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Interactive effects of light, water, soil type and competition on the endangered *Minuartia smejkalii* vary over time

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Abstract: Understanding drivers of species performance is crucial for their effective conservation. Despite a range of studies on the effects of single biotic and abiotic factors on plant performance, very little is known about interactions among multiple factors and their effects over time. We studied competition and abiotic interactions in an endemic species of the Czech Republic, serpentinophyte *Minuartia smejkalii*, over four years. In a full factorial experiment, we evaluated the performance of *M. smejkalii* alone, in the presence of a competitor, *Festuca ovina,* and under different abiotic conditions, including different types of soil, light exposure and water regime, and observed its changes over time. The results indicate very complex interactions among these factors. Competition had negative effects on the performance of *M. smejkalii* (1.2 times larger plants and 1.8 times more flowers in the absence of the competitor), but abiotic factors had stronger effects than competition alone. The effects of *F. ovina* on *M. smejkalii* also varied depending on whether shaded or not and soil conditions. Biotic and abiotic factors had contrasting effects on plant and number of flowers, suggesting that investment in growth and reproduction are context dependent. The size of plants grown in shaded areas was 2.7 times larger than those grown in full sun, whereas plants under full sun produced 1.7 times more flowers than those grown in shaded conditions. Type of soil did not affect plant area, but plants produced 1.5 times more flowers in non-serpentine soils. Our results suggest that the effects of competition are very complex, interact with abiotic factors and vary over time. We highlight the importance of long-term studies to identify competitive interactions and the importance of studying competition under multiple conditions. Understanding how competition might affect performance of the endangered *M. smejkalii*, under certain abiotic conditions (i.e. soil, water, shading), provides essential information for implementation of more efficient long-term conservation strategies.

Keywords: competition, competitive ability, conservation, facilitation, long-term experiment, sandwort, endemic, serpentine

Introduction

Plants interact with their abiotic and biotic environment in complex ways. Some biotic interactions can be negative, for example herbivory that can cause structural damage, while other plants can produce certain allelochemicals that have detrimental effects on other plant species, by affecting their germination or growth. Among the most important

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biotic interactions are competition and facilitation (Callaway & Walker 1997). Competition in plants occurs when interactions with neighbouring individuals result in negative effects on growth or fitness due to a decrease of resource availability (Callaway & Walker 1997). In contrast to competition, facilitation occurs when the occurrence of a species positively influences the development of another species (Hunter & Aarssen 1988, Callaway 1995).

Competitive and facilitative interactions are strongly affected by abiotic (e.g. temperature, salinity, water availability) and biotic (e.g. life stage, physiology and indirect interactions with other species) factors (Callaway & Walker 1997). The balance between these two interactions are context dependent, varying in both space and time. Many studies have shown changes in interactions between competition and facilitation over time among seasons or years (e.g. Alberti et al. 2008, Alba et al. 2019, Sinclair et al. 2020) and along environmental gradients defined by abiotic stress (e.g. Pugnaire & Luque 2001). The stress gradient hypothesis (SGH) affirms that competition is more common in low abiotic stress conditions, whereas facilitation should increase in frequency as abiotic stress increases (Bertness & Callaway 1994, Brooker & Callaghan 1998). This hypothesis has received mixed support (Michalet et al. 2014), some studies confirm it (e.g. Liancourt et al. 2005, Dohn et al. 2013, Ziffer-Berger et al. 2014, López et al. 2016), even in systems other than plants (Adams et al. 2022); some contradict it (e.g. Tielbörger & Kadmon 2000, Maestre & Cortina 2004, Butterfield et al. 2016) and others report mixed results (Grant et al. 2014, Chaieb et al. 2020). These findings emphasize the SGH relationship varies a lot depending on specific gradients and conditions and there is a need to know a lot more about this variation (He et al. 2013).

Understanding how plants interact with their environment and the balance between competitive and facilitative interactions provides important insights into drivers of species dynamics under changing conditions (Brooker & Callaghan 1998, Michalet et al. 2014). However, the level of complexity quickly increases when all spatial-temporal and abiotic-biotic conditions are considered. One way to address this complexity is to separate the effect of these processes in controlled experimental studies (Connell 1983, Schoener 1983). Due to time and space associated logistic difficulties, most experimental studies focus on complex competitive interactions in a short-term up to one year (Goldberg & Barton 1992, Bachmann et al. 2005). However, long-term studies (more than a year) have shown that plant interactions sometimes change over time from facilitation to competition (e.g. Metz & Tielbörger 2016, Alba et al. 2019). Similarly, Chaieb et al. (2020) demonstrated that drought intensity promoted short-term facilitation supporting the stress gradient hypothesis, while facilitation decreased in the long-term.

Species adapted to serpentine habitats are useful systems for studying the relationship between competition and tolerance to abiotic stressful conditions. Serpentine soils contain low levels of nutrients (potassium, phosphorous, nitrogen) and high levels of toxic heavy metals such as chromium, cobalt, nickel and magnesium (Brady et al. 2005). In addition to the poor quality substrate, these habitats are often characterized by high temperatures, high solar radiation and low water availability. Such characteristics act as selective pressures resulting in many endemic species (Kazakou et al. 2008, Anacker 2014) and usually small populations with low rates of regeneration (Brady et al. 2005). As a consequence, there are few other species at these localities and the incidence of competition is low.

The low levels of competition combined with high stress-tolerance allow serpentine species to thrive in these stressful habitats. However, the competitive abilities of these species under less stressful abiotic conditions are not well characterized. Studies have shown that serpentine species performed worse in productive, low-stressful environments than in their native high-stress environments (Jurjavcic et al. 2002, Going et al. 2009), probably due to their inability to compete in non-serpentine habitats (Kruckeberg 1954). Other studies, however, found higher competitive abilities in serpentine compared with non-serpentine species in high nutrient low-stress habitats (Powell & Knight 2009). In addition, studies comparing serpentine and non-serpentine relatives, suggest that serpentine species are more tolerant to abiotic stress (e.g. Reeves & Baker 1984, Taylor & Levy 2002) and have higher genetic diversity than their non-serpentine relatives (e.g. Moore et al. 2013), which enables them to colonize serpentine environments.

