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Maternal temperature effects on dormancy influence germination responses to water availability in *Arabidopsis thaliana*

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ABSTRACT

With climate change, germination cuing to water availability is expected to be especially important for seedling survival. Here, we examined germination responses to low water potential and tested whether dormancy status mediates these responses. We considered both genetically based dormancy (genotypes with allelic variation in dormancy genes) as well as dormancy imposed by the environment (low seed-maturation temperature or short duration of dry afterripening). We examined (a) germination capacity at low water potential, (b) germination acceleration in response to pre-incubation at low water potential, and (c) secondary dormancy induction by low water potential. We found that both environmentally imposed dormancy and genetically based dormancy influenced germination responses to low water potential. Specifically, dormancy established via introgression of a strong dormancy allele and dormancy induced by low seed-maturation temperatures both reduced the ability to germinate at low water potential. Pre-incubation at low water potential accelerated germination, but the rate differed between both dormancy-inducing environments and among dormancy genotypes. Prolonged incubation at low water potential induced secondary dormancy, and this effect was greater in fresher (more dormant) seeds and in seeds that were matured at low temperature (a dormancy-inducing treatment). Although genotypes also varied in secondary dormancy induction, their level of primary dormancy did not predict their induction into secondary dormancy. Environmentally induced dormancy also influenced the expression of genetic differences in germination responses to low water potential. Thus environmentally determined dormancy influences not only germination responses to low water potential but also their evolutionary potential.

1. Introduction

Plant performance often depends on the accurate use of environmental cues to control phenology, or the seasonal timing of biological events. Phenology is considered to be one of the primary factors to influence the performance of organisms in novel climates that result from climate change or dispersal (Bradshaw and Holzapfel, 2008; Chuine and Beaubien, 2001; Menzel et al., 2006; Parmesan, 2006; Walther et al., 2002; Willis et al., 2008). The phenology of germination is particularly consequential, not only because the seedling stage is vulnerable to many environmental factors, but also because the seasonal timing of seed germination can influence the environmental conditions experienced by all subsequent life stages (Baskin and Baskin, 1998; Donohue et al., 2005; Eriksson, 2002; reviewed in Gutterman, 1994; Weinig, 2000). As a consequence, the seasonal timing of germination can be under extremely strong natural selection (Donohue et al., 2005; Huang et al., 2010), is likely to be a strong selective sieve for populations colonizing novel environments (Kronholm et al., 2012; Montesinos-Navarro et al., 2012), and it can have ramifying effects on whole life cycles (Burghardt et al., 2015b; Chiang et al., 2013). Identifying the major environmental factors that contribute to variation in germination behavior is therefore necessary to predict plant performance under diverse environmental conditions that accompany climate change or range expansion.

Seed dormancy prevents germination under environmental conditions that would normally permit germination in non-dormant seeds (Baskin and Baskin, 1998; Bewley, 1997; Simpson, 1990). Physiological dormancy is the most prevalent form of seed dormancy (Baskin and Baskin, 1983), and it allows seeds to postpone germination until specific environmental conditions are

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encountered that release the constraint on germination. High dormancy is associated with low germination proportions and a reduced ability to germinate over a wide range of conditions, whereas low dormancy is associated with higher germination proportions at a wider range of conditions. Dormancy is a dynamic state that can be distinguished as two types: primary dormancy, which is established during seed maturation and can vary with seed-maturation conditions such as temperature, and secondary dormancy, which is induced by environmental conditions experienced after dispersal and subsequent to the loss of primary dormancy (Baskin and Baskin, 1998; Bewley et al., 2013; Cadman et al., 2006). Primary dormancy is gradually alleviated through a process called afterripening, and when seeds become imbibed, secondary dormancy can be induced if seeds are exposed to unfavorable conditions. It is the interaction between factors that break primary dormancy, elicit germination, and induce secondary dormancy that ultimately determine germination timing (Baskin and Baskin, 1998; Forcella et al., 2000).

Once dormancy is broken, water availability strongly regulates the timing and probability of germination (Baskin and Baskin, 1998; Bewley et al., 2013). Rainfall can be highly variable within and between years (Clauss and Venable, 2000) and is not always indicative of suitable growing conditions if moisture is ephemeral. In some cases, seeds that germinate quickly after the onset of rain may gain a head start over others, but rapid germination could also result in mortality if drought occurs soon after. Seeds must therefore respond appropriately to such ephemeral cues. In annual plant species, one strategy is to capitalize on moisture resources as soon as they become available in order to increase the chances of establishment. Alternatively, the risk of germinating into an unfavorable environment can be spread across the seed cohort, such that only a fraction of seeds are competent to germinate when moisture conditions are permissive (Gremer and Venable, 2014; Venable and Lawlor, 1980). A third option is to not germinate until moisture conditions are optimal and persistent.

