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REVIEW

Maternal and zygotic temperature signalling in the control of seed dormancy and germination

Sarah Kendall[1] and Steven Penfield[2]*

[1]CNAP, Department of Biology, University of York, PO BOX 373, York YO10 5DD, UK; [2]School of Life and Environmental Sciences, Geoffrey Pope Building, University of Exeter, Stocker Road, Exeter EX4 4QD, UK

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Abstract

Temperature has a key influence over seed dormancy and germination, allowing wild plants to synchronize their life history with the seasons. In this review we discuss the signalling pathways through which temperature is integrated into seed physiology and the control of primary and secondary dormancy, with an emphasis on understanding maternal effects and responses dictated by the zygotic tissues. A key emerging paradigm is that temperature signalling in seeds must be understood in relation to whole plant genetics and physiology, as overlapping pleiotropic roles for temperature sensing and hormone signalling pathways are commonplace.

Keywords: alternating temperatures, chilling, maternal effects, temperature, thermoinhibition

Introduction

In temperate zones plants use environmental temperature as a key signal to synchronize their life history with the seasons. Thus temperature is an important regulator of a number of developmental processes, including seed dormancy and germination. For annual plants chilling or alternating day and night temperatures are often strong germination-promoting cues, while daily maximum temperature during key windows of seed maturation is important for determining the level of primary dormancy. For secondary dormant seeds lying buried in the soil seed bank, temperature, together with soil moisture content, is the predominant signal that allows dormancy to cycle on a seasonal basis (Bewley and Black, 1994).

Climate change is predicted to be most apparent in the northernmost latitudes, where significant warming has already taken place compared to standard measures of 20th-century mean temperatures (IPCC, 2007). Because dormancy and germination are temperature-dependent processes, it is possible that climate change will alter annual plant life history and, over time, select new life-history variants from existing populations (Kover *et al.*, 2009). One study has even concluded that in Europe, over 30% of all herbaceous plant species may be driven to extinction primarily through an effect of climate warming on dormancy cycling in seeds and buds (Thuiller *et al.*, 2005). However, predicting the effects of a changing climate on natural populations is extraordinarily challenging, as existing and new variation may provide material for deriving populations capable of thriving in the modified conditions. Thus we need to understand the genetic basis of the link between temperature and plant life history, the key processes underlying the control of key life-history traits, and how these might evolve. This is a big challenge, even in a model species such as *Arabidopsis thaliana*, which is an excellent model system for the study of life-history evolution as well as the genetic basis of plant traits (Metcalf and Mitchell-Olds, 2009). Such information can also be expected to inform future plant breeding initiatives, for instance to breed crops with new combinations

*Correspondence
Email: S.D.Penfield@exeter.ac.uk

of traits better adapted to growing in future climate scenarios.

Temperature during seed maturation determines primary dormancy depth

During seed maturation, environmental stimuli such as temperature and photoperiod are important determinants of many characteristics of seeds, which in turn can potentially affect the developmental stages of the plant that follow. Effects of such stimuli on seed characteristics such as seed size and weight have been noted since the early 1950s. *Chenopodium polyspermum* L. seeds from mother plants grown in long days have lower germination frequencies and thicker seed coats in comparison to seeds from mother plants grown in short days (Pourrat and Jacques, 1975). Maternal temperature also influences the germination of seeds from the mother plant and, in almost every reported case, higher temperatures during seed maturation correlate with increased germination (Fenner, 1991). One interesting and often overlooked feature of this phenomenon is that the temperature applied to vegetative tissues pre-anthesis has been shown to influence dormancy of seed subsequently produced. Two clear examples have been shown using tobacco (Thomas and Raper, 1975) and wild oats (Sawhney *et al.*, 1985), and we show here that the same phenomenon can be observed with *Arabidopsis thaliana* (Fig. 1). Therefore plants can pass a memory of previous temperatures to their offspring. Our understanding of how the maternal environmental temperature leads to changes in dormancy is still poor. More recently, work on *Arabidopsis* and rice has begun to demonstrate the genetics important for the influence of the maternal experience of temperature on primary seed dormancy (Gu *et al.*, 2006; Schmuths *et al.*, 2006; Donohue *et al.*, 2008; Chiang *et al.*, 2009; Kendall *et al.*, 2011).

