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Germination Success and Seedling Development of *Argania spinosa* under Different Climatic Conditions and Browsing Intensity

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The present study assesses whether the germination and establishment success of *Argania spinosa* seeds are affected by the environmental conditions under which the mother plant has grown. Seeds from three populations with different climatic conditions and herbivory intensity were collected and sown in the laboratory after different treatments. Our study suggests that the seed germination process and initial stages of seedling growth are adaptive. Seeds from the population of Agadir with the highest herbivory pressure and high air relative humidity in summer (due to the proximity to the sea) were stimulated by acid treatment, and showed a lower root/stem ratio, which allows them to take advantage of the atmospheric water resources. Seeds from the Mountain population, where the most arid environmental conditions were found, produced early-germinating seeds with the highest root/stem ratio that would facilitate seedling establishment when the harshest environmental conditions appear in summer.

Keywords: Herbivory, Germination treatments, Root/stem ratio, Root elongation, Timing of emergence.

One of the most important factors influencing reproductive success in forest communities is seedling emergence. Seedling emergence responds to environmental resource gradients such as light, water and nutrients, which can result from a variety of disturbance regimes [1]. Timing of emergence has important consequences on the survival and fitness of seedlings [2], and often determines whether a plant will compete successfully with its neighbors, or will be consumed by herbivores, infected with diseases, and finally whether it will mature properly by the end of the growing season [3]. All the events occurring during juvenile stages are extremely important for habitat selection by tree species [4,5]. In this way, a few days delay in the emergence can be magnified into large differences in final biomass and reproduction, especially under competitive situations [2]. Early emergence and establishment may be of critical importance when competition for resources is intense [6], as occurs in arid and semi-arid environments where *Argania spinosa* grows.

Seedlings of large-seeded and late successional species, as is the case with *A. spinosa*, have usually higher survival rates than small-seeded species, even under stressful environmental conditions such as water scarcity, shade, and damage by pathogens or herbivores [5,7,8].

Root development is also important for plant growth, since the capacity of nutrient and water acquisition depend on total root length and root architecture [9,10]. Especially when soil resources are limited, the capability of an acclimatory plasticity of the root system is important to plant success [11]. Once the carbon has been assimilated, the distribution of plant biomass is also affected by many factors (water, nutrients, climate), so the root shoot ratio (ratio of belowground versus above ground biomasses) has a valuable meaning, improving the rate of carbon assimilation and nutrient uptake of plants [12].

Argania spinosa (L.) Skeels is an endemic Moroccan tree subjected to a constant regression due to overexploitation. The high herbivory pressure, the use of the wood for carpentry and fuel, and the fruit for oil production have decreased their populations, and the recruitment of new individuals is almost non-existent. Germination and initial growth of seedlings are critical stages, and plant regeneration is strongly dependent on environmental conditions. Thus, the relationship between anthropogenic pressure, environmental conditions and plant regeneration performance has become important for understanding germination dynamics of this native species, mainly due to the fact that nowadays its regeneration is essential for the conservation of the ecosystem that has merited the inclusion of the UNESCO Biosphere Reserve Arganeraie. Although interest in research on this species has increased in the last years and some studies have been undertaken about different aspects of the germination and seedling survival [13-17], no studies have been carried out comparing germination dynamics in different populations of its biogeographical area.

The present study assesses whether the germination and establishment success of *A. spinosa* seeds are affected by the environmental conditions where the mother plant has grown. The following question was posed: Does seed origin affect emergence success, emergence timing and stem and root allocation?

Seeds from three populations with different climatic conditions and herbivory intensity were collected and sown in the laboratory after different treatments. The study areas were:

1. Douar Chwihiya (hereafter North). Located on a North oriented smooth slope close to the Beni Snassen Mountains, and to the coastal plane, at an altitude of 210 m (Figure 1). Vegetation is an open forest, where *A. spinosa* is accompanied by *Pinus halepensis* and *Olea europaea*. Until the settlement of a protection fence within a Government preservation programme 2 years before the study, the