In the present study, we focus on *Minuartia smejkalii*, an herbaceous perennial serpentinophyte species, endemic to the Czech Republic. Individuals of *M. smejkalii* grow very fast, forming well-defined rosettes in serpentine habitats, and can even produce seeds in the first season. Despite this fast early growth, the individuals can live for more than a decade. In its natural serpentine habitat, *M. smejkalii* grows in very sparse vegetation usually without any neighbouring plants. In the last few decades, anthropogenic activities related to urban constructions and agriculture expansion caused environmental changes in these serpentine habitats (Stojanova et al. 2020, 2021), producing more favourable conditions for other plants to colonize and subsequently reducing the populations of *M. smejkalii* (Pešout 2001). In many places, the previously open serpentine rocks are being colonized by self-seeded pine trees, causing a decrease in temperature and an increase in shading and moisture. In addition, accumulating litter is covering the serpentine rocks, reducing the effects of its chemistry, allowing non-adapted more "generalist" species to colonize these sites and increasing the level of competition for *M. smejkalii*.

Understanding how different biotic and abiotic conditions affect the performance of *M. smejkalii* and how they might change over time is crucial for designing efficient long-term conservation strategies for this species. This is particularly relevant for perennial species such as *M. smejkalii* which can live for at least 19 years (Lozada-Gobilard et al., personal observation). Usually, perennial plants flower only after an extended vegetative phase but *M. smejkalii* can flower in the first year. Different stages (seedling and adult) might be affected differently by competitors and abiotic factors, especially seedlings, which are more prone to drought due to their smaller root system.

The aim of the present study was to compare the performance of *Minuartia smejkalii* when grown alone and competing with its common competitor *Festuca ovina* under different abiotic conditions of water and light availability, and different types of soil, over an extended period of time. The following questions are addressed: (i) How does *M. smejkalii* respond to the presence of the competitor *F. ovina,* different types of soil, watering regimes and shading? (ii) Do the effects of the competitor depend on environmental conditions? (iii) Do these effects change over four years? We hypothesize that (i) performance of *M. smejkalii* will be strongly reduced by the presence of the competitor and in non-serpentine, shaded and wet conditions (i.e. non-natural conditions of *M. smejkalii*), (ii) the negative effects of competition will get stronger in non-natural conditions and (iii) the intensity of competition will increase over the four-year period of this study.

Methods

Experimental setup

Seeds of *M. smejkalii* were collected in June 2016 from a natural population in the Czech Republic at Želivka (49°41'14.2"N, 15°06'04.8"E), the population referred to as Z2 in previous studies (Lozada-Gobilard et al. 2020, Stojanova et al. 2020, 2021). Seeds were germinated in a mixture of serpentine and common garden soil (50:50) for approximately six months (from November 2016 to April 2017) in greenhouse conditions. In the experiment non-serpentine and serpentine types of soil were used. Non-serpentine soil was a mixture of common garden soil (50%) and sand (50%). It contained approximately 0.06% nitrogen, 0.67% carbon and 23.2 mg/1000 g of 0.002% phosphorous (Münzbergová et al. 2017). Serpentine soil was a mixture of the soil collected in the field (population Z2) during management interventions in the area and from a serpentine quarry located close by. The soil was collected in autumn 2016 and contained approximately 0.77 % nitrogen, 13.48% carbon and 4.47 mg/1000 g (0.0004%) of phosphorous. The non-serpentine mixture is a good representation of productive areas, mainly due to its higher content of phosphorus, which is usually the most limiting element.

In April 2017, when the seedlings reached ~3 cm in diameter, they were transplanted to the garden into 1-liter individual pots containing either serpentine or non-serpentine soil described above. The pots were arranged into a blocked design full factorial setup. After three months, in July 2017, we started the experiment collecting the corresponding data.

A total of 160 individuals were divided in eight abiotic treatments differing in watering regime, soil type and light exposure, each combined with presence/absence of the competitor (i.e. 10 pots of each type). Watering included daily watering (until the soil was saturated) vs no water addition, where water intake only came from natural rainfall. Mean annual precipitation at Průhonice is 577 mm, driest in February (28 mm) and wettest in July (83 mm) (https://weather-and-climate.com/). In rare events (11 days) of extreme drought (temperature > 35 °C) when the plants showed signs of wilting, water was added to the pots in order to avoid high losses of individuals. Light exposure was divided into "shade" and "full sun" mimicking two different growing conditions for *M. smejkalii* in nature: shaded areas in forest and open areas on rocks. Even though shading conditions in nature are driven by other plant species (usually pine trees), in this study we consider shading as an abiotic factor based on the amount of light received. Shading was implemented by using green garden net that transmitted 30% of the light, which was used to cover the treated plants inside a cage of ~1.5 m high and 2 × 1 m long.

Competition was divided into presence or absence of the most common grass found in natural populations, *Festuca ovina*, whose plants can grow up to 20 cm tall and 10 cm in diameter and overgrow *M. smejkalii* in serpentine habitats. Like *M. smejkalii*, the *Festuca* tussocks are also perennial. Half of the individuals of *M. smejkalii* were grown in a pot together with two surrounding tussocks of *F. ovina*, while the rest of the *M. smejkalii* individuals were grown alone (Fig. 1). In spring (March) prior to the experiment, *F. ovina* plants were collected directly from the serpentine habitat. Whole plants were dug up in the field and kept in the same serpentine soil in the garden until the start of the experiment. In July 2017, *Festuca* tussocks were separated into single ramets and two ramets were transplanted next to each *Minuartia* plant.

