic stress.

When the accuracy of predictive germination increases the optimal germination fraction is expected to increase, because low germination fractions form a buffer against mistakenly germinating and dying (Venable & Lawlor, 1980). The probability to correctly predict favourable conditions for seedling establishment can be expected to increase with germination being restricted to higher water potentials. Therefore, a negative correlation between the ability to germinate under water stress and germination fraction is expected.

Edaphic factors may still be important determinants of germination behaviour in relation to osmotic stress. Certain habitats may constrain the range of feasible water potentials for germination. Though coarse soils generally provide more favourable moisture conditions for plants in arid regions than fine soils, fine soils will, due to capillary rise, provide higher moisture level for a longer time near the surface than more coarse soils (Alizai & Hulbert, 1970). Seeds in sand therefore have to germinate at high water potentials to ensure that seedlings will be able to keep up with the rapidly descending water. We predict that species of coarse soils will cease to germinate at higher water potential than species of fine soils.