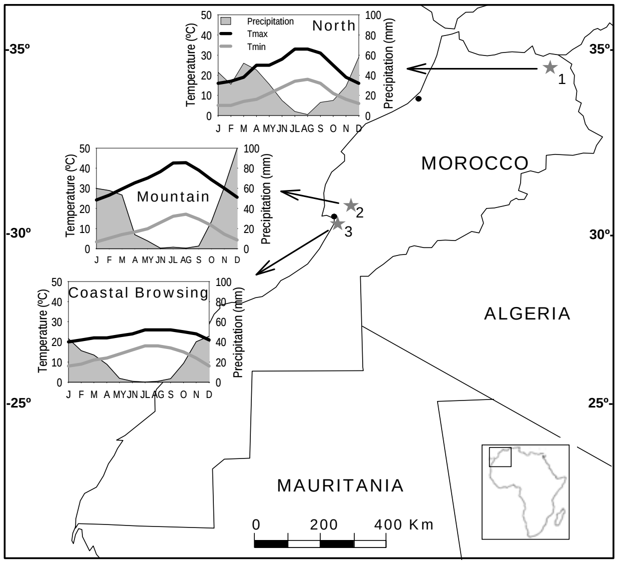

Figure 1: Location and ombrothermic diagram of the 3 studied areas: 1 North; 2 Mountain; 3 Coastal browsing.

area had been used for goat pasture, which prevented the natural regeneration of the argan forest.

he climate is Mediterranean, with an annual rainfall of 337 mm, concentrated from September to May. Monthly average temperatures are 30°C in summer and 5°C in winter. Relative humidity ranges between 58-60% in summer to 65-75% in winter. The site was selected for its intermediate climatic conditions and its isolation (800 km from main distribution area).

2. Tassademt (hereafter Mountain). Located 70 km NE of Agadir, in the first foothills of the Atlas Mountains. The studied population grows on a slight slope at 810 m of altitude. The argan forest is the predominant vegetation type, an open forest with broad gaps covered with a grass community (Figure 1). Woody vegetation is scarce and scattered, mainly composed of spiny shrubs. The climate is more extreme than in Agadir, with marked continental character. Monthly average temperatures are 40°C in summer and 3°C in winter (Figure 1); however it can drop to -5ºC. Rainfall is scarce (385 mm) and almost totally absent in summer, which, combined with high temperatures, turn summer especially severe. Relative humidity for this population was the lowest of all three (40-50% in summer to 60-70% in winter). The extreme climatic conditions at this site, close to the species' natural distribution limit, were the reason for its selection.

3. Admine Forest (hereafter Coastal Browsing). Located in the suburbs of Agadir city, 5 km inland, 107 m of altitude, in a strongly humanised area, traditionally managed for agriculture and livestock raising. Apart from the dominant *A. spinosa*, natural vegetation is scarce. The climate is temperate due to marine influence, with maximum temperatures never surpassing 30ºC, and minimum never below 7ºC. Annual rainfall is scarce, 232 mm, and concentrated from October to April (Figure 1). Relative humidity for this population was the highest of all three (from 65 to 75% throughout the year). This area is considered [18] as the ecological optimum for the species and the center of its distribution area. It was selected by the high herbivory pressure, mainly by goats.

Seed germination experiments

A. spinosa fruits are sessile drupes with a hard endocarp protecting an oil rich kernel. Flowering occurs mainly in spring, with great variation between individuals. Therefore, fruit production extends over a long period, and fruits can be found in different ripening phases from April to September [19].

Fruits of similar size were collected in June from 20 trees within each population and then pooled to homogenize tree individual variations. Fruits were peeled to obtain the seeds (endocarp plus kernel), which were stored in natural conditions in paper bags until they were sown in the following mid-September.

Seeds were individually planted in 250 mL container pots in the greenhouse of the University of Seville in a substrate composed of a 70:30 mixture of commercial compost (plant organic matter) and perlite, and watered daily. Seventy seeds were used for each treatment and population (70 seeds*3 population*4 treatments). Burial of the seeds was avoided for a better control of germination timing and, because burying does not occur under natural conditions, due to the seeds big size.

Physical dormancy has already been reported for this species. Alouani and Bani-Aameur [13] proved that gibberellic acid and cold storage treatment increased germination rates, while other authors have proved the effect of temperature (25ºC being the optimum), oxygenated water, and warm water [15]. The treatments selected in this study had the objective of simulating natural processes in argan seed germination. This assay was carried out under natural sunlight and greenhouse temperature conditions (from 19 to 26ºC for this period). Seed sowing occurred at the end of September, coinciding with the first rains and the decrease in the high summer temperatures.

