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SPECIALTY SECTION

This article was submitted to
Forest Ecophysiology,
a section of the journal
Frontiers in Forests and Global Change

RECEIVED 08 September 2022

ACCEPTED 30 December 2022

PUBLISHED 19 January 2023

CITATION

Magni CR, Poch PL, Espinoza SE, Yáñez MA,
Martínez EE, Promis AA and Mancilla GA (2023)

Provenance influences seed germination
and phenotypic responses to water restriction
in the endemic *Beilschmiedia miersii* (Gay)
Kosterm.

Front. For. Glob. Change 5:1039908.

doi: 10.3389/ffgc.2022.1039908

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Provenance influences seed germination and phenotypic responses to water restriction in the endemic *Beilschmiedia miersii* (Gay) Kosterm

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The higher drought intensity recorded in the last decades in the Mediterranean zone of Chile increased the level of threats of the endemic *Beilschmiedia miersii* (Gay) Kosterm and has raised concern about its capacity to face drought. In this study, we assessed the effect of seed provenance and mother tree on seed germination traits, seedling growth, biomass allocation, presence of cotyledons, and survival responses of *B. miersii* cultivated under two water treatments (well-watered versus water stress. Average pre-dawn plant water potentials of -0.9 and -4.5 MPa, respectively). The germination stage of this trial showed significant differences in germination capacity, germination energy, and the maximum value of Czabator. Provenances from the southern range of the species, with higher precipitation (Cantillana and El Arbol) had a better germination performance, however, once germinated, the ability of the seedlings to survive in the nursery was high only in two of the five provenances under study. The coastal and interior provenances with lower precipitations (El Pobre, Longotoma, and Antumapu) were not able to survive to the seedling stage (<5% survival). Seedling growth and survival varied significantly between the two remaining provenances and the two watering treatments. The provenance El Arbol, exhibited a higher survival, growth, presence of cotyledons, and biomass traits. This provenance also exhibited a higher presence of cotyledons in both watering treatments and an unaltered root to shoot ratio between the well-watered and the water stress treatments. Our results suggests that there is important phenotypic variation for seed germination and seedling survival associated to the provenance origin, emphasizing the importance of a nursery-evaluation phase before the beginning of restoration projects at the landscape level.

KEYWORDS

provenance origin, water restriction, restricted range species, Mediterranean-type ecosystems, recruitment, restoration, recalcitrant-seeded tree species

1. Introduction

Seed source studies in forest trees are a valuable tool to identify better seed sources when planning ecological restoration actions, particularly in regions where the Mediterranean drylands are affected by drought (Broadhurst and Boshier, 2014). In these areas, the restoration of Mediterranean-type ecosystems has had limited success because climate warming and increased aridification are changing the habitat to which populations have been adapted, altering species range, phenology and vegetation types, and threatening tree recruitment and survival (Vallejo et al., 2012; Benito-Garzón et al., 2013; Gazol et al., 2018). Besides, factors such as anthropogenic disturbances (Mandle et al., 2011), lack of governmental restoration plans, poor quality and quantity of the planting stock, low survival after outplanting (Bannister et al., 2019; Acevedo et al., 2021), and lack of adequate seed supply (León-Lobos et al., 2020) constrain forest landscape restoration. In addition, there is lack of information on the early responses of seedlings to water stress, as a tool to guide the selection of appropriate seed sources for restoration.

In the Mediterranean-type ecosystems of central Chile *Beilschmiedia miersii* (Gay) Kosterm (Lauraceae) is an endemic and threatened recalcitrant-seeded tree species with hypogeal germination, a very limited distributional range (Henríquez and Simonetti, 2001) and the largest seeds among Mediterranean flora (Fuentes et al., 1986). Its overall geographical range extends no more than 200 km from coastal areas (32° S) and altitudes close to the sea level, to interior areas (34° S) with altitudes close to 1,200 m.a.s.l (Donoso, 1998). The species has been considered as Vulnerable (Benoit, 1989; MINSEGPRES, 2008) because of threats such as land conversion for agricultural uses, damage by livestock, leaf litter removal, drought (Henríquez and Simonetti, 2001; Becerra et al., 2004; Kremer et al., 2019) and fire (de la Barrera et al., 2018). Recently, Venegas-González et al. (2022) reported a decline in growth of *B. miersii* forests since the early 1900s as a consequence of climatic variability. Besides, seed viability has been negatively affected by rodents, insects and other herbivores, diminishing the sexual regeneration of the species (Serra et al., 1986; Gajardo et al., 1987; Henríquez and Simonetti, 2001; Morales et al., 2015).

Adaptations to ecological conditions can lead to differences in growth performance in seedlings of different provenances (Gratani et al., 2003; Vasques et al., 2013) and trees respond to changes in environmental conditions through phenotypic plasticity (i.e. the ability of a genotype to alter its morphology and physiology in response to changes in the environmental conditions) (Bradshaw, 1965; Nicotra et al., 2010), which allows species to grow in a range of environments (Corcuera et al., 2010). *Beilschmiedia miersii* is a relict species (Cabrera, 1959) that has been typically restricted to humid and shaded environments (Becerra et al., 2004; Novoa, 2004), but phenotypic plasticity has allowed populations to prosper under different environmental conditions in the last decades. The geographic area where the species develops has been subjected to an uninterrupted sequence of dry years from 2010 to 2018 (Garreaud et al., 2020) with the consequent negative effects on vegetation development (Garreaud et al., 2017; Miranda et al., 2020). In this context, given the contrasting environmental conditions within the limited area where *B. miersii* currently develops, it is expected phenotypic variation in seed germination and seedling responses, especially to environmental stresses such as drought,

