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Pre- and post-harvest temperatures influence the germination response to supra-optimal temperature in contrasting tomato (*Solanum lycopersicum*) MAGIC genotypes

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Abstract

Seeds rely on temperature to adjust their germination timing by modulating primary and secondary dormancy. The knowledge regarding an intraspecific variation in the germination responses to supra-optimal temperatures during imbibition within the *Solanum lycopersicon* species and its relation with pre- and post-harvest environments is limited. Here, we studied the impact of imbibition at 35°C in 17 genotypes selected from a multiparent advanced generation intercross (MAGIC) population. We discovered a high genetic variability in the germination responses to heat, leading to thermotolerance, thermoinhibition or thermodormancy with different depths. While thermodormancy appeared more profound than primary dormancy, there was no correlation between the deepness of primary and thermodormancy. Post-harvest treatments influenced considerably germination at supra-optimal temperatures. Dry storage beyond the apparent loss of primary dormancy led to an increased proportion of thermotolerant or thermoinhibited seeds at the expense of thermodormancy in a genotype-dependent manner, thereby revealing cryptic genetic variation. Prolonged cold imbibition also led to increased thermodormancy in genotypes that produced thermotolerant and thermoinhibited seeds. The thermal history before and after flowering influenced primary dormancy and the germination response to heat during imbibition in a genotype-dependent manner, with high temperatures leading to increased thermotolerance or thermoinhibition at the expense of thermodormancy, suggesting transgenerational plasticity despite the domestication of the species. The high potential of the MAGIC population for quantitative trait loci mapping and causal polymorphism identification will be helpful in deciphering the regulatory mechanisms that lead to the plasticity of thermoinhibition or thermodormancy, as well as their connection to the parental environment.

Introduction

Global warming has not only raised average temperatures but also increased the risks of extreme weather conditions and impacted the pattern of daily–nightly temperatures according to regional specificities. Additionally, it has affected seasonal patterns, causing spring to start earlier and winter to begin later. In Europe, the average surface temperature increase has become alarming since 2014, resulting in longer and warmer summer periods (Wang et al., 2021). Temperature is widely recognized as an important environmental cue for plants and seeds. It governs both transitions between vegetative and reproductive stages, namely flowering and germination, which are both key components of plant fitness. Seeds rely on the temperature, perceived during both their development and imbibition, to adjust their germination timing by modulating primary and secondary dormancy (reviewed in Batlla and Benech-Arnold, 2015; Huo and Bradford, 2015; Soltani et al., 2019; Buijs, 2020; Iwasaki et al., 2022; Reed et al., 2022). Dormancy is defined as an innate dynamic state of the seed that results in the blockage of germination despite permissive conditions to do so (Bewley et al., 2013; Batlla and Benech-Arnold, 2015). Primary dormancy is acquired during seed development and progressively released through after-ripening that depends on the seed water content and temperature during storage (Basbous-Serhal et al., 2016) and/or environmental cues (e.g. cold stratification and light) during imbibition (Chahtane et al., 2016). Secondary dormancy is induced by stressful conditions such as anoxia, temperature or water stress in non-dormant seeds, or it can be re-induced in seeds that were once primarily dormant. This induction is also a dynamic process depending not only on the stress intensity and duration but also on primary dormancy (Symons et al., 1987; Auge et al., 2015; Batlla and Benech-Arnold, 2015; Huang et al., 2015; Edwards et al., 2016; Coughlan et al., 2017; Soltani et al., 2019). In wild species, primary and secondary dormancy form a continuum that serves as a bet-hedging strategy against

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unpredictable environmental fluctuations to ensure plant survival and successful reproduction (Huang et al., 2015; Fernández-Pascual et al., 2019; Gianella et al., 2021; Postma and Ågren, 2022). While in crops, domestication has led to a strong decrease in primary dormancy, there are examples of secondary dormancy in a wide range of agronomical species including sunflower (Corbineau et al., 1988), barley (Leymarie et al., 2009), *Brassica oleraceae* (Awan et al., 2018) and tomato (Geshnizjani et al., 2018).

Temperature influences germination in multiple ways. Seeds germinate in a range of temperatures between a base temperature (T_b) and a ceiling temperature (T_c), which depend both on the species (for a meta-analysis, see Maleki et al. (2024)) and on the depth of primary dormancy and genotype within a species (Batlla and Benech-Arnold, 2015; Huo and Bradford, 2015). Between these cardinal temperatures, the optimal temperature T_o is the temperature at which germination speed is the highest. At increasing supra-optimal temperatures, germination of non-dormant seeds will be first delayed, then impeded by the establishment of one of two seed physiological responses: thermoinhibition or thermodormancy (Huo and Bradford, 2015). According to these authors, thermoinhibition is a process when the germination of seeds that have been imbibed at supra-optimal temperature is prevented, but the seeds will germinate when the imbibition temperature is decreased. Thermoinhibition is, therefore, temporary and can be alleviated by lowering the temperature. In contrast, thermodormancy is a type of secondary dormancy that is induced by imbibition at warm temperatures. Thermodormant seeds are inhibited in their germination, even when the temperature of imbibition is reduced, indicating that a more persistent type of inhibition has been induced (Huo and Bradford, 2015). A dormancy release treatment such as stratification and/or the addition of nitrate during imbibition is necessary to induce germination in these thermodormant seeds. The dual response to supra-optimal temperatures leading to either thermodormancy or thermoinhibition depends on the genotype (Argyris et al., 2008; Geshnizjani et al., 2018). In tomatoes, the genetic architecture and quantitative trait loci (QTL) of thermoinhibition and thermodormancy have been described using a recombinant inbred line (RIL) population from a cross between *Solanum lycopersicum* cv. Moneymaker and *Solanum pimpinellifolium*, a wild species. Secondary dormancy was only induced in the cultivar Moneymaker but not in *S. pimpinellifolium* (Geshnizjani et al., 2018). This work, together with the QTL analysis in lettuce (Argyris et al., 2008), also identified genotypes producing seeds that were thermotolerant, i.e. capable of germinating above supra-optimal temperatures.

There is a wealth of evidence, mostly coming from studies on Arabidopsis, showing that temperature during seed development affects the depth of primary dormancy (Springthorpe and Penfield, 2015; Burghardt et al., 2016; Coughlan et al., 2017; Huang et al., 2017; Awan et al., 2018; Iwasaki et al., 2022) and dormancy cycling in the soil following shedding (Finch-Savage and Footitt, 2017). Typically, cold temperature during seed maturation leads to enhanced (or deeper) primary dormancy and an increased susceptibility to induce secondary dormancy. This is influenced by genotype-by-environment interactions (Coughlan et al., 2017; Soltani et al., 2019), involving flowering genes such as FLOWERING LOCUS C (Springthorpe and Penfield, 2015; Burghardt et al., 2016). In wild species, such thermal regulation both before and after shedding determines whether seeds germinate and the timing of seedling emergence in seasonal climates in conjunction with flowering time (Springthorpe and Penfield,

2015). In crops, such thermal regulation prior to shedding should also determine whether, within the same genotype, seeds will be thermotolerant, thermoinhibited or thermodormant, but this is not well documented. In various lettuce genotypes, thermosensitive seeds become thermotolerant when produced at supra-optimal temperatures (Kozarewa et al., 2006). In tomatoes, seeds from the RIL population between Moneymaker and *S. pimpinellifolium* produced with different nitrate and phosphate concentrations throughout the culture show genetic variation in their germination response to heat that interacts with the maternally supplied nutrient conditions (Geshnizjani et al., 2019). However, whether the germination response to heat exhibits intraspecific variation with cultivated genotypes and how it is impacted by thermal history remains poorly explored.

