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Interactive effects of seed size and drought stress on growth and allocation of *Quercus brantii* Lindl. seedlings from two provenances

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Abstract: *Quercus brantii* is an important tree species in Zagros forests. Summer drought imposes severe limitations in *Q. brantii* forests, making reforestation with this species in general very difficult. This is further complicated by the limited ecophysiological information for this species. To improve our understanding of factors affecting the drought tolerance of *Q. brantii* at early critical life stages, we explored the influence of seed size and provenance on growth and survival of *Q. brantii* seedlings under drought. As expected, drought reduced growth and survival and increased the root-to-shoot ratio, with larger acorns rendering more vigorous growth than small ones. There was a positive correlation between seed size and root-to-shoot ratio under severe drought stress only for the provenance from the wetter region. Our results indicate that large seeds of *Q. brantii* from populations with good genetic material can render restoration programs in the Zagros forests more successful.

Key words: Maternal environmental, Mediterranean forests, reforestation, root-to-shoot ratio

1. Introduction

The seedling stage is an important, often critical, phase in the regeneration of woody species under natural conditions; the risk of lethal environmental stress is high at this stage. Water availability is a widespread limiting factor for regeneration of many woody species including oaks (Aschmann 1984). Poor seedling quality, especially in the Mediterranean environment, which is characterized by seasonal and episodic droughts, frequently accounts for the failure of oak plantations (Clark et al. 2000). Among oaks there is wide variation in seed size within species (Khan and Shankar 2001). Seed size can be affected by the maternal environment, primarily due to seed sensitivity to resource availability (Krannitz et al. 1999; Wulff et al. 1999; Ramirez-Valiente et al. 2009). In general, growth parameters of seedlings such as height, diameter, and fresh weight increase as seed size increases (Karrfalt 2004). Large seed size has often been linked to enhanced seedling survival and regeneration success (Armstrong and Westboy 1993; Bonfil 1998), because seed mass represents the amount of reserve an embryo contains to start its first life stage (Quero et al. 2007). The effect of seed size on seedling performance is highly variable and depends on environmental conditions such as drought (Leishman and Westoby 1994). In fact, seed size variation is thought to be important for the establishment of seedlings under different ecological conditions (Quero et al. 2007), and larger seeds can improve the establishment of seedlings under competitive and resource-limiting conditions (Moles and Westoby 2004). For example, Khurana and Singh (2000) found that seedlings from smaller seeds were better under moderate levels of water stress; however, under severe water stress seedlings from large seeds were more tolerant. Ramirez-Valiente et al. (2009, 2010) also found that larger seeds of *Quercus suber* from drier populations exhibited the highest survival rates under dry conditions.

Quercus brantii Lindl. is one of the most abundant and widespread species in the Zagros mountain forests of western Iran. *Quercus brantii* is distributed from north to south in the Zagros mountain forests, but the other 2 Zagros oak species (*Q. infectoria* and *Q. libani*) are distributed only in the north. In fact, *Q. brantii* grows in a mixed environment with 2 other oak species in the Baneh provenance (north of Zagros). The occurrence of 2 (or even more) oak species in a forest stand certainly contributes to the adaptive potential of the species by increasing genetic diversity (Finkeldey 2001) and providing a basis for selection due to the differentiation in species' adaptive traits, such as water use efficiency. Study of the genetic

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variation (CVG) of *Q. brantii* growth parameters from different provenances of the Zagros forests have also shown that the Baneh population has higher genetic variation than the other Zagros forest populations (Karimi 2012). On the other hand, these forests are characterized by a Mediterranean climate and extreme summer aridity, and soil in the north of the Zagros forests is wetter and more fertile than in other parts of these forests. More than 1.7×10^6 ha of the Zagros forests has been destroyed since 1962 due to human activities such as cattle grazing (Ghazanfari et al. 2004). Due to low growth rates and survival percentages, plantations of *Q. brantii* established to restore these destroyed forests have not been successful, making the search for effective reforestation strategies timely and crucial. However, despite all efforts to understand the responses of *Q. brantii* to drought stress, the information is far from complete, particularly regarding the combined effects of seed size and drought stress on the growth of *Q. brantii* seedlings. The present study was designed to determine the combined effects of seed size and drought stress on early growth in *Q. brantii* from 2 climatically and genetically different provenances (north and south Zagros forests). The aim of this paper is to contribute to the development of a strategy for the extensive production of high quality seedlings of this species for reforestation in the Zagros forests of Iran.