which is projected to increase in areas with Mediterranean-type climate (Seager et al., 2019). However, population growth is not always related to climate variation (Peterson et al., 2021), and in *B. miersii* this is still poorly understood. Studies with species from Mediterranean-type climate areas (e.g., *Quercus ilex* L. and *Quillaja saponaria* Mol.) have shown that seed germination and seedling survival is high in provenances with annual precipitation close to 500 mm, whereas the lowest germination and survival values were reported in provenances with annual precipitation close to 900 mm (Caliskan, 2014; Magni et al., 2019). In field experiments with *B. miersii* it was found that seedling survival improved with irrigation, and the response depended on the site canopy conditions and the presence of leaf litter (Kremer et al., 2019), whereas, under laboratory conditions, seedling survival was not affected by irrigation (Becerra et al., 2004). However, as these studies only used one local provenance origin, the results are limited geographically because it is known that performance increases as local seed is planted near to their home site (Joshi et al., 2001).

Provenance differentiation for seed germination and seedling growth in Chilean native species has been investigated at the field (Espinoza et al., 2020) and nursery level (Magni et al., 2019). Seedling performance in large- recalcitrant seed species is influenced by traits such as the root to shoot ratio (RSR) and the presence of cotyledons. The RSR confers adaptability to harsh environments because it is a critical factor for optimizing the balance between water uptake and loss to avoid summer drought damage (Grossnickle, 2000), whereas the cotyledons store nutritional substances that determine the initial development of seedlings (Yi and Wang, 2016). However, there is still little knowledge about the provenance variation and the phenotypic variation of different seed sources to stresses such as drought at the seedling stage, as a tool to guide the restoration of *B. miersii*. This information is relevant to select better seed sources and diminish the high mortality rate observed in seedling establishment of woody Mediterranean species (Davis, 1989). As young seedlings are more susceptible to drought than adult trees (Cavender-Bares and Bazzaz, 2000), information at the seedling stage might give indications of the capacity of a species to grow and survive under water- restricted environments. In this context, the aim of this study was to analyze the variation for seed germination and the phenotypic responses to water restriction of *B. miersii* provenances. We analyzed germination traits in five provenances (seed sources) with germinated seeds, and then we assessed responses in survival, growth and biomass partitioning under contrasting watering regimes in two provenances that survived to seedling stage. As *B. miersii* is a recalcitrant-seeded species that needs moisture to germinate, we expect a better germination capacity and seedling performance from the wettest provenances and higher RSR in seedlings from the drier provenances.

2. Material and methods

2.1. Plant material

This study included seeds from five provenance origins from coastal and inland areas of Central Chile (Table 1). These provenances comprise the narrow range of distribution (maximum distance of 190 km) and environmental conditions where the species

currently develops. From February to early April 2013, ripe seeds were directly collected from trees on each provenance and the plantation from 40 mother trees randomly selected, and stored at 4°C under similar conditions until use. ISTA standards were followed to clean seeds (ISTA, 2006). The number of mother trees varied by provenance (Table 1). The study was conducted in a nursery located at the Universidad de Chile, La Pintana, Chile (33° 34' S, 70° 37' W, 611 m.a.s.l) and in April 2013 the seeds were soaked in tap water for 24 h, and those that floated and with insect damage were discarded. Approximately sixteen viable seeds from each of 40 mother trees (i.e., a total of 3,168 seeds) were sown in 150-mL pots filled with a mixture of composted bark, local topsoil, and sand (1:1:1 v). Then, they were cultured under similar ambient conditions during 12 months until early April 2014 under daily irrigation according to the season of the year (1.25 L m² in fall-spring, and 5 L m² during the summer months). No fertilizer was added to the growing substrate.

2.2. Assessment of seed germination

Germination was recorded daily on those seeds with emerged cotyledons. The germination capacity (GC) was obtained as the proportion between the germinated seeds and the total seeds sown. The maximum value of Czabator (MV) was obtained as the maximum quotient derived from all of the cumulative full-seed germination percentages on any day divided by the number of days to reach these percentages (Czabator, 1962). Additionally, we determined the germinative energy (GE), as the accumulated percentage of germination on the day that MV occurs, and the energy period (EP), as the number of days in which MV occurs (FAO, 1985; ISTA, 2006).

2.3. Seedling experiment and watering treatments

After the seed germination finished the provenances El Pobre, Longotoma, and Antumapu were excluded from the analysis due to the low number of germinated seedlings. Provenances Cantillana and El Arbol were represented with 7 and 11 mother trees (synonym families and coded as C and A, respectively), and the total number of seedlings in this phase was 1,265. The watering experiment was established in April 2014 with the germinated seeds of the germination experiment (i.e., 1-year-old seedlings) and it was arranged following a split-plot in an incomplete block design with 11 replicates. Two watering treatments were the whole plot treatment [well-watered (WW) and water stress (WS)], and the provenances were the split-plot treatment. As both provenances had an heterogenous number of germinated seedlings, we used incomplete blocks but we took care that each family was present in more than three replicates in each watering treatment and containing at least three seedlings. Watering regimes were defined based on pre-dawn plant water potentials (ψ_{pd}) measured by using a Scholander pressure chamber (PMS Instrument, Albany, USA). In the WW treatment, seedlings were watered daily until reaching an average ψ_{pd} of -0.9 MPa. In the WS treatment, water was withheld from April 11th to May 6th 2014 (i.e., one 26-days cycle of water withholding) and seedlings reached an average ψ_{pd} of -4.5 MPa.