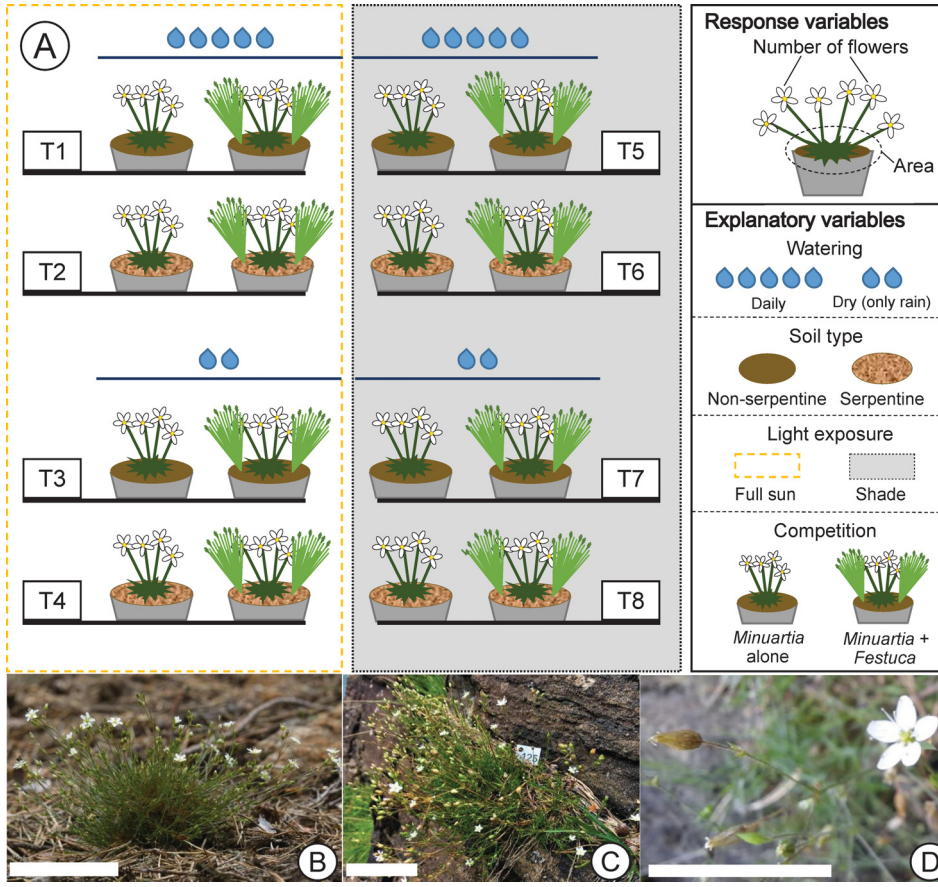

Fig. 1. Schematic representation of the experimental design and of *M. smejkalii* individuals in natural conditions. A total of eight treatments were evaluated differing in watering regime, type of soil and light exposure. Within each treatment a total of 20 individuals, 10 without and 10 with the competitor (*Festuca ovina*), were evaluated (A). Growth of *M. smejkalii* in the open (B) and on steep serpentine rocks (C) forming a clear rosette. Detail of flower and fruit (D). Scale bar = 10 cm. Area and number of flowers were measured, and competition response ratio calculated based on Goldberg et al. (1999).

To characterize plant performance, we recorded plant area and number of flowers produced per individual. We calculated plant area as the area occupied by an individual using the ellipse area equation ($Area_{ellipse} = \pi \times length/2 \times width/2$), where length was the longest dimension of the space occupied by an individual and width was the distance orthogonal to the length. We counted the total number of flowers in 10 randomly selected stems per individual. We estimated the number of flowers produced by an individual by multiplying the total number of flowering stems per individual by the mean number of flowers per stem. At the beginning of the experiment in July 2017, these variables were measured monthly from July 2017 to November 2017 and later only once a year in July between 2018 and 2020 when plants were at peak flowering. At the end of the experiment

in 2020, aboveground biomass of the competitor *F. ovina* was harvested, dried and weighed. A more detailed examination of the biomass of the competitor over time was not done because it is destructive and could have biased the results. Biomass of *M. smejkalii* was not measured due to its complex morphology and its tendency to completely dry out at the end of each season. Our long-term field demographic data indicate that plant area, as estimated here, is a very good predictor of long-term performance (survival and flowering) of *M. smejkalii* (H. Pánková et al., unpublished). Therefore, plant area is a very reliable proxy of biomass for assessing the performance of *M. smejkalii.*

Statistical analyses

Plant performance, characterized by area and number of flowers, was evaluated by considering time to be a continuous explanatory variable measured in days since the beginning of the experiment. A generalized linear mixed model (GLMM) with a gamma distribution, was applied for both area and flower number to evaluate the effect of time, competition (presence vs absence of competitor), type of soil (non-serpentine vs serpentine), light exposure (full sun vs shade) and watering regime (dry vs wet) including pot ID as a random effect to account for the repeated measurements. The total variance explained by the entire model, including both fixed and random effects, was calculated using the r.squaredGLMM function in the MuMIn R package (Bartoń 2009). Since plants started flowering in September 2017, values recorded from July–August 2017 were not included in the analysis of the number of flowers. Dead plants were excluded from the analyses from the time of their death (23 individuals in total).

In order to detect whether there was any evidence of competition or facilitation, the log response ratio (RR) in terms of plant area and number of flowers was calculated following Goldberg et al. (1999) using the formula:

$$RR = \ln\left(\frac{X_{alone}}{X_{mix}}\right)$$

where X represent the response variable; X_{alone} = variable measured for the focal species in the absence of the competitor (*M. smejkalii* alone) and X_{mix} = variable measured for the focal species grown with the competitor (*M. smejkalii* + *F. ovina*). Positive values of RR indicate competition and negative values facilitation (Goldberg et al. 1999). Due to normality of the data, competitive response was evaluated using a linear mixed effect model including time, light exposure and watering regime as predictors and pot ID as a random effect to account for the repeated measurements.

In addition, we assessed the effect of type of soil, light exposure and watering regime on the performance (biomass) of the competitor *Festuca ovina*. Its biomass was measured at the end of the experiment and was normally distributed and therefore analysed using ANOVA. All analyses were performed in R version 4.0.3 (R Core Team 2019), using the package lme4 for mixed effects models.

Results

Average plant area was 95.5±145.8 cm^2 (mean±SD) and mean number of flowering stems was 23.3±43.8 (mean±SD). All the tested factors (time, light exposure, watering regime, type of soil and presence of the competitor) had significant effects on plant area or number of flowers. Plant area was similar in both types of soil (both ~100 cm^2; Fig. 2A), but plants produced 1.5 times more flowers in non-serpentine soils than in serpentine soils (Fig. 2E). When shaded, plants were 2.7 times larger than those exposed to full sun, but under full sun, plants produced 1.7 times more flowers than those in the shade (Fig. 2B, F). Plants grew larger when shaded, independent of type of soil (Supplementary Fig. S1A); in non-serpentine soil, plants produced 2.5 times more flowers under full sun compared to when shaded, while in serpentine soil light exposure did not affect flower number (Supplementary Fig. S1B). Watered plants were 1.5 times larger and produced 1.6 times more flowers than those in dry conditions (Fig. 2C, G). In the absence of the competitor, plants were 1.2 times larger and produced 1.8 times more flowers than plants with the competitor (Fig. 2D, H).

