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Maternal Environment Modulates Dormancy and Germination in *Vaccaria hispanica*

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Abstract

Offspring performance is affected by mother plants via genes and maternal environment. Seed characteristics such and dormancy and vigour are affected by the environmental resources during plant development. Intra and inter-variation in seed dormancy and longevity are considered as a bet-hedging strategy to reduce the recruitment failure across years under environmental uncertainty. In this study, the effects of drought and herbivory, two common environmental stresses, were investigated on biomass and seed quality in *Vaccaria hispanica* (Mill.) Rauschert, an annual forb. Plants were subjected to different levels of water and simulated herbivory stress. Maternal water stress suppressed seed mass, but it stimulated dormancy in seeds. Progenies from the maternal stress environment were more persistent than those from the maternal control environment after being exposed to 45°C and 100% RH for 8 days. The findings highlighted the importance of the water maternal effect versus herbivory on seed dormancy and longevity in this species. The results may help us understanding the life cycle and population dynamics of *V. hispanica* in successive years.

Keywords: *Vaccaria hispanica*; Vigour; Dormancy; Maternal effect; Water stress; Simulated herbivory

Introduction

Fitness of offspring can be affected by maternal environment in different ways [1]. Unpredictable biotic and abiotic maternal environment may have a crucial role in determining germination fractions and seedling recruitment. Bet-hedging is an important strategy to reduce the risk of failure under environmental uncertainty [2]. Spreading germination over time by producing seeds with different dormancy and longevity can help reducing the risk of recruitment failure in any one year [3]. It is well known that, seeds are less vulnerable to environmental stresses than seedlings [2].

Persistent seed banks buffer populations in unfavourable environmental condition [3,4]. Seed longevity and dormancy can increase the seed bank of populations. Both the environment and genetics of plants are responsible for recruitment variation. The environment of the parental plant can influence offspring fitness by changing dormancy and germinability. This is very important for annual wild populations to have longer lived seed-lots to ensure survival from one generation to the next.

The species selected as the experimental organism was *Vaccaria hispanica* (Mill.) Rauschert, which occurs in Europe, Asia and has been introduced to North America. The species is an annual forb, which produces gray to brown rounded seeds. In Iran, this species is found in both agricultural and pasture areas. In pastures it often experiences herbivory (being grazed by livestock) and/or drought stress and mostly germinates in September and flowers in May (Cici, pers.obs.).

The main objective of this study was to test the hypothesis that increasing stress causes changes in seed characteristics and seedling recruitment of *V. hispanica* species. This will help to provide a better understanding of the recruitment biology and seed plasticity of this species in an environmentally fluctuating habitat.

Materials and Methods

Source of seeds

The study site was located on semi-arid slopes in the vicinity of Mallard in northwest of Alborz (35°43'53"N; 51°0'5"E), Iran. It has a long-term average rainfall of 260 mm and temperature of 21°C. The area has vegetation dominated by Asteraceae and Chenopodiaceae. In early spring, seeds were harvested at the time of dispersal from 50 randomly selected maternal plants located within a 15 m radius and transported in paper bags. They were pooled together, dried at 15°C and stored at 4°C for 6 months.

Plant Growth

To avoid undesirable carry-over environmental effects on species performance two sequential generations of *Vaccaria hispanica* were grown in a controlled environment with no biotic or abiotic stress.

Initially, seeds were placed in 90 mm plastic Petri dishes with filter paper drenched with GA3 at 1.0 g L^{-1} to stimulate germination and kept 2 days in a dark room at 15°C and 5 days in alternating 12 h light (30 μ mol m^{-2} s^{-1}) and 12 h darkness [3]. When cotyledons were fully evident, seedlings were transplanted to 50 plastic pots (2 L) filled with a commercial potting soil and moved in the greenhouse with an average temperature of 21 ± 3 and 15 ± 2°C during day and night time,

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respectively. The daytime light intensity was about 800 µmol m^{-2} s^{-1}. The soil was watered to the field capacity every other day with tap water. Once established, seedlings were thinned to one plant per pot to ensure the highest similar initial size. Seeds from these plants were collected and kept in paper bags. One year later these seeds were planted in the same environmentally controlled greenhouse and the same procedure was repeated.

