Maternal environmental control of progeny seed physiology: a review of concepts, evidence and mechanism

Review Paper

Corresponding author:
Steven Penfield;
Email: steven.penfield@jic.ac.uk

William Bezodis and Steven Penfield (ORCID)

John Innes Centre, Norwich, UK

Abstract

The environment experienced by a plant before and after reproduction can have a profound effect on the behaviour of the progeny after shedding. Maternal environmental effects on seeds are important for phenology and fitness in plants, especially for bet-hedging reproductive strategies. Maternal tissues that disperse with seeds are important for dormancy in many species, particularly those with coat-imposed dormancy and those that disperse in indehiscent fruits. Maternal nitrogen status, temperature and photoperiod modify maternal tissues and also influence the developing zygote. During seed development on the mother, the progeny may acquire environmental information directly, but there is also evidence for maternal–filial signalling and the epigenetic inheritance of environmental information through the germline.

The maternal environment and its influence on progeny physiology

The transition from embryo to seedling is perhaps the most critical transition in the life history of seed plants. Quiescent orthodox dry seeds are extremely robust to adverse environmental conditions, even after imbibition in the soil seed bank. Once the developmental decision to germinate is taken, the plant soon after enters a seedling stage particularly vulnerable to adverse conditions. Primary seed dormancy describes the phenomenon of fresh, viable seeds not germinating despite permissive environmental conditions (light, moisture and suitable temperature). Dormancy allows for seed physiology to be optimized such that germination occurs when there is the best chance of seedling survival, optimal phenology and maximal reproductive fitness (Baskin and Baskin, 2014).

Maternal environment effects on seed behaviour describe the phenomenon by which seeds of the same genotype behave differently when sown in the same conditions due to variation in the environment experienced by the mother (Fenner, 1991). Light, temperature, nutrients and water availability during growth of the mother affects the dormancy of its seeds (the progeny). Extensive evidence for maternal environmental effects on seed dormancy has been collected across a wide range of seed plant species (Roach and Wulff, 1987; Gutterman, 2000; Baskin and Baskin, 2014). These descriptions of maternal environmental effects are complicated because, in practise, it is challenging to differentiate between zygotic responses to the environment as seeds develop on the mother plant and effects of the environmental experience of the mother itself (Gutterman, 2000; Penfield and MacGregor, 2017). Truly maternal effects act transgenerationally and, therefore, must involve an intergenerational control mechanism and genotype * environment interactions in both the mother and progeny. Gutterman (2000) considers that maternal environmental effects take place after fertilization but before seed dispersal. Nonetheless, there are *bona fide* examples of effects of the maternal environment during vegetative growth that affect seed physiology. The earliest description of this seems to be by Thomas and Raper (1975), who showed that tobacco (*Nicotiana tabacum*) seedlings exposed to colder temperatures produced more dormant seeds even when transplanted to warmer temperatures before the apex had become reproductive. In wild oat (*Avena fatua*), Sawhney et al. (1985) showed that maternal temperature before anthesis affected the germination of the resultant seed. This was also genotype-specific so demonstrates a double genotype * maternal environment * progeny environment interaction. This has also been shown in the model plant *Arabidopsis thaliana* where different locally adapted ecotypes have different levels of dormancy (Postma and Ågren, 2015) and temperature treatments given to the mother prior to fertilization of any ovules give rise to dormancy phenotypes in the progeny (Chen et al., 2014; Auge et al., 2017).

The adaptive value of maternal environment effects

For *A. thaliana*, studies of soil seed banks show that, at any given time, around 90% of the population diversity is below ground in the soil seed bank (Lundemo et al., 2009). Primary

dormancy is a likely pre-requisite for the entry of newly dispersed seeds into the soil seed bank. However, rapid cycling accessions require low dormancy if newly dispersed seed is to give rise to another generation in the same growing season. The adaptive advantage of the production of seeds with variable germination strategies is known as 'bet-hedging'. Bet-hedging is the hypothesis that the mother maximizes her fitness by producing a range of seeds in which, regardless of conditions, a portion is likely to be successful and a portion is not, thereby hedging bets with a distribution of seeds (see Penfield (2017) for further discussion). In addition to the timing of germination, Hamilton and May (1977) showed theoretically that the optimal and evolutionarily stable strategy for a parent organism is to disperse a certain fraction of offspring where survival is riskier and keeps a fraction around the parent where the parent's own survival and reproduction indicate a lower risk. Germination ends spatiotemporal progeny dispersal in seed-bearing plants. Therefore, variable dispersal requires that the mother impart variation in dormancy across its progeny even if this is unfavourable for specific individual seeds (discussed further by Penfield (2017)). For these reasons, the promotion of bet-hedging behaviour should always be under genetic control of the mother plant. The production of seeds with variable dormancy leads to optimum maternal fitness in variable environments globally and across seed plant taxa (Zhang et al., 2022).

