Under pressure: maternal effects promote drought tolerance in progeny seed of Palmer amaranth (*Amaranthus palmeri*)

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Abstract

The environmental conditions under which parental plants are reared can affect the seed characteristics of the progeny. The variation originating from such maternal effects has rarely been incorporated into models of seed germination. Here, using Palmer amaranth (*Amaranthus palmeri* S. Watson), we examined the effects of water stress during the growth of parental plants on the progeny seed characteristics, including weight, size, final germination, and parameters of a hydrotime germination model. We grew two populations (from California and Kansas) under continuous water-deficit or well-watered conditions. In both *A. palmeri* populations, progeny seeds originating from water-stressed plants were heavier and larger than those from well-watered plants. Plants exposed to water stress also produced seeds that were ~30% less dormant than seeds from control plants. To test whether the maternal environment affects the parameters of a hydrotime model, progeny seeds were subject to five water potentials (0, −0.2, −0.4, −0.6, and −0.8 MPa) and incubated at 20 and 30 C; germination was monitored daily. The estimated median base water potential ($\Psi_{b(50)}$), that is, the water potential at which 50% of seeds cannot germinate, was consistently lower for seeds from water-stressed plants than for seeds from well-watered plants. Our results showed that *A. palmeri* plants experiencing drought during their growth produce seeds that are less dormant and can germinate from drier conditions—a maternal response that seems to be adaptive. These findings also call for development of germination models that incorporate the environmental conditions of both the current and past seasons to better describe the variability in germination of weed seeds.

Introduction

Seed germination is highly regulated through environmental cueing (Donohue et al. 2010), and weeds often exhibit high levels of variation in timing and extent of germination (Baskin and Baskin 1985; Egley and Williams 1991; Forcella et al. 2000). Variation in seed germination is determined, however, not only by the immediate microenvironment of the seed but also by the conditions experienced by parental plants (mainly maternal; Baskin and Baskin 2019) during the preceding growing season (Fenner 1991; Roach and Wulff 1987). Maternal environment effects on seed germination have been reported for a wide range of plant species in response to temperature (Donohue et al. 2008), soil moisture (Wright et al. 1999), CO_2 (Farnsworth and Bazzaz 1995), daylength (Nurse et al. 2004), solar irradiance (Adkins and Armstrong 2007), light quality (Van Hinsberg 1998), nutrients (Allison 2002), herbicides (Andersson 1996), competition (Nurse and DiTommaso 2005), viral infection (Kathiria et al. 2010), and even presence (or absence) of earthworms in the soil (Laossi et al. 2010).

Variability in germination (dormancy) patterns acts as a bet-hedging strategy whereby some weed cohorts can escape control measures or unsuitable environments. Repeated applications (e.g., of herbicides) during the season are often necessary to control the staggered cohorts that result from temporally nonuniform germination patterns. Therefore, understanding what regulates the observed variation in germination patterns not only is a fundamental question in weed seed ecology but also has implications for management of weeds.

Environmental maternal effect adds another layer of complexity to germination studies, as the observed responses to current experimental factors are not independent of seed's past exposure to different environmental conditions. Maternal effect, therefore, markedly constrains our ability to predict weed seed germination (and seedling emergence), as current germination/emergence models are developed solely using the present microenvironment experienced by the seed. The inconsistencies that we sometimes observe in germination studies are often interpreted as experimental errors but in part may have sound biological underpinnings due to maternal effects.

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Interestingly, it seems that seed germination responds to certain maternal environments in a predictable manner. A literature review by Fenner (1991) showed that high temperatures, short days, red light, drought, and high nitrogen during seed development were consistently associated with increased germinability in the progeny (Fenner 1991). A good example of such predictable changes is an early study by Von Abrams and Hand (1956) on hybrid roses that found a strong (positive) linear relationship ($R^2 \approx 0.99$) between the progeny seed germination and the mean average daily temperature 30 d before seed harvest. These observations suggest that the predictive power of germination (emergence) models can be improved by incorporating the information about the environment of the previous growing season. Such "transgenerational models" can be developed by quantifying changes in the attributes of an established model as a function of certain maternal environmental variables (e.g., soil moisture levels in which the mother plants have grown).