1. Water treatment: seeds were submerged in water at environment temperature (24-28ºC) for 24 hours. This treatment simulated the first autumn rains after summer rainfall shortage.

2. Acidic pH treatment: seeds were submerged in water that had been acidified with 35% hydrochloric acid to attain a pH value of 3 for 15 minutes and then rinsed with water. This treatment simulated the passage through the goat's digestive system, which reaches this acidity during digestion.

3. Endocarp breakage treatment: the thick endocarp, that protects the kernel, was partially broken with a hammer to simulate the possibility of breaking when chewed by goat.

4. Another series of 70 seeds per site were planted as controls with no treatment.

Seedling emergence was defined as the moment when the radicle goes through the tegument (endocarp). Days to emergence was defined as the period from the date of sowing to the date of seedling emergence. Total germination proportion was then calculated as the percentage of the number of germinated seeds from the total number of seeds initially sown per population and treatment. Germinated seeds were counted and marked daily. The experiment was stopped when no germination was observed for 10 days in any of the treatments.

At the end of the germination experiment the following items were measured: seedling height (stem elongation), as the distance from the soil surface to the shoot apex, and root elongation as the distance from soil to root apex. Total number of leaves per seedling was counted.

Differences in total germination (%) among populations and treatments were tested by the G-test of independence. The Habermann test was used to compare pairwise differences.

Table 1: Seed characteristics of *A. spinosa* trees in the study sites. Lower-case indicate post hoc Tukey test results. (+ Data from [20]).

	North	Mountain	Agadir
+Seed mass (g)	2.52 ± 0.8 **a**	1.88 ± 0.7 **b**	2.48 ± 0.7 **a**
+Endocarp mass (g)	2.25 ± 0.7 **a**	1.59 ± 0.6 **b**	2.21 ± 0.6 **a**
+Kernel mass (g)	0.27 ± 0.1 **a**	0.28 ± 0.1**a**	0.27 ± 0.1**a**
One kernel mass (g)	0.25 ± 0.1 **a**	0.16 ± 0.1 **b**	0.23 ± 0.1 **a**
+Nº Kernels/seed	1.08 ± 0.2 **a**	1.78 ± 0.7 **b**	1.16 ± 0.3 **a**

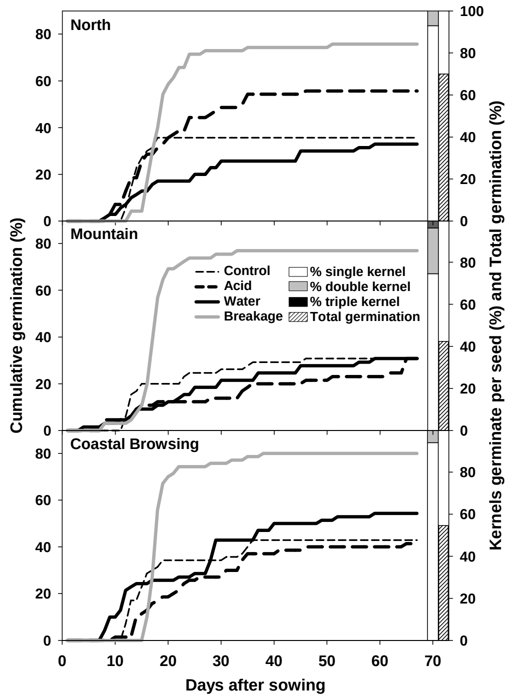

Figure 2: Seedling emergence dynamics of *A. spinosa* subjected to 4 germination treatments, and percentage of germination of single, double and triple seedlings per individual seed in three populations.

Two parameters were calculated to analyse germination dynamics: t_0 (number of days between sowing and the first germination), and t_{50} (days needed to reach 50% germination of the total germinated seeds). Days to emergence were compared among sites and treatments by means of a two-way ANOVA.

MANOVA was used to evaluate the influence of the root/stem elongation ratio of the seedlings. Seedlings were categorized in 5 classes by stem height (<60 mm, 60-100 mm, 100-150 mm, 150-190 mm, and >190 mm) within each population, and were analyzed using a three-way ANOVA where population, treatment and stem height category were the crossed factors. Post-hoc Tukey test was used to compare pairwise differences.