2. Materials and methods

In early November 2009, acorns from 40 *Quercus brantii* mother trees were collected from 2 provenances, Yasouj (south Zagros forest) and Baneh (north Zagros forest) (Table 1). Trees of each provenance (20 trees) were separated by a minimum of 100 m to reduce consanguinity. Healthy acorns were selected and different traits such as weight, length, width, and seed volume were measured; seed weight was not significant between the 2 provenances. Acorns from each provenance were then separated into 3 size classes consisting of small, medium, and large seeds (Table 2). Next, 100 acorns of each size class were sown in 5-L plastic pots containing forest soil modified by 20% sand by volume (50.6% sand, 24.4% silt, and 25.2% clay). Seedlings were grown under field conditions at Yasouj University and were irrigated regularly until July 2010. Prior to the onset of the experiment, soil moisture characteristics including field capacity (FC) and permanent wilting point (PWP) were determined by pressure-plate apparatus (Richards 1947). The water holding capacity of the soil at one-third (100% FC) and at 15 atm (PWP) was 25.7 and 12 w/w percentage, respectively (PWP 45% of FC). In July 2010, seedlings were divided into 2 groups, control and drought treatments. Both groups were harvested at 3 time points of 4, 8, and 14 days after withholding water in the drought-treated group. Control seedlings (optimal condition) were irrigated regularly at all 3 harvesting points, such that their soil FC remained at about 100% during the experiment.

Table 1. Location and climate of the 2 provenances.

Provenance	Location		Climate parameters					
	Latitude	Longitude	AP	AT	GP	GT	NDD	Xi
Yasouj	30°41′43.7″	45°35′5.1″	922.18	15.00	92.3	21.27	195	329.5
Baneh	35°55′33.9″	45°49′0.4″	707.90	14.65	151.7	21.93	160	258.1

AP = annual precipitation (mm), AT = annual temperature (°C), GP = precipitation of growth period (mm), GT = temperature of growth period (°C), NDD = number of drought days, Xi = xerothermic index (Grossmann et al. 2002).

Table 2. Seed size classes used from each of the 2 provenances.

Provenance	Seed weight classes											
	Small				Medium				Large			
	LS	WS	VS	W	LS	WS	VS	W	LS	WS	VS	W
Yasouj	4.1 ± 0.07	1.4 ± 0.03	4.5 ± 0.2	5.2 ± 0.1	4.4 ± 0.07	1.65 ± 0.02	6.4 ± 0.2	7.2 ± 0.1	4.5 ± 0.07	1.75 ± 0.03	7.50 ± 0.3	9.8 ± 0.1
Baneh	3.4 ± 0.05	1.4 ± 0.01	3.5 ± 0.1	3.9 ± 0.1	3.9 ± 0.06	1.6 ± 0.02	6.2 ± 0.2	6.6 ± 0.1	4.1 ± 0.09	1.90 ± 0.05	8.08 ± 0.5	10.6 ± 0.2

LS = length of seed (cm), WS = width of seed (cm), VS = volume of seed (cm^3), W = weight of seed (g).