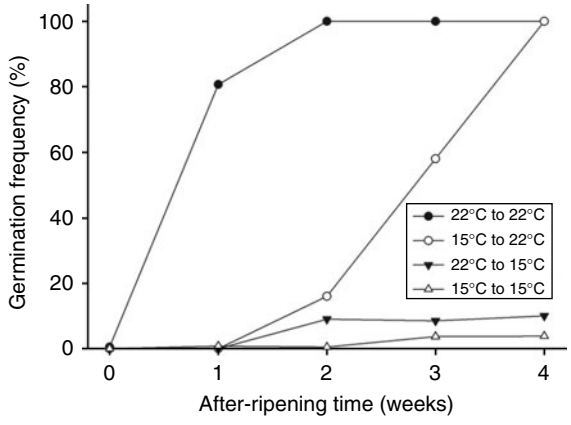

Figure 1. Environmental temperature before and after anthesis of the mother plant influences *Arabidopsis* seed dormancy. Plants were grown to anthesis of the first flower at either 15°C or 22°C, and then swapped to the other temperature. Seed dormancy was compared to control plants maintained for the whole life cycle at either 15°C or 25°C. Data represent the mean germination of five independent seed lots per treatment.

In *Arabidopsis*, low temperature during seed maturation leads to high primary dormancy levels, whereas warm temperatures lead to lower dormancy. This effect can be observed across a wide range of genetic backgrounds, with only strongly dormant ecotypes such as CVI showing insensitivity to this effect (Schmuths *et al.*, 2006; Penfield and Springthorpe, 2011). Lower seed maturation temperatures are likely to be experienced in the wild, either in winter annuals setting seed early in the spring, or in late-setting summer annuals whose reproduction lasts into autumn. In the latter case low seed maturation temperatures are often essential for seeds to make the necessary transition into secondary dormancy, required for overwintering in the soil seed bank (Penfield and Springthorpe, 2011). This is because in many ecotypes where low seed maturation temperatures are not experienced, the prolonged cold and dark incubation of seeds required to shift *Arabidopsis* seeds into secondary dormancy (Finch-Savage *et al.*, 2007) causes germination of seeds even in the absence of light, suggesting that these seeds are committed to germinating in the same growing season as they are set (Penfield and Springthorpe, 2011). For seeds set in warmer times of the year, germination conditions may be more favourable for immediate resumption of the life cycle, or further genetic dormancy-inducing mechanisms may confer an after-ripening requirement that delays germination until a set of dormancy-breaking conditions have been fulfilled. The complex mechanism regulating the coupling of dormancy level to temperature is only just starting to be unravelled.

The relationship between primary seed dormancy and seed maturation temperature is also critically important for seed quality in cereal crops. In addition to rainfall, environmental temperature is an important determinant of the frequency of pre-harvest germination and pre-harvest sprouting, both of which damage grain quality in a range of cereals, including barley, wheat and sorghum (Cochrane, 1993; Rodriguez *et al.*, 2001). Importantly, Rodriguez *et al.* (2001) were able to localize the period of barley seed maturation in which dormancy was maximally sensitive to temperature to a short window, using a simple thermal time model. This study also revealed that during this window eventual germination correlated with daily mean temperature, rather than the maximum or minimum. Elucidation of such details is necessary to predict the performance of crops species in new environments.

Temperature regulation of primary seed dormancy shares gene networks with other developmental

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pathways, such as flowering. *FLOWERING LOCUS C (FLC)* negatively regulates a number of genes that promote flowering, and confers a vernalization requirement on winter annuals (recently reviewed in Kim *et al.*, 2009). Epigenetic regulation represses *FLC* following vernalization through chromatin remodelling, thus allowing the expression of *SUPPRESSOR OF OVER-EXPRESSION OF CONSTANS 1* (*SOC1*) and *FLOWERING LOCUS T* (*FT*) in spring. *FLC* has been shown to have a maternal role in the regulation of dormancy, but this regulation is apparent only when seeds are matured at low temperatures and then incubated at cool imbibition temperatures (Chiang *et al.*, 2009). Under these conditions near isogenic lines (NILs) containing strong alleles of *FLC* display higher germination when imbibed at 10°C in comparison to the wild type, but this phenotype is extremely weak at higher germination temperatures (Chiang *et al.*, 2009). This increase in germination is correlated with an increase in the abscisic acid (ABA) catabolic gene *CYP707A2*, and the gibberellic acid (GA)-biosynthesis gene *GIBBERELLIN 2-OXIDASE 1* (*GA2ox1*) expression during imbibition, suggesting that *FLC* can regulate metabolism associated with hormone balance. Surprisingly, expression of *DELAY OF GERMINATION 1* (*DOG1*), a gene identified as a quantitative trait locus which is involved in regulation of seed dormancy (Bentsink *et al.*, 2006 l Kendall *et al.*, 2011) also appears to be up-regulated in the high *FLC* expressing line and this is usually characteristic of seeds displaying high dormancy levels.