Consistently producing highly vigorous seeds, regardless of environmental conditions, is essential for increasing crop yield (Finch-Savage and Bassel, 2016). This is particularly important for high-value seeds like tomato, one of the most important horticultural crops worldwide, grown in various climate regions and often exposed to high-temperature stress in greenhouses and fields (Bineau et al., 2021). Understanding the effects of high temperatures on seed germination behaviour and the impact of warm temperatures during seed production is needed for breeding programmes aimed at producing more resilient seeds towards climate change (Reed et al., 2022). In tomatoes, quantitative trait dissection has been especially challenging due to its low genetic diversity and strong population structure (Pascual et al., 2015). This is underscored when primary and secondary dormancy are concerned because they represent a dynamic state of the seed that is subject to within-species adaptation to local environments.

The objective of this work was to characterize the genetic variation in the germination response to heat during imbibition among *S. lycopersicon* genotypes and whether this response exhibits plasticity in relation to the thermal seed history before and after harvest. To this purpose, selected genotypes of the tomato multiparent advanced generation intercross (MAGIC) population were cultivated under three temperature settings in the greenhouse that are relevant for seed production and tested for their level of thermotolerance, thermoinhibition and thermodormancy. The MAGIC population was developed using eight founder parents from two evolutionarily distinct groups during domestication: *Solanum lycopersicum* var. *lycopersicum* group giving large fruits and the cherry tomato group *S. lycopersicum* var. *cerasiforme* (Blanca et al., 2015; Pascual et al., 2015). Since temperature also influences primary dormancy, we furthermore investigated how the depth of primary dormancy influences these germination responses to heat during imbibition. Considering that radicle emergence is mechanically controlled by the embryo growth potential and endosperm cap resistance (Toorop et al., 2000; Steinbrecher and Leubner-Metzger, 2017; Nonogaki, 2019), we also evaluated the contribution of the embryo and seed coverings in inhibiting germination in a deeply thermodormant genotype.

Material and methods

Plant material and growth conditions

Tomato genotypes were selected from the tomato MAGIC population (Pascual et al., 2015) based on the germination data obtained from seeds that were produced under two contrasting temperature conditions, as described in Bizouerne et al. (2023).

Selected genotypes included six of the founder lines that were used to create the MAGIC population: four lines with big fruits from the *S. lycopersicum* var. *lycopersicum* group (Levovil, Stupicke, LA0147 and Ferum) and two founder lines with small fruits from *S. lycopersicum* var. *cerasiforme* (Criollo and LA1420). From the generation intercross population, the following final lines were used: H10-55, H10-107, H10-131, H10-179, H10-165, H10-205, H10-221, H10-242, MagicTom 41 (MT41) and MagicTom 209 (MT209). These genotypes were selected to represent the various impacts of heat during seed production on the germination phenology (Bizouerne, 2021). In addition, the cultivar Moneymaker was included as a genotype whose seed development and thermodormancy have been previously characterized (Geshnizjani et al., 2018; Bizouerne et al., 2021a, b).

Seeds were imbibed in the dark at 20°C as described below, and seedlings were transferred in 10 L pots containing Irish peat, perlite and coconut fibre (50/40/10, v/v/v). Four to six plants/genotypes were grown under greenhouse conditions in Angers, France, with 16 h of light (250 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and daily supplementation of a nutrient solution (NPK 15/10/30, 1.5 g/l). Genotypes were randomized within the greenhouse module. To manipulate temperature during seed development, three sowings were started sequentially in December (winter culture), March (spring culture) and May (summer culture), and mature red fruits were collected, respectively, in April–May, July and August–September according to the genotype. Day and night temperatures were recorded (Fig. 1). Flowering (date of the first open flower on the 2nd truss) and harvest dates (fruits from the 2nd truss) were recorded to calculate the thermal time of the vegetative growth and fruit development using 7 and 5.2°C as base temperatures, respectively (Boote et al., 2012).

Seeds were extracted from red fruits between the 2nd and 5th truss by incubating the locular tissues for 1 h in 100 ml of solution containing 400 mg/l of pectolytic enzymes (Lafazym CL®, Laffort, France) under gentle shake at room temperature. After extensive washing with tap water, seeds were rapidly dried under an airflow at 43% relative humidity (RH) at 20°C in the dark and subsequently hermetically stored at 4°C until all seeds were collected. We also used Moneymaker seeds that were obtained from a previous study (Bizouerne et al., 2021a) using growth conditions as described above. Fruits were harvested at

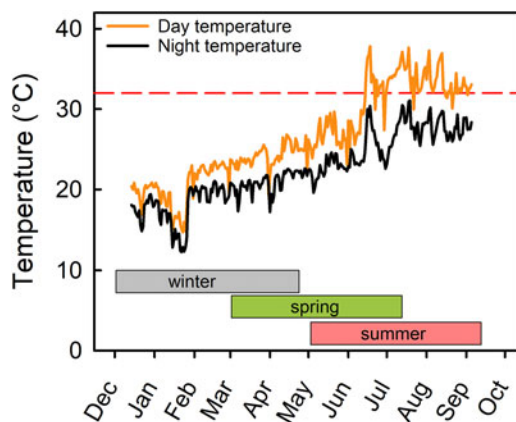


Fig. 1. Temperature profile during the three consecutive cultures used in this study. The bars indicate the average length of the cultivation period from sowing to harvest. The dashed line at 32°C represents the threshold temperature above which the developing tomato fruits are considered to be under heat stress.

the Breaker stage and thereafter incubated for 14 days in dim light (25 $\mu\text{mol m}^{-2} \text{s}^{-1}$) or in light (300 $\mu\text{mol m}^{-2} \text{s}^{-1}$), both provided by LED lamps with a 16 h photoperiod at 23/20 or 32/26°C.

Germination assay and primary dormancy determination

Three repetitions of 30–50 seeds were imbibed with 4 ml of water on one filter paper (Whatman No. 1) in 9 cm diameter Petri dishes in the dark at 20°C for up to 7 days. All handling of the seeds was conducted under a green safe light. Germination was scored when the radicle protruded more than 2 mm out of the seed coat. The first germination test to assess primary dormancy was performed, respectively, after 8, 4 and 1 week of dry storage at 4°C following harvest and seed drying for the winter, spring and summer cultures, respectively, so that the same imbibition conditions were used for the three cultures. The storage at 4°C was chosen to severely slow down after-ripening prior to the germination assays. Thereafter, seeds were after-ripened by dry storage at 20°C and 65% RH, during which germination was assessed periodically. These germination measurements were used to assess the depth of primary dormancy as the number of days of seed dry storage required to reach 50% germination (DSDS_{50PD}) from storage at 20°C onwards. Data were fitted with a logistic regression using a sigmoid function.