In this study, we examined the effects of maternal water environments on properties of the hydrotime model of germination in progeny seeds of Palmer amaranth (*Amaranthus palmeri* S. Watson). Hydrotime models have been successfully used to describe the temporal pattern of germination in response to reduced water in many species, including weeds (Batlla and Benech-Arnold 2004; Bradford 1990; Bradford and Still 2004; Gianinetti and Cohn 2007; Gummerson 1986). Specifically, our objective was to quantify potential changes in base water potential, $\Psi_{b(g)}$, for seed germination of *A. palmeri* in response to maternal water stress. Base water potential represents a water potential threshold at or below which no germination will occur. As a key parameter in the hydrotime model, $\Psi_{b(g)}$ measures the germination tolerance of species (population) to drought: lower (more negative) $\Psi_{b(g)}$ values indicate that seeds can germinate from drier conditions (e.g., soils). The present study tests the hypothesis that plants grown under water stress will produce seeds characterized with lower $\Psi_{b(g)}$ values and will therefore be capable of germinating under drier conditions compared with seeds originating from well-watered plants. This study represents the first step in developing transgenerational germination models that incorporate environmental conditions before and after seed dispersal. This study used *A. palmeri*, which is one of the most troublesome weeds in the United States, and hopefully could help with the development of decision support systems for effective management of this pervasive weed.

Materials and Methods

Seeds of two populations of *A. palmeri*, one from California (CA) and one from Kansas (KS) were provided by Anil Shrestha (California State University, Fresno, CA) and Dallas E. Peterson (Kansas State University, Manhattan, KS), respectively. A greenhouse experiment was conducted at the Orchard Parks greenhouse facilities of the University of California, Davis, during the summer of 2018. Round plastic pots (2.37 L) were filled with a soil mix (1:1 sand/peat) plus a controlled-release fertilizer (15–9–12, 150 g 75 L^{-1}; Scotts Osmocote® PLUS, Mississauga, ON, Canada). Approximately 10 seeds from each *A. palmeri* population were sown into a total of 200 pots, 100 for each population. Plants were grown in a greenhouse with a temperature range of 32/22 C (day/night) and daylength of 16 h provided through supplementary lighting. Seedlings were thinned randomly to achieve one plant per pot by the 4-leaf stage. All plants received normal

irrigation using four emitters inserted into the potting medium to deliver 65 ml of water min^{-1} for 2 min, twice per day (7:00 AM and 2:00 PM). For each population, when plants reached the 6-leaf stage, 50 pots (replicates) were randomly assigned to water-stress treatment by removing three out of four drip emitters, which reduced the amount of water by ~75% (field capacity 6% to 13%). The remaining 50 pots continued to receive normal irrigation (field capacity 35% to 42%), as described earlier. Seeds were harvested at full maturity as determined by inspecting the inflorescences for the presence of black, firm seeds (Mesgaran et al. 2019).

Seed Weight and Size Measurements

One month after harvest, 10 seed subsamples from each population by maternal water treatment combinations, containing 100 seeds each, were weighed using a precision scale (ME104E™, Mettler-Toledo, Columbus, OH) to obtain 1,000-seed weight data. Seeds (40 to 70 seeds) were imaged using a Leica M205 FA stereomicroscope (Leica Microsystems, Wetzler, Germany) equipped with a digital camera (Leica MC190 HD Camera) and built-in image analytical software (LAS X Core) to measure the seed size based on the surface area.