It remains unclear; however, how much variation within progeny dormancy is noise or 'leakiness' in the encoded dormancy programme and how much is under selection. Abley et al. (2021) found natural variation for variability in the depth of dormancy and proposed a molecular mechanism that could account for this involving variation at the *DELAY OF GERMINATION 6* (*DOG6*) locus. Whether this is relevant for bet-hedging under real environmental conditions is unknown, not least because *DOG6* acts through modulation of ABA sensitivity in the zygote rather than from the maternal genome (Bentsink et al., 2010). Boyd et al. (2007) report that germination differs between branch positions on the *Arabidopsis* inflorescence and that this positional effect on germination depends on genotype and environmental conditions, suggesting that this could be a mechanism to introduce variation between seeds from a single parent. This positional effect has been observed in a range of species, which Fenner (1991) described as being due to a 'maternal microenvironment' informed by the maternal environment.

The environment experienced by the mother is non-random and can be determined, in a large part, by the timing of germination and the control of flowering time. Each stage of reproductive development sometimes has a narrow temperature optimum (for example, see Bykova et al., 2012). Considering seed set, we previously showed that theoretically Col-0 *Arabidopsis* plants set seed around a mean of 15–16°C (Springthorpe and Penfield, 2015). The interaction between the warming maternal environment and the effects on progeny seed dormancy creates bet-hedging behaviour in the absence of other mechanisms because seeds produced later in development are progressively less dormant. Similar observations have been made in wild populations. A great example is *Lactuca serriola* growing in the Negev desert (Gutterman, 1992 and references therein). *L. serriola* flowers in response to long days, but seed set can be observed from spring to early autumn. Harvested seeds have low dormancy in midsummer but higher dormancy in spring and autumn. These observations tally with laboratory experiments, which show that seed set in long days has lower dormancy. Simply by exploiting a prolonged seed set period, *L. serriola* can generate seeds of different dormancy depths, which enable a bet-hedging strategy adapted to unpredictable desert rainfall (Gutterman, 1992).

Stochastic yet seasonally predictable environmental conditions may allow bet-hedging, but seasonal changes in dormancy can also facilitate germination synchrony in primary dormant seeds. For instance, seed set in shorter days and cooler spring conditions can use higher dormancy to persist until autumn, while seeds set in warmer long day summer conditions require less dormancy to do so. In *Polygonum aviculare*, primary dormancy is mediated by maternal photoperiod and the resulting change in progeny dormancy varies the time needed between seed set and germination, facilitating synchronous germination in responses to dormancy-breaking signals in autumn (Fernández-Farnocchia et al., 2019). This was also shown to have a strong effect on fitness.