After 4, 8, and 14 days of withholding water, seedlings from the drought treatment group reached 65% FC or mild stress, 45% FC or moderate stress, and 25% FC or severe stress, respectively (Figure 1). In this experiment, both control and drought treatment seedlings were harvested at 3 time points (Figure 1). The seedlings were examined in terms of growth and morphological traits such as seedling height (cm); root length (cm); shoot, leaf, and root weight (g); total fresh weight (g); root-to-shoot ratio (R/S); specific leaf area (SLA) ($cm^2 g^{-1}$); number of leaves; and vitality. At the end of each treatment, seedling roots were washed gently to remove soil, and seedling height and root length were measured. Seedlings were then separated into roots, shoots, and leaves, and the fresh weight of each part was measured

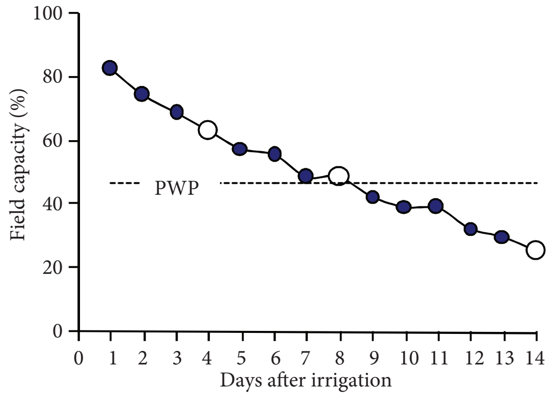

Figure 1. Trend of soil field capacity during experiment. Harvest points are indicated with white circles and PWP is shown with a dashed line.

separately. R/S was estimated by dividing root weight by shoot weight; total fresh weight by adding root, shoot, and leaf weights; and vitality by dividing the number of green leaves by the number of total leaves. In order to calculate SLA, the first fully developed leaf from each seedling was scanned together with a scale, and then leaf area was measured with Image J software. SLA was then calculated by dividing leaf area by leaf dry weight. In addition, the seedling survival percentage was recorded by calculating numbers of living seedlings compared to total seedlings at the end of the experiment (25% FC). The experiment was designed as a completely randomized full factorial scheme (2 provenances, 3 harvest times, 2 treatments, and 3 seed size classes) with at least 5 replicates for each combination. For all investigated parameters, analysis of variance was performed using SPSS 16.0 (SPSS Inc., Chicago, IL, USA). Significant differences among mean values were compared by Duncan's test. Pearson's correlation coefficient was determined among seed weight and the different seedling traits from each provenance and treatment.

3. Results

3.1. Effects of seed size

Significant differences were observed for leaf, shoot, root fresh weight, and total fresh weight in seedlings from different seed size classes (Table 3). Seedlings from larger seeds had higher values for these traits among all water conditions than those from small seeds (Table 4). Interactions of seed size by treatment and seed size by

Table 3. Statistical results (ANOVA) for the different traits of seedlings as affected by provenance, water deficit, and seed weight.

Source of variation	Traits of seedlings									
	H	RL	FWL	FWS	FWR	TFW	R/S	SLA	NL	Vitality
Provenance	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Time	ns	ns	ns	ns	ns	ns	**	ns	ns	*
Treatment	ns	ns	**	ns	**	**	ns	ns	ns	*
Seed size	ns	ns	**	*	**	**	ns	ns	ns	ns
Time × provenance	ns	*	ns	ns	ns	ns	ns	ns	ns	*
Treatment × provenance	ns	ns	ns	ns	*	ns	**	ns	ns	ns
Seed size × provenance	ns	ns	ns	ns	ns	ns	ns	*	ns	ns
Time × treatment	ns	ns	**	ns	ns	ns	ns	ns	ns	*
Time × seed size	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Treatment × seed size	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Time × provenance × treatment	ns	ns	ns	ns	ns	ns	*	ns	ns	ns
Time × provenance × seed size	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Treatment × seed size × provenance	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Time × treatment × seed size	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Time × treatment × seed size × provenance	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

** $P < 0.01$, * $P < 0.05$; ns: not significant. H = height of seedling, RL = length of root, FWL = fresh weight of leaf, FWS = fresh weight of shoot, FWR = fresh weight of root, TFW = total fresh weight, R/S = root to shoot ratio, SLA = specific leaf area, NL = number of leaves.