Seed Germination Tests

Germination (both parental and progeny generations) was tested under five nominal water potentials (0, −0.2, −0.4, −0.6, and −0.8 MPa) at two constant temperatures of 20 and 30 C representing suboptimal and optimal temperatures for germination of *A. palmeri*, respectively (Guo and Al-Khatib 2003; Steckel et al. 2004). Experiments were conducted with four replicates (petri dishes) per treatment and repeated twice. Experimental runs were rotated between two growth chambers (Conviron® CMP 6010, Winnipeg, Canada). Solutions were prepared by dissolving appropriate amounts of polyethylene glycol 8000 (Sigma-Aldrich, St. Louis, MO) in deionized water according to Michel (1983). Filter papers (Whatman® Grade 2; Sigma-Aldrich) were soaked in each solution containing the desired water potential for 12 h before the experiment, as recommended by Hardegree and Emmerich (1990). The water potential of each solution was tested twice: before and after adding the filter papers to the solution using a Wescor Vapro osmometer (Wescor, Logan, UT, USA). For each treatment, 40 seeds from each population were placed in a 9-cm petri dish lined with moistened filter paper and sealed with Parafilm® to reduce water loss from the dishes.

Hydrotime Model and Statistical Analysis

The hydrotime model is based on a linear relationship between germination rate, GR (i.e., the inverse of time to a given germination percentile, $1/t_g$) and the medium water potential, Ψ (Bradford 2002; Gummerson 1986):

$$GR = \frac{1}{t_g} = \frac{\left(\Psi - \Psi_{b(g)}\right)}{\theta_H} \qquad [1]$$

where t_g is time to germination of a given percentile g (the subscript "g" indicates the germination percentile), θ_H is hydrotime constant describing the amount of time (in MPa day or MPa hour units) required for germination of any fractions of the seed subpopulation. The main feature of the hydrotime model is that base water potential varies among seeds (hence the subscript "g" in $\Psi_{b(g)}$), giving rise to variaiton in timing of germination for each
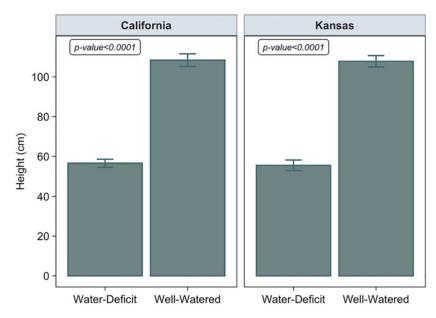
Figure 1. Plant height for *Amaranthus palmeri* populations (California and Kansas) grown under continuous water-deficit or well-watered irrigation conditions. Vertical lines on bars indicate SE.

individual seed, as shown below after rearranging Equation1 for $\Psi_{b(g)}$:

$$\Psi_{b(g)} = \Psi - \left(\frac{\theta_H}{t_g}\right) \qquad [2]$$

Variability in $\Psi_{b(g)}$ in a seed population can be described by various statistical frequency distributions (Mesgaran et al. 2013; Watt et al. 2010), but most often is assumed to be normally distributed with its respective mean (median), $\Psi_{b(50)}$, and standard deviation, $\sigma_{\Psi b}$ (Bradford 1990, 2002). Assuming a normal distribution, the cumulative germination of seeds, g, over time, t, at any given water potential, Ψ, can be obtained by:

$$g(\Psi, t_g) = \Phi(\Psi_{b(g)}, \Psi_{b(50)}, \sigma_{\Psi b})$$

Replacing $\Psi_{b(g)}$ with Equation 2 gives:

$$g(\Psi, t_g) = \Phi\left(\Psi - \left(\frac{\theta_H}{t_g}\right), \Psi_{b(50)}, \sigma_{\Psi b}\right) \qquad [3]$$