The *hy2-1* mutant has reduced levels of all five phytochromes (Chory *et al.*, 1989) and, like the wild type, shows high dormancy levels when matured at 10°C. However, cold stratification and after-ripening have no dormancy-breaking effects in this background, whereas approximately 80% germination can be obtained following cold stratification of seed matured at warmer temperatures (Donohue *et al.*, 2008). This suggests that primary dormancy levels are higher in *hy2-1* and that phytochromes not only respond to temperature during imbibition, but also to the maternal environment. Since the low-temperature-induced dormancy in *hy2-1* is not broken by any stratification treatment nor after-ripening, it seems that lack of phytochrome can induce a state in which seeds are not responsive to dormancy-breaking signals. Interestingly, Donohue *et al.* (2008) show that low-temperature induced dormancy is only alleviated by a period of warm stratification followed by cold stratification. This warm/cold stratification did not promote germination in *phyB* and *phyD* mutants and, following after-ripening, this stratification regime does not break dormancy. Recently, we have shown that seed maturation temperature controls the level of both *phyB* and *phyE* transcripts in dry seeds, suggesting that temperature can modify the light requirement for germination by impacting directly on phytochrome levels (Kendall *et al.*, 2011).

Dormancy and germination are both regulated by a fine balance of ABA and GA signalling, and shifts in the ratio of ABA to GA can cause different dormancy states. Levels of ABA are considerably higher in dry seeds matured at 10°C in comparison to 20°C. GA levels show the opposite, whereby levels are lower in the low-temperature matured seeds (Kendall *et al.*, 2011). This change was coupled with the increased expression of two *GIBBERELLIN 2-OXIDASE 6* isoforms by lower temperatures, *GA2ox2 and GA2ox6.* Expression of *CYP707A2* is also down-regulated in seeds matured at low temperature (Chiang *et al.*, 2009; Kendall *et al.*, 2011), whereas *NCED4*, which is involved in ABA biosynthesis, is up-regulated. This suggests that metabolism of both ABA and GA may be key to the mechanism by which temperature regulates primary dormancy, and that the levels of ABA and GA in mature seeds correlate strongly with dormancy depth. Low temperature during seed maturation causes an up-regulation in *DOG1* (Bentsink *et al.*, 2006; Kendall *et al.*, 2011). A summary of our understanding of the genetics of the influence

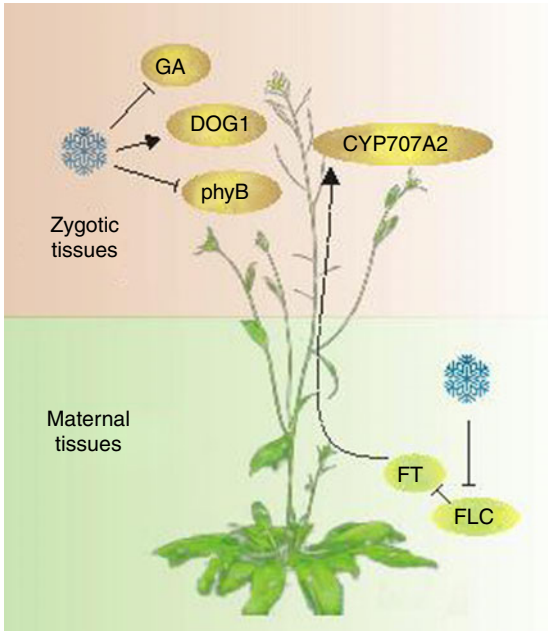

Figure 2. The genetic control of primary dormancy by environmental temperature experienced by the mother plant, and during seed maturation. Maternal temperature is sensed by pathways known to be important in the control of the timing of the floral transition (Chiang *et al.*, 2009), but it is unclear which tissues are important. During seed maturation, temperature influences the gibberellic acid (GA) content of the dry seed, and the level of *DOG1* and phytochrome expression (Kendall *et al.*, 2011). (A colour version of this figure can be found online at http://journals.cambridge.org/ssr).

