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Seedling root traits strongly influence field survival and performance of a common bunchgrass

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Abstract

Seedling survival is a limiting factor in arid-land restoration. We investigated how variation in the root traits of glasshouse-reared seedlings related to the field performance of different genotypes from two populations of *Elymus elymoides* (squirreltail), a common bunchgrass native to the Western United States. Seeds from 100 *E. elymoides* individuals were collected from two sites in northern Nevada. We planted offspring of these 100 individuals in the glasshouse to characterize 10-day root traits of each maternal family. Root traits of glasshouse-reared plants and seed size measures were correlated with the performance of siblings grown in field plots close to the seed collection sites. Seedling root traits were related to performance of siblings at both sites. We estimate that within-population variation in root traits was associated with a more than six- to nine-fold increase in seedling survival probability and a two-fold increase in height at the less productive site, and a two-fold increase in survival and 1.2-fold increase in size at the more productive site. At both sites, effects of root traits were complex, with extreme values of some traits favoured and intermediate values of other traits favoured. There is a recognized need to integrate understanding of plant functional traits into larger conceptual frameworks of ecological restoration. Here we show that within-population variation in a suite of root functional traits relates to large variation in seedling survival and size of an arid-land grass species, improving our understanding of how trait variation affects performance in the field. Understanding such variation may be used to positively impact restoration outcomes.

Zusammenfassung

Das Überleben der Sämlinge ist ein limitierender Faktor bei der Renaturierung in trockenen Gebieten. Wir untersuchten wie die Variation von Wurzelmerkmalen bei im Gewächshaus gezogenen Sämlingen sich zur Freilandperformanz von unterschiedlichen Genotypen aus zwei Populationen von *Elymus elymoides*, einem häufigen, einheimischen Tussockgras des Westens der Vereinigten Staaten verhält. Samen von 100 Individuen von *E. elymoides* wurden auf zwei Flächen in Nord-Nevada gesammelt. Wir pflanzten die Nachkommen dieser 100 Individuen im Gewächshaus aus, um nach zehn Tagen die Merkmale der Wurzeln jeder Mutterfamilie zu beschreiben. Die Wurzelmerkmale der Pflanzen aus dem Gewächshaus und die gemessenen Samengrößen wurden mit der Performanz von verwandten Individuen korreliert, die auf Freiflächen nahe den Sammelstellen wuchsen. Die

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Wurzelmerkmale der Sämlinge standen auf beiden Flächen in Beziehung zur Performanz der Geschwister. Wir kalkulierten, dass die Variation der Wurzelmerkmale innerhalb einer Population mit einer sechs- bis über neunfachen Zunahme der Überlebensrate der Sämlinge verbunden war und mit einer 1.2-fachen Größenzunahme auf der produktiveren Fläche. Auf beiden Flächen waren die Effekte der Wurzelmerkmale komplex, wobei bei manchen Merkmalen extreme Werte, bei anderen aber intermediäre Werte begünstigt wurden. Es besteht ein anerkannter Bedarf dafür, das Verständnis von funktionalen Pflanzenmerkmalen in das konzeptionelle Bezugssystem der ökologischen Renaturierung zu integrieren. Hier zeigen wir, dass die Variation einer Reihe von funktionellen Wurzelmerkmalen innerhalb einer Population mit der großen Variationsbreite von Überlebensrate und Größe der Sämlinge einer Grasart der Trockengebiete zusammenhängt. Dies verbessert unser Verständnis davon, wie diese Variation die Performanz im Freiland beeinflusst. Und das Verständnis derartiger Variabilität kann genutzt werden, um die Ergebnisse von Renaturierungen positiv zu beeinflussen.

Keywords: *Bromus tectorum*; *Elymus elymoides*; Great Basin; Restoration; Root architecture; Root development; Root size; Seed mass

Introduction

Roots are a major area of interface between plants and their environment. Root architecture, i.e. the surface characteristics, branch morphology, and gross topology of root tissue (after Fitter, 1987), is known to influence nutrient uptake (Busso, Briske, & Olalde-Portugal, 2001), stress resistance (Rundel & Nobel, 1991), interaction with competitors (Casper & Jackson 1997), and interaction with soil microorganisms (Hetrick, 1991; Nibau, Gibbs, & Coates, 2008; also reviewed by Hodge, Berta, Doussan, Merchan, & Crespi, 2009). While simulation models have shown that the length, depth, and arrangement of roots can affect the rate, amount and location of nutrient uptake (e.g. Somma, Hopmans, & Clausnitzer, 1998), experimental studies of the ecological importance of root form are difficult, due to the extreme plasticity of root traits and to the practical difficulty of directly observing processes in soil. As a result, we understand some of the drivers of plastic changes in root form and we can associate differences in root architecture with changes in resource capture (see reviews by Lynch, 1995; Casper & Jackson, 1997; Hodge et al., 2009), but we still know little about how variation in root form affects plant survival and function (Lynch, 1995; Pacheco-Villalobos & Hardtke, 2012).

Among species, variation in root traits is believed to have important effects on the ecology of plant species. This is certainly the case for plants in water-limited environments, where adequate root proliferation is necessary to take advantage of scant rain during the growing season (Gregory 2008). However, roots are costly to produce, and overproduction of roots could increase the risk of water loss in dry soils. Correctly balancing these conflicting pressures is thought to be crucial for plants growing in arid environments (Canadell et al., 1996; Jackson et al., 1996; Schulze et al., 1996). For grasses growing in arid environment, it is believed that proliferation of shallow roots aids water capture during sporadic rain events, although the exact relationship between root form and ecological function is still unknown (Rundel & Nobel, 1991; Donovan & Ehleringer, 1994; Gibbens & Lenz, 2001).

Within-species, most studies have focused on the importance of plastic variation in root form, e.g. in response to varying resource abundance (reviewed by Lynch, 1995; Casper & Jackson, 1997). However, non-plastic, heritable within-species variation in root form is also known to exist, particularly for crop species and model organisms (reviewed by Pacheco-Villalobos & Hardtke, 2012). In crop species, root traits have been linked to performance in water-limited environments (Manschadi, Hammer, Christopher, & deVoil, 2008). In model organisms like *Arabidopsis*, rice, and tomato, rapid progress is being made in our understanding of the genetic controls over root architecture in these species (reviewed in Nibau et al., 2008). Much less is known about how within-species variation in root form affects the performance of wild plants, however Rowe and Leger (2011) showed that invasion by *Bromus tectorum* was associated with changes in a large number of root traits of the arid-land native grass *Elymus multisetus*, including changes in root length, diameter, and branching patterns. This variation was also found to affect competitive performance in a glasshouse experiment.

Understanding the relationship between seedling traits and field performance is important for understanding the ecology of arid plants, but it may also provide information that is important for land stewardship. For example, disturbance by fire, climate change, and invasion represent major threats to Great Basin ecosystem health and natural resource quality (Reynolds et al., 2007; UNCCD, 2012). Restoration to combat natural resource loss requires the use of appropriate native seed sources, but how best to identify such seed sources is the subject of a large and long-lasting debate in restoration ecology (see McKay, Christian, Harrison, & Rice, 2005; Broadhurst et al., 2008; Vander