Germination response to heat and secondary dormancy determination

Germination response to heat was assessed using the protocol by Geshnizjani et al. (2018) with modifications (Fig. 2A). Seeds were first after-ripened through dry storage at 20°C for lots exhibiting primary dormancy. When seed lots exhibited a minimum of 90% of germination at 20°C, they were tested for their response to heat. For this purpose, seeds were imbibed for up to 7 days at 35°C in the dark. Thereafter, the germinated seeds were counted and these were noted as thermotolerant (Fig. 2A). Then, non-germinated seeds were returned to 20°C for 7 days, after which those that had germinated were noted as thermoinhibited by the imbibition at 35°C. Finally, Petri dishes that still contained non-germinated seeds were submitted to a stratification treatment, consisting of 5 days at 4°C in the presence of 30 $\mu\text{mol KNO}_3$ followed by a further 7 days at 20°C in the dark. Germinated seeds after this treatment were noted as thermodormant. A 5-day incubation at 35°C was routinely used to compare the responses to heat among genotypes and treatments. However, to assess the dynamics of thermodormancy induction, the percentage of thermodormant seeds was monitored incrementally at 35°C for up to 7 days and the time to induce 50% thermodormancy (TD₅₀) was calculated from the fit with a logistic regression using a sigmoid function. In one experiment, thermodormant seeds were also imbibed in darkness or continuous white neon light at 20°C (277 $\mu\text{mol m}^{-2} \text{s}^{-1}$) for 15 days and then transferred to 25°C. For germination assays, all handling of the seeds was conducted under green safe light, except for the dormancy-breaking treatment, when seeds were briefly exposed to ambient light before moving the seeds in the cold room. To assess the depth of secondary dormancy, thermodormant seeds were dried to 43% RH after the imbibition at 35°C, and germination was assessed at 20°C periodically during dry storage at 20°C in the dark. DSDS₅₀ of thermodormancy (DSDS_{50TD}) was calculated as described for primary dormancy.

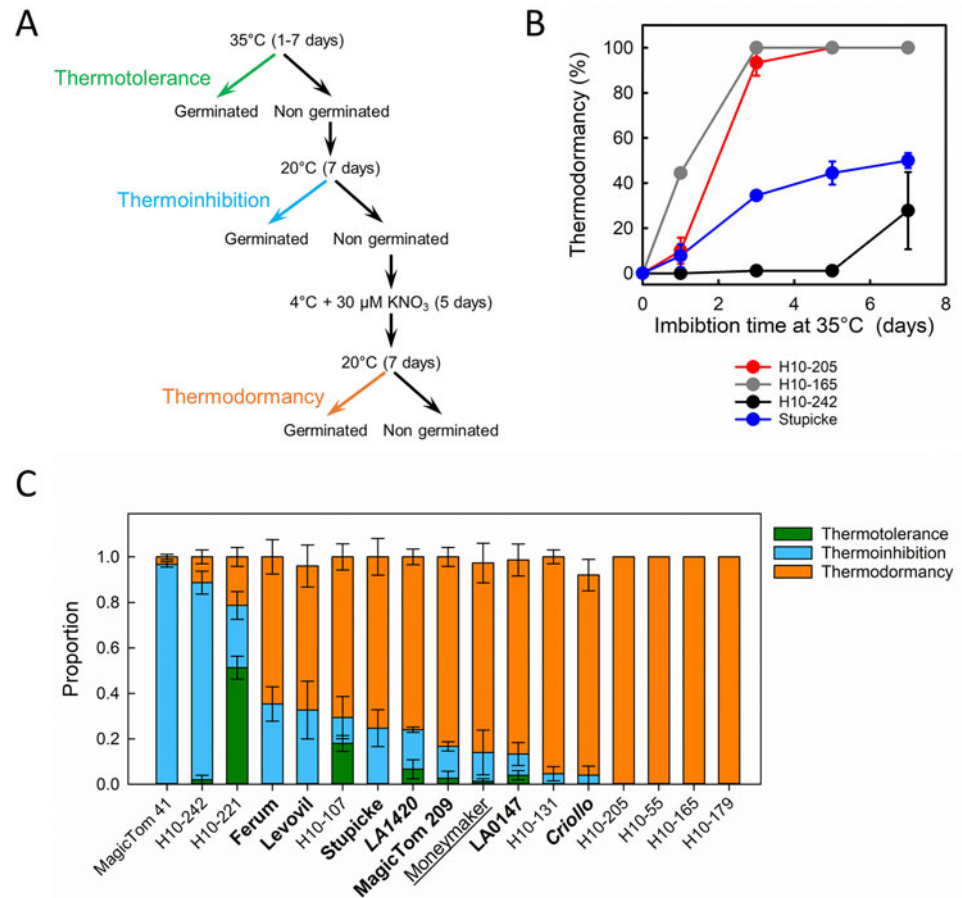


Fig. 2. The germination response is genotype-dependent. (A) An experimental design is used to assay thermotolerance, therminhibition and thermodormancy. All steps were performed in the dark. (B) The effect of imbibition time at 35°C on the induction of thermodormancy in the indicated genotypes. (C) Proportion of thermotolerant, therminhibited and thermodormant seeds of the indicated genotypes after imbibition for 7 days at 35°C. Genotypes in bold and bold italic fonts refer, respectively, to the parental lines of the *S. lycopersicum* var. *lycopersicum* group and the *S. lycopersicum* var. *cerasiforme* group of the MAGIC population. MoneyMaker is underlined as it is not part of the MAGIC population. Seeds were used from the winter culture (see Fig. 1). Data are the average triplicates of 50 seeds (\pm SD).

Contribution of the endosperm and embryo growth to secondary dormancy

After-ripened and dried thermodormant seeds of the genotype H10-205 obtained from the winter culture were first imbibed for 6 h at 20°C in the dark to allow dissection of the seed parts. The seed coat was carefully peeled off at the chalazal end without altering the underlying endosperm. Seeds with slit endosperm were prepared by making a small incision at the chalazal end using a surgical blade. To assess the growth rate of the embryo, 10–30 intact embryos were isolated with forceps after removing part of the endosperm and transferred on a wet filter paper (Whatman No. 1). Thereafter, embryo length was monitored using Image J (<https://imagej.net/ij/>) for 0, 3, 4 and 5 days during incubation at 20°C in the dark at 100% RH. The experiment was repeated with five embryos that were isolated from 16 h-imbibed seeds.

Statistical analysis

All assays were performed with triplicates of 30–50 seeds unless otherwise indicated. Significant differences ($P < 0.05$) were calculated after probit transformation of the germination percentages, using analysis of variance (ANOVA) followed by a Tukey post-hoc test for mean comparison, or through a two-tailed *t*-test (XLSTAT, Lumivero, Denver, CO, USA). To test the effects of the genotype and maternal temperatures on secondary dormancy and to test whether these effects differed among primary dormancy, the probit values of germination at harvest and after thermodormancy induction were analysed using ANCOVA. The

genotypes were treated as fixed factors, with maternal temperatures and primary dormancy as covariates, respectively. A full model that included all interactions was analysed to test for a significant three-way interaction. To test the effects of thermodormancy on embryo growth, the Kruskal Wallis test ($P < 0.05$) was used for multiple comparisons between the dormancy status and time of incubation. The growth rate was calculated from the slope of the regression between the time of incubation and embryo length.

Results

Genotypic differences in the response to supra-optimal temperature during imbibition

Using mature seeds obtained from the winter culture, a pilot experiment was performed using a restricted number of genotypes to calibrate the exposure time at 35°C necessary to induce thermodormancy. The dynamics of thermodormancy induction at this supra-optimal temperature was different for the four genotypes tested (Fig. 2B). A 3-day incubation was sufficient to fully induce thermodormancy in H10-205 and H10-165 seed lots, whereas the seed lots of Stupicke and H10-242 responded slower, reaching, respectively, 50 and 32% of thermodormancy after 7 days at 35°C. From this, a 5-day incubation period was chosen for the remainder of the experiments as the best time point to capture the genetic variation in thermodormancy. Since light is a permissive condition to allow germination in thermodormant seeds of MoneyMaker (Geshnizjani *et al.*, 2018), we tested its effect on our material (Supplementary Fig. S1). Imbibition in

continuous white light at 20°C did not result in full germination, and the response was genotype-dependent (Supplementary Fig. S1). For example, light did not affect the germination of the thermodormant H10-55 and H10-165 seeds after 14 days of imbibition but resulted in around 40% of germination in the H10-131 and H10-179 genotypes. Therefore, an incubation temperature of 20°C in the dark for 7 days was chosen to express thermodormancy.