Table 4. Mean values for seedling traits measured in *Quercus brantii* under different provenances, seed size classes, drought treatments, and times.

		H (cm)	RL (cm)	FWL (g)	FWS (g)	FWR (g)	TFW (g)	R/S	SLA ($cm^2 g^{-1}$)	NL	Vitality
Provenance	Yasouj	6.43a	42.7a	0.51a	0.82a	2.9a	4.1a	1.9a	6.6a	8.9a	0.87a
	Baneh	6.59a	46.9a	0.58a	0.67a	3.4a	4.7a	2.4a	7.5a	8.9a	0.83a
Seed size	Small	6.08a	46.5a	0.45b	0.56b	2.3c	3.3c	2.0a	7.0a	7.2a	3.20a
	Medium	6.55a	46.5a	0.52b	0.79a	3.0b	4.3b	2.1a	7.5a	8.2a	3.10a
	Large	6.93a	41.3a	0.66a	0.89a	4.1a	5.4a	2.4a	6.6a	8.1a	3.50a
Drought treatment	Control	6.47a	43.3a	0.62a	0.80a	3.6a	5.1a	2.1a	7.0a	9.0a	0.94a
	Drought	6.54a	45.8a	0.49b	0.71a	2.8b	3.9b	2.2a	7.0a	8.8a	0.80b
Time	65% FC	6.40a	45.4a	0.56a	0.70a	3.5a	4.8a	1.3b	7.1a	8.3a	-
	45% FC	6.30a	45.3a	0.54a	0.84a	3.0a	4.2a	2.4a	6.9a	9.0a	0.91a
	25% FC	6.80a	43.3a	0.54a	0.65a	2.9a	4.1a	2.6a	7.1a	9.4a	0.75b

Different letters in each column denote significant mean differences at P < 0.05 based on Duncan's test. H = height of seedling, RL = length of root, FWL = fresh weight of leaf, FWS = fresh weight of shoot, FWR = fresh weight of root, TFW = total fresh weight, R/S = root to shoot ratio, SLA = specific leaf area, NL = number of leaves.

time were not significant for any seedling trait (Table 3). Seed size was positively correlated with growth parameters such as fresh weight of leaf, shoot, and root and total fresh weight of seedlings from both provenances under optimal condition or 100% FC; however, there was no correlation with height of seedlings, length of root, R/S, number of leaves, or vitality (Table 5). In addition, there was no significant correlation between seed size and measured parameters under any level of water stress in Yasouj provenance seedlings (Table 5). However, Baneh provenance seedlings showed a higher positive correlation between seed size and fresh weight of leaf, shoot, and root and total fresh weight under drought treatment than under optimal conditions. In fact, there was a positive correlation between seed size and R/S under severe drought stress (25% FC) in seedlings from the latter provenance. We also found an interaction between seed size and provenance. Seedlings from medium-size Baneh provenance seeds had higher SLAs than seedlings from small and large size seeds; however, the SLA of Yasouj seedlings did not differ significantly for any seed size class (Figure 2a). Seed size did not significantly affect survival rate.

Table 5. Correlation between seed weight and different traits of *Q. brantii* seedlings in each provenance and drought treatment.

Provenance	Treatment	H	RL	FWL	FWS	FWR	TFW	R/S	SLA	NL	Vitality
Yasouj	100% FC	0.43	–0.03	0.38*	0.17	0.4*	0.45**	0.26	–0.03	–0.25	0.0001
	65% FC	0.26	0.19	0.49	0.3	0.28	0.42	–0.34	–0.11	0.52	-
	45% FC	0.08	–0.24	0.39	0.34	0.26	0.29	–0.17	–0.27	0.32	–0.29
	25% FC	–0.01	–0.08	0.09	0.06	0.44	0.37	0.29	0.18	0.27	0.10
Baneh	100% FC	–0.13	–0.06	0.17	0.49**	0.51**	0.52**	0.03	–0.24	0.34	0.04
	65% FC	–0.05	–0.34	0.38	0.49	0.78**	0.77**	0.42	–0.26	–0.04	-
	45% FC	0.48	–0.26	0.54**	0.68**	0.72**	0.69**	0.04	0.08	0.28	0.16
	25% FC	0.25	0.15	0.62**	0.04	0.65**	0.67**	0.45*	–0.15	0.33	–0.33