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of maternal and zygotic seed maturation temperature on seed dormancy is shown in Fig. 2.

Chilling and dormancy control in the imbibed seed

Chilling after imbibition is a widely conserved dormancy-breaking stimulus, and chilling requirements can vary enormously between species. An interesting conundrum that is not understood is how low temperature promotes dormancy during seed maturation but promotes germination during imbibition. Thus there must be a mechanism that ameliorates the dormancy-promoting effect of chilling in imbibed seed, and a second which attenuates the dormancy-breaking effect of chilling during seed maturation. It is often assumed that chilling can have both dormancy-inducing and dormancy-breaking effects simultaneously (Batlla and Benech-Arnold, 2009). Similarly, extended chilling times can induce secondary dormancy, especially in *Arabidopsis* (Finch-Savage *et al.*, 2007; Penfield and Springthorpe, 2011), and this requires that low temperature again induces dormancy. Germination promotion by chilling during imbibition is dependent on expression of *GA3ox1*, involved in later steps of the GA-biosynthetic pathway, which is upregulated at 4°C in comparison to 22°C and leads to an increase in bioactive GA levels (Yamauchi *et al.*, 2004). This may be a clue to the mechanism, as in vegetative tissues of many species, low temperatures have been consistently shown to slow growth by inducing *reductions* in GA content (Tonkinson *et al.*, 1997; Stavang *et al.*, 2005; Achard *et al.*, 2008). In *Arabidopsis*, this reduction in GA content has been shown to be mediated by cold-induced expression of three APETALA2-domain transcription factors known as C-REPEAT BINDING FACTORS (CBFS; Stockinger *et al.*, 1997; Achard *et al.*, 2008), genes also important in the development of freezing tolerance. These slow growth by promoting the transcription of *GA2ox3*, which leads to inactivation of GAs. Interestingly, in imbibed seeds no up-regulation of *CBF* expression is detected in response to low temperature, showing that a mechanism exists to prevent the temperature-regulation of *CBF* transcription in seeds (Kendall *et al.*, 2011). This must be important because expression of high *GA2ox3* levels in seed in response to chilling would not be expected to lead to germination and, indeed, *CBF* overexpression causes a germination inhibition that can be overcome by exogenous GA (Kendall *et al.*, 2011). In contrast, absence of *CBF* leads to a reduction in *DOG1* and *GA2ox6* and to low dormancy expression in dry seeds exposed to low temperature during seed maturation, suggesting that CBF action in maturing seeds can contribute to dormancy control by low maturation temperatures.

Interestingly, the role of phytochromes during seed imbibition appears to be temperature dependent. PHYE contributes to germination at low temperatures, whereas PHYA is important for germination at warm temperatures. PHYB, on the other hand, is important for germination over a range of temperatures (Heschel *et al.*, 2007). This therefore suggests that the phytochromes are not only important for responding to light signals but are able to exert influence over temperature signal transduction. Light and temperature also regulate the transcription factor *SPATULA (SPT)*, a member of the PHYTOCHROME INTERACTING FACTOR sub-family of bHLH proteins. SPT can act as a positive or negative regulator of germination depending on the ecotype background (Penfield *et al.*, 2005; Gan *et al.*, 2007). In L*er*, the standard *Arabidopsis* laboratory accession Landsberg erecta, SPT is a germination promoter and the *spt-2* mutation blocks chilling-responsive germination and the induction of *GA3ox* expression by cold. Chilling stabilizes the SPT protein in seedlings, where it also acts to repress growth (Sidaway-Lee *et al.*, 2010), showing that temperature can directly impact the SPT protein. Thus chilling may promote germination in part through stabilization of the SPT protein. SPT is also expressed during seed development, and so may be important for establishing the chilling-responsiveness of primary dormancy, but less important in the imbibed seed. SPT can also interact with DELLA proteins, linking temperature signalling to hormone response pathways. Elucidation of the targets of SPT will help uncover its precise mode of action.