where Φ is the cumulative distribution function of a normal distribution. Equation 3 was fit to germination data using the drcSeedGerm package (Onofri et al. 2018) in R (R Core Team 2020). The hydrotime model (Equation 3) was fit to germination data of each temperature and population separately. To obtain robust standard errors for model parameters, we implemented the delete-a-group jackknife technique (Onofri et al. 2014) using the *jackGroupSE()* function available in drcSeedGerm package (Onofri et al. 2018). This method provides more accurate estimates of standard errors for cumulative data such as germination curves (Onofri et al. 2014). To test whether the germination curves differed between the two maternal watering levels, a reduced hydrotime model that ignored the maternal treatment as grouping factor was fit to the data. Using the *anova()* function in R (R Core Team 2020), an *F*-test was conducted to test whether the size of error in

the reduced model is significantly larger than that of the full model: the full model included the maternal water environment as a grouping factor. A significant P-value ($\leq$0.05) indicates that the germination curves significantly differ between the two maternal water conditions.

Parental plant height and progeny seed weight and seed size were compared across the two maternal water treatments (water-deficit vs. well-watered) using the *t*-test with Proc TTEST in SAS (v. 9.4; SAS Institute 2019). As a surrogate measure of dormancy level, the total percent germination at 0 MPa and 30 C treatment, representing the optimal conditions for germination of *A. palmeri* (Steckel et al. 2004), was further analyzed using generalized linear mixed models with PROC GLIMMIX in SAS (v. 9.4). In this analysis, a binomial distribution with the logit function was used, and maternal water treatment was considered the fixed effect, while the experimental run was incorporated as the random effect. Data from each population were analyzed separately. Visual assessment of residuals (plotted against fitted values) showed no evidence of variance heteroscedasticity.

Results and Discussion

Our irrigation scheme was effective in causing stress in the water deficit treatment, as evidenced by significant reduction in plant height of both *A. palmeri* populations (P-value < 0.0001). Plant height was almost halved in plants exposed to the water deficit treatment (Figure 1).

Seed Weight and Area

Analysis of progeny 1,000-seed weight showed significant differences between the two maternal water treatments both in the California (P-value = 0.0003) and the Kansas (P-value = 0.0003) populations. In both populations of *A. palmeri*, seeds produced under water stress were 18% heavier than those produced by plants under normal irrigation (Figure 2). The 1,000-seed weights of original (parental) seeds were 290.7 mg (SE: 8.5) and 279.5 mg (SE: 8.2) for the California and Kansas collections, respectively.
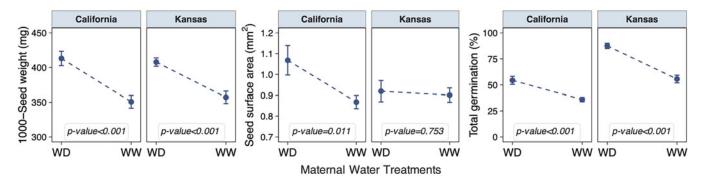
Figure 2. Differences in 1,000-seed weight, seed surface area, and total germination (dormancy) of progeny seeds from two *Amaranthus palmeri* populations (California and Kansas) grown under continuous water-deficit (WD) or well-watered (WW) irrigation conditions. Vertical bars on data points indicate SE.