There was a large genetic variation in the response to heat during imbibition for the winter culture (Fig. 2C). MT41, H10-242 and H10-221 seed lots did not display thermodormancy; the two former genotypes produced seeds that were thermoinhibited by heat during imbibition, whereas H10-221 displayed 51% thermotolerance. Seed lots from seven genotypes of the MAGIC population (including the founder parents Ferum, Levovil, Stupicke, LA1420 and LA0147) were susceptible to the induction of thermodormancy, but with a small proportion of seeds that remained thermoinhibited, ranging from 10% (LA0147) to 35% (Ferum and Levovil, Fig. 2C). Four genotypes were found with the highest potential for thermodormancy induction: H10-205, H10-55, H10-165 and H10-179. The cultivar Moneymaker, which is not part of the MAGIC population, also exhibited thermodormancy.

Relation between primary dormancy and thermodormancy

To investigate if a relationship exists between primary and secondary dormancy, we first assessed the depth of primary

dormancy by calculating the time during dry storage necessary to obtain 50% of germination by after-ripening ($DSDS50_{PD}$, Fig 3A–C, Supplementary Fig. S2). For this, seeds obtained from the winter culture were used. There was a large genetic diversity in the $DSDS50_{PD}$ values, spanning over 120 days among the genotypes tested (Fig. 3D). Seeds of Stupicke, Criollo, H10-221 and H10-55 exhibited a shallow dormancy as the $DSD50$ was less than 10 days of dry storage after harvest (Fig. 3D). In contrast, seeds of MT209 and H10-165 took 115 days to reach 50% germination, indicating a deeper dormancy. A cold stratification of 5 days at 4°C was able to release dormancy for all genotypes except for H10-165, suggesting that this genotype requires additional cues to release dormancy (Supplementary Fig. S3).

Next, the $DSDS50_{PD}$ was compared with the dynamics of thermodormancy induction. To this end, using the four genotypes from the pilot experiment shown in Fig. 2B, we calculated the time to induce TD_{50} . TD_{50} values decreased exponentially with increasing $DSDS50_{PD}$ values (Fig. 4A), showing that deeper primary dormancy results in a faster induction of thermodormancy. When $DSDS50$ values of primary dormancy were plotted on a logarithmic scale, the relationship was linear ($R^2 = 0.99$). This is consistent with previous works in Brassicaceae, suggesting that the capacity for induction of secondary dormancy is associated with some degree of primary dormancy (Auge et al., 2015; Finch-Savage and Footitt, 2017; Soltani et al., 2019).

Thermodormancy was partially released by a 5-day stratification period at 4°C without nitrate in MT209, H10-131 and

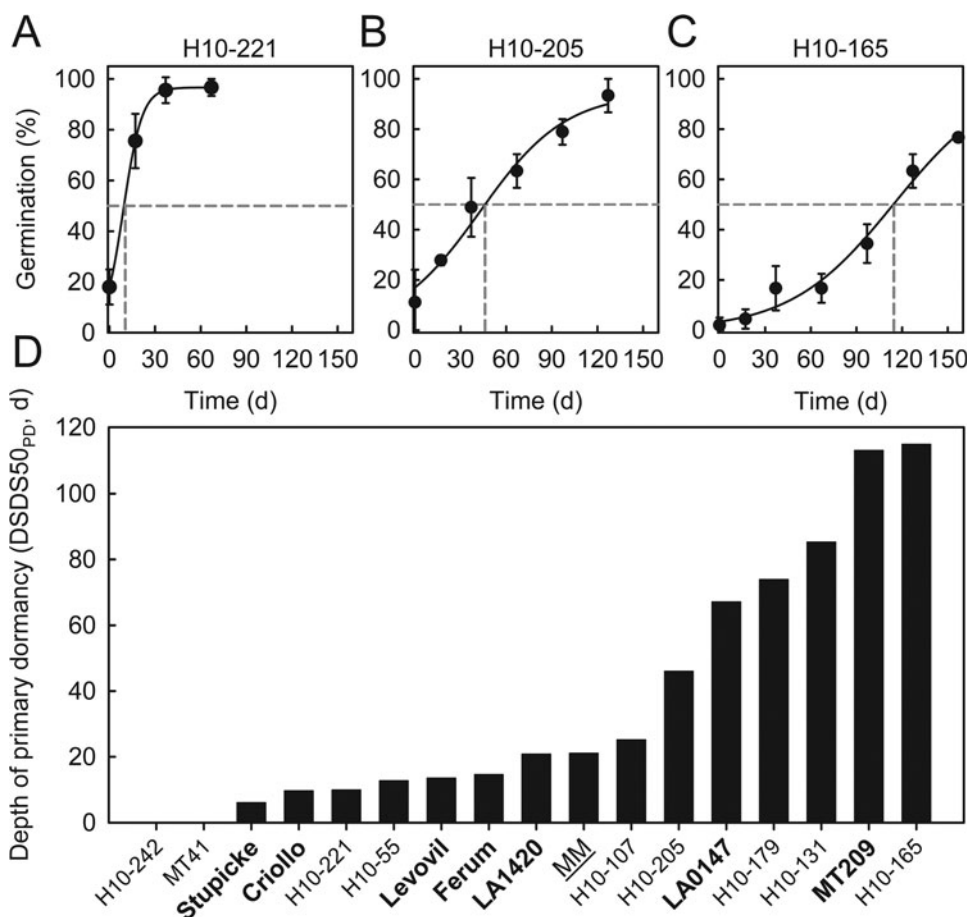


Fig. 3. Depth of primary dormancy is genotype-dependent. (A–C) Changes in the percentages of germinated seeds during hermetic storage at 20°C in the dark. Germination was performed at 20°C in the dark. Data are the average of triplicates of 30 seeds (\pm SD) and were fitted with logistic regression to assess the number of days of seed dry storage required to reach 50% of germination ($DSDS50_{PD}$). (D) Depth of primary dormancy in the indicated genotypes assessed by $DSDS50_{PD}$. Seeds were used from the winter culture.

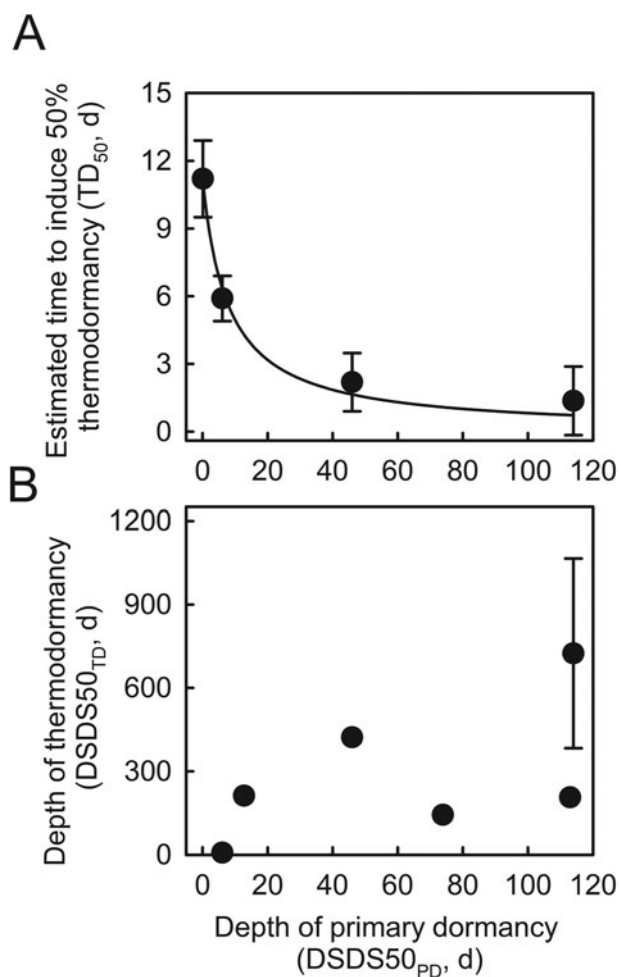


Fig. 4. The relationship between the depth of primary dormancy (DSDS50_{PD}) and capacity to induce secondary dormancy (A, TD₅₀) and the estimated depth of thermodormancy (B, DSDS50_{TD}). Data are the means of three independent replicates (\pm SD). Seeds were used from the winter culture.