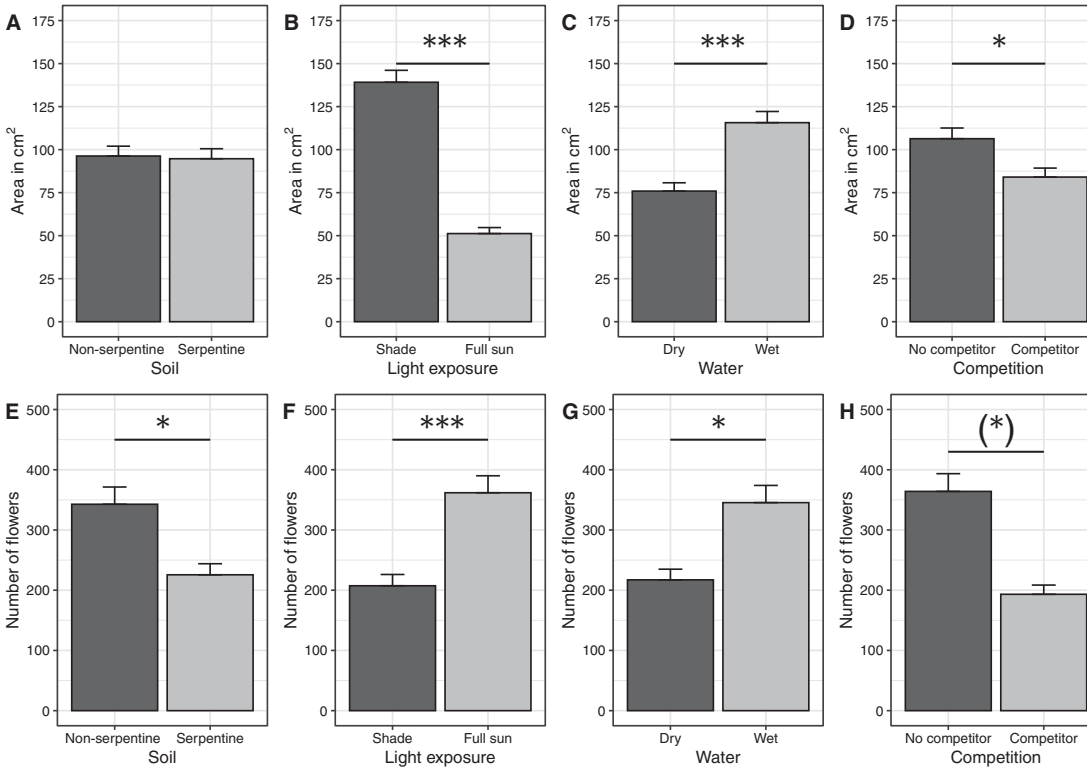

Fig. 2. Effect of the single treatments on plant area and number of flowers. Effect of single predictors on type of soil, light exposure, water regime and presence of competitor on plant area (A–D) and number of flowers (E–H). (*) P < 0.1; * P < 0.05; ** P < 0.01; *** P < 0.001.

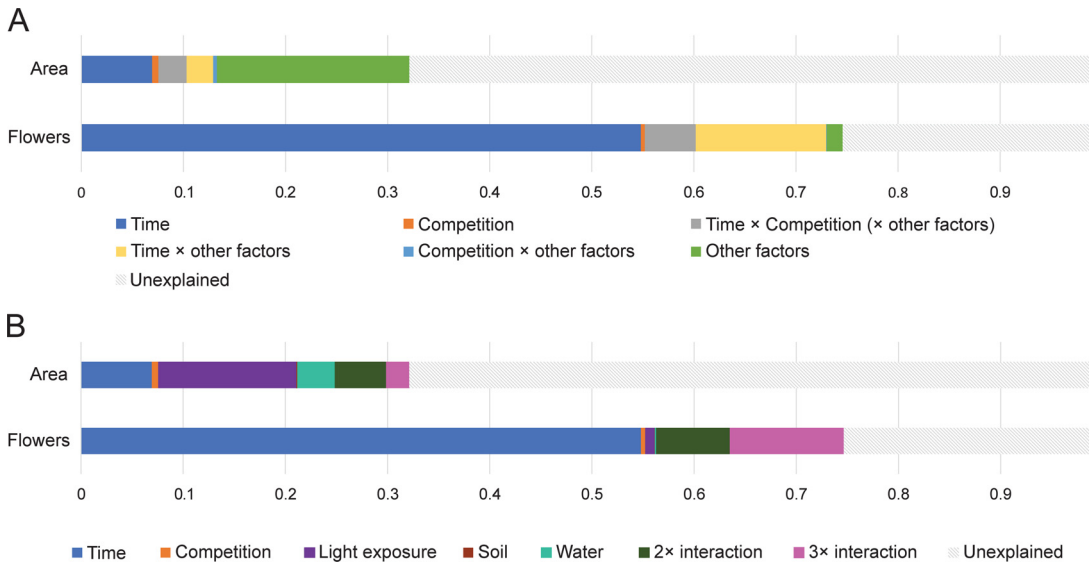

Fig. 3. Proportion of explained variance in plant area and number of flowers. Proportion of variance explained by the model are in in Table 1. In (A) proportions are divided to focus on time and competition and other factors represent light exposure, soil and water. In (B) 2× and 3× interactions represent variance explained by interaction among any of the tested factors.

The model of plant area explained 32% of the total variance, and light exposure was the best predictor (14%) (Fig. 3). In the case of number of flowers, the model explained 75% of the total variance and the predictor that explained most of the variance was time (55%) (Fig. 3).

Effects of competition

On average, competition resulted in a smaller plant area and fewer flowers (Fig. 2D, H, Supplementary Fig. S2), but the effect changed over time and the response to competition was affected differently depending on plant area or number of flowers and abiotic factors (Table 1). Competition × time interaction only affected plant area, whereas competition × time × light exposure interaction only affected the number of flowers (Table 1). Competition alone and in interaction with other factors contributed little to explaining plant performance; up to 0.1% for plant area and 0.4% for number of flowers (Fig. 3A).

Log response ratio (RR) calculated for area was significantly affected by light exposure, its interaction with type of soil, and light exposure × type of soil × time triple interaction (Table 2). Log response ratio (RR) calculated for number of flowers was significantly affected by light exposure × type of soil × time and water regime × type of soil × time triple interactions (Table 2). On average, area-based responses under full sun in non-serpentine soil indicated competition (RR area > 0, mean±SE = 0.6±0.08) while responses when shaded indicated facilitation (RR area < 0, mean±SE = –0.6±0.09). No significant competition effect was recorded in serpentine soil (RR area ~0, mean±SE = 0.07±0.06 in full sun and –0.05±0.08 in shade; Fig. 4A).