Progeny seed size, as measured by the seed surface area, differed between maternal water treatments in the California population (P-value = 0.0117) but not in the Kansas population (P-value = 0.7534). In the California population, progeny seed surface area increased by 23% in response to maternal water stress (Figure 2). The surface areas of parental seeds used in the study were 0.656 mm² (SE: 0.023) for the California population and 0.621 mm² (SE: 0.037) for the Kansas population. As seed surface area in the Kansas population was constant across the two maternal conditions, the increase in seed mass observed with the water-deficit treatment should have resulted from the increase in seed thickness and/or density. Previous studies with crop plants such as lentil (*Lens culinaris* Medik.) (Sehgal et al. 2017), soybean [*Glycine max* (L.) Merr.] (Wijewardana et al. 2019), and canola (*Brassica napus* L.) (Hatzig et al. 2018) have shown that applying water stress to parental plants may negatively affect yield-related traits and reduce final seed weight. In cereal crops such as rice (*Oryza sativa* L.), maize (*Zea mays* L.), and wheat (*Triticum aestivum* L.), water stress at the grain-filling stage translated to a shorter grain-filling period, eventually leading to lower seed weight (Saini and Westgate 1999). However, similar to our findings, a greenhouse study with redroot pigweed (*Amaranthus retroflexus* L.) showed that plants subjected to water stress produced heavier seeds (greater mass) than those grown without drought (Chadoeuf-Hannel and Barralis 1982). Greater seed mass in *A. retroflexus* was also associated with drier environments in the correlative study of Schimpf (1977). Three of four *Polygonum* spp. (i.e., ladysthumb [*Polygonum persicaria* L.], tufted knotweed [*Polygonum cespitosum* Blume], and pale smartweed [*Polygonum lapathifolium* L.]) tested by Sultan (2001) produced larger achenes in dry rather than moist environments. Interestingly, the noninvasive species marshpepper smartweed (*Polygonum hydropiper* L.) was the only species that produced smaller achenes in dry soils. Whereas our study shows that maternal drought can markedly affect seed mass and size in *A. palmeri*, shading, even as high as 87%, had no effect on seed weight of *A. palmeri* (Jha et al. 2010).

Seed Dormancy

Progeny seed dormancy was evaluated by testing the germination of *A. palmeri* seeds at optimal temperature (i.e., 30 C; Steckel et al. 2004). Maternal water stress significantly affected the dormancy level in progeny seeds of both the California (P-value = 0.0004) and Kansas (P-value < 0.0001) populations. Plants that experienced water stress produced the least dormant seeds (Figure 2).

For example, in the Kansas population, the total germination for seeds originating from water-stressed plants was as high as 87.5% (SE: 2.6) but dropped to 55.6% (SE: 3.7) in seeds from plants receiving normal irrigation (Figure 2). In the California population, the total germination for seeds from the water-deficit treatment was 20% higher than for the control. The parental seeds used in the study exhibited dormancy levels similar to those produced by well-watered plants: California parental seeds germinated 30.6% (SE: 2.3), while parental seed sourced from Kansas reached 65.0% (SE: 3.7) germination.

In several other weed species such as johnsongrass [*Sorghum halepense* (L.) Pers.] (Arnold et al. 1992) and *A. retroflexus* (Karimmojeni et al. 2014), when parental plants were exposed to water stress during seed production, progeny seeds showed increased germination rates compared with seeds of plants grown under control irrigation conditions. However, an opposite trend has been recorded for germination of seeds from maternally stressed plants in crops. In soybean, increasing maternal drought stress translated into lower seed germination rates (Wijewardana et al. 2019). For canola, differences in mean germination time between seeds of genotypes grown under water stress was not conclusive, although some genotypes grown under water stress took longer to germinate than the control (Hatzig et al. 2018). Differences between crop plants and weedy species may be explained due to evolutionary changes related to historical domestication and breeding processes. One of the main features of plants that have undergone strong domestication processes is reduced seed dormancy through changes in seed coat thickness (e.g., physical dormancy) or biochemical seed composition (e.g., physiological dormancy) (Abbo et al. 2014). Different drought stress responses were reported when weedy and domesticated populations of sunflower (*Helianthus annuus* L.) were compared (Koziol et al. 2012).