H10-179, whereas there was no effect on H10-205, H10-55 and H10-165 (Supplementary Fig. S4). This indicates that there is a genetic component to the depth of secondary dormancy. To further investigate this, the depth of thermodormancy was assessed by measuring the time to reach 50% germination during dry storage (DSDS50_{TD}) across six genotypes exhibiting a wide range of primary dormancy depths, with DSDS50_{PD} values spanning from 6 to 115 days (Fig. 4B, Supplementary Fig. S5). DSDS50_{TD} was, on average, 10-fold higher than that of primary dormancy across the tested genotypes. However, there was no relation between the depth of primary dormancy and that of thermodormancy for these six genotypes (Fig. 4B, Pearson coefficient correlation = 0.567, P -value = 0.267).

In Brassicaceae, it was shown that a high percentage of germination obtained as a result of after-ripening cannot exclude the possibility that some residual primary dormancy is still present (Soltani *et al.*, 2019). Hence, stress-induced secondary dormancy in this condition has been construed as an expression of primary dormancy (Auge *et al.*, 2015; Batlla and Benech-Arnold, 2015; Soltani *et al.*, 2019). This was further tested by examining whether dry storage, after the apparent loss of primary dormancy, could influence the response to heat during imbibition (Fig. 5). Five genotypes exhibiting a wide range of primary dormancy depths

were used, with DSDS50_{PD} values spanning from 6 to 74 days. For the genotypes with lower DSDS50_{PD} values [Stupicke (DSDS50_{PD} = 6 days), H10-107 (DSDS50_{PD} = 21 days) and Moneymaker (DSDS50_{PD} = 25 days)], 6 months of storage led to a decrease in the propensity to induce thermodormancy compared to 3 months, resulting in an increased proportion of thermoinhibited seeds (Fig. 5C). For those genotypes with higher DSDS50_{PD} [H10-205 (DSDS50_{PD} = 46 days) and H10-179 (DSDS50_{PD} = 74 days)], even 8 months of dry storage did not influence the induction of thermodormancy (Fig. 5). Interestingly, after 8 months of storage, an increased proportion of thermotolerant seeds was observed for H10-107 (Fig. 5C). This observation led us to investigate the effect of dry storage on the germination response to heat of H10-221, a genotype with a shallow primary dormancy (DSDS50_{PD} = 10 days), which displayed the largest fraction of thermotolerant seeds at harvest (i.e. 51%, Fig. 2C). After 6 months of dry storage (i.e. 5 months after the apparent loss of primary dormancy, Fig. 3A), the proportion of thermotolerant seeds was increased to more than 80% at the expense of both the thermodormant and thermoinhibited fractions (Fig. 5B). Thus, dry storage beyond the apparent loss of primary dormancy impacted the germination response to heat with genotypic differences leading to an increased proportion of thermotolerant or thermoinhibited seeds at the expense of thermodormancy, thereby revealing cryptic genetic variation.

Temperature during fruit development influences the germination response to heat during imbibition in a genotype-dependent manner

Considering the importance of parental temperatures on primary and secondary dormancy in *Arabidopsis* (Coughlan *et al.*, 2017), we tested the impact of temperature during the entire culture using three cultures grown in greenhouse conditions for which sowings were shifted. Five genotypes were selected based on their different thermodormancy depths. Fruits of the winter culture were exposed to a daily average temperature of 22/19°C (Fig. 1). During the spring and summer cultures, the average temperature during fruit development was, respectively, 27/22 and 31/25°C with 18 and 57 days above 32°C.

First, we evaluated how parental temperatures influenced primary dormancy based on percentages of germination at harvest (Supplementary Table S1, Fig. 6). There was a significant impact of the sowing date on the primary dormancy that was dependent on the genotype. Warm temperatures led to a decrease in primary dormancy, although the extent depended on the genotype. H10-55 and H10-107 were the most temperature-sensitive genotypes. In contrast, for MT209, the warmest temperature had only a little, although significant, effect on the percentage of primary dormant seeds.

There was also a genetic and culture effect on thermodormancy (Supplementary Table S1, Fig. 6). Overall, high temperatures during the summer culture reduced seed susceptibility to thermodormancy during imbibition at 35°C, except for H10-242, which produced seeds that remained thermoinhibited regardless of the maternal temperature. This was particularly pronounced at 32°C. The decreased thermodormancy observed for the summer culture resulted in an increased proportion of thermoinhibited seeds, except for H10-107, which produced thermotolerant seeds instead of thermodormant seeds. Furthermore, the maternal temperature had also an effect on the dynamics of