Germination timing in response to dynamically fluctuating temperature and water availability has been accurately predicted in agronomic applications using hydrothermal time models (Alvarado and Bradford, 2002; Bradford, 2002, 2005; Hardegree et al., 2003). Empirically estimated parameters that describe germination responses to temperature and water availability (i.e. water potential, or Ψ) are used to predict the rate of progress towards germination. The key parameters used to describe germination responses to water availability include base water potential, Ψ_b, or the lowest water potential at which germination can be completed, and minimum water potential, Ψ_{min}, or the lowest water potential necessary for metabolic advancement to occur while still preventing radicle protrusion. Germination speed is proportional to the difference between ambient Ψ and Ψ_b, with larger differences resulting in faster germination. Seeds with a high (less negative) Ψ_b therefore have a narrower range of moisture conditions that permit germination, and they exhibit slower germination compared to seeds with a low Ψ_b. Under field conditions, seeds with a higher Ψ_b could prevent precocious germination when water is available but growing conditions are otherwise unfavorable for growth. In a recent long-term field study of a community of desert annuals, low Ψ_b was shown to be significantly associated with higher germination proportions within a year, later germination during the season, and higher demographic variance across years (Huang et al., 2015), indicating that germination responses to water potential can have important phenological and demographic consequences in natural systems.

Lack of emergence does not necessarily mean that germination-related processes are static, as processes related to germination and dormancy can still proceed even at water potentials that do not permit germination. For instance, seeds may still accumulate progress towards germination at water potentials below Ψ_b if the ambient water potential is above Ψ_{min}. Under low-moisture conditions, seeds may become partially imbibed and achieve a head start on germination, as evidenced by faster germination upon subsequent exposure to permissive hydric conditions. This enhancement effect on germination is often utilized in agriculture to improve crop performance – in practice, it is referred to as seed priming – and studies have identified multiple cellular processes that occur during seed priming, including protein synthesis, nucleic acid synthesis, and DNA repair mechanisms (Chen and Arora, 2013; Paparella et al., 2015). In nature, seeds on the soil surface experience fluctuating cycles of wetting and drying throughout the year, and a number of studies have reported improved predictions of field emergence by accounting for priming dynamics (Allen et al., 2000; Cheng and Bradford, 1999; Rowse and Finch-Savage, 2003). In contrast to priming, prolonged exposure to non-permissive water potentials may actually induce secondary dormancy (Auge et al., 2015). Advancement towards germination at non-permissive water potentials is not always a desirable response, if the onset of rain, for example, coincides with other environmental conditions that are unfavorable. In this instance, the ability of seeds to re-enter dormancy can prevent germination under unfavorable conditions and may be crucial for seedling survival.

The dormancy status of a seed influences the range of environmental conditions that are permissive for germination; as dormancy is lost, the permissive range broadens (Forcella et al., 2000). Hydrothermal models of germination have incorporated dormancy dynamics as changes in Ψ_b, and thereby the range of Ψ over which germination can occur, as dormancy is alleviated (Bair et al., 2006; Batlla and Benech-Arnold, 2004; Bauer et al., 1998; Christensen et al., 1996; Hardegree et al., 2013; Meyer et al., 2000). The empirical accuracy of such models suggests that changes in dormancy may directly influence germination responses to water potential. Both genetic and environmental mechanisms contribute to dormancy levels, but it has yet to be determined if dormancy induced by these different mechanisms leads to similar germination responses to moisture. To understand how dormancy contributes causally to germination responses to Ψ requires direct manipulation of genetic and environmental factors that control dormancy. Exploring how environmentally and genetically based variation in dormancy influences sensitivity to Ψ is necessary to understand how germination phenology may vary across environments with different water availability, including environments of the future.

Arabidopsis thaliana offers unique potential for investigating the genetic basis of germination responses to seasonal environmental factors, including Ψ. It is broadly distributed across diverse seasonal environments and exhibits a range of life-histories caused by variation in flowering and germination timing (Ratcliffe 1965; Donohue, 2009; Thompson, 1994). Environmental factors associated with flowering time, especially temperature during seed maturation, have strong effects on dormancy and germination in this species, such that seed maturation under cool conditions induces strong dormancy (Chiang et al., 2011; Donohue et al., 2007; Kendall and Penfield, 2012; Springthorpe and Penfield, 2015). Natural allelic variants of loci involved in dormancy have been identified (Alonso-Blanco et al., 2003; Bentsink et al., 2010; Huang et al., 2010; Laserna et al., 2008) and introgressed onto a common genetic background, allowing experimental studies of the combined effects of genetically and environmentally based differences in dormancy on germination responses to specific environmental factors, such as water availability.

Here, we examined germination responses to water potential and tested whether genetically and environmentally determined dormancy status mediates these responses. To manipulate