2.4. Assessments

Seedling height (H, cm), root collar diameter (D, mm), and survival (SUR, %), and the presence of cotyledons in each seedling (COT, %) were measured after the watering treatments had finished. SUR and COT were assessed as categorical variables. For SUR, 1 represented an alive seedling, and 0 represented a dead seedling. For cotyledons, 1 represented a present cotyledon, and 0 represented an absent cotyledon. Afterward, cotyledons were extracted from each seedling and weighed at ± 0.01 (Wcot, g). Finally, all seedlings were harvested and oven-dried at 65°C until constant weight. The dry weight fractions of roots (RDW), leaves (LDW), stems (SDW) were determined (± 0.01 , g). The total dry weight (TDW) was derived as RDW+LDW+SDW, and the root:shoot ratio (RSR) was derived as $RSR = RDW/(SDW+LDW)$.

2.5. Data analyses

Seed germination traits were analyzed using the full data set ($n = 3,168$ sown seeds) of the four provenances and the plantation, and the linear mixed model presented in Equation 1. Otherwise, survival, growth, cotyledons, and biomass traits were analyzed using a reduced dataset containing only seedlings from provenances Cantillana and El Arbol ($n = 1,265$ seedlings), and the linear mixed model presented in Equation 2. We examined the assumptions for normality and homogeneity of variance required for the analysis of variance, and used Box-Cox transformation when necessary. The survival and the presence of cotyledons; measured as categorical values (i.e., 1, 0), were analyzed by using a generalized linear model with binomial distribution and a logit link function (Stroup, 2012). The analyses of variance for each trait was carried out on a family-mean basis.

$$Y = \mu + R + P + R \times P + M(P) + R \times M(P) + e \quad (1)$$

$$Y = \mu + W + R + e_1 + P + M(P) + W \times P + W \times M(P) + e_2 \quad (2)$$

Where, Y is the observed phenotypic value, μ is the overall mean, W is the fixed effect of watering regime, R is the fixed effect of replicate, P is the fixed effect of provenance, $M(P)$ is the random effect of the mother tree nested within the provenance. In Equation 1, e represents the experimental random error. In Equation 2, e_1 is the error associated with the whole plot, and e_2 is the error associated with the split-plot. Mean comparisons were made using the Tukey test at $P \leq 0.05$. In this equation, a significant effect of W indicates the existence of phenotypic plasticity in response to water stress for the trait considered, whereas a significant genotype by environment interaction (i.e., interaction $W \times P$), indicates the existence of genetic differences in plasticity (Schlichting, 1986).

Because our interest was also to analyze the survival of seedlings in the WS treatment, we used the reduced dataset containing two provenances ($n = 1,265$ seedlings) to conduct simple regression analysis with family means in order to assess the relationships between seedling SUR with seedling responses in growth (D and H), biomass partitioning (SDW, LDW, RDW, RSR, and TDW), and cotyledons (COT and Wcot). We checked assumptions of normality and homogeneity of variances and the goodness of fit

TABLE 1 Location and climate for the provenances and plantation of *Beilschmiedia miersii* under study.

Provenance	Mother trees	Location	Latitude	Longitude	Altitude (m.a.s.l)	MTCM	MAP	PWQ	MAT	De Martonne aridity index
El Pobre	3	Coastal	283178	6431833	300	6.3	150	105	14.6	6.1
Longotoma	10		277436	6415907	15	7.1	300	200	14.2	12.3
Antumapu*	3	Interior	348552	6284350	610	2.7	397	276	20.5	13.0
Cantillana	12		321221	6256492	600	6.2	439	366	16.0	16.8
El Arbol	12		313852	6252048	800	4.5	502	375	13.1	21.7

MTCM, minimum temperature of the coldest month (°C); PWQ, precipitation of the wettest quarter (mm); MAP, mean annual precipitation (mm); MAT, mean annual temperature (°C). The De Martonne aridity index was estimated as $MAP/(MAT + 10)$. The higher the index, the lower the aridity.

*This corresponds to a plantation established with seed collected in an interior provenance. Provenances are ordered according to the De Martonne aridity index.

for the regression model was assessed by computing the coefficient of determination and the Pearson's coefficient of correlation. In addition, we used Path analysis to quantify simultaneously the direct and indirect contributions of seedling attributes on seedling survival. We assessed the influence of D, H, RDW, LDW, SDW, COT, and Wcot on seedling SUR in the WS treatment. In this analysis we omitted those traits derived as ratios or as the sum of individual traits (i.e., RSR and TDW), to avoid multicollinearity among the independent variables. All the analysis were carried out using the SPSS software v18 (SPSS Inc, Chicago, Illinois, USA) and INFOSTAT software version 2018 (Group Infostat, Universidad Nacional de Córdoba, Argentina).

3. Results

3.1. Provenance differences in seed germination

Provenance El Arbol exhibited the highest GC, and GE, while the other provenances did not differ among them (Table 2). On average, GC and GE were 108 and 95% higher in provenance El Arbol in comparison to the other provenances. For MV, provenance El Arbol had significantly higher values than provenance El Pobre, while the other provenances had intermediate values. No differences were observed for EP in any of the provenances under study, but provenances El Pobre and Antumapu exhibited a long EP with a low variability due to the homogeneity values for this trait among mother trees.