In many species, a linked syndrome of fruit morphology, dispersal characters and seed dormancy is controlled in concert by the maternal genome as a clear bet-hedging strategy. For example, in grasses of the genus *Aegilops*, it has been shown in multiple species that two caryopses remain together during dispersal, but the seeds within each differ in dormancy such that they germinate in different years: a clear bet-hedging strategy with a 'second chance' for progeny establishment (Gutterman, 1980). Perhaps the clearest example is in the Brassiceae tribe, where around 40% of species have heteroarthrocarpy, in which the fruits are bisected into two segments that each produce seeds. This has evolved multiple times independently in the Brassiceae (Hall et al., 2011) and in a range of plant taxa. This leads to variation in dispersal, facilitated by variable seed dormancy within these heterocarpic fruits (Imbert, 2002). In *Mesembryanthemum nodiflorum* (Aizoaceae), seeds form three distinct groups within the dispersed capsule that have higher to lower germination from the terminal to basal sections (Gutterman, 1994). In *Cakile*, which also has fruit and seed heteromorphy as a dispersal adaptation, one large non-dormant seed is produced in a dehiscent distal locule, whereas an indehiscent locule has a small dormant seed that can be dispersed by wind (Barbour, 1970; Donohue, 1998). A similar trait is present in *Diptychocarpus strictus* (Brassicaceae) but via morphologically distinct siliques. Upper dehiscent siliques shed winged seeds that exhibit lower dormancy, while seeds retained in lower, indehiscent siliques remain dormant for over a year (Lu et al., 2010). There is also evidence that the evolution of fruit traits affecting dispersal occurs together with changes in seed physiology (Willis et al., 2014), such that they are likely controlled by a common mechanism. A particularly clear example showing the linked traits of fruit dispersal and dormancy, both controlled by the maternal environment, comes from work on *Aethionema arabicum*. Arshad et al. (2019) showed that the two propagule types of *Aethionema* have very different dispersal properties, with dehiscent fruits producing seeds with limited dispersal as well as indehiscent fruits with a morphology allowing greater aerial dispersal. Within indehiscent fruits, seeds had maternal pericarp-imposed dormancy due to the indehiscence, as well as higher physiological dormancy imposed during seed maturation. Importantly, the ratio of these propagule types is under strong maternal environmental control with a greater proportion of dispersed indehiscent fruits produced when the mother plant is grown in colder conditions (Lenser et al., 2016). This suggests that the maternal genotype × environment interaction is controlling the ratio of dispersed and non-dispersed propagules depending on environmental conditions to optimize the success of the whole cohort of offspring overall. Maternal environmental effects on pericarp-imposed dormancy can also occur without

major morphological variation. For example, in sunflower, the embryo, endosperm, seed coat and pericarp can impose dormancy, and under different conditions, maternal and zygotic tissues impose dormancy including at times exclusively the pericarp (Lachabrouilli et al., 2021). Interestingly, the pericarp-imposed dormancy increases with maturation temperature, while embryo dormancy may be greater at lower temperatures, particularly earlier in development (Bodrone et al., 2017). Even in *Arabidopsis* that does not exhibit notable fruit phenotypic plasticity or dispersal of fruit tissues with seeds, it has been shown that dehiscence can be prevented by the same low-temperature treatments that induce higher primary seed dormancy (Li et al., 2018). Thus, in *Arabidopsis*, bet-hedging involves the coordinated effect of maternal temperature experience on fruit development and seed dormancy.

Such a transgenerational genotype * environment interaction as described, in which the environment of both generations interacts with the genotype of both generations, implies the existence of a particularly complex system to integrate multiple environmental variables from both generations with transgenerational signalling mechanisms. The mixture of generations and genotypes present during reproduction creates complications and opportunities for experimental seed physiologists. A mature seed is made up of the endosperm, embryo and seed coat and sometimes pericarp or perisperm, with different genomes derived from the mother and the male and female gametophytes (Rensing and Weijers, 2021). Seed development and, therefore, the development of two 'individuals' with different genomes (embryo and endosperm) also takes place entirely enclosed within maternally derived tissues of the seed coat and fruit. Fundamentally, three methods could be hypothesized by which a seed acquires its dormancy state: (1) part of the zygote, either embryo or endosperm, could sense the environmental conditions and modify its own response, (2) the maternal or paternal parent could sense the environmental conditions and transmit this information to the progeny epigenetically or (3) the mother plant could sense the environmental conditions and transmit this information to the progeny via intergenerational signalling during fruit and seed development or via plasticity in the development of the maternal tissues surrounding the seed. These hypotheses are not mutually exclusive and are shown diagrammatically in Fig. 1.

