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Plant Root Mass Fraction Response to Soil Resource Limitation in the Context of Dry Mediterranean Rangeland

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Abstract

Root mass fraction (RMF) was proposed as a stable measurement of plant resource partitioning that can represent plant acquisition–conservation trade-offs. We examined the effects of soil resources availability on RMF of abundant annual plant species of water-limited rangeland. We used data from controlled experiments in which nine species were grown under variable water and nitrogen availabilities and their root and shoot biomass were examined at flowering time. In legumes we examined also presence of N_2-fixation. In all of the species, reduced water and/or nitrogen availability was associated with increased RMF. However, the magnitude of variation in RMF found between the resource availability treatments was different among the annual species. At the intra-specific level, plant size was negatively related to RMF. Finally, in legumes RMF corresponded to the species' N_2-fixation status.

Introduction

Annual plant species are typical of water-limited environments, and are represented in high diversity in Mediterranean rangelands, in which amounts and distribution of rainfall are highly unpredictable and confined to a short season. During this limited growth period, the annual plants' partition biomass between root and shoot in order to optimize resource capture (McConnaughay and Coleman 1999) and maximize fitness (Weiner et al. 2009). Thus, variation in the total biomass of annual plants at the end of the growing season reflects differences in resource capture and biomass production rate, whereas variation in biomass partitioning may reflect the adaptation and adjustment of species in their coping with variation in resource availability (Dovrat et al. 2019a). Previous works have shown that plant species respond to soil resource limitation by altering their biomass partitioning in order to better capture and preserve limited resources (see in Poorter et al 2011). However, these works mainly focused on resource allocation physiology and did not deal with the biomass partitioning patterns of a particular plant assemblage.

Since the size and seed production of annual plant species are directly related to the environmental conditions prevailing during a defined growth period (i.e., one growth season), annual plant communities provide a unique opportunity to study patterns of resource capture and allocation in relation to environmental conditions. However, to date, only few empirical studies have examined the magnitude and patterns of biomass partitioning traits with respect to total plant biomass within and among plant species and under varying resource availability (Chanteloup and Bonis 2013, Nathan et al. 2016, Dovrat et al. 2019b). In recent works, we empirically studied the extent and pattern in which plant size is related to resource partitioning within and among key annual plant species and under varying resource availability (Dovrat et al. 2019a, Dovrat et al. 2020a).

Unlike root-to-shoot ratio, the use of root mass fraction (RMF) had been proposed as a stable measurement of resource partitioning (Poorter and Nagel 2000). In annual species, measurements of RMF at fixed phenological phases, such as flowering time, allow ontogenetically controlled comparisons among plants. In this work we examined RMF response within and among annual plant species of water-limited rangeland, under varying soil resource availability.

Methods and Study Site

We have reanalysed annual species biomass production data. The selected species represent a range of sizes (Osem et al. 2004) and constitute a major portion of the plant abundance and productivity of the annual plant community at Lehavim Long-Term Ecological Research Station. The climate in Lehavim is semi-arid with a short winter, and the average annual rainfall is 295 mm. The vegetation is characterized by sparse shrubland, with diverse herbaceous vegetation growing in large open patches between the shrubs. The herbaceous vegetation comprises mainly of annual species (130 identified species). The area has been used for livestock grazing (mainly sheep and goats) since prehistorical times (5000–8000 years, Perevolotsky and Seligman,1998).

Controlled experiments were conducted at the Volcani Center, Israel. Each of the species was grown as a single plant in a separate pot under three water levels (eight species) and two nitrogen levels (nine species). Destructive measurements of root and shoot biomass were conducted at flowering (81-86 days). Each treatment was performed in 5-10 replicates (pots). More details on the experimental methods can be found in Dovrat et al. (2018, 2019a). Biomass of shoots and roots was measured following oven drying (60° for 72 hours). Root mass fraction was calculated by dividing plant root dry biomass by the total dry biomass. Flowering time was determined for each treatment according to petal opening or, in the case of grass, according to the appearance of stamens.

In order to examine the effects of species, water availability and nitrogen availability, on plant total biomass and RMF, a Multifactorial ANOVA test was used. Basic assumptions for ANOVA tests i.e., normal distribution of error and homogeneity of variances, were examined using the Kolmogorov–Smirnov test and Levene's test, respectively. Data not corresponding to these assumptions was mathematically transformed. All statistical analyses were conducted with the SPSS 25.0 software (SPSS Inc, Chicago, IL, USA).

Results

In all nine annual species examined, decrease in water and nitrogen availability caused an increase in RMF. Multifactorial analysis results showed significant effects of water and N availabilities on species' RMF, as well as significant interspecific differences in RMF and total biomass. Interspecific differences in the extent of the response to N-availability were reflected through significant N×sp. interaction on RMF. Additionally, no significant N×water interaction effects were found, indicating an independent effect of water and N availabilities on RMF.

Discussion

Annual species respond to changes in soil resources availability and reorganize through resource partitioning, as we have presented here, via changes in RMF. Reorganization allows better use of available resources and maintenance of reproductive effort (Dovrat et al. 2019a). All studied species decrease in size and increase in RMF in response to decrease water availability. However the magnitude of variation in plant size as well as in RMF found along the soil-resource availability treatments was different among the annual species. This interspecific variation reflects a range of biomass allocation strategies present in the plant community of the studied water-limited rangelands site, which allows fast response to rainfall amount and distribution (Dovrat et al. 2020b).

Using soil resources manipulation, we demonstrated in recent works that annual species size (flowering size) was negatively related to root to shoot ratio at the intraspecific level, but no relationship was found between size and biomass partitioning at the interspecific level (Dovrat et al. 2019a). However, we found that species size was negatively related to stress resistance. This tradeoff between species size and stress resistance emerges as a consistent property of fundamental importance in shaping annual plant communities along resource gradients (Dovrat et al. 2019a). In another work we showed that RMF of annual Fabaceae species was higher in uninoculated (without bacterial inoculation) plants compared to N_2-fixing plants. The root mass fraction was similar in inoculated plants of all species regardless of dramatic differences in nitrogen availability, and was not influenced by the different sizes of plants at flowering time (Dovrat et al. 2020a).

Biomass partitioning trade-offs can explain the presence and abundance of species along resource availability gradients and are primary drivers of community productivity patterns (Nathan et al. 2016). Future work is required to understand the importance of these mechanisms in plant community response to herbivory, as well as in invasive weed dynamics in these water-limited rangelands.

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