Plant growth under different maternal environment

Seeds of the second generation were used for this main experiment. The establishment and growth conditions were the same as previously for all plants up to 3 weeks and then the following experimental procedures were applied.

A complete random block design was considered for the experiment. Plants were grouped into two watering treatments: Control and Drought, with plants being watered to field capacity every 2 and 10 days, respectively. At the same time, half of the plants from each watering treatment were subjected to simulated herbivory (80% defoliation). The herbivory treatment performed only once. Undamaged plants had no sign of herbivory at the end of the experiment. Scissors were used to remove 80% of leaf area and leaves. This level of defoliation has been observed in the pasture (Cici, pers. obs.). There were 40 plants (pots) per group. Forty five days after treatments were initiated, number of branches, number of leaves and index of architecture (number of branches/main stem length) were determined for each plant. Each plant was harvested when there was a total lack of chlorophyll present. At harvest, plants in each treatment were collected separately and divided into roots, shoots and seeds. Seeds of each plant were collected in paper bags and later counted. The roots were gently washed free of soil. Root and shoot biomass was oven-dried at 75°C for 48 h in paper bags and weighed.

Seed vigour experiment

An accelerated aging test was conducted to study vigour of freshly collected seeds from different maternal sources in the above experiment. The viability of seeds prior to the start of the experiment was checked by cutting seeds (100/seedlot) vertically and examining of the endosperm. Seeds were scored as unviable if dark or mushy endosperm was present. White and firm endosperms were scored as viable. The percentage of unviable seeds was below 2%, irrespective of maternal seed source.

Seeds were placed in an incubator (SMI4E; Sheldon Manufacturing, Cornelius, USA) operating at 45°C and 100% relative humidity [5]. Four incubation periods were tested: 0, 2, 3, 4 and 8 days. After incubation, seeds were washed and immediately placed into a germination test. Four replicates per incubation time and per maternal treatment were put in completely randomized blocks and exposed to 30 days of altering day/night temperature (20/10°C) under dark [6]. Fifty seeds per replicate were placed on two layers of Whatman No.1 filter paper moistened with 2.5 mL of distilled water in 5 cm-diameter plastic Petri dishes. Germinated seeds were counted and removed every 2 days during a period of 30 days. Seeds were considered germinated when their seedlings produced healthy cotyledons.

The viability of ungerminated seeds was tested by the TTC method [5]. Embryos were placed in a 1% solution of 2,3,5-triphenyl-2 H-tetrazolium chloride and those that turned pink were considered viable. The experiment was run twice.

Seedling recruitment

To investigate the maternal effect (of both drought and herbivory) on seedling recruitment in the next autumn, freshly collected seeds from each maternal source were sown in micro plots outside. A randomized block design with ten replicates was used in a seedbed filled with a potting soil. The size of each micro plot was 20 cm long × 10 cm wide. One hundred seeds were planted at a depth of 1 cm in each micro plot. Counts of seedling emergence were made at weekly intervals from mid-September 2012 to mid-May 2013. Between May and June 2013, all remaining seeds were exhumed using a wet sieving technique and their viability was tested by the TTC method as mentioned above [5].

Statistical analysis

All the data were analyzed for normality and homogeneity of variance prior to analysis. Variables were analysed by a two-way ANOVA (fixed factors: Herbivory and drought) using Minitab version 14 [7]. Three-way ANOVA was used to determine the effects of maternal environment on seed vigour. Tukey's HSD test was performed for multiple comparisons to determine significant ($p<0.05$) differences among levels in each treatment. For the seed vigour experiment, the two runs were not significantly different so the data were pooled over runs.

Results

Morphological traits

Neither drought nor herbivory damage affected the survival of plants (data are not shown). Final stem height, number of stems and leaves, mass accumulation and seed production were significantly affected by treatments (Table 1). Water supply had the major influence on maternal plants, with plants grown in drought conditions being significantly shorter, and producing less leaves and stems compared with plants subjected to herbivory (Figure 1). Total plant biomass decreased more significantly in response to drought in undamaged and damaged plants. It was found that the herbivory treatment neutralized plant responses to water shortage. Significant reduction in shoot: root ratio was observed in undamaged plants under water shortage. This response to water shortage was not obvious in plants subjected to damage (Figure 1).