The role of maternal reproductive tissues in progeny seed dormancy

The seed coat and pericarp are well known for their essential roles in the imposition of progeny dormancy. Many species exhibit physical dormancy in which permeability of the seed coat to water controls whether the seed will germinate. Physical dormancy occurs in at least 14 families of angiosperms, and seed coat properties often vary with environmental conditions (Baskin and Baskin, 2014). Although *Arabidopsis* dormancy is imposed by the endosperm, mutants that affect seed coat properties, such as the *TRANSPARENT TESTA* mutants, are altered in dormancy (Debeaujon and Koornneef, 2000). It seems therefore that an intact and functional seed coat is necessary for endosperm-mediated dormancy to be maintained in *Arabidopsis* (Debeaujon et al., 2000). This interaction has been recently explained by the observation that the seed coat is required for the synthesis of a cuticular layer deposited on the outer tangential walls of the developing endosperm (Loubéry et al., 2018).
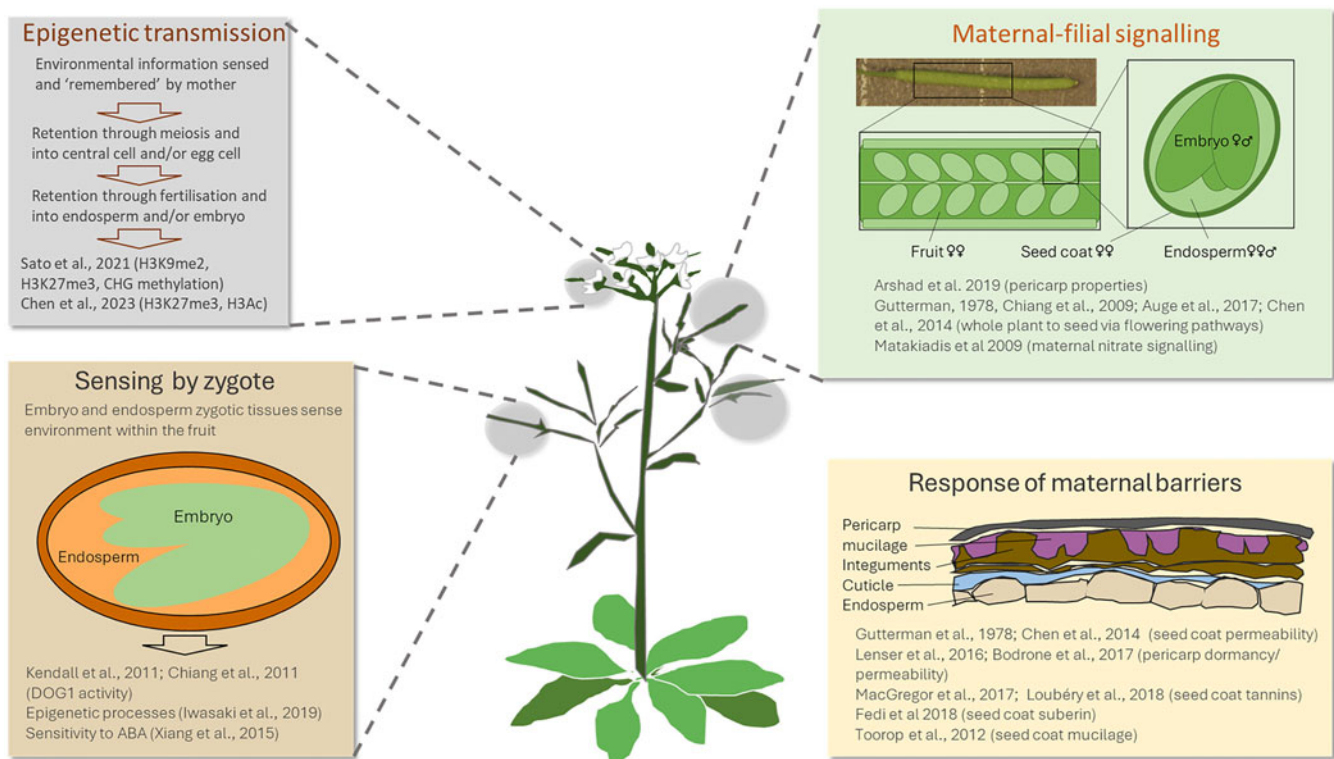

Figure 1. Illustration of the routes by which progeny seed dormancy can be influenced by the maternal environment. This includes epigenetic transmission through the germline from maternal to zygotic tissues, maternal–filial signalling to zygotic tissues, sensing of the maternal environment after fertilization by the progeny itself, and modification of maternal barriers such as seed coat and pericarp that disperse with mature seeds. Examples illustrating maternal effects mediated by these mechanisms in a range of species are indicated and further discussed in the text.