3.2. Provenance differences in growth, survival, and biomass allocation under the water restriction

Before imposing the water restriction treatment, D and H were 6 and 11% higher in the provenance El Arbol than Cantillana, respectively. The magnitude of these differences between provenances was maintained after the watering restriction cycle (8 and 12%, respectively). The effect of provenance was significant for growth, biomass, survival, and cotyledons. The provenance El Arbol exhibited the highest D, H, SUR, SDW, LDW, RDW, TDW, COT, and Wcot (Table 3). The phenotypic plasticity due to the watering treatment was significant for most of the seedling traits except SDW, LDW, and Wcot, whereas the genetic differences

among provenances within watering treatments (i.e., genotype by environment interaction) were significant for RSR and COT. The Provenance Cantillana had a high RSR in the WW treatment, but this was reduced in the WS treatment, while RSR in the provenance El Arbol was similar in both treatments. Moreover, RSR in Cantillana was higher than El Arbol in the WW treatment but lower in the WS treatment (Figure 1A). The provenance El Arbol had a higher percentage of cotyledons (COT) than Cantillana in both watering treatments (Figure 1B), but in both provenances COT was significantly reduced by the WS treatment. We also reported a family variation for H, SUR, COT, Wcot, RDW, and TDW (Table 3 and Figure 2), which was mainly explained by family A_16 from provenance El Arbol that exhibited the highest H, SUR, COT, RDW, and TDW, and family C_2 from provenance Cantillana, which showed the opposite pattern in almost all the abovementioned traits.

3.3. Correlation between seed and seedling characteristics

When comparing the correlations among survival with seedling responses in growth, biomass and cotyledons characteristics; with the exception of RSR, they were mostly medium-low and positive correlations (Figure 3). However, the Path analysis indicated that only H and COT had significant direct and positive effects on seedling survival (Table 4). We also observed positive and indirect effects of the other traits under study. The trait with the greatest indirect effect on seedling SUR was D, followed by LDW, RDW, Wcot and SDW. Consistently, those traits, via positively affecting H, indirectly affected seedling SUR. In the case of Wcot, via positively affecting COT, indirectly affected seedling SUR.

4. Discussion

4.1. Provenance differences in germination traits

Our results indicated that the provenance effect considerably impacted the germination traits. GC, GE, and MV of *B. miersii* were significantly higher in the El Arbol provenance seed and a large number of seeds were able to survive to the seedling stage from this provenance. The coastal provenances El Pobre and Longotoma and the interior plantation Antumapu were not able to survive in

TABLE 2 Means and standar error for the seed germination parameters by provenance of *Beilschmiedi miersii*.

Trait	Provenance				
	El Pobre	Longotoma	Antumapu	Cantillana	El Arbol
Germinative capacity (GC, %)	30.0 ± 8.9b	34.4 ± 8.1b	48.4 ± 12.3b	41.8 ± 2.9b	80.4 ± 3.4a
Germinative energy (GE, %)	27.2 ± 6.1b	26.7 ± 9.4b	43.3 ± 12.1b	32.0 ± 3.5b	62.8 ± 6.1a
Maximum value (MV, % per day)	0.11 ± 0.02b	0.17 ± 0.06ab	0.18 ± 0.04ab	0.23 ± 0.03ab	0.40 ± 0.03a
Energy period (EP, days)	246 ± 1a	206 ± 50a	246 ± 1a	145 ± 12a	172 ± 16a

Different lowercase letters indicate significant differences among provenances at $P \leq 0.05$.

TABLE 3 Main effects in growth, survival, and biomass parameters tested through 2-Way ANOVA using watering treatment (*W*) and provenance (*P*) as fixed factors and family (*F*) as a random nested factor in provenance (*F(P)*).

Trait	Water treatment		Provenance		Main effects of factors and interactions				
	Well-watered	Water stress	Cantillana	El Arbol	Watering	Provenance	<i>W</i> × <i>P</i>	<i>F(P)</i>	<i>W</i> × <i>F(P)</i>
D	4.55 ± 0.11	3.94 ± 0.08	4.05 ± 0.15	4.37 ± 0.08	<0.000	0.009	0.153	0.151	0.633
H	14.02 ± 0.52	12.31 ± 0.57	12.24 ± 0.71	13.72 ± 0.46	0.002	0.026	0.803	0.030	0.296
SUR	70.73 ± 3.25	52.85 ± 2.73	50.17 ± 4.43	68.45 ± 2.34	<0.000	0.003	0.732	0.001	0.980
SDW	0.73 ± 0.04	0.64 ± 0.03	0.59 ± 0.04	0.74 ± 0.03	0.142	0.001	0.056	0.270	0.055
LDW	1.00 ± 0.06	0.88 ± 0.06	0.81 ± 0.08	1.01 ± 0.05	0.073	0.017	0.162	0.082	0.065
RDW	1.23 ± 0.07	0.98 ± 0.06	0.93 ± 0.08	1.21 ± 0.06	0.003	0.003	0.254	0.013	0.414
TDW	2.98 ± 0.18	2.51 ± 0.15	2.33 ± 0.20	2.98 ± 0.14	0.025	0.002	0.121	0.044	0.089
RSR	0.73 ± 0.02	0.66 ± 0.02	0.70 ± 0.02	0.69 ± 0.02	0.026	0.766	0.019	0.222	0.922
COT	69.48 ± 3.17	62.17 ± 2.85	56.11 ± 4.16	71.08 ± 2.34	0.023	0.001	0.034	0.008	0.982
Wcot	2.83 ± 0.18	2.71 ± 0.17	2.18 ± 0.22	3.07 ± 0.14	0.532	0.008	0.070	0.016	0.619