Seed germination is regulated by several plant hormones, mainly abscisic acid (ABA) and gibberellic acid (GA) accumulated in the embryo during seed development (Bewley 1997; Kermode 2005). Physiological seed dormancy is regulated by ABA/GA ratio, where ABA prevents and GA promotes seed germination. ABA level increases during initial seed development and decreases during seed maturity; however, this process can be affected by environmental signals (Bewley 1997). In grain sorghum [*Sorghum bicolor* (L.) Moench.] seeds, water stress decreased both embryo content and sensitivity to ABA (Benech Arnold et al. 1991). Elevated ABA levels were recorded in seeds of *A. palmeri* plants grown under 87% shade compared with 0% shade conditions (Jha et al. 2010).
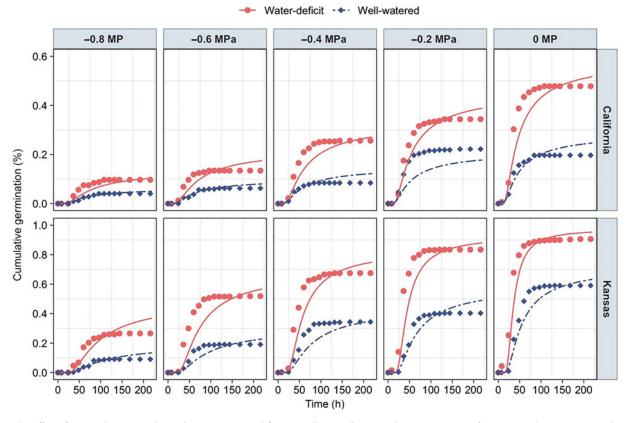
Figure 3. The effect of maternal water conditions (continuous water-deficit vs. well-watered) on cumulative germination of progeny seeds in two *Amaranthus palmeri* populations (California and Kansas) tested under various water potentials at 20 C. Lines are fitted values obtained from the hydrotime model, Equation 3, $g(\Psi, t_g) = \Phi\left(\Psi - \left(\frac{\theta_H}{t_g}\right), \Psi_{b(50)}, \sigma_\Psi b\right)$, with parameter estimates shown in Table 1.

Hydrotime Germination Model

With few exceptions, the hydrotime model adequately described the germination time courses of *A. palmeri* at both tested temperatures as shown by fitted curves (Figures 3 and 4) and small root mean-square error (RMSE) as shown in Table 1. There were marked differences in progress toward germination between the two maternal water conditions. In both *A. palmeri* populations, seeds from water-stressed plants achieved greater germination percentages (almost double) than those from plants with no water stress across all levels of water potentials tested in this study (Figures 3 and 4).

The observed changes in germination capacity of seeds (Figures 3 and 4) can largely be attributed to shifts in population base water potential ($\Psi_{b(50)}$) and to a lesser extent to its standard deviation (i.e., $\sigma_{\Psi b}$), as hydrotime constant (θ_H) was not affected by the maternal environment (Table 1). Base water potential exhibited a consistent pattern of response to maternal water treatments across the two tested temperatures and in both *A. palmeri* populations. Maternal drought significantly shifted the distribution of base water potential in progeny seed subpopulations toward more negative values (Figure 5), implying that the resultant seeds have become more tolerant to water limitation and hence can germinate from drier conditions. For example, in the Kansas population, the estimated $\Psi_{b(50)}$ was −0.63 MPa (SE: 0.036) at 30 C when seeds matured on water-stressed plants, which was three times more negative than the $\Psi_{b(50)}$ (i.e., −0.21 MPa, SE: 0.025) of seeds produced by nonstressed plants. These $\Psi_{b(50)}$ values suggest that if seeds from nonstressed plants are planted into a medium with

a water potential of −0.63 MPa, only 18% of them are predicted to germinate as contrasted to 50% germination for seeds from water-stressed plants. Maternal water stress also reduced the variance of $\Psi_{b(g)}$ in seed subpopulations as indicated by smaller $\sigma_{\Psi b}$ values with the only exception being the progeny seed from California population tested at 30 C (Table 1; Figure 5). As parameter $\sigma_{\Psi b}$ in the hydrotime model is a measure of germination uniformity, reduction in $\sigma_{\Psi b}$ implies a higher uniformity for *A. palmeri* seeds originating from maternally stressed plants.