** P < 0.01, * P < 0.05. H = height of seedling, RL = length of root, FWL = fresh weight of leaf, FWS = fresh weight of shoot, FWR = fresh weight of root, TFW = total fresh weight, R/S = root to shoot ratio, SLA = specific leaf area, NL = number of leaves.

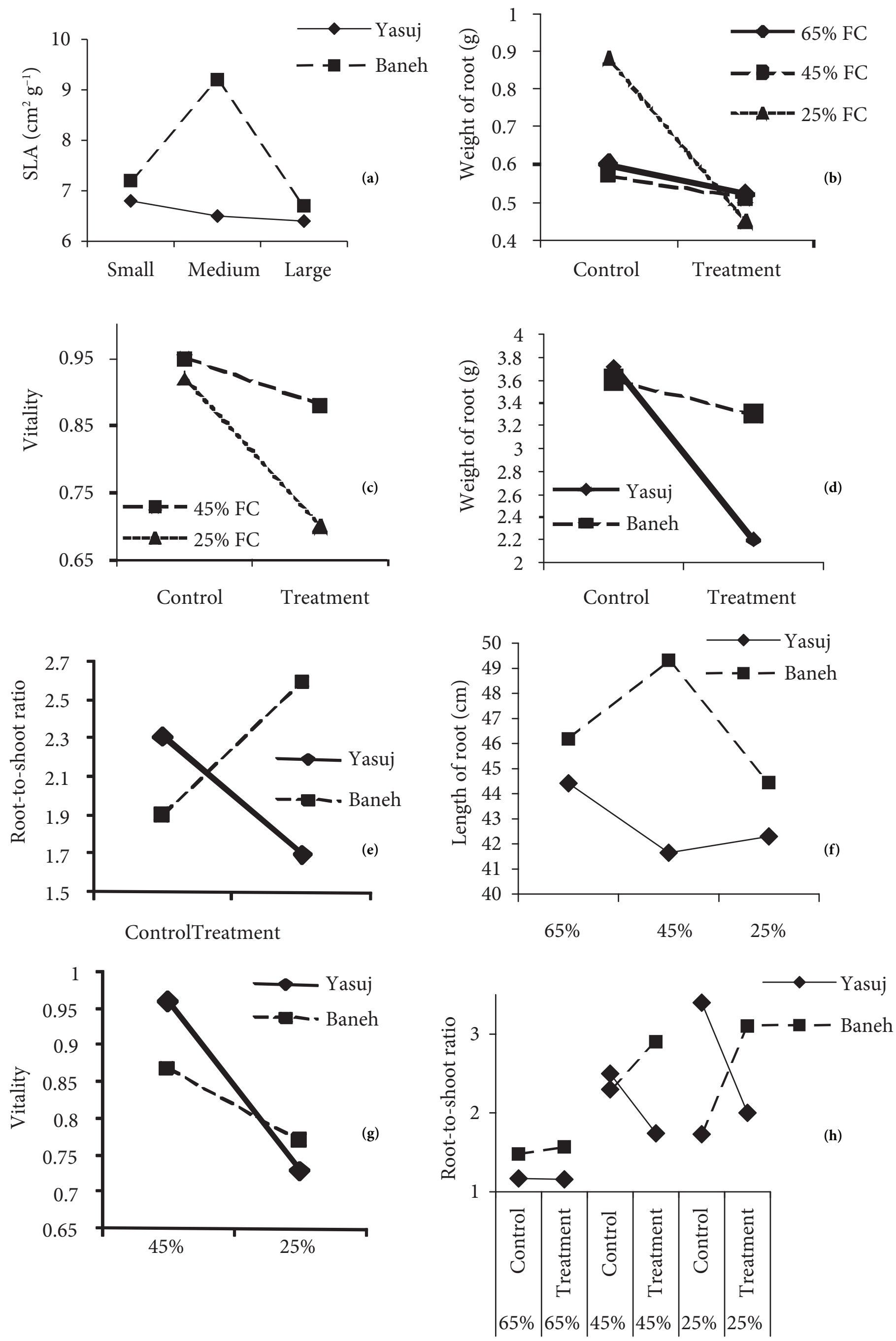

Figure 2. Interactive effects of seed size, drought stress, time, and provenance (Yasouj and Baneh) on seedling traits.

3.2. Effects of drought stress

Analysis of variance showed that the effect of drought was significant for fresh weight of leaf and root, total fresh weight, number of leaves, and vitality (Table 3). These traits significantly decreased under drought regardless of provenance and seed size (Table 4). The effect of time was significant for R/S and vitality (Table 3). R/S was 1.4, 2.4, and 2.6 under mild, moderate, and severe water deficit stress, respectively, and it was significantly lower under mild stress than under other drought stress levels (Table 4). Indeed, this result showed changes in allocation patterns in response to water deficit, with a higher allocation toward roots under higher drought stress. Vitality under 25% FC significantly decreased with increasing drought stress

(Table 4). A significant interaction between treatment and time for fresh weight of leaf and vitality was observed (Table 3). Fresh weight of leaf and vitality in the drought treatment was significantly lower than in the control at severe stress, and this was not the case under mild or moderate stresses (Figures 2b and 2c).

3.3. Effects of seed source (provenance)

The main effects of provenance were not significant for all measured traits of *Q. brantii* seedlings (Table 3). However, there was a significant interaction of treatment by provenance for R/S and fresh weight of root (Table 3). These results demonstrated that the impact of drought stress on the seedlings differed between the 2 provenances. Both traits (R/S and fresh weight of root) decreased in seedlings from Yasouj under drought treatment compared to optimal conditions (Figures 2d and 2e). However, weight of root in Baneh seedlings did not change