Statistically significant values ($P \leq 0.05$) are in bold. D, root collar diameter (mm); H, height (cm); SUR, survival (%); SDW, stem dry weight (g); LDW, leaves dry weight (g); RDW, root dry weight (g); TDW, total dry weight (g); RSR, root to shoot ratio; COT, percentage of cotyledons (%); Wcot, weight of the cotyledon (g).

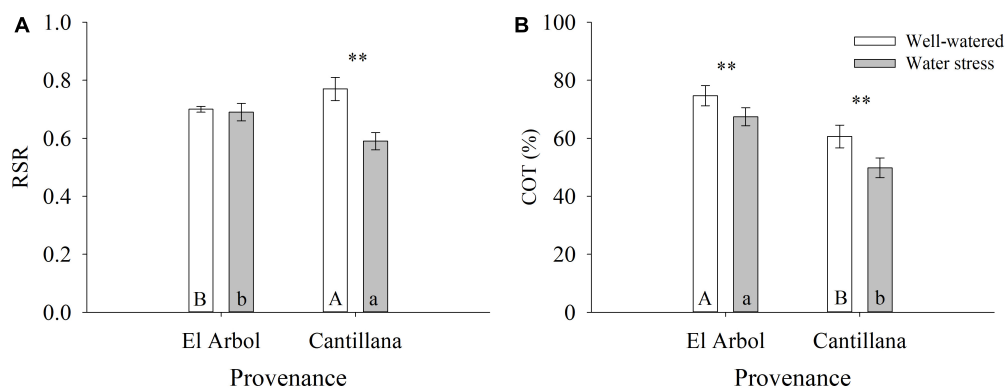


FIGURE 1

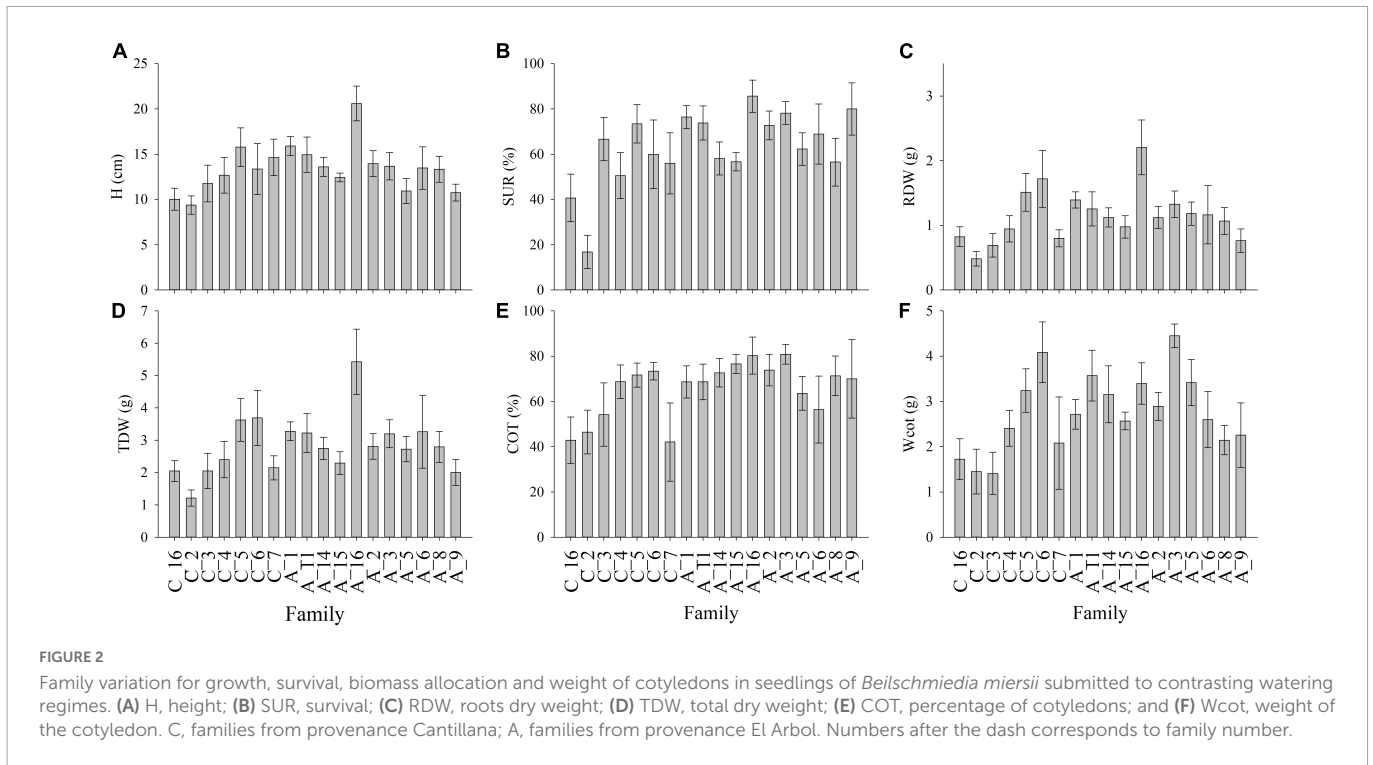
Provenance variation by watering regime for RSR (A) and COT (B). **Indicate significant differences within a provenance at $P \leq 0.05$. The same lowercase and uppercase letters indicate no significant differences ($P \leq 0.05$) between the provenances in the well-watered and water stress treatment.