Table 1. Effect of water regime, light exposure, type of soil and presence of competitor on plant area and number of flowers produced per individual by *Minuartia smejkalii* over time. Significant effects are shown in bold.

Factor		Area		Flowers	
	df	χ^2	P	χ^2	P
Water	1	54.1	**< 0.001**	4.6	**0.032**
Light exposure	1	190.7	**< 0.001**	37.6	**< 0.001**
Soil	1	1.7	0.195	5.2	**0.022**
Competition	1	6.3	**0.012**	3.6	0.056
Time	1	39.9	**< 0.001**	259.3	**< 0.001**
Water × Light exposure	1	8.6	**0.003**	1.2	0.267
Water × Soil	1	3.4	0.065	1.7	0.190
Water × Competition	1	0.5	0.483	0.9	0.351
Water × Time	1	1.1	0.288	0.0	0.907
Light exposure × Soil	1	4.7	**0.030**	10.6	**0.001**
Light exposure × Competition	1	0.1	0.805	0.2	0.650
Light exposure × Time	1	9.9	**0.002**	14.2	**< 0.001**
Soil × Competition	1	3.4	0.067	0.1	0.724
Soil × Time	1	2.3	0.130	2.8	0.094
Competition × Time	1	14.4	**< 0.001**	3.4	0.065
Water × Light exposure × Soil	1	7.7	**0.006**	0.8	0.363
Water × Light exposure × Competition	1	0.3	0.569	2.8	0.094
Water × Light exposure × Time	1	0.1	0.770	49.7	**< 0.001**
Water × Soil × Competition	1	1.9	0.163	0.3	0.596
Water × Soil × Time	1	1.9	0.167	2.0	0.154
Water × Competition × Time	1	3.0	0.082	3.3	0.071
Light exposure × Soil × Competition	1	0.0	0.875	0.5	0.500
Light exposure × Soil × Time	1	2.8	0.093	1.0	0.306
Light exposure × Competition × Time	1	1.9	0.174	14.4	**< 0.001**
Soil × Competition × Time	1	0.9	0.337	1.9	0.163

Table 2. Effect of water regime, light and type of soil on the response to competition based on plant area and the number of flowers produced per individual of *Minuartia smejkalii* over time. Log response ratio was calculated by dividing area or number of flowers of *M. smejkalii* in the absence of competitor (*Festuca ovina*) by the values in presence of the competitor (*M. smejkalii* + *F. ovina*). See Methods section for details. Significant effects are in bold.

Factor		RR [area]		RR [flowers]	
	df	F	P	F	P
Water	1	0.5	0.470	1.5	0.228
Light exposure	1	21.1	**< 0.001**	0.2	0.687
Soil	1	0.4	0.510	0.3	0.584
Time	1	0.1	0.781	1.1	0.293
Water × Light exposure	1	0.8	0.368	0.0	0.921
Water × Soil	1	0.0	0.838	1.8	0.186
Light exposure × Soil	1	22.5	**< 0.001**	2.2	0.138
Water × Time	1	0.0	0.983	0.6	0.434
Light exposure × Time	1	2.6	0.108	0.0	0.881
Soil × Time	1	3.7	0.055	0.2	0.644
Water × Light exposure × Soil	1	2.0	0.158	1.3	0.252
Water × Light exposure × Time	1	0.0	0.877	3.0	0.082
Water × Soil × Time	1	1.9	0.170	12.4	**< 0.001**
Light exposure × Soil × Time	1	14.7	**< 0.001**	4.3	**0.039**

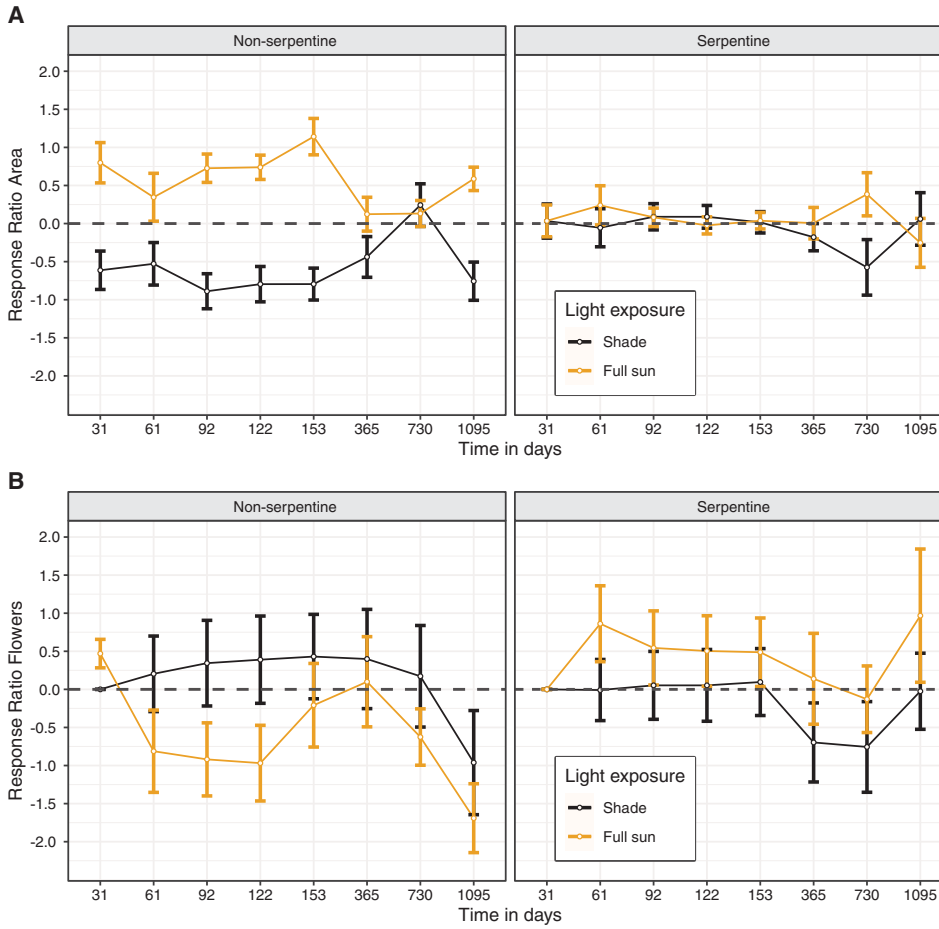

Fig 4. Log response ratio based on (A) plant area and (B) number of flowers and its response to light exposure and type of soil. Positive values of the index indicate competition, negative values facilitation. Points indicate mean values ± SE. There is a significant effect of light exposure, light × soil and light × soil × time interaction for area and only significant light × soil × time interaction for number of flowers.