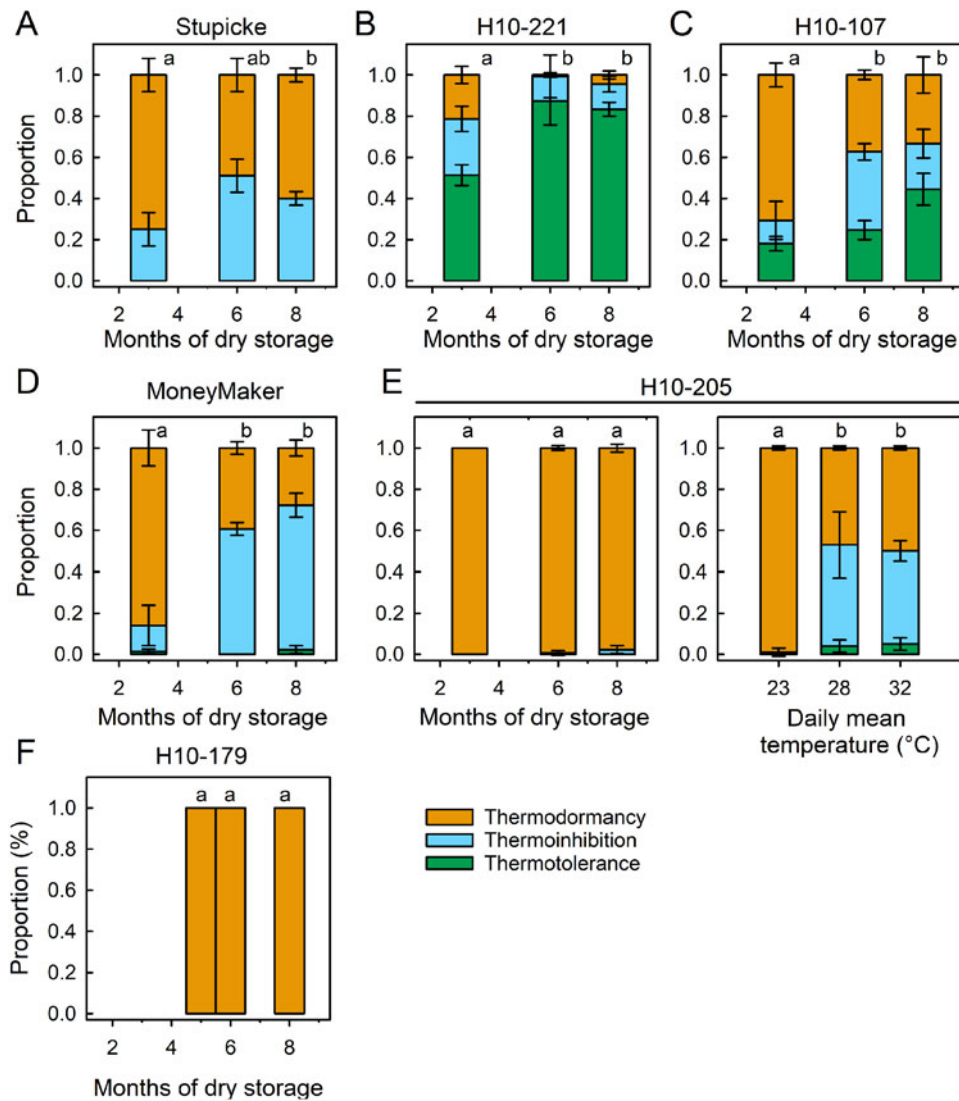


Fig. 5. Changes in thermotolerance, thermoinhibition and thermodormancy in the indicated genotypes as a function of time of dry storage time at 20°C. Genotypes (A, Stupicke; B, H10-221; C, H10-107; D MoneyMaker; E, H10-205; F, H10-179) are ranked from the least to the highest primary dormant genotypes (Fig. 3D). Seeds were obtained from the winter culture except for H10-205, for which the effect of temperatures during fruit ripening on the response to 35°C imbibition was also tested for seeds stored for 6 months. Data are the average triplicates of 30 seeds (\pm SD). Different letters correspond to significant differences ($P < 0.05$).

thermodormancy during dry storage. This was assessed with H10-205, showing that 6 months of storage led to an increased proportion of thermoinhibited seeds obtained from plants grown at temperatures above 28°C compared to seeds harvested from the 23°C culture (Fig. 5E). Like for primary dormancy, the interactions between genotype and thermal times of the vegetative and reproductive phases were significant and contributed to a similar extent to the variance explained (Supplementary Table S1).

The genotype effect on the duration of fruit development due to different sensitivities to temperature could explain the differences in primary and secondary dormancy by indirectly impacting the seed maturity level at harvest and, hence, the depth of dormancy. To test this, we investigated how the genotype, accumulated thermal time during the vegetative and reproductive phases and their interactions had a significant effect on primary dormancy (Table 1). First, we noted that the accumulated thermal times of both phases depended on the genotype (Supplementary Fig. S6). For example, the accumulated thermal times of the vegetative phase were the smallest in H10-242, H10-55 and H10-107 and increased significantly between the three different cultures. In H10-165, the accumulated thermal time of the reproductive

phase increased significantly in the summer culture compared to the other two cultures, but not the vegetative phase (Supplementary Fig. S6). There were significant genotype and accumulated thermal time effects on primary dormancy (Table 1). However, the contributions of their interactions were equally important in inducing primary dormancy as shown by the F -values (respectively, 19.4 and 20 before and after flowering), which were higher than the genotype effect ($F = 10.592$, Table 1). Likewise, for thermodormancy, the genotype and its interaction with the accumulated thermal time were equally important in their contribution to the explained variance (Table 1). Therefore, the phenology of the entire tomato life cycle plays an important role in determining primary and secondary dormancy.

While the temperature was manipulated by delayed sowing, the progressive increase in light intensity from December to July might also have contributed to the germination response to heat. To assess the effect of a combination of light and temperature, we used MoneyMaker fruits that were harvested at the Breaker stage (when fruits turn from green to orange) and subsequently incubated for 14 days under standard temperature (23°C day/20°C night) or high temperature (32°C/26°C) and two different light regimes: a standard light regime (16 h photoperiod,

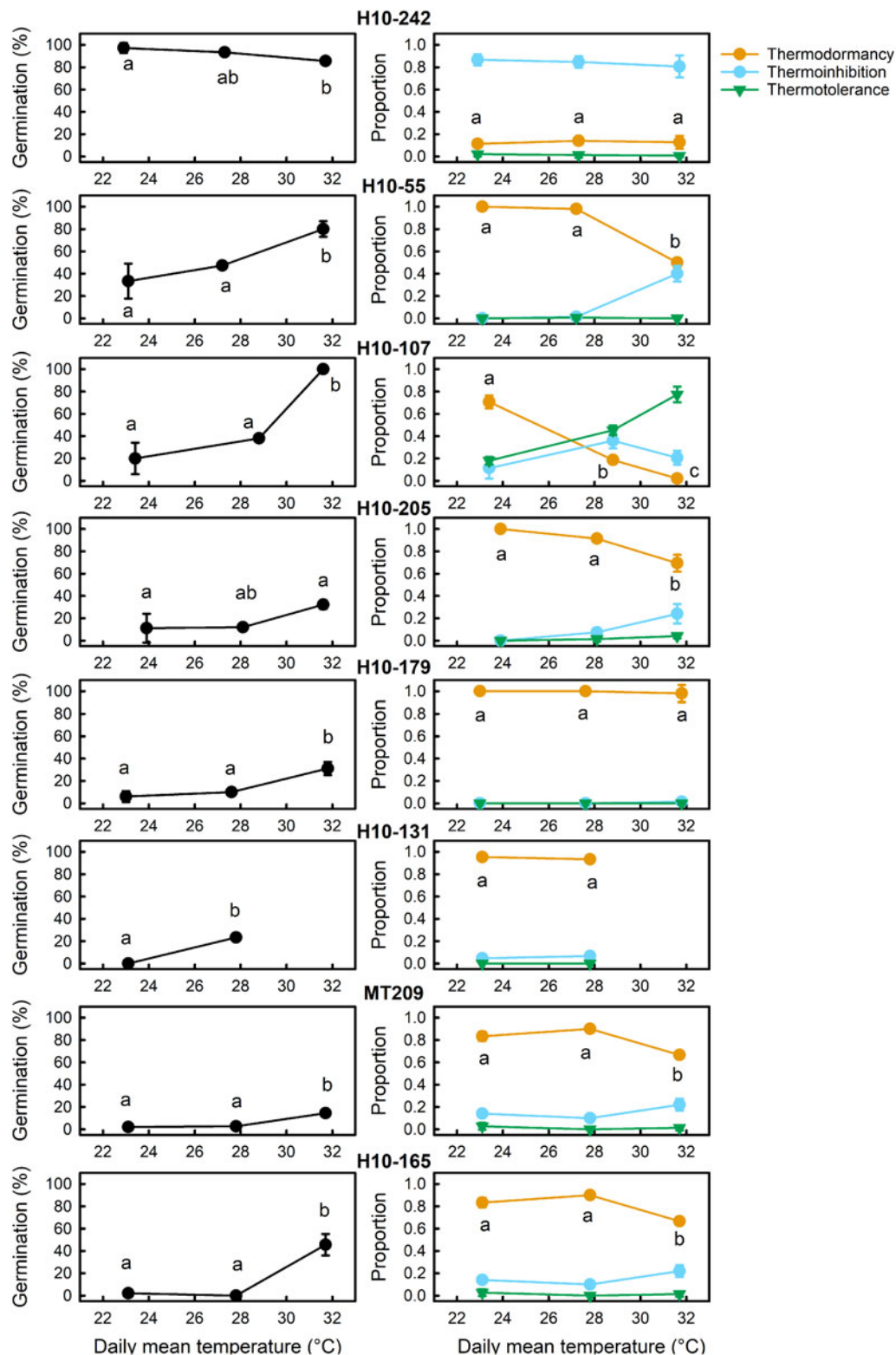


Fig. 6. The impact of parental temperature during fruit ripening on the primary dormancy (left panels) and germination response to heat (right panels) as described in Fig. 1. Genotypes are indicated on the top of the panels. Data are the average of three replicates of 50 seeds. Different letters indicate significant differences ($P < 0.05$).