Similar principles occur in species with indehiscent fruits in which the seeds disperse from the rest of the mother plant contained within fruits. Seed dormancy variation in tomato (*Solanum lycopersicum*) has been shown to involve the progeny genotype as well as activity by the maternal seed coat and fruit tissue. It seems that ABA content of the zygotic tissues plays a relatively small role in the determination of dormancy in species like tomato, while aspects of fruit (maternal) tissue like osmotic potential are more important (Hilhorst, 1995). The indehiscent dispersal fruits of *Aethionema* described above also exhibit this phenomenon of ABA synthesis by maternal tissues that disperse with the fruit and assist in imposing dormancy in response to environmental temperature (Arshad et al., 2019). Environmentally plastic modifications to the physiology and development of maternal reproductive tissues that surround the seed and disperse with the zygote are a mechanistically relatively simple way by which the mother can influence progeny. In *Arabidopsis,* seed coat tannin and suberin content increase with lower maternal temperatures, suggesting that variation in seed coat polymers can be important for variation in dormancy (MacGregor et al., 2015; Fedi et al., 2017). In *Capsella bursa-pastoris*, not only does seed coat colour change with temperature but also the presence of mucilage (Toorop et al., 2012). This requires phenotypic plasticity by the mother but, on its own, does not require any intergenerational transmission of information nor any coordination between maternal and zygotic behaviour, as the maternal tissues disperse with the progeny, and these act on the mature zygote after dispersal.

Maternal effects of nitrate on progeny seed dormancy

Exogenous nitrate is well known to promote the germination of dormant seeds and plants well-supplied with nitrogen produce seeds that are less dormant via maternal effects. This has been shown in a range of plant taxa and conditions (Thomas and Raper, 1975; Alboresi et al., 2005; Geshnizjani et al., 2019 (and works cited within); Duermeyer et al., 2018) and occurs during seed development, as well as in mature seeds. However, in *Amaranthus retroflexus*, while intermediate levels of maternal nitrogen fertilization increased germinability/reduced dormancy, higher levels of nitrogen fertilization started to increase progeny dormancy (Karimmojeni et al., 2014). It has been suggested in sugar beet that additional nitrogen fertilization may lead to the production of germination and growth inhibitors in seed balls (Inoue and Yamamoto, 1977; Chiji et al., 1980). Commercial sugar beet seed balls are polished and washed to remove this outer pericarp, which has been shown to remove germination inhibitors, including ABA, and the wash water from this process itself has a strong inhibitory effect on germination (Ignatz et al., 2019). The pericarp, which gets removed in seed processing, also acts as the major nitrate store for the seed (Mäck and Tischner, 1990). Taken together, it seems that in sugar beet propagules, the maternal fruit tissues that disperse with the seed can act to both inhibit and promote germination after dispersal, because before dispersal their loading with these pro- or anti-germination molecules seems to depend on the maternal environment even before flowering. There are also rare cases where maternal nitrogen availability does not have an effect on seed dormancy. For example, Gualano and Benech-Arnold (2009) did not observe any effect of nitrogen on seed dormancy in barley, but instead observed strong effects of temperature and drought, suggesting that other environmental traits can have a stronger effect in different circumstances.

A maternal effect of nitrogen on seed dormancy has also been shown in *Arabidopsis* (Alboresi et al., 2005; Matakiadis et al., 2009). There is also evidence that nitrate itself acts in a maternal–filial signalling function. Nitrate reductase mutants (which accumulate free nitrate) produce less dormant seeds via a maternal effect, whereas plants deficient in nitrate uptake produce more dormant seeds (Alboresi et al., 2005). This is despite the nitrate reductase mutants exhibiting symptoms of nitrogen deficiency due to their inability to incorporate the nitrate into metabolism, suggesting that this maternal effect of nitrogen is not just nutritional (Alboresi et al., 2005). It may, therefore, be that nitrate loading by maternal tissues into seeds is important for any putative signalling function. Indeed, there is some evidence for the maternal environmental regulation of nitrate loading into seeds (Huang et al., 2018). However, there is no direct correlation between seed nitrate content and dormancy, suggesting that the key effects of nitrate are in the mother plant.