Seed vigour (Seed longevity)

Vigour of seeds decreased with increasing time at 45°C and 100% relative humidity. It was significantly affected by maternal soil water but not by maternal herbivory (damage). About 65% and 100% of seeds from well watered maternal plants were dead after an incubation time of 4 and 8 days, respectively. Progeny from the drought environment were more persistent. Ninety and 10% of these seeds were alive after the incubation time of 4 and 8 days, respectively (Figure 2).

Seedling recruitment

Seeds produced by plants grown under different treatments were tested for germination and dormancy status in order to determine possible maternal effects. There were significant differences in final emergence percentages between seeds produced by well watered maternal plants and drought exposed maternal plants, respectively. After one year, about 20% and 60% of seeds from well watered and drought exposed maternal plants were still dormant. Maternal herbivory damage did not have any significant effect on the proportion of dormant seeds produced by treated plants (Figure 3).

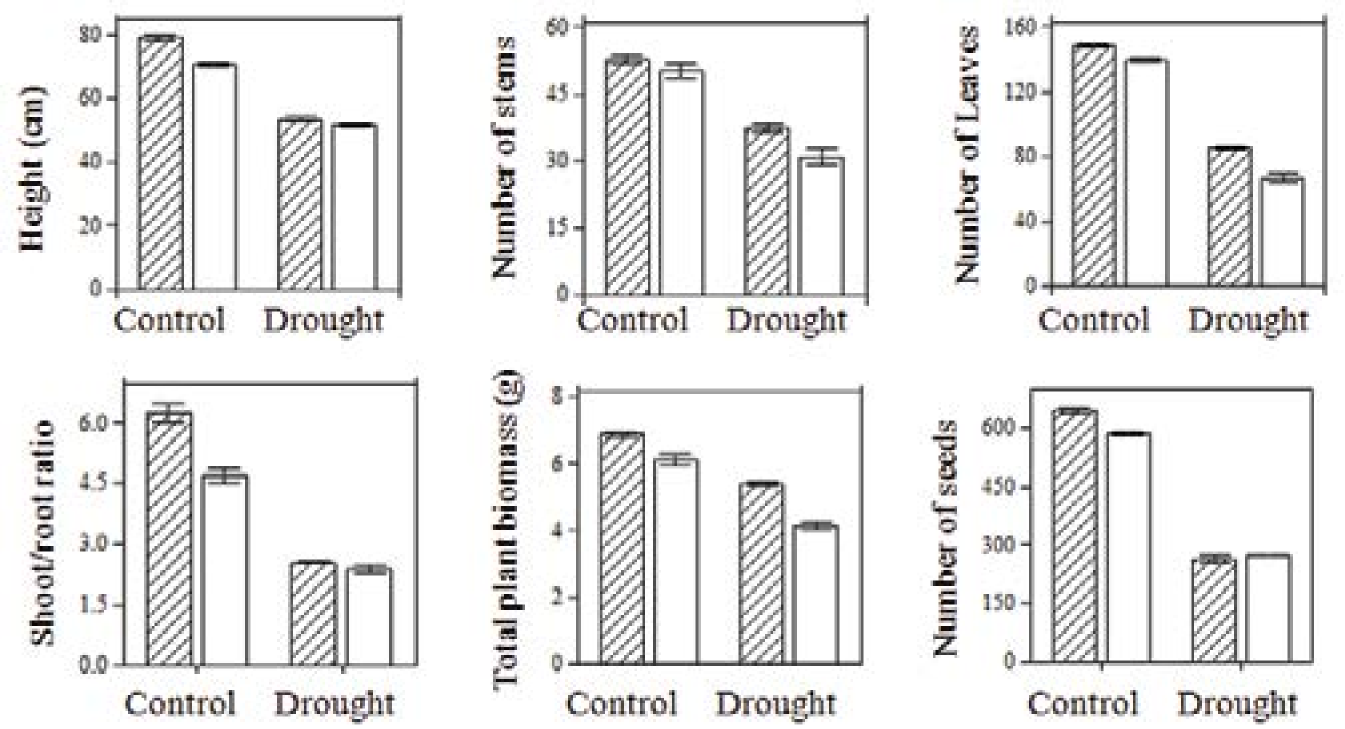

Figure 1: Effect of experimental drought and herbivory on different traits of *Vaccaria hispanica* plants. Hatched bars: undamaged plants; open bars: damaged plants.

