Research article

Light limitation shapes the community seed mass of annual but not of perennial weeds

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ARTICLE INFO

ABSTRACT

How seed mass determines plant performance is dependent on the type of herbaceous community. Here, we hypothesized that life span is a decisive driver of the seed mass response to an environmental gradient. We examined whether separating community data into annuals and perennials sheds new light on seed mass importance in herbaceous weed vegetation of arable fields. We studied the seed mass response to a gradient of light limitation and tested the prediction that seed mass will increase with light limitation but that the trend will differ in annuals compared to perennials. In summary, only the seed mass of annuals reacted to the light limitation gradient. The seed mass community-weighted mean (CWM), controlled for crop type and seasonality, was positively linked with crop coverage, i.e., a proxy for light limitation. The seed mass CWM of perennials exhibited a random distribution. In annuals which are strongly dependent on seeds, large seeds are advantageous under dense crop canopies. We showed that considering the relevance of a trait for a particular strategy can improve our understanding of community assembly. This approach can help to explain some differences among published studies regarding the effect of an environmental gradient on the community seed mass.

1. Introduction

Studying the patterns of trait changes along environmental gradients is one of the major topics of trait-based ecology. In particular, regeneration traits such as seed mass are very often considered (Lhotsky et al., 2016; Metz et al., 2010; Santini et al., 2017). Seed mass is one of the three components of the LHS (leaf-height-seed) plant ecology strategy scheme (Westoby, 1998), a key trait in the dynamics of community structure (Leishman, 2001) and a part of the leading dimension of variation between species (Díaz et al., 2016; Westoby et al., 2002). In herbaceous vegetation, the role of seed mass in structuring communities has been thoroughly studied but the evidence is mixed (Coomes and Grubb, 2003; Fenner, 1985; Klimešová et al., 2016; Levine and Rees, 2002). The relevance of seed mass varies according to the type of vegetation and type of plants (summarized in Coomes and Grubb, 2003). This uncertainty of the importance of seed mass in herbs can be obscured by the significant proportion of perennial herbs relying on clonal propagation instead of seed production (Klimešová et al., 2016). In annuals, however, seed mass is a trait involved in all important aspects of plant ecology, such as dispersal, colonization, recruitment, tolerance of environmental hazards and competition.

Large-seeded plants are thought to have an advantage over small-seeded plants beyond seedling establishment (Metz et al., 2010); however, this advantage is dependent on site conditions (e.g., the level of shade, soil nutrients or disturbance). Light limitation (sensu Borer et al., 2014) is a key factor in plant communities (Hautier et al., 2009), and it is closely associated with site productivity. In line with the tolerance-fecundity trade-off (Muller-Landau, 2010), it has been hypothesized that seedlings from large-seeded plants better endure stressful shading (Bergholz et al., 2015; Leishman et al., 2000; Manning et al., 2009) because of at least two mechanisms. First, higher resource reserves provide a competitive advantage as plants can spend additional resources on shoot biomass. Large-seeded species, therefore, should be better competitors for light (Tilman, 1988). Second, seed reserves boost survival below denser canopies, i.e., plants with larger seeds tolerate lower levels of light in closed vegetation (Manning et al., 2009) or under litter (Lönnberg and Eriksson, 2013; Thompson, 1987). Nevertheless, Bergholz et al. (2015) recently suggested that the hypothesized positive relationship between community seed mass and plant canopy density is not linear but rather U shaped. If soil nutrients are considered (positively correlated with canopy density), these shifts appear to be the consequence of site productivity (competition for light) and the varying stress tolerance of seeds. On the one hand, large seeds can be advantageous under oligotrophic conditions (Adler et al., 2013;

Dainese and Sitzia, 2013), because these better provisioned seeds have a higher chance of reaching maturity. On the other hand, productive sites also select for large-seeded species because non-limiting nutrients enhance light competition and stressful shading, which are necessary for seedlings to overcome (Bergholz et al., 2015; Hautier et al., 2009).

Arable weed communities are an excellent example of annual-dominated and frequently disturbed communities (Lososová et al., 2006) where seed mass is a vital trait (Manning et al., 2009). Weeds grow in the crop understorey and shade impacts them during their whole life cycle. Recently, trait-based studies that dealt with seed mass as an essential part of the LHS scheme (Westoby, 1998) questioned its relevance in herbs (Klimešová et al., 2016) or arable communities (Perronne et al., 2015). Currently, the relationship between community seed mass and light limitation gradients is under debate. While some studies found a positive linear relationship (Leishman et al., 2000; Manning et al., 2009; May et al., 2013), others reported non-linear trends (Bergholz et al., 2015; Guerrero et al., 2014) or found weak or no evidence (Lhotsky et al., 2016; Lönnberg and Eriksson, 2013; Santini et al., 2017). Moreover, it should be noted that the majority of studies reporting an increase in seed mass along plant density or productivity gradients were conducted on annuals (Harel et al., 2011; Manning et al., 2009; Santini et al., 2017) or annual-dominated communities (Guerrero et al., 2014; May et al., 2013), but see Bergholz et al. (2015). This finding suggests that life span might play an important role in the association between seed mass and environmental conditions.