There is also good evidence that nitrate and ABA signalling for dormancy/germination interacts. Matakiadis et al. (2009) showed that exogenous nitrate given to imbibed seeds and maternally supplied nitrate both strongly promoted the germination of *Arabidopsis* seeds. Maternal nitrate acts to lower the level of ABA in mature seeds through upregulation of the ABA-degrading enzyme *CYP707A2*. In imbibed seeds, this occurs via the activity of *NIN-LIKE PROTEIN 8* (*NLP8*), which is a nitrate-responsive transcription factor that directly binds the promoter of *CYP707A2* (Yan et al., 2016). Interestingly, the upregulation of *CYP707A2* by maternal nitrate seems to occur during seed development, either within silique tissue or in developing seeds (Matakiadis et al., 2009). Additionally, although *cyp707a2* mutants do not show lower seed ABA in response to maternal nitrate, the dormancy phenotype still responds. This contrasts with the effect of exogenous nitrate supplied to imbibed seeds, which acts via CYP707A2 to lower ABA (Matakiadis et al., 2009). This suggests that the maternal control of dormancy by nitrate is more complex than the direct action of nitrate loaded from the mother plant during imbibition.

Does DOG1 mediate a maternal effect?

Previously we and others have suggested that the *DELAY OF GERMINATION1* (*DOG1*) gene is important for responses to the maternal temperature variation (Chiang et al., 2011; Kendall et al., 2011). *DOG1* is a locus originally identified as a major QTL controlling seed dormancy (Alonso-Blanco et al., 2003). *DOG1* has been cloned (Bentsink et al., 2006), although its molecular function and mechanism of action in seed dormancy remain unclear (for a review, see Carrillo-Barral et al. (2020)). *DOG1* transcript levels in mature seeds are increased at low temperatures; furthermore, *dog1* mutants have reduced sensitivity to low-temperature treatments applied during seed maturation (Kendall et al., 2011). Simplistically, this implicates changes in *DOG1* levels to temperature. More recent thorough analysis showed that *DOG1* transcription likely ceases before desiccation, and that in common with many seed maturation-associated genes, differences in *DOG1* levels in mature seeds arise from the effect of temperature on RNA decay rates (Chen et al., 2021). Importantly, strong *DOG1* alleles behave in a dominant fashion, affecting dormancy from the genotype of the zygote (Bentsink et al., 2006). So *DOG1* is not an obvious candidate for a gene mediating a maternal effect. However, natural variation at *DOG1* appears to be important for latitudinal adaptation, with

Arabidopsis accessions at cooler latitudes being more likely to have weaker *DOG1* alleles (Kerdaffrec et al., 2016). A possible explanation for this is that *DOG1* evolves to counter the effect of the maternal environment on dormancy rather than to mediate it, for instance, by reducing seed sensitivity to low-temperature signals. Thus, at higher colder latitudes, developing seeds are less sensitive to the induction of dormancy by low-temperature signals if they have weaker *DOG1* alleles.

Maternal effects due to seasonal variation in temperature and photoperiod

There is considerable evidence that maternal photoperiod affects seed dormancy across many species. One of relatively few experiments to directly test whether the maternal environment is sensed by seeds or by the mother plant. Gutterman (1978) exposed *Trigonella arabica* plants to different photoperiods during seed maturation. This led to changes in seed coat morphology, including permeability to water, which imparts different degrees of physical dormancy on the offspring. Most importantly, this occurred regardless of whether the fruits containing the developing seeds were covered in foil completely blocking light (Gutterman, 1978). This can only be explained by a maternal signal that must originate from outside the fruits themselves that acts on the seeds at some distance. Blocking light from the developing seeds excluded any seed environmental sensing, and applying the treatment long after fertilization excluded the possibility of epigenetic inheritance of the signal from the maternal tissue that formed the germline.

Changes to *FLOWERING LOCUS C* (*FLC*) expression, mediated by epigenetic modification, act as a memory system for winter cold through vernalization. *FLC* itself also has a maternal role in determining seed dormancy in *Arabidopsis* (Chiang et al., 2009). Loss of function *FLC* alleles, in general, confer low dormancy and a reduced effect of maternal low temperatures on progeny seed dormancy (Chen et al., 2014; Chen and Penfield, 2018). In agreement with this, vernalization of the mother plant reduces progeny seed dormancy (Auge et al., 2017). This contrasts with the observation that among different accessions, higher expressing *FLC* lines are associated with lower dormancy, creating some confusion in the literature (Chiang et al., 2009). Strong *FLC* alleles are mainly found at higher colder latitudes, where seed dormancy is lower due to the presence of weak *DOG1* alleles (Kerdaffrec et al., 2016), so one possibility is that this correlation is spurious. It remains to be clarified in which tissue FLC acts to affect dormancy. The maternal epigenetic state is initially inherited into the female gamete and early developing seed (Luo et al., 2020). It is therefore possible that epigenetic inheritance is important in mediating maternal effects, particularly those that involve sensing from before anthesis that therefore must be 'remembered' in order to impact seeds. However, nobody has yet ruled out that FLC acts in maternal sporophytic tissues where it impacts seed coat permeability and tannin content (Chen and Penfield, 2018).