Flower-based responses under full sun in non-serpentine soils indicated facilitation (RR flowers < 0, mean±SE = –0.5±0.1); while responses when shaded indicated competition (RR flowers > 0, mean±SE = 0.2±0.1). The opposite pattern was recorded in serpentine soils: competition in full sun conditions (RR flowers > 0, mean±SE = 0.4±0.1) vs facilitation when shaded (RR flowers < 0, mean±SE, –0.15±0.1; Fig. 4B). There was a larger variation in competition response values based on number of flowers in both light exposure and type of soil treatments, compared to the responses based on plant area (Fig. 4).

A significantly higher biomass of the competitor *Festuca ovina* was found in wet, full sun and non-serpentine soil conditions (Table 3, Fig. 5).

Table 3. Performance of the competitor (*Festuca ovina* measured as biomass) in response to water regime, light exposure and soil treatments. Significant effects are in bold.

Factor	df	Mean sq	F-value	P
Water	1	102.49	24.65	**<0.001**
Light exposure	1	74.82	17.99	**<0.001**
Soil	1	53.66	12.91	**<0.001**
Water × Light exposure	1	212.19	51.03	**<0.001**
Water × Soil	1	0.00	0.00	0.99
Shading × Soil	1	0.69	0.17	0.69
Water × Light exposure × Soil	1	2.92	0.70	0.40

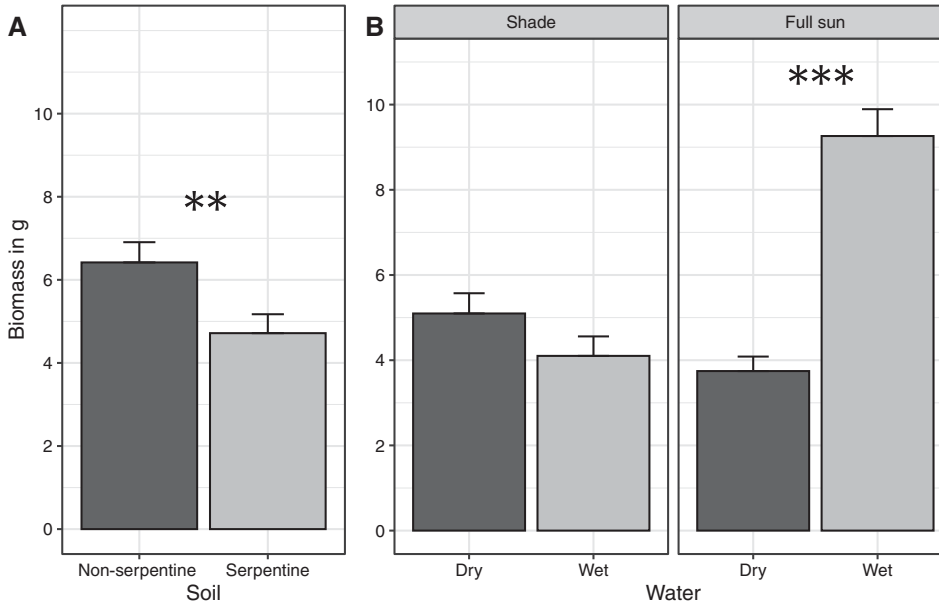

Fig. 5. Effect of A) type of soil and B) water regime and light exposure on biomass of the competitor *Festuca ovina* measured at the end of the experiment. There is a significant effect of water, light, soil and water × light interaction. (*) P < 0.1; * P < 0.05; ** P < 0.01; *** P < 0.001.

Effects of time

Time alone explained 55% of the total variance in number of flowers, but only 7% of plant area (Fig. 3). Time interacted with most of the other variables tested (Table 1). The interaction of time with competition (including their triple interactions with other factors) explained more variation (3% for area vs; 5% for flowers) than competition alone (0.6% for area; 0.4% for flowers) (Fig. 3A). Interactions of time with other factors had a stronger effect on number of flowers (13%) than on plant area (3%) (Fig. 3A). Other factors (light exposure, type of soil, water regime and their interactions) independent of time explained most of the variation in the case of plant area (19%), but very little in the case of number of flowers (2%) (Fig. 3A).

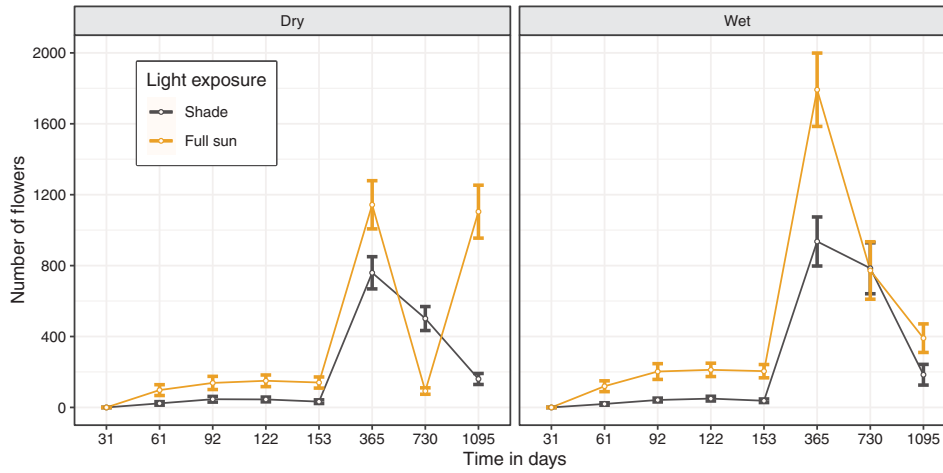

Fig. 6. Effect of light exposure and watering regime on number of flowers over time. Points indicate mean values ± SE. There is a significant effect of water, light, soil, time, light × soil, light × time and water × light × time interaction on number of flowers.