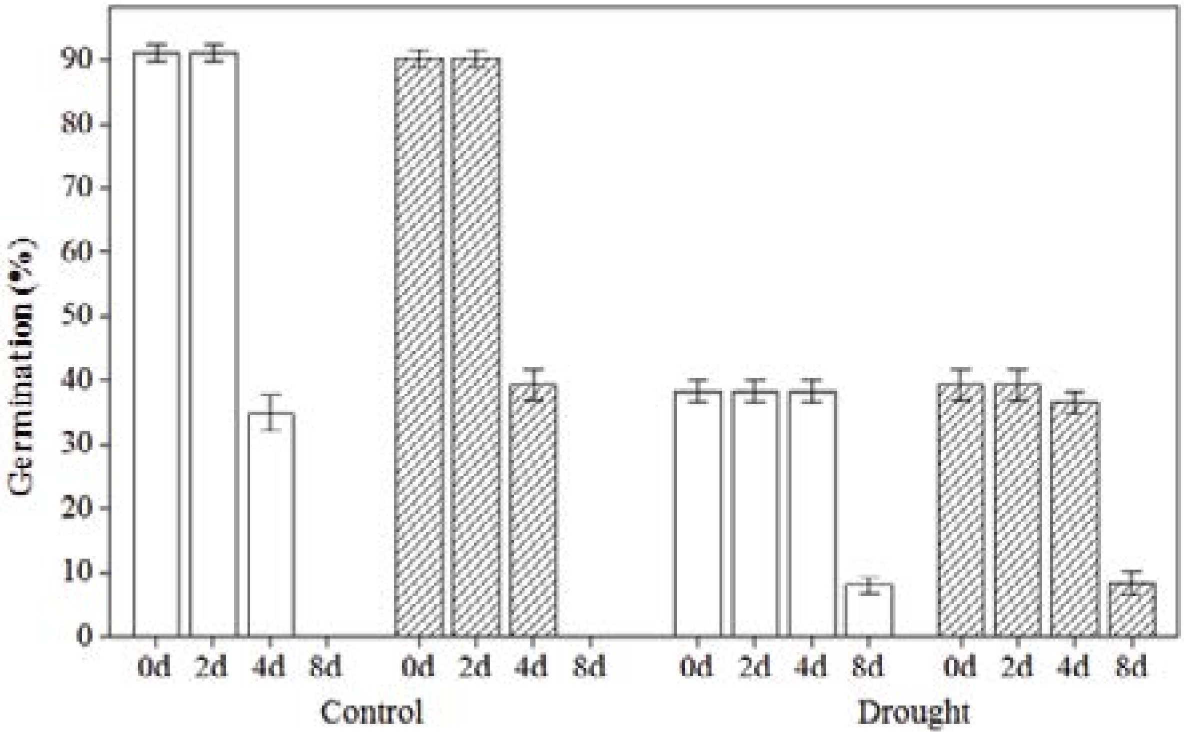

Figure 2: Effect of maternal plant environment (drought and herbivory) of *Vaccaria hispanica* on seed vigour of offspring using accelerated aging test (seeds were exposed to 45°C and 100% RH for 0, 2, 4, 8 days (d) in an incubator). Hatched bars: seeds from undamaged maternal plants; open bars: seeds from damaged maternal plants.