In the context of control of flowering time, *FLOWERING LOCUS T* (*FT*) is a major mobile signal and its expression is partly controlled by photoperiod and partly by floral repressors such as *FLC* (see Turnbull (2011) for a review). In common with other photoperiod pathway mutants, *FT* mutants have increased dormancy, while ectopic *FT* expression promotes high germination. We showed that these effects are maternal in origin (Chen et al., 2014). Interestingly, fruit tissues are the site of maximum

FT expression in *Arabidopsis*, and FT is important to mediate temperature-dependent accumulation of tannins in the seed coat via the regulation of *FLC* (Chen and Penfield, 2018).

ABA as a signal of dormancy from mother to progeny

The role of ABA in promoting seed dormancy has been studied extensively, indeed having been described as the dormancy-inducing hormone *dormin* prior to molecular characterization. ABA-deficient genotypes of *Arabidopsis* universally lack dormancy (Koornneef et al., 2000). Both the mother plant and the zygote of Arabidopsis are known to synthesize ABA, and synthesis by the zygote is clearly important for seed dormancy (Karssen et al., 1983), as is the observation that ABA biosynthesis inhibitors applied to seeds can have a dormancy-breaking effect. A similar dominant effect of zygotic ABA was observed in tomato seeds (Groot and Karssen, 1992). The maternally derived ABA in seeds reaches a peak level during the onset of seed maturation, while a second later peak of ABA levels in seeds is controlled by the zygotic genotype. These observations can be repeated in *Brassica oleracea* where we showed that the early peak in ABA levels was restricted to the seed coat and the endosperm, whereas the later zygotic peak could be observed in the endosperm/seed coat and embryo fractions (Chen et al., 2021). Reciprocal backcrosses of ABA-insensitive mutants to WT show that the genotype of the mother but not the father has an influence in the susceptibility of progeny seeds to applied ABA (Finkelstein, 1994). There is some further evidence for a maternal effect of ABA in tomato (*S. lycopersicum*). There is also some evidence of long-distance transport of ABA; for example, water stress increases ABA levels in the phloem exudate, and this can lead to an increase in the ABA levels of seeds (Hoad, 1978) though it is not clear whether this can have an effect on dormancy in any species or conditions. Despite this, ABA applied exogenously to maternal tissues has not been shown to increase dormancy, despite its ability to complement other ABA-deficient phenotypes such as drought susceptibility (Koornneef et al., 1989), and in *Nicotiana plumbaginifolia*, it was shown that ABA is graft transmissible from roots and did enter seeds but that this root-derived ABA could not restore dormancy (Frey et al., 2004). Therefore, it has long been assumed that ABA from distal maternal tissues does not influence seed dormancy and it has been recorded in *Sorghum* that maternal ABA (when increased under drought conditions) can reduce dormancy through decreased ABA sensitivity in the progeny (Benech-Arnold et al., 1991). Although, as discussed above, in a number of species with pericarp-imposed dormancy, ABA in the maternal tissues that disperse with the seed does seem to act to impose dormancy in the shed seed such as in *Aethionema* (Arshad et al., 2019) or sugar beet (Ignatz et al., 2019)

Epigenetic mechanisms

In addition to signalling from maternal to zygotic tissues or control by maternal tissues that disperse with the seed, there is the potential for information about the maternal environment to be transmitted through the germline. Information about environmental conditions experienced by the mother plant before the start of reproduction could be encoded epigenetically, such that zygotic gene expression may be influenced by the maternal environment independently of any maternal–filial signalling.

Epigenetic effects in the sense of DNA and chromatin modification are well known to affect seed dormancy in the form of parent of origin effects. The dormancy of resultant seed from crosses between genotypes of *Arabidopsis* with different levels of dormancy depends on which accession is the male or female (Piskurewicz et al., 2016). This difference co-occurs with the presence of genomic imprinting of genes, some of which were shown to regulate seed dormancy or germination-related processes such as storage protein mobilization (Piskurewicz et al., 2016). Importantly, this work established that genomic imprinting at some loci remains stable beyond seed shedding, and that after-ripening and other processes can abolish imprinting during the epigenetic re-programming that occurs during germination.