Triple interactions of time × light exposure × competition and time × light exposure × watering regime were only significant for number of flowers (Table 1, Fig. 6). A large increase in flower number was detected at 365 days, with a higher number of flowers recorded under full sun and wet conditions (Fig. 6). In dry conditions, an abrupt decrease in number of flowers was recorded in the second year with a recovery in the third year under full sun, while a constant decrease in the second and third year was recorded under wet conditions and when shaded independently of the water regime (Fig. 6).

Discussion

In the present study, we compared the performance of *Minuartia smejkalii* grown in different types of soil type, exposure to light, water regimes and presence of a competitor (*Festuca ovina*) in a full factorial common garden experiment and evaluated how the responses changed over four years. We hypothesized that the performance of *M. smejkalii* would be reduced in non-natural conditions (i.e. non-serpentine soil, shaded and wet conditions), and in the presence of the competitor. We found that the presence of the competitor had a negative effect on the performance of *M. smejkalii,* but contrary to our expectations, non-natural conditions did not negatively affect *M. smejkalii* (except for the negative effect of shade on the number of flowers). We further expected that the level of competition would be higher in non-natural conditions, however, this was not the case. Performance of *M. smejkalii* depended on abiotic factors with contrasting facilitation/competition responses depending on plant size and number of flowers under non-natural conditions (i.e. non-serpentine soils and shade). Finally, we hypothesized that competition would increase over time. Competition varied over time, in particular in relation to light exposure and type of soil, but it did not increase over the four years.

Effects of Festuca ovina on Minuartia smejkalii and interactions with abiotic factors

Presence of the competitor *F. ovina* had a negative effect on plant area and number of flowers (Fig. 2D, H, Supplementary Fig. S2), but *M. smejkalii* did not perform better in its typical habitat conditions (i.e. serpentine, full sun, dry), except for more flowers under full sun than when shaded conditions (Fig. 2). These results suggest that this species occurs in habitats that are not abiotically ideal. They are, however, free of competitors and possibly also natural enemies. Thus, it is likely that *M. smejkalii* would thrive in more productive environments in the absence of biotic constraints. One of the most important reversible abiotic factors constraining plant growth in serpentine soils is nutrient availability (Turitzin 1982, Chiarucci et al. 1998a, b). For instance, *Cochlearia pyrenaica* and other serpentine species grow better when the nutrient limitation is removed (Nagy & Proctor 1997). Like this species, *M. smejkalii* might be a "latent competitor", since it can tolerate stressful conditions but can rapidly respond in an opportunistic way when the conditions are favourable (Nagy & Proctor 1997).

Biomass of the competitor *Festuca ovina* was larger in non-serpentine soils, suggesting its performance is poorer in serpentine soils. As for *Minuartia*, this might be due to nutrient limitation in serpentine soils. Previous studies showed that *F. ovina* has or might have tolerance to heavy metal present in serpentine habitats (e.g. Snaydon & Bradshaw 1961, Garland & Wilkins 1981, Baker 1987). Since the *F. ovina* used in the experiment was collected in the same serpentine habitat, the expectation is that these plants have serpentine-specific genotypes. However, a better performance of *F. ovina* in non-serpentine soils and wet conditions suggests that this species can tolerate stressful conditions but could also rapidly respond in an opportunistic way when conditions are favourable, similar to *M. smejkalii*. Biomass production of *F. ovina* was found to be larger under constant water and high soil moisture conditions, which promoted higher nutrient acquisition (Misra & Tyler 2000). In our case, highest biomass production of *F. ovina* was recorded under full sun and wet conditions (Fig. 5). In addition, increase in soil moisture might be favourable for *F. ovina*. During the period of the experiment, there was a slight (but not significant) increase in soil moisture after the first year (Supplementary Fig. S3), which might have affected *Festuca* growth.

Log response ratio based on plant area was significantly positive, only under full sun and when grown in non-serpentine soil, suggesting a competitive effect of *F. ovina* on *M. smejkalii* under these conditions. Log response ratio based on number of flowers was positive when grown in both types of soil, but this depended on light exposure, suggesting a competitive effect of *F. ovina* on *M. smejkalii* under full sun and grown in serpentine soils, but not when shaded and grown in non-serpentine soils. This dependence on whether plant area or number of flowers is used, suggests that the investment in growth and reproduction in *M. smejkalii* differs as it ages. Changes in competition along life history stages has a long-term effect on community structure and composition (Leger & Espeland 2010), with potentially important consequences for the plant-plant interaction when *M. smejkalii* interacts not only with *F. ovina* but also other different neighbours in rapidly changing serpentine habitats.

Previous studies show that rare species are restricted to stressful habitats due to their poor competitive abilities under normal conditions (e.g. Gurevitch 1986, Rünk et al. 2004, Moora & Jőgar 2006, Imbert et al. 2012), but see Powell & Knight (2009). In the

presence of *F. ovina* the growth and reproduction of *M. smejkalii* was reduced, an outcome that is expected from a pot experiment in which adding more plants to a pot usually reduces per-plant performance, regardless of the identity of the competing plant. This, however, does not indicate the competitive ability of *M. smejkalii* is poor in its natural habitat. In order to assess whether *M. smejkalii* is a poor competitor, future studies should focus on intraspecific competition among *M. smejkalii* plants, on other plant species and the effect of *M. smejkalii* on *F. ovina*. We did not perform such a comparison here as the aim was to simulate the two scenarios occurring in the field, i.e. *M. smejkalii* growing alone or in competition with another species (*M. smejkalii* stands are never dense enough for intraspecific competition to occur).

Production of flowers by Minuartia smejkalii was mainly affected by time, light exposure and water regime

Time explained most of the variation in number of flowers, which largely changed over time. Plants started producing flowers after two months, with the peak in flowering after one year and a decrease in the second year. Previous studies have shown specific effects of the environment on different plant stages, from seedling establishment and recruitment to entire plant life cycle, in different habitats (e.g. Knappová et al. 2013, Kladivová & Münzbergová 2016). In this study, light exposure and watering regime were the most important factors affecting flowering and the effects of these factors changed over time.