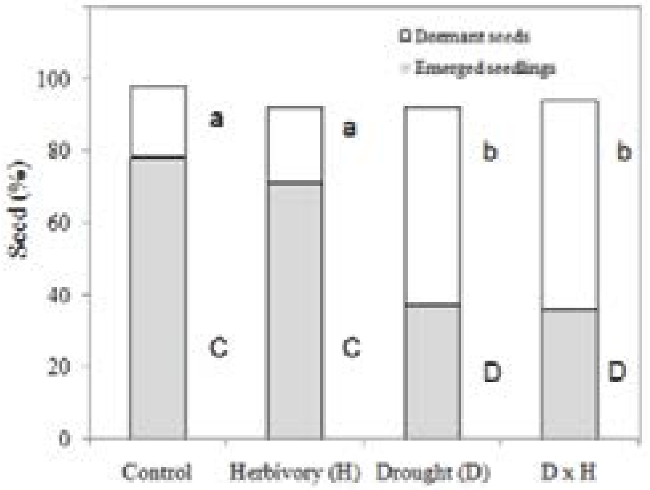

Figure 3: Effect of maternal plant environment (drought and herbivory) of *Vaccaria hispanica* on seedling emergence and seed dormancy in the following autumn. Bars with different letters are significantly different (Tukey's HSD, P=0.05).

	Drought (D)	Herbivory (H)	D × H
Final height (cm)	848^{***}	19.5^{*}	17.63^{*}
Number of stems	300^{***}	6.8^{*}	4.6^{*}
Index of architecture	3.35^{ns}	0.2^{ns}	11.7^{*}
Number of leaves	1341^{***}	130^{**}	7^{*}
Shoot/root ratio	422^{***}	15^{*}	22.12^{*}
Total plant biomass	372^{***}	58.11^{*}	8.39^{*}
Seed number	2344^{***}	17.68^{*}	24.23^{*}

*P<0.05; ***p<0.001; ns p>0.05. Main factors: Drought, Herbivory. F-values are shown along with statistical significance.

Table 1: Summary of two-way ANOVA showing the effects of drought and herbivory on different traits of *Vaccaria hispanica* plants.

Discussion

The population dynamics of plants is affected by climate change [8]. Diversity and composition of a plant community is affected by seeds as new offspring. Plants change their reproductive partitioning in terms of the mass, dormancy and longevity to acclimate to varying environments [9]. When offspring produced by each maternal plant shows different dormancy level, it may be an example of bet-hedging. Our study revealed that the dormant: non dormant seed ratio of *Vaccaria hispanica* is controlled by maternal water conditions but not by plant herbivory. While dormant seeds are more persistent and represent the low risk strategy, non-dormant seeds have high germinability and represent a high risk strategy [3,10]. A delay in germination of some of seeds would provide a reserve of seeds to germinate in future years. Such a bet-hedging strategy decreases the risk of reproductive failure under temporal environmental uncertainty [11].

Morphological traits

While maternal water limitation reduces the number of seeds, its effect on dormancy and emergence is more complex. Drought had the major influence on maternal plants. *V. hispanica* plants were highly plastic and displayed a phenotypic response to the environmental conditions, particularly drought, observed as changes in plant size, along with changes in seed mass [12].

Seed vigour

The changes induced by maternal growth environment were also passed on to the progeny [13]. While seeds from the water stressed maternal environment were all alive after being exposed to high temperature and humidity for 4 days (accelerated aging test), only 40% of the seeds from the control maternal plants remained alive. Seed vigour and longevity is a critical aspect in the population dynamics of a species. There was therefore evidence for a trade-off between fecundity and seed persistence in *V. hispanica* in a water shortage condition. Herbivory did not have any significant effect on seed vigour.

Seedling recruitment

Seeds from different maternal plants showed varying dormancy status. Variability in dormancy and germination of seeds from a plant reduces the risk from all siblings simultaneously suffering unfavorable conditions. Maternal environment drought had strong effects on seed dormancy in *V. hispanica*. Seeds produced by plants grown at low maternal water availability had lower germination percentage than those produced by plants that experienced no drought or herbivory alone. Previous work demonstrated that seeds from maternal plants grown in drought showed higher dormancy than seeds from a low water stress environment [14]. Maternal effects that have a significant influence on offspring fitness may confer a fitness advantage in environmental conditions similar to those experienced by the parents [15].

Conclusion

The current study shows that water status influences the population dynamics and seed persistence in *Vaccaria hispanica* and that variation in the seed bank (seed mass, seed vigour and dormancy) of *V. hispanica* are more dependent on water availability than herbivory. Seed dormancy and longevity as a bet-hedging strategy is likely to be an important contributor to stable species coexistence in the novel environmental conditions expected with climate change.

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