More recent work has also shown that this mechanism can transmit environmental information to influence dormancy. Imprinting of the germination-promoting gene *ALLANTOINASE* (*ALN*) occurred in the endosperm by non-canonical RNA-directed DNA methylation (RdDM) and is promoted by low temperatures during seed maturation (Iwasaki et al., 2019). Components involved in the RdDM pathway were shown to be upregulated during seed development by maternal cold, a mechanism that could allow the co-regulation of many imprinted genes that affect seed dormancy or germination (Iwasaki et al., 2019). Several mutants compromised in RdDM show seed dormancy phenotypes when seed are set in the cold, although the importance of *ALN* imprinting in these dormancy phenotypes remains to be clarified. This provides evidence of an environmental component for parental control of dormancy by imprinting and suggests that the effect of the maternal environment on dormancy of the progeny could be mediated by this or a similar mechanism. These processes are reviewed in more detail elsewhere (Iwasaki et al., 2022). *VERNALIZATION5/VIN3-LIKE 3* (*VEL3*) acts in the central cell of the female gametophyte and is also required for the induction of seed dormancy by low temperatures. VEL3 associates with histone-modifying complexes and is needed for correct deposition of histone marks to establish a dormancy-promoting transcriptional programme during endosperm development (Chen et al., 2023). It is particularly notable that this happens in the central cell, which is part of the female gametophytic tissue. It remains unclear whether these epigenetic processes modify sensitivity to a separately derived environmental signal controlling dormancy, or whether epigenetic modifications transfer environmental information from mother to progeny.

Conclusions and research perspectives

While there is clear evidence that the maternal environment, potentially long before reproduction, has important effects on seed dormancy, the mechanisms behind how this is mediated remain far from clear. We have discussed how there is a strong evolutionary advantage to the mother to be able to control the level of dormancy of its progeny, affecting dispersal in space and time and maximizing the chance of survival and reproduction of its progeny. There is also a clear advantage to the seeds themselves of retaining information about the maternal environment from which they developed as it carries crucial information about seasonal timing that is needed to inform life history and when to germinate. Recent work on epigenetic mechanisms for transgenerational inheritance of environmental information controlling dormancy has revealed the diversity of maternal processes affecting seed dormancy, but maternal–filial signalling can better explain some of the results observed from physiological experiments. Whether maternal tissues transmit environmental information from mother to progeny remains to be understood. The evidence discussed suggests that a combination of (1) transgenerational epigenetics, (2) maternal–filial signalling and (3) plastic development of maternal embryo-surrounding tissues can be involved in fine-tuning progeny responses to the maternal environment.

While an understanding of the mechanistic basis of how these systems work to determine the germinability of a particular seed is particularly important in the context of adapting ecosystems and agriculture to a changing environment, different approaches to seed science are needed to properly address these questions. In particular, while the majority of tests of seed dormancy focus on mature dried seed, considering dormancy at stages prior to shedding has the potential to simplify the experimental system (Benech-Arnold et al., 1991; Alboresi et al., 2005). Many developmental and physiological processes occur between early seed development and maturity, and these make *bona fide* maternal effects more difficult to separate from environmental effects on zygotic tissue.

When testing specific mutants for their effects on dormancy, it is especially important and informative to perform crosses to identify maternal sporophytic effects. While this has long been used to explore maternal effects on dormancy (e.g. Koornneef et al., 1989), it is worth doing routinely, particularly with the prevalence of reverse genetics in model species like *Arabidopsis*. We have also used a genetics approach to show that *VEL3* has a dormancy effect acting via the female gametophyte (Chen et al., 2023) and therefore is maternal but not sporophytic. This emphasizes the need to consider the alternation of generations in reproduction, particularly when trying to find when exactly maternal effects are inherited. Finally, it is vitally important that different tissue types within seeds and reproductive tissues are considered separately, and that 'seed' is not regarded as a single tissue because this contains both maternal and zygotic tissues within. Low-input sequencing methods, cell sorting and single-cell omics technologies are likely to be key for new insights in the future.

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