300 $\mu\text{E m}^2 \text{s}^{-1}$) or dim light (16 h photoperiod, 25 $\mu\text{E m}^2 \text{s}^{-1}$) (Bizouerne *et al.*, 2021a). Heat during *ex planta* fruit ripening produced thermoinhibited seeds compared to the standard

temperature incubation, after which seeds were thermodormant, consistent with our findings for the MAGIC genotypes (Supplementary Fig. S7, Fig. 6). There was no effect of the light

Table 1. Primary dormancy and thermodormancy and their interactions with thermal history during the vegetative phase from sowing to flowering fruit (vegetative heat sum, Veg HS) and the reproductive phase from flowering until seed harvest (Reproductive heat sum, Rep HS).

Effect	d.f.	Primary dormancy			Thermodormancy		
		SSq	F	P-value	SSq	F	P-value
Genotype	6	0.269	10.592	<0.0001	11.727	70.278	<0.0001
Veg HS	1	0.037	8.841	0.005	0.011	0.385	0.538
Rep HS	1	0.022	5.215	0.027	0.150	5.401	0.025
Gen × Veg HS	6	0.494	19.437	<0.0001	14.262	85.467	<0.0001
Gen × Rep HS	5	0.425	20.079	<0.0001	7.121	51.210	<0.0001

Note: First a full model that included all interactions was tested. Since the interaction Veg HS × Rep HS was not significant, it was removed in a second analysis. d.f., degree of freedom; gen, genotype, SSq, sum of squares.

regime on the shift from thermodormancy to thermoinhibition (Supplementary Fig. S7).

Prolonged cold during imbibition promotes the induction of thermodormancy

Since sub-optimal temperatures during plant growth and fruit development favoured the production of thermodormant seeds (Fig. 6), we tested whether cold imbibition after harvest could induce thermodormancy in genotypes that produced

thermotolerant (H10-221) or thermoinhibited seeds (H10-242 and MT41). After cold imbibition, seeds were dried for 2 days at 44% RH before testing the germination response at 35°C. We verified that such a drying treatment did not impact the germination response to heat compared to undried seeds. A temporal study using H10-242 showed the longer the cold imbibition at 4°C, the higher the proportion of thermodormant seeds, reaching 50% after 14 days of cold (Fig. 7A). Likewise, 8-day imbibition at 4°C led to an increase of up to 50% of thermodormant seeds at the expense of thermotolerance and

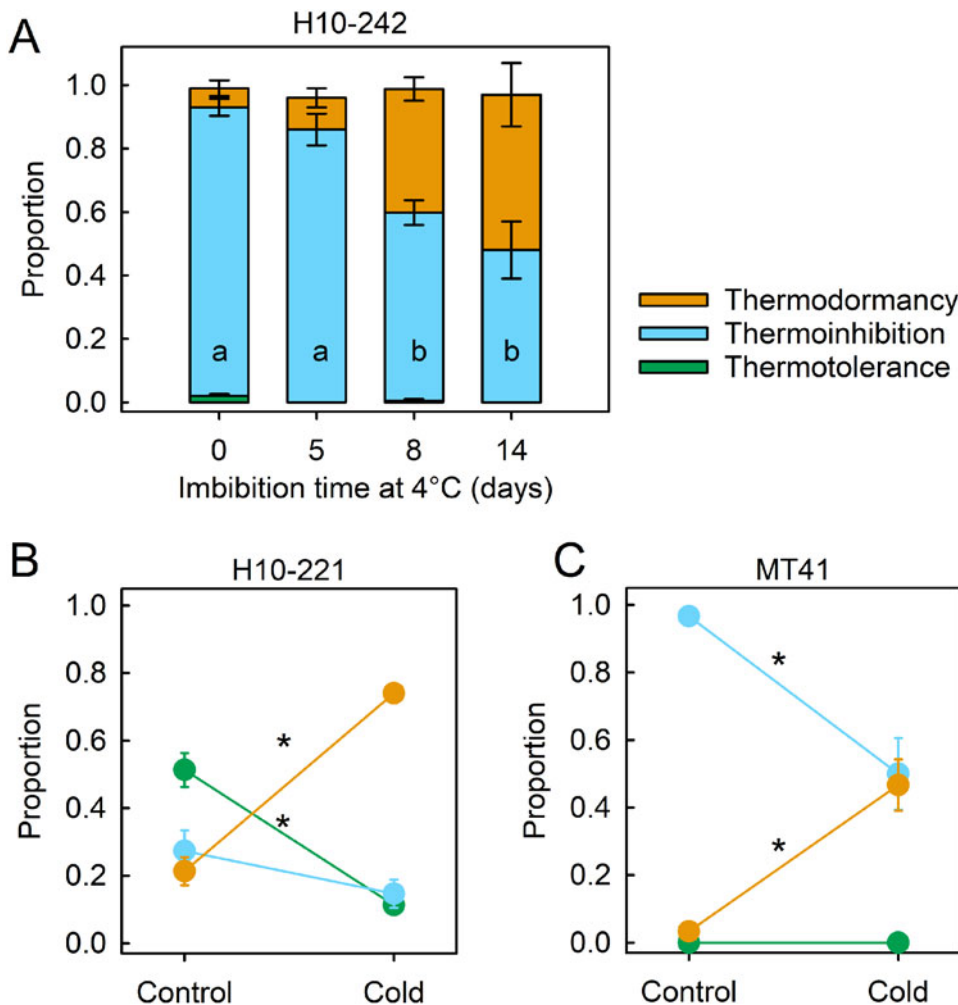


Fig. 7. Incipient cold imbibition impacts the germination response to heat. (A) The effect of the duration of cold imbibition on thermoinhibition and thermodormancy levels in the genotype H10-242. Letters indicate significant differences ($P < 0.05$) using ANOVA and Tukey's test. (B, C) Effect of 8-day cold imbibition on the heat response of germination in indicated genotypes. Control represents seeds without cold imbibition. Stars indicate significant differences between controls and cold imbibition ($P < 0.05$) using a two-tailed t -test. Data are the average of triplicates of 50 seeds (\pm SD). Seeds were used from the winter culture.