large number to the seedling stage, which might be because those provenances are located in the dry edge of the species distribution (i.e., the lower the De Martonne aridity index in Table 1), with the consequent low individual performance (Brown, 1984). This lack of ability to survive to the seedling stage might be also related to lack of pollinators and inbreeding in those populations. A worldwide decline of pollinators (Rodger et al., 2021) has critically impacted the Mediterranean-type ecosystem of Chile (Vieli et al., 2021).

The differences in precipitation, altitude, and temperature across provenances, might have also caused the variations in germination

capacity. *B. miersii* is a recalcitrant seeded-species that needs moisture to germinate. Recalcitrant seeds are highly sensitive to desiccation and lose their viability in dry sites (Bewley et al., 2006). The cumulated precipitation from the year before the seed release to the month of seed dispersal and seed collection (i.e., from January 2012 to April 2013) averaged 212 mm in the three coastal provenances, while the interior provenance El Arbol averaged 529 mm of precipitation in the same period.¹ In this context, the

¹ <https://agrometeorologia.cl>



higher precipitation in El Arbol than in the other provenances may partially explain the differences in seed germination, but this needs further research because we used only viable seed in our experiment.

On the other hand, provenances that survived to the seedling stage (Cantillana and El Arbol) come from areas with higher altitude (close to 800 m.a.s.l.), while those provenances that were not able to survive to the seedling stage are mainly from coastal areas close to the sea level. Provenances Longotoma and El Arbol have similar annual temperature but they differed in altitude and aridity, with the latter provenance being present at higher altitudes with higher precipitation and lower aridity. In general, seeds from higher altitudes have higher germination rate than those from the lower altitudes, which is related to the size of cotyledons, i.e., seed from higher altitudes are heavier than those of lower altitudes because they have to survive under severe environments (Mariko et al., 1993). Average winter temperature in provenances El Arbol is 2.8°C, compared to the 6.9°C of coastal provenances (see text footnote 1).

Due to the large number (3,168) and size of seeds, we assessed viability according to the simple floating method and not by more accurate methods (i.e., cutting and tetrazolium methods). Thus, another explanation for the lower germination rate experienced by coastal provenances might be the presence of insect-infested seeds; probably by *Hypothenemus* sp. (data not shown), that did not float in the test. The acorns of large-seeded species infested by insects experience lower germination (Branco et al., 2002; Yi and Zhang, 2008) and *B. miersii* has large seeds that are usually damaged during seed dispersal (Serra et al., 1986; Gajardo et al., 1987; Henríquez and Simonetti, 2001). It has been reported that damaged seeds have a decrease in germination rate, and the surviving seedlings have low performance and high mortality (Hou et al., 2010). By visual inspection in our field campaigns, we observed low seedling regeneration in

El Pobre and Longotoma provenances, but not in the Cantillana and El Arbol provenances. This could indicate a superior seedling recruitment in the latter provenances which may be associated with fewer pest insects. However, this assertion needs further research.

4.2. Provenance differences in growth, survival and biomass allocation under water restriction

In general, we found that water stress did not affect growth and survival, but affected belowground adaptations (RSR) and percentage of cotyledons (COT). Both parameters are associated with water absorption and carbohydrates reserves within the plant (Bewley and Black, 1994; Grossnickle, 2005) and may counteract decreases in carbon assimilation during water stress. As the provenances from drier environments did not survive to the seedlings stage, no assessments of RSR were made to test our hypothesis about this trait. However, the plasticity for RSR was higher in the provenance Cantillana whereas the provenance El Arbol exhibited null plasticity for this trait as it remained unaffected between watering treatments. The phenotypic plasticity of both provenances does not fit the theory of specialization proposed by Lortie and Aarssen (1996). This theory proposes that genotypes adapted to unfavorable conditions (provenance Cantillana with higher aridity), may have superior performance in restrictive environments but are unable to take advantage of favorable conditions. On the contrary, genotypes adapted to favorable environments (provenance El Arbol with lower aridity), present a superior performance in these environments, but this is reduced when conditions are limiting. According to the De Martonne index of Table 1, both provenances come from similar dry conditions (semiarid and Mediterranean type climate for Cantillana and El Arbol, respectively),