significantly between drought and optimal conditions, and the reverse result was observed for R/S (Figures 2d and 2e). Time-by-provenance interaction was significant for length of root and vitality (Figures 2f and 2g), indicating different responses between seedlings of Baneh and Yasouj provenances to different levels of drought stress (Table 3). Length of root in Baneh seedlings increased from 65% FC to 45% FC, and this pattern was reversed in Yasouj seedlings (Figure 2f). Additionally, the vitality of Baneh seedlings did not change significantly under different drought stresses; however, vitality of Yasouj seedlings decreased significantly from moderate stress to severe stress (Figure 2g). A significant 3-way interaction (treatment, time, and provenance) was found for R/S (Table 3), because under mild stress R/S was not significant between control and drought treatment in both provenances. By increasing water deficit stress from 45% to 25% FC the reverse result was found for the 2 provenances (Figure 2h), and under drought conditions the R/S in seedlings from Yasouj and Baneh was lower and higher than in the control, respectively (Figure 2h). Survival at the end of the experiment was similar for the 2 provenances (27.1% for Yasouj seedlings and 21.3% for Baneh seedlings).

4. Discussion

In the present study, large seeds exhibited larger growth parameters than small seeds regardless of drought conditions. Similar results were reported by Navarro et al. (2006) in oak and Cicek and Tilki (2007) in chestnut. However, these results are inconsistent with studies by Indira et al. (2000), Moles and Westoby (2006), and Tilki and Alptekin (2005), which reported that seed size had no effect on growth. Survival and vitality had no significant relation with seed size. Navarro et al. (2006) found that seedlings from larger seeds did not survive better than seedlings from smaller seeds under drought conditions, findings similar to the results of this study. This is in contrast to studies by Gomez (2004) in *Quercus ilex* and by Bonfil (1998), which found that larger seeds result in higher seedling survival.