We are only aware of a single study that has examined the effect of maternal water level on the germination tolerance of progeny seed to water limitation. Seed of wild tomato (*Lycopersicon chilense* Dunal) (an endemic tomato species in Chile) from mother plants grown under water deficit were able to germinate at a lower water potential than those from plants receiving ample water supply (Maldonado et al. 2002). Low temperature during seed maturation reduced the ability of mouseear cress [*Arabidopsis thaliana* (L.) Heynh.] to germinate at low water potential (Edwards et al. 2016).

Our results suggest that a transgenerational hydrotime model can be developed by adjusting $\Psi_{b(50)}$, and perhaps $\sigma_{\Psi b}$, to adequately describe the progeny seed germination. A shift in $\Psi_{b(50)}$ toward more negative values has been associated with reduced dormancy in other studies (Batlla and Benech-Arnold 2004; Bradford 2002). For example, temporal change in seed dormancy of prostrate knotweed (*Polygonum aviculare* L.) was also modeled by using $\Psi_{b(50)}$ alone, as the θ_H and $\sigma_{\Psi b}$ parameters changed only slightly with dormancy level (Batlla and Benech-Arnold 2004).
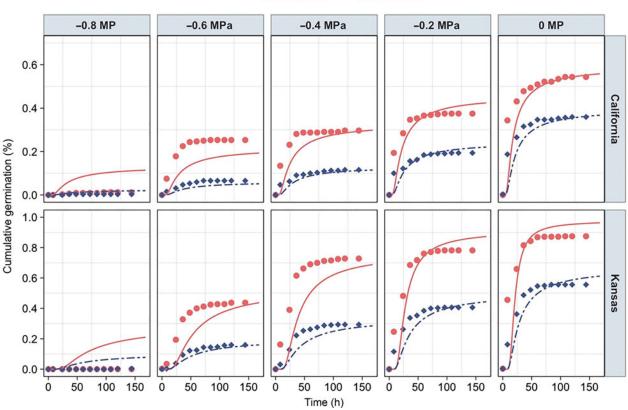
Table 1. Parameter estimates of hydrotime model of germination, Equation 3, $g(\Psi, t_g) = \Phi\left(\Psi - \left(\frac{\theta_H}{t_g}\right), \Psi_{b(50)}, \sigma_{\Psi_b}\right)$, for progeny seeds of two *Amaranthus palmeri* populations (California and Kansas) grown under contrasting maternal water conditions.[a]

Population	Maternal environment	20 C					30 C				
		$\Psi_{b(50)}$	σ_{Ψ_b}	θ_H	RMSE[b]	P-value[c]	$\Psi_{b(50)}$	σ_{Ψ_b}	θ_H	RMSE[b]	P-value[c]
					—%—					—%—	
California	Water deficit	−0.13 (0.03)	0.61 (0.05)	24.07 (2.03)	5.7	<0.001	−0.14 (0.03)	0.59 (0.06)	9.22 (0.96)	7.1	<0.001
	Well watered	0.46 (0.12)	0.83 (0.11)	23.19 (2.92)			0.12 (0.03)	0.46 (0.04)	6.63 (0.82)		
Kansas	Water deficit	−0.81 (0.02)	0.39 (0.03)	30.47 (1.59)	8.5	<0.001	−0.63 (0.04)	0.31 (0.03)	14.04 (1.14)	11.6	<0.001
	Well watered	−0.33 (0.03)	0.55 (0.05)	31.98 (2.27)			−0.21 (0.02)	0.47 (0.04)	12.71 (1.09)		
Parental seed source											
	California	0.23 (0.07)	0.47 (0.08)	49.50 (8.37)	2.4		0.09 (0.04)	0.54 (0.06)	27.24 (3.16)	4.3	
	Kansas	−0.55 (0.04)	1.03 (0.11)	30.81 (3.52)	8.3		−0.39 (0.03)	0.50 (0.06)	7.39 (0.75)	12.4	

[a] Germination assays were conducted at two temperatures (20 and 30 C), and the hydrotime model was fit to data of each temperature separately. Also shown are the parameter estimates for the original (parental) seed sources used to grow plants under the two maternal water treatments. Values in the parenthesis indicate SE.
[b]RMSE, root mean-square error. Note that a single hydrotime model that included the maternal water environment as a covariate was fit to the germination data of each population. As result, there is one RMSE for both maternal water conditions.
[c]P-value indicates the overall significance level for the difference between the germination curves (models) of the two maternal water levels, i.e., water-deficit vs. well-watered treatments.