To reach the normality assumptions of the ANOVA, days for germination were log (x) transformed, and root elongation, stem height and leaf·density were square-root transformed.

Pearson's correlations were performed between t_0 and stem height, root elongation, and root/stem elongation. All statistical analyses were performed using SPSS 14 for Windows.

Endocarp, seed mass, and number of kernels per seed are significantly different among populations while total kernel mass per seed was similar [20].

Although the Mountain population had the smallest seeds and individual kernels (Table 1), it also had the biggest number of kernels per seed (1.8 kernels per seed, with up to 4 kernels), and, as a consequence, total kernel mass was similar to that of the other populations.

Table 2: t_0 (number of days between sowing and the first germination), t_{50} (days needed to reach 50% germination of the total germinated seeds), t_{mean} (mean number of days needed for germination), t_{total} (number of days between sowing and the last germination) and % G (total percentage of germination).

	Treatment	t_0	t_{50}	t_{mean}	t_{total}	% G
North	***Control***	12	13.6	14.9	18	35.7
	Water	9	15.5	19.4	46	55.7
	Acid	8	17.5	25.1	59	32.9
	Break	13	17.6	19.4	51	75.7
Mountain	Control	12	13	19.4	46	30.8
	Water	8	33.6	34.2	65	30.8
	Acid	4	23	26.8	58	30.8
	Break	8	17	17.7	33	76.9
Coastal	Control	12	14.6	14	36	42.9
	Water	10	21.5	24.8	65	41.9
	Acid	8	11.7	23.2	59	54.3
	Break	16	16.7	18.3	38	80.0

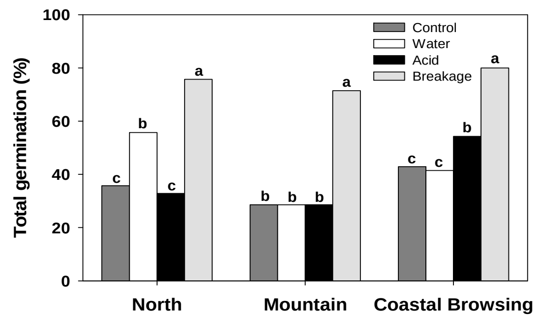

Figure 3: Total germination percentage for each treatment in the three study populations. Lower-case indicate Habermann test results.

Two way ANOVA showed differences in germination time between populations (F2=3.31, P=0.037), treatments (F3=8.84, P=0.001) and more importantly, interaction between them (F6= 2.61, P=0.017). Seedling emergence began 4 days after sowing for acid treatment in the Mountain population, followed by 8 days for the acid (North and Coastal Browsing) and water treatments (Mountain population). The last seedling emergence occurred on day 59 from acid treatment in the North population, and day 65 in the Mountain and Coastal Browsing from water treatment (Figure 2).

Germination dynamics for the control treatment were similar in all populations, with the radicle emerging 12 days after sowing, and time to complete t_{50} was reached about 13-14.5 days after sowing. Acid treatment was the most effective in stimulating early germination, t_0 being the lowest of all treatments (4-8 days). However, in spite of the fast germination of acid treated seeds, t_{50} was higher than in other treatments. Water treatment was more effective for early germination than controls or breakage, but not for achieving early 50% of seed germination. Breakage was effective for neither early germination nor 50% of germination compared with the control treatment, although total percentage germination within this treatment was the highest in all populations (Table 2). When germination dynamics were compared between populations, it could be observed that seeds from the Mountain population were the fastest to germinate, although days needed for 50% germination were longer than in the North. Seeds from Coastal Browsing showed the slowest germination.

Differences between populations in germination percentage (Figure 3) were found for water and acid treatments (G-test, $P_{water}<0.001$, $P_{acid}<0.05$). However, differences between treatments

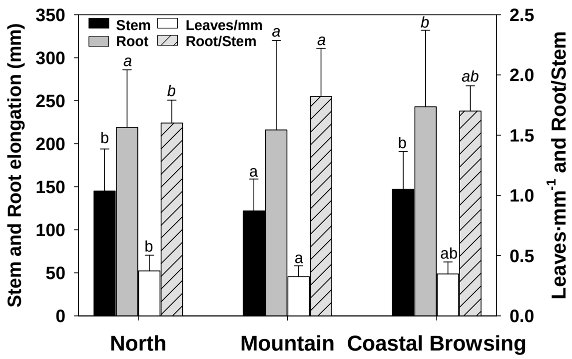

Figure 4: Root elongation, stem height, leaf density (leaves per mm) and root/stem elongation ratio (mm·mm^{-1}) of seedlings of the study populations (± sd). Lower-case indicate results of the post hoc Tukey test.