In this study, we investigated whether inconsistent and contra-dicting evidence in the literature stems from the disparity of plant strategies: annual and perennial life span. As far as we know, no study has challenged the established theory of seed mass changes in response to environmental variation from the separated perspective of annuals and perennials. It is, therefore, essential to provide a study that could reveal clear patterns in seed mass changes in annuals and perennials due to variation in one of the most often studied ecological filters (light limitation). Hence, we tested the following hypothesis: average seed mass (community-weighted mean CWM) increases along a crop coverage gradient (proxy of light limitation or productivity), i.e., species with a higher seed mass are favoured under high crop coverage because these species exhibit better light limitation (stressful shading) tolerance. We specifically tested whether the changes in the seed mass CWM along a crop coverage gradient are consistent or differ according to life span strategy (Fig. 1).

2. Material and methods

2.1. Study sites and sampling

The study area (Fig. 2) covers 11,000 km^2 in northern and central Moravia, which is located in the northeastern part of the Czech Republic (49° 08′–50° 27′ N, 16° 43′–18° 52′ E). The mean annual temperature is 4.5–8.5 °C, and the annual precipitation ranges from 575 to 1 300 mm. The altitude of the study sites spans from 195 to 815 m a. s. l. We recorded vegetation data on arable land for the period 2001–2003. We used a stratified sampling scheme for obtaining a stratified dataset, which produced land categories (polygons) with unique combinations of soil, climate and potential natural vegetation. For more details about the stratifying procedure see Cimalová and Lososová (2009). We sampled in both cereal (autumn seeding: wheat and rye; spring seeding: oat and barley) and root crops (sugar beet, potatoes). Plots of a standard size of 20 m^2 were randomly situated along edges where the effects of herbicide use are relatively low in conventionally managed fields. The total number of sampled plots was 233.

2.2. Traits and variables

We retrieved average seed mass data from the databases BiolFlor (Klotz et al., 2002) and LEDA (Kleyer et al., 2008). A total of 208
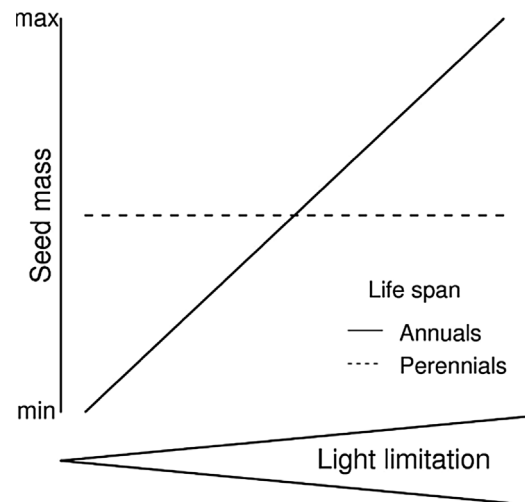

Fig. 1. The hypothesis tested in this study. The strength of the relationship between community seed mass and increasing light limitation is dependent on seed mass relevance. Here, we hypothesized that this relevance differs in annual and perennial weeds. When plant performance is largely dependent on seed mass (annuals), a response is detectable. On the other hand, one can observe no response in cases where recruitment is weakly dependent on seed mass (perennials with clonal reproduction). Note that the slope and intercept of the regression line change according to relevance.

species were recorded (103 annuals and 105 perennials; listed in Appendix A). For the species *Armoracia rusticana* we found no data; hence, its seed mass was estimated from the regression model of the inter-trait relationship between seed mass and plant height (data from LEDA database). To assess the impact on weed community seed mass, we used three variables: (1) crop coverage (estimated cover of the planted crop), (2) crop type (cereals: barley, oat, rye and wheat; root crops: beet and potato) and (3) sampling period (part of the season coded as a number of days since the start of the year). We used crop coverage as a suitable proxy for the light availability gradient. Weeds grow in the understorey; hence, the density of the crop canopy has to be strongly correlated with the light availability. We determined the crop coverage gradient by visual estimation of percentage cover on the van der Maarel scale (van der Maarel, 1979).

Weed communities are specifically shaped by cultivated plants and their associated management, and exhibit significant seasonal variation (Cimalová and Lososová, 2009; Gross et al., 2015; Nowak et al., 2015). Crop type is often used as an approximate measure of the differences in agricultural practices (like disturbance, sowing date, herbicide use or inherent traits of the crop; Lososová et al., 2004; Nowak et al., 2015; Šilc et al., 2009) that have been shown to be influential drivers of the seed mass response (Gaba et al., 2014; Gunton et al., 2011). We treated the crop type (an indicator of management practices) and season (an indicator of phenological changes in weed vegetation) as confounding variables. Crop coverage was the variable of direct interest.

2.3. Data processing and software

Prior to analysis we excluded crops, juvenile trees and non-seeded plants from the dataset. Prior to CWM calculation, we divided recorded plants into two groups based on the life span (annuals or perennials) and log-transformed their seed mass values. The seed mass CWM (weighted by percentage cover of each species) was calculated separately for each group in each plot. To explore the effect of light limitation on the seed mass CWM, we first tested the significance of the interaction term: life span x crop coverage. To do so, we combined annual and perennial datasets and fitted a linear model using the *lm* function in R (version 3.3.1; R Core Team, 2016) with all other predictors. Life span was treated as a binary variable. Given the non-constant proportions of annuals or perennials in sampled plots, we also