Figure 4. The effect of maternal water conditions (continuous water-deficit vs. well-watered) on cumulative germination of progeny seeds in two *Amaranthus palmeri* populations (California and Kansas) tested under various water potentials at 30 C. Lines are fitted values obtained from the hydrotime model, Equation 3, $g(\Psi, t_g) = \Phi\left(\Psi - \left(\frac{\theta_H}{t_g}\right), \Psi_{b(50)}, \sigma_{\Psi_b}\right)$, with parameter estimates shown in Table 1.

Future studies need to use multiple levels of maternal water limitation to determine the shape of relationships between maternal water level and $\Psi_{b(50)}$ and σ_{Ψ_b}; for example, whether they are linear or nonlinear. Our study used continuous water stress (from 6-leaf stage onward); however, it is likely that only stress at the reproductive stage (i.e., when seed develops) will be important in driving maternal effects, as shown in several studies (reviewed by Baskin and Baskin 2014). Applying water stress at different

parental growth stages can inform us about the most influential stage that can produce maternal effects.

Conclusions

Our results show that *A. palmeri* plants experiencing water stress during their growth can produce less dormant and larger seeds that may give rise to competitive and vigorous seedlings. Moreover, we
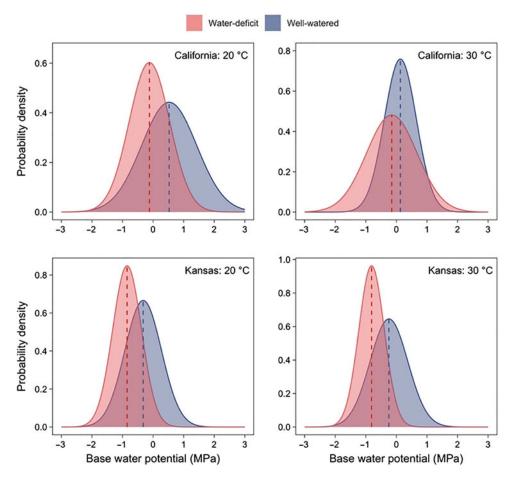
Figure 5. Shifts in distribution of base water potential of progeny seeds from two *Amaranthus palmeri* populations (California and Kansas) grown under contrasting maternal water conditions (continuous water-deficit vs. well-watered). Seed germination was tested at two temperatures (20 and 30 C) under five water potentials. A hydrotime model, Equation 3, $g(\Psi, t_g) = \Phi\left(\Psi - \left(\frac{\theta_H}{t_g}\right)\Psi_{b(50)}, \sigma_{\Psi b}\right)$, was fit to estimate the median base water potentials, $\Psi_{b(50)}$ (vertical dashed lines), and their respective standard deviations, $\sigma_{\Psi b}$, to produce these probability density curves of normal distribution (see Table 1 for parameter estimates). Note that the area under the curve for base water potential values >0 indicates the proportion of seeds that have not germinated (i.e., dormancy level).

showed, for the first time, that *A. palmeri* parental plants grown under water-deficit conditions can produce seeds that are more drought tolerant and hence can germinate under drier conditions compared with seeds from nonstressed plants. These maternal effects seem to be adaptive, as the mother plant exposed to stress produced progeny somewhat primed (prepared) to cope with the harsh environments similar to maternal conditions. The consistency in germination responses of progeny seed to maternal conditions suggests that further models of germination (and emergence) need to be transgenerational, as the "memory" of past environment can have a marked influence on the responses of seeds to current conditions.

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