Table 3: Summary of the three-way MANOVA on the effects of population (P), treatment (T), and stem height categories (C) for root and stem elongation, leaf density (leaves·mm^{-1}), and root/stem elongation ratio (Tukey test results in Figs 4 and 5). * Indicate significant differences.

		Root		Stem		Leaves·mm^{-1}		Root/Stem	
	fd	F	P	F	P	F	P	F	P
Population	2	2.22	0.111	0.15	0.855	3.1	0.006*	1.01	0.117
Treatment	3	11.44	0.001*	1.45	0.227	2.25	0.082	9.02	0.001*
Category	4	21.85	0.001*	68.21	0.001*	1.19	0.314	11.32	0.001*
P*T	5	4.09	0.001*	3.22	0.008*	3.69	0.003*	8.43	0.001*
P*C	8	0.91	0.509	0.749	0.649	1.58	0.130	0.91	0.503
C*T	12	0.86	0.589	0.83	0.615	0.95	0.491	0.846	0.603
P*T*C	10	1.527	0.130	0.653	0.767	1.105	0.359	1.820	0.051

in germination percentage were detected in the 3 populations (G-test P<0.001 for the 3 populations). Germination percentage varied between 31% in control, acid, and water treatments of the Mountain population, to 77-80% in breakage treatment (Table 2). Breakage was the best treatment in all populations; acid was effective only in Agadir and water treatment was effective only in the North population. The best total mean germination results were obtained in the Agadir population, with 54.6% of seeds germinated, of which 6% were double-kernelled (two seedlings were produced per one single seed). As a result, 162 seedlings were obtained in this population. On the other side, the Mountain population had the lowest germination percentage (42.3%), although the number of seedlings obtained was the highest (166 seedlings) because of the high number of seeds with double and triple germination (21.8% of the seeds produced two seedlings per single seed and 4.0% of the seeds produced three seedlings per single seed, Fig 2). The lowest number of seedlings was obtained in the North population (150 seedlings, 7% of which were double-kernelled) with total germination of 43.6%. When all populations were compared independently of the treatment, seedlings from Coastal Browsing showed a significantly greatest elongation of root, while stem elongation was similar in North and in Coastal Browsing and shorter in Mountain (Table 3, Figure 4). Leaf density was highest in the North population and lowest in Mountain (ranking from 0.32 to 0.36 leaves·mm^{-1}). The highest root/stem ratio was found in the Mountain population (1.6-1.8 mm·mm^{-1}).

When stems were categorized by height classes, it could be appreciated how root/stem ratio decreased significantly (R= 0.428, P= 0.001) with stem height until seedlings reached 100-150 mm. At this point stabilisation of this variable could be observed in North and Mountain populations, but it still decreased in Coastal Browsing (Figure 5, Table 3). t_0 was correlated to root elongation (R= 0.639, P= 0.025), but nor to stem height (R= 0.180, P= 0.558).

Our results show that *A. spinosa* can reproduce easily from seed.

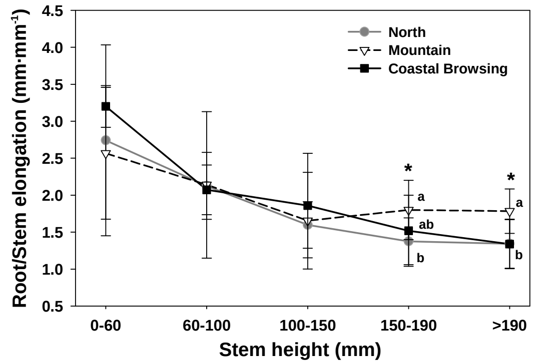

Figure 5: Root/stem elongation ratio at 5 categories of stem height in the 3 study sites. Root/stem ratio values are mean of each stem category (± sd). * Indicate P<0.05. Lower-case indicate results of Tukey test.