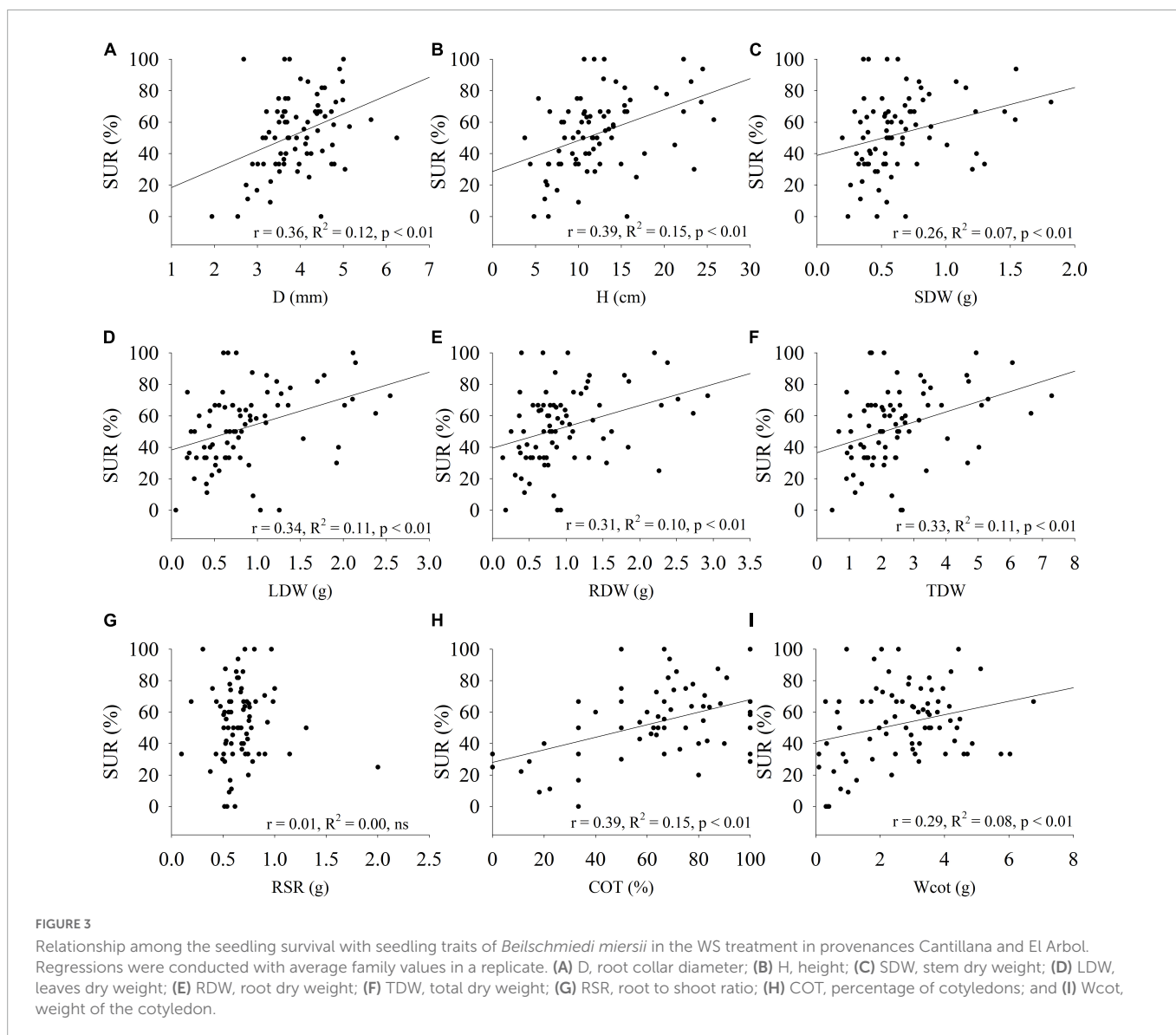


TABLE 4 Path analysis of the relationships between seedling survival in the WS treatment and the various independent variables (growth, biomass and cotyledons).

Factors	Direct effect	Indirect effect							Total correlation
		D	H	COT	Wcot	RDW	SDW	LDW	
D	-0.05	–	0.28	0.08	0.01	0.05	0.05	-0.05	0.36***
H	0.40**	-0.04	–	-0.01	-0.03	0.07	0.07	-0.08	0.39***
COT	0.32**	-0.02	-0.01	–	0.11	-0.01	-0.02	0.00	0.39***
Wcot	0.16	-0.01	-0.06	0.23	–	-0.01	-0.02	0.01	0.30***
RDW	0.09	-0.03	0.28	-0.02	-0.01	–	0.07	-0.08	0.31***
SDW	0.10	-0.03	0.29	-0.06	-0.04	0.07	–	-0.08	0.26**
LDW	-0.09	-0.03	0.32	0.00	-0.02	0.08	0.08	–	0.33***

D, root collar diameter; H, height; COT, percentage of cotyledons; Wcot, weight of the cotyledon; RDW, root dry weight; SDW, stem dry weight; LDW, leaves dry weight. RSR and TDW were omitted from this analysis.

** and *** the correlation is significant at the $p < 0.05$ and $p < 0.01$ level.

thus their behavior might be explained because some organisms; particularly in the early stages of development, have the ability to alter their patterns of carbon allocation in response to certain environmental stimuli (Bloom et al., 1985). It might be possible

that the low-water treatment was not sufficiently low to trigger further physiological responses in provenance El Arbol or that the presence of heavier cotyledons buffered the response. The low plasticity of El Arbol suggests a higher phenotypic stability