Thermoinhibition of germination

Dormancy is often related to the control of the permissive temperature range within which germination can occur, with more dormant seeds germinating only after the experience of a narrower window of germination conditions. However, high temperatures can suppress the germination of seeds with little or no dormancy in a phenomenon known as thermoinhibition. Expression of the ABA biosynthesis genes *NCED2, NCED5* and *NCED9* is higher in seeds imbibed at 34°C in comparison to 22°C, thus suggesting that they contribute to enhanced ABA biosynthesis at high temperature (Toh *et al.*, 2008). A significant reduction in expression of the ABA catabolic genes *CYP707A1, CYP707A2* and *CYP707A3* was also observed at 34°C. In addition to regulation of ABA in response to high temperature, GA also plays an important role. Levels of both GA_1 and GA_4 are reduced in seeds imbibed at high temperature and this is due to a reduction in expression of GA biosynthesis genes. This suppression requires ABA since *aba2-2* mutants display increased expression of these genes at high temperature.

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Mutants isolated from a screen for high temperature resistant germination included a new *abi3* allele, *abi3-14*, and *transparent testa* (*tt*) mutants (Tamura *et al.*, 2006). The isolation of mutants affected in dormancy control in genetic screens for thermoinhibition insensitivity suggests that this effect is an extreme form of dormancy. The role of ABA synthesis in the thermoinhibition of germination appears to be conserved across species, as a key quantitative trait locus (QTL) for high temperature germination in lettuce also corresponds to an *NCED* orthologue (Argyris *et al.*, 2011).

Germination promotion by alternating temperatures

This is still a very poorly understood physiological process and there is only limited understanding of how and why alternating temperatures appear to be critical for germination in many dormant species. A favoured theory is that vegetation cover can reduce the daily amplitude of temperature oscillations and that the alternating temperature response is an adaptation to germination after canopy removal (Toole *et al.*, 1956). An interesting early demonstration of the importance of alternating temperatures was by Stotzky and Cox (1962), who realized that germination of *Musa balbisiana* seeds was strongly inhibited in their greenhouse in winter, when it was artificially heated to maintain temperature. Mechanisms touted as candidates were the need for sequential destruction of inhibitor and synthesis of activators, or the regulation of some aspect of metabolism, or light signalling (Toole *et al.*, 1956). The adaptive significance of the alternating temperature response was probed in an important multi-species study of germination responses on seeds from various ecosystems (Thompson *et al.*, 1977). This showed that seeds from habitats which experience seasonal flooding have clear requirements for alternating temperatures, and also confirmed that canopy removal increases the daily temperature amplitude. Thus the requirement for large daily temperature amplitudes may be an adaptation to time germination to a seasonal dry spell in wetland areas. Alternating temperatures have been shown to be important for the germination of many species, and even promote increased germination in dormant *Arabidopsis* seeds (Ali-Rachedi *et al.*, 2004) and one complete temperature cycle is sufficient for many species.

Germination promotion by alternating temperatures may be a phenomenon related to thermoperiodism (Went, 1944). Thermoperiodic growth responses have been observed in many species and are characterized as a growth promotion by oscillating day and night temperatures, compared to a constant warm temperature alone. Thermoperiodism acts, at least in part, through the regulation of GA levels (Stavang *et al.*, 2005). In *Arabidopsis*, disruption of circadian rhythms has been shown to attenuate germination promotion by alternating temperatures, suggesting that entrainment of the circadian clock to temperature signals may be important for germination, or that the circadian clock might be necessary for the measurement of temperature differentials (Penfield and Hall, 2009). Because of the importance of alternating temperatures as a dormancy-breaking cue, further work is required to understand the mechanism underlying the effect.

Conclusions

Seeds use environmental temperature in a variety of ways to co-ordinate germination timing, but the mechanisms of temperature signal transduction have only recently begun to be understood. Because temperature influences a wide variety of seed traits, a better understanding of the molecular mechanisms underlying temperature signalling is essential to breed crops giving consistently high seed quality in a variety of seed maturation environments. Our best hope for this is to combine knowledge of the genetic basis of key traits gleaned from model systems to identify candidate targets for selection during breeding. A second important consideration is the genotype of the parent plants, and understanding how and when environmental signals are influencing traits of interest. Finally, because of pervasive pleiotropy in the control of seasonal events in plants (Chiang *et al.*, 2009; Kover *et al.*, 2009) it is critical to understand the overlap between the control of seed traits and other crop characters vital to performance.

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