Under favourable conditions where the cost of reproduction is low, plants may allocate more resources to flower and fruit production. It was previously shown, for instance, that intermediate soil moisture (von Euler et al. 2012), soil depth and sun exposure (Ågren et al. 2008) positively affected flower and fruit production. We expected that more flowers would be recorded in *M. smejkalii* typical natural habitat (i.e. serpentine soil, dry conditions and full exposure to sun). Contrary to our expectations, we found more flowers in non-serpentine soils and wet conditions, but higher number when exposed to full sun than when shaded (Fig. 2). These results suggest that *M. smejkalii* tolerates its "typical conditions" probably due to the low level of competition and responds positively when the conditions are favourable (i.e. non-serpentine well-watered soils).

On the other hand, flowering could also be a response to stress (Wada & Takeno 2010, Takeno 2016). Under "typical" dry and full exposure to sun, there was an abrupt decrease in number of flowers in the second year, followed by a recovery in the third, which might indicate a better adaptation to these conditions over time; while a steady decrease over time was recorded in wet conditions. These results might indicate that typical natural condition for *M. smejkalii* might be stressful and therefore a higher production of flowers could be a response to stress. However, an alternative explanation could be that plants grown under dry and full sun conditions saved resources in the second year for use the next year, when they were better prepared to take advantage of favourable conditions for reproduction.

Number of flowers recorded was higher in full sun, whereas plant area was greater when grown in shaded conditions. These results might indicate that shaded plants tried to increase photosynthesis by investing more energy in vegetative biomass than flower production (e.g. Valiente-Banuet & Gutierrez-Ochoa 2016).

Conservation application and recommendations

Understanding the balance between competition and facilitation and the interaction with the abiotic environment is essential for the design of successful ex situ and in situ conservation strategies for endangered species (Raven 2004, Volis & Blecher 2010). However, long-term experiments on these interactions are scarce and there is usually a trade-off between the levels of complexity (i.e. number of interactions and duration of the experiment). In addition, even the most complex experiments only include a small fraction of the natural conditions and might provide unrealistic conditions that could lead to erroneous biological conclusions (Chaieb et al. 2020) as any additional factor interacts with the previously considered, as indicated by our results.

Even though the results presented indicate that optimal habitats for *Minuartia smejkalii* growth are those with wet and non-serpentine soils, such conditions are not recommended for ex-situ conservation of *M. smejkalii* since they could easily cause the loss of adaptations to serpentine conditions. Loss of adaptations is a crucial problem in ex-situ cultivations (Ensslin et al. 2011, 2015), and particular relevant for species restricted to extreme habitats, such as *M. smejkalii*. Therefore, we suggest that this species is grown in serpentine soils under full sun and with restricted watering, without the presence of any competitor or other species to mimic the "typical" natural serpentine habitat conditions in order to preserve its tolerance for serpentine habitats. Such conditions together with an appropriate management of ex-situ facilities, including avoidance of interspecific hybridization (Lozada-Gobilard et al. 2020), consideration of population origin, degree of gene flow and inbreeding depression (Stojanova et al. 2020, 2021) and its dispersal ability (Zhu et al. 2021) are likely to provide a solid baseline for successful long-term conservation of *M. smejkalii* in the Czech Republic.

Conclusions

The results of this study demonstrate that plant responses to different conditions change over time and depend on different abiotic factors (type of soil, water regime and exposure to light). We found evidence of competition in both types of soil and when shaded or in full sun. Competitive interactions mainly depended on light exposure and soil conditions with opposite tendencies depending on the performance variable measured (plant area vs number of flowers). Shading promoted larger plants with fewer flowers, whereas exposure to full sun resulted in greater number of flowers especially when growing in non-serpentine soils. These contrasting results obtained by using plant area or number of flowers suggest that abiotic conditions modify vegetative and reproductive investment of *M. smejkalii*. These results highlight the importance of long-term experiments for improving the understanding of how plant-plant interactions are affected by different environmental factors, which is essential for designing successful long-term conservation strategies, especially for endangered species such as *Minuartia smejkalii*.

Supplementary materials

Fig. S1. – Effect of light exposure and soil type on (A) plant area and (B) number of flowers.
Fig. S2. – Effect of soil type, light exposure and water regime by presence of competitor.
Fig. S3. – Soil and air temperature and moisture variation by year during the experiment.

Supplementary materials are available at www.preslia.cz

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Interakce vlivu světla, vody, půdního typu a kompetice na ohrožený druh kuřičku hadcovou (*Minuartia smejkalii*) se mění v čase

Pochopení faktorů ovlivňujících růst rostlinných druhů je zásadní pro jejich účinnou ochranu. Přestože existuje řada studií o vlivu jednotlivých biotických a abiotických faktorů na růst rostlin, stále víme velmi málo o interakcích mezi více faktory a jejich vlivu v čase; proto jsme po dobu čtyř let studovali kompetici a abiotické interakce u endemického druhu České republiky, hadcového specialisty *Minuartia smejkalii*. V plně faktoriálním pokusu jsme pěstovali *M. smejkalii* samostatně a v přítomnosti kompetitora *Festuca ovina* za různých abiotických podmínek, zahrnujících vliv půdního typu, světla a zálivky. Hodnotili jsme růst *M. smejkalii* a sledovali změny v čase. Naše výsledky ukázaly velmi složité interakce mezi sledovanými faktory. Kompetice sice měla negativní vliv na růst *M. smejkalii* (1,2× větší rostliny a 1,8× více květů v nepřítomnosti konkurenta), ale abiotické faktory měly silnější vliv než samotná kompetice. Vliv *F. ovina* na *M. smejkalii* se lišil v závislosti na zastínění a půdních podmínkách. Biotické a abiotické faktory měly odlišný vliv na velikost kuřičky a počet květů, což naznačuje, že investice do růstu a reprodukce závisí na kontextu. Oslunění snížilo velikost rostlin (rostliny ve stínu byly 2,7× větší než na plném slunci), ale zvýšilo 1,7× tvorbu květů. Typ půdy neměl vliv na velikost rostlin, ale rostliny produkovaly 1,5× více květů v nehadcové půdě. Naše výsledky naznačují, že kompetice působí velmi komplexně, vzájemně se ovlivňuje s abiotickými faktory a její působení se mění v čase. Proto je třeba zdůraznit význam dlouhodobých studií pro pochopení kompetičních vztahů a důležitost studia kompetice v různých podmínkách. Pochopení vlivu kompetice na růst ohroženého druhu *M. smejkalii* v různých abiotických podmínkách (tj. půda, voda, zastínění) poskytuje důležité informace pro realizaci účinnějších dlouhodobých ochranářských opatření.

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