in balancing the extraction and losses of water even in a water restricted condition, which could be linked to a specialization to adverse environments, and a conservative resource-use strategy (Baquedano et al., 2008). Seedlings with an adequate size (Villar-Salvador et al., 2012) and a balance between the shoot transpirational surface to the root absorbing surface (i.e., RSR) could have a better chance to survive in sites with water restrictions. In these sites, a high proportion of roots may ensure water supply for the plant over the first summer (Richards and Lamont, 1996). Provenance El Arbol also produced larger seedlings (H) with the highest body mass (TDW) compared with Cantillana provenance. The higher aboveground growth of the provenance El Arbol could be coupled with a higher water demands, but this is likely compensated by a greater water uptake and food reserves due to its higher mass of cotyledons (Wcot) and roots mass (RDW) in comparison to the Cantillana provenance. It is known that partial or total removal of cotyledons can reduce biomass production and even cause death in young seedlings (Armstrong and Westoby, 1993). The presence of heavier cotyledons is an adaptive character to environmental stresses (Jurado and Westoby, 1992) and might explain the high number of seeds that survive to the seedling stage in these provenances. At the mother tree level, and with the exception of mother C_6 from provenance Cantillana, most of mother trees from El Arbol provenance exhibited higher percentages and mass of cotyledons than those from Cantillana provenance. This suggests that seedling growth in *B. miersii* has an important maternal effect that needs to be further investigated.

4.3. Relationships between seedling survival in the WS treatment and the various independent variables

Our Path analysis provides evidence that seedling height (H) positively influenced the survival of seedlings in the water restricted treatment. The seedling diameter (D) did not directly contribute to seedling survival but did indirectly influence this trait through its positive effects on H. Height and diameter are considered good predictors of seedling survival (Grossnickle and MacDonald, 2018), and large seedlings have a better survival because of the larger roots that allow seedlings to reach moisture in deep soil horizons (Oliet et al., 2009; Cuesta et al., 2010; Villar-Salvador et al., 2012); however, larger seedlings can also have large transpiratory demands (Grossnickle, 2012) with the consequent risk of desiccation. It is known that the larger roots systems allows the supply of enough water to the foliage (Grossnickle, 2005; Manzoni et al., 2015) and the presence of heavier cotyledons promotes seedling survival because of their greater resource storage capacity (Metz et al., 2010). In our experiment, despite seedlings of provenance El Arbol were taller and had higher transpiratory surface (LDW); probably depleting the water pot more quickly than the provenance Cantillana, they had higher mass of cotyledons and root mass (Wcot, RDW). Both traits were significantly positively correlated with seedling SUR and had an indirect influence on seedling SUR via their positive effects on H and COT. Seed mass; which is a functional trait that positively affects germination and seedling survival in recalcitrant seeded species (Chacón and Bustamante, 2001), has

been found to be highly correlated with storage-type cotyledons in larger seeded species (Green and Juniper, 2004). Thus, the higher Wcot and RDW might have helped to compensate larger transpiratory demands with water uptake and food reserves.

From a conservation point of view, knowledge of seed germination ability and seedling survival of *B. miersii* is important and may provide an insight on survival and distribution range of the species in the era of climate change. This study showed that *B. miersii* has phenotypic variation among provenances on seed and seedling characteristics and this variation seems to be related to the climate of the seed source origins. Provenances from driest locations had low germination capacity and were unable to survive to the seedling stage. As Mediterranean-type climate areas are expected to become drier in the coming decades (Seager et al., 2019; Fernández et al., 2021), the natural regeneration of these provenances could be seriously compromised by the lack of water to germinate and to assure seedling establishment. Recalcitrant-seeded tree species such as *B. miersii* are highly sensitive to dehydration (Berjak and Pammenter, 2004), and, unlike orthodox seeds, they must germinate quickly before dehydration or die (Berjak and Pammenter, 2008). On the contrary, the provenances from sites with lower aridity produced larger seedlings with abundant and heavier cotyledons. In a global change context, this differentiation in important functional traits such as the weight of cotyledons might suggest that the southern provenance El Arbol (with heavier cotyledons to survive under harsh conditions) has the potential to provide options for re-forestation. However, this potential needs to be established in the context of future work examining fruit traits and the effect of local environmental factors on fruit development. Germinated seeds of this provenance were able to survive to the seedling stage in a severe water restricted treatment (-4.5 MPa of water potential) and were able to optimize the balance between the moisture extraction capacity of the roots relative to the transpiring shoots (RSR). In other large- recalcitrant seed species from Mediterranean-type climate areas (e.g., *Quercus* spp.) seedling growth and survival are negatively affected when the cotyledons are removed (Yi et al., 2019), corroborating the role of cotyledons in supporting seedling development (Yi and Wang, 2016).

Data availability statement

The data analyzed in this study is subject to the following licenses/restrictions: The data that support the findings of this study are available from the Universidad de Chile, but restrictions apply to the availability of these data, which were used under license for the current study, and so are not publicly available. Data are however available from the authors upon reasonable request and with permission of Universidad de Chile. Requests to access these datasets should be directed to CM, crmagni@uchile.cl.

Author contributions

CM, GM, and PP conceived and designed the study. PP performed the experiments and collected the results. SE and MY analyzed and interpreted the data, and were major contributors in writing the manuscript. AP, EM, GM, PP, CM, SE, and MY revised the manuscript. All authors read and approved the final manuscript.

Funding

This work was supported by the Fondo de Investigación del Bosque Nativo, from the Corporación Nacional Forestal (CONAF) through the project “Permanencia de Bosques de *Beilschmiedia miersii*. Regeneración según contenido de humedad del suelo y presencia de hojarasca” (grant number 033/ 2012).

Acknowledgments

We thank the staff from the Centro Productor de Semillas y Arboles Forestales (CESAF) from the Universidad de Chile, specially to Betsabé Abarca and Iván Grez.

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