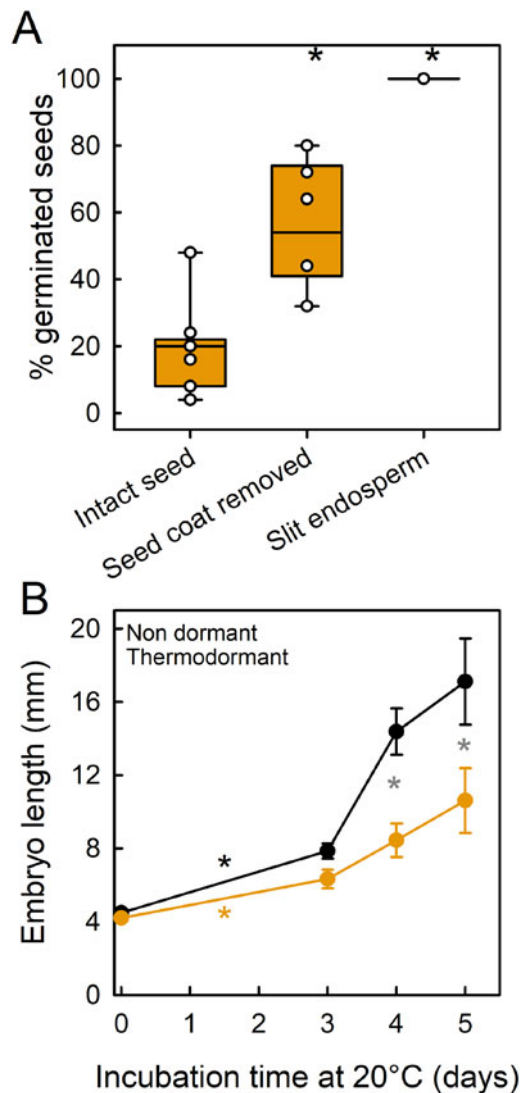


Fig. 8. Contribution of seed tissues to thermodormancy in the H10-205 genotype. Thermodormancy was induced as explained in Fig. 2A. (A) Germination of thermodormant seeds after removal of the seed coat and slitting of the endosperm. Data represent five replicates from two independent experiments using 30 seeds. (B) Length of naked embryos isolated from 6 h-imbibed non-dormant and thermodormant seeds as a function of incubation time at 20°C in the dark. Data represent the average of 10–30 embryos \pm SE. Stars indicate significant differences ($P < 0.05$) between factors as follows: black and orange between 0 and 3 days of incubation of non-dormant and thermodormant embryos, respectively; grey between non-dormant and thermodormant at 4 and 5 days of incubation. Seeds were used from the winter culture.

thermoinhibition for seeds from genotypes H10-221 and MT41 (Fig. 7B, C).

Contribution of the embryo and the endosperm to secondary dormancy

Tomato seed germination depends on the balance of the opposing forces between the constraint of the endosperm and seed coat at the chalazal end on one side and the embryo growth potential on the other side (reviewed in Steinbrecher and Leubner-Metzger, 2017; Nonogaki, 2019). To investigate which tissue contributed the most to thermodormancy, H10-205, the genotype that produced seeds with a very deep thermodormancy was used.

Slitting the endosperm led to 100% germination, whereas surgically removing the seed coat led to 50% germination (Fig. 8A). A similar result was obtained for primary dormant seeds (Supplementary Fig. S8A), showing the importance of the endosperm in tomato seed dormancy. After 3 days of incubation, the elongation of isolated non-dormant and thermodormant embryos was significant compared to 0 day, but there was no significant difference between these two states (Fig. 8B). Thus, there was no delay in the elongation from thermodormant embryos after the extraction of the seeds. After 4 days, the thermodormant embryos grew significantly slower than non-dormant embryos, resulting in a lower growth rate of 1.22 mm/day (± 0.28 , $P = 0.045$) for dormant embryos compared to 2.5 mm/day (± 0.68 , $P = 0.066$) for non-dormant embryos. These results, which were confirmed in an independent experiment (Supplementary Fig. S8B), suggest that besides the endosperm, the embryo growth potential also contributes to thermodormancy and that both tissues need to be considered for the molecular understanding of thermodormancy in tomato seeds.

Discussion

With the prospect of global warming, it is expected that seeds will be increasingly exposed to supra-optimal temperatures during both their production and germination. Using a selection of genotypes from the tomato MAGIC population, our data show that the thermal history before and after harvest strongly modulates germination response to heat during imbibition. There is also a genetic component that underlies the differential responses to temperature during the growth of the culture. This thermal sensing occurs both before and after flowering and after harvest. It is also influenced by dry storage, even after the apparent loss of primary dormancy. These data clearly show that seeds of cultivated tomatoes exhibit a complex phenotypic plasticity in relation to their thermal history. As previously argued by Batlla and Benech-Arnold (2015), the possibility of temperature inducing either thermodormancy or thermoinhibition may confound the interpretation of the lack of germination during imbibition under stressful conditions. This can be problematic for crop seeds, such as tomatoes, in both seed vigour testing and breeding programmes aimed at producing seeds that are resilient to climate change (Reed *et al.*, 2022). This work underscores the need to thoroughly analyse the origin of stress-induced germination arrest within both genetic and environmental contexts.

Induction of secondary dormancy depends on primary dormancy in Brassicaceae (Auge *et al.*, 2015; Coughlan *et al.*, 2017; Soltani *et al.*, 2019) and wild oats (Symons *et al.*, 1987). Our data support this observation for tomatoes using germination percentage as an assessment of dormancy. When developing seeds were continuously exposed to temperatures above 32°C after the seed set (Fig. 1), both primary dormancy and thermodormancy were reduced (Fig. 6). Furthermore, when pre-harvest temperature was taken into account, the effect of primary dormancy on thermodormancy was higher than the genotype effect (with F -values of 48 and 24, respectively, Supplementary Table 1).

There is no correlation between the deepness of primary dormancy and thermodormancy for the six genotypes tested (Fig. 4B). In *Arabidopsis*, secondary dormancy was also maintained after 150 days of dry storage regardless of the DSDS_{50pD} values that were obtained genetically by introgressing fragments of DELAY OF GERMINATION 1 (DOG1) alleles of different accessions in the Ler background (Buijs *et al.*, 2020). Thirdly,

two genotypes without primary dormancy under our culture conditions that exhibit either thermotolerance or high levels of thermoinhibition were found to express thermodormancy when cold imbibition was prolonged to 8 days instead of 5 days (Fig. 7). Thus, the genetic wiring related to the depth of primary and secondary dormancy appears to be partially different.

The molecular mechanisms associated with the genetic and environmental plasticity of the germination response to heat remain to be elucidated, but our study shows that both the embryo and the seed coverings play a role. In the Moneymaker cultivar, naked embryos did not grow during incubation at 37°C, which led the authors to conclude that thermodormancy was solely due to the embryo (Geshnizjani et al., 2018). However, they did not report whether lower temperatures after the induction of thermodormancy led to an inhibition of embryonic growth. In our study, isolated dormant embryonic axes of H10-205 grew to a lesser extent than non-dormant axes when incubated at 20°C (Fig. 8), suggesting that the growth potential had been affected by the induction of thermodormancy. Likewise, chilling-induced secondary dormancy in sugar beet resulted in a reduction in the embryo's growth potential (Hourston et al., 2022). Furthermore, breaking the endosperm integrity of H10-205 seeds resulted in 100% germination at 20°C (Fig. 8). This suggests a role for the endosperm as a component of thermodormancy, at least for this genotype, in agreement with the consensus that dormancy is imposed by tissues enclosing the embryo in tomato and other species (Hilhorst and Downie, 1995; Steinbrecher and Leubner-Metzger, 2017; Nonogaki, 2019), including the secondary dormant sugar beet seeds (Hourston et al., 2022). However, another possible explanation for the role of testa and endosperm in preventing germination would be to act as an oxygen barrier. Since testa peeling led only to 50% germination (Fig. 8), it might be possible that the endosperm slitting increased the oxygen usability of the embryos more efficiently than the testa peeling. In two tomato breeding lines, radicle emergence was found to be inhibited when the partial oxygen pressure was below 10 kPa (Dahal et al., 1996). Above this very low oxygen level, respiration was reduced without any effect on germination timing. It remains to be tested whether a putative oxygen barrier of the endosperm creates a hypoxic environment that impairs the conversion of ACC to ethylene by the embryo, thereby stimulating germination, as found for thermodormant sunflower seeds (Corbineau et al., 1989).

The observation that further dry storage beyond apparent primary dormancy release by after-ripening reveals genetic differences in the germination response to heat and adds an additional layer of complexity has been unexplored so far in tomatoes (Fig. 5). Seeds of H10-221 and H10-107 became progressively thermotolerant at the expense of the dual forms of germination arrest, whereas seeds from genotypes H10-205, H10-179 and Stupicke remained thermodormant after 8 months of storage (Fig. 5). Seeds were stored in the dry state at 20°C