Drought stress had negative effects on survival percentage and growth parameters such as weight of root and leaf and total fresh weight. This was expected, due to results in other tree species (Bauerle et al. 2006; Fort et al. 1997; Humara et al. 2002). There was also a consistent shift in resource allocation from shoot to root under moderate and severe drought stress (45% FC and 25% FC). Khurana and Singh (2000) found similar results and argued that this increased root weight helped seedlings with water uptake, further benefiting plants under drought. All growth parameters of seedlings from Baneh provenance (wetter site) were higher than those from Yasouj provenance (drier site), although this trend was not significant.

We found here that larger seeds produced larger seedlings, and seedlings from Baneh provenance had higher weight of root and R/S under drought stress, which was due to a positive correlation between seed size and R/S of Baneh provenance seedlings under severe drought stress. It has been suggested that relatively larger seeds provide sufficient energy for growth when photosynthetic activity is limited (Khurana and Singh 2000). This pattern is consistent with other studies that demonstrated better performance of larger seeds under drought (Seiwa 2000; Gomez 2004; Ramirez-Valiente et al. 2009). A study of the seedlings from a Mediterranean oak showed a positive correlation between seed weight and root weight (Quero et al. 2007). There was a significant relationship between seed size and seedling traits only for Baneh provenance under drought stress. Lopez et al. (2009) found similar results in *Pinus canariensis*, and there was no correlation between seed size and growth parameters in some populations under drought stress. In fact, the lack of significant correlations between seed size and growth parameters in Yasouj seedlings revealed not only significant variation between provenances regarding this influence in *Q. brantii* seedlings, but also a genetic component potential in oak seedling response to maternal environmental effects. This has been argued, for instance, in *Quercus douglasii* (Rice et al. 1993). Gapare et al. (2011) also found that populations with higher genetic variation had higher growth parameters and survival rates. Khurana and Singh (2000) found a decrease in SLA under 3 months of drought stress in seedlings of *Albizia procera*. However, this was not observed in this experiment, and SLA did not change under drought stress. Perhaps the drought period imposed here was too short for morphological acclimation.

Although significant differences in survival between seedlings from the 2 provenances were not found under drought stress, differences in vitality, weight of root, and R/S were observed between them. Collectively, these results suggest the lower quality of Yasouj provenance seedlings, particularly with respect to the vigor of their root systems and lack of significant of survival rate; this might be due to pot medium. Because study of Baneh and Yasouj provenance seedlings under field conditions (common garden) took almost 1 year, it was indicated that survival rates of Baneh provenance seedlings, which had higher genetic variation and came from the wetter north, were higher than in Yasouj seedlings (Karimi 2012). This is in contrast to the results of Ramirez-Valiente et al. (2009, 2010), who found that seedlings from the drier populations fared better under drought stress. Thus, our findings reveal that the effects of seed size depend on the genetics of the seed source, as the *Q. brantii* population from the drier site (Yasouj) was not any better adapted to dry conditions than the population from the wetter site (Baneh). Our results suggest that *Quercus brantii* can tolerate high levels of drought stress, and better performance is achieved by seedlings originating from the wetter parts of the Zagros forests, with their higher genetic diversity, than those originating from drier areas. In addition, collecting larger seeds can help with plantation success. However, the discarding of small seeds should not be practiced unless there is good genetic evidence to demonstrate that the practice does not eliminate whole families with possible good growth potential, as discussed by Karrfalt (2004). Our results also suggest that drought acclimation during growth increases R/S and the weight of the roots and could favor drought tolerance beyond the seedling stage. Moreover, collecting larger seeds with good genetic material should be considered for successful reforestation programs of the Zagros forests with *Q. brantii*, although more provenances in these forests should be tested before providing general recommendations. This research demonstrates that the correct choice of genetic material can be critical to early survival and production under drought stress.

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