Therefore, the factors preventing natural recruitment of new individuals must be related to the harsh weather conditions where the species grows, such as drought periods [16], and salinization problems [14], and also by biological factors such as herbivory or pathogens. In this context, trees from each population produce seeds that present differences in germination and establishment strategies, from seed size, germination success, and root and stem allocation in seedlings.

Germination percentage obtained in this study with control seeds (30-40%) fits with the values obtained in control treatments (32-35%) in earlier studies [13, 16]. Some have reported higher values of germination success, but in all these cases the seeds had received either a pre-treatment or had been cultivated at optimal temperature.

Seed germination of many species may be stimulated by animal ingestion. Several works have demonstrated the effect of ingestion on fruits over the endocarp that protects the seeds, allowing them to germinate if conditions are suitable [21, 22].

When fruits are swallowed, seeds pass through the digestive tract and receive an acid treatment that softens the endocarp and prepares them for germination. In our study, acid treatment speeded up the germination process in all populations, but when cumulative germination was reviewed, this treatment was effective only in the Coastal browsing population, with centuries of high herbivore pressure. Nevertheless, breakage was the most effective treatment in terms of germination rate.

The fact that t_0 was correlated with root elongation, but not with stem height, suggests the importance of a quick germination for root development. This improves the capacity of nutrient and water acquisition against competitors or even the capacity to renew photosynthetic material after herbivory [9-11]. Seeds from the Mountain population were the fastest to germinate, probably because the lowest investment in endocarp of these seeds facilitates the breakage. As shown by Zunzunegui *et al*. [20], fruits from this population are the ones with the thinnest endocarp. In this site, where the most adverse climatic conditions were found, early timing of germination could be advantageous for seedling survival. A fast seedling development and, as a consequence, a big root development would facilitate seedling establishment before the harsh conditions of summer. In addition, a big root development would be beneficial in this population for surviving to the absence of precipitation and the low relative air humidity of summer. On the contrary, cumulative germination success in this population was low, probably because of the low mass of the kernels of its seeds. This fact could also be the cause of the lower (stem and root) seedling growth from this site in comparison with the other populations, as seed size has been described to be related to relative growth rate [4, 23].

Resources allocation to defense and storage can influence survival by providing a buffer against temporary resource deprivation (e.g. restoring tissue after herbivore attack [23, 24]. In addition, changes in allocation patterns in response to the environment determine the plants' survival ability [25, 26]. In our experiment, root/stem ratio diminished significantly with stem height indicating that at the seedlings' first stage the main allocation in resources was root elongation, until a stem height of 100-150 mm was reached. From this moment onwards, root/stem ratio followed a different pattern depending on the origin of the population of the seed: it could continue decreasing (Coastal Browsing), increasing (Mountain), or even remain stable (North).

In this way, seeds from the population with the highest herbivory pressure produced the seedlings with the longest root and stem, but the lowest root/stem ratio. Moreover, this population is located in the area with the best climatic conditions for the species [18, 19], close to the ocean (5 km) whose influence maintains relative humidity high even in summer (close to 65%). These favourable conditions throughout the year could allow seedlings from this population to allocate resources towards stem growth, taking advantage of the atmospheric water resources that do not occur for the Mountain population. On the contrary, the highest root investment by stem was located in the Mountain population. Most likely, this would improve the seedling's probability of surviving the next dry season. An increase in root/stem ratio has been documented in *Quercus ilex* trees growing in a xeric site compared with plants from a mesic site [27-28]. It has also been suggested by Schulze [29] that water depletion modified the allocation pattern to favour supporting organs and thus to improve the uptake and transport of the available resources. According to Tazi *et al.* [17], the higher root/stem ratio in this population could be due to the lower sensibility to an increase in the arid conditions of the root than stem. These authors found that seedling stems tended to be more affected by water stress than roots.

Our study suggests that the seed germination process and initial stages of seedling growth are adaptive because of the different responses found by comparing the seeds of the study populations. Seeds from the Coastal Browsing population with the highest herbivory pressure and high air relative humidity were stimulated by acid treatment, and showed a lower root/stem ratio, which allows them to take advantage of the atmospheric water resources. In contrast, seeds from the Mountain population, where the most arid environmental conditions were found, produced early-germination seeds with the highest root/stem ratio that facilitated seedling establishment when the harshest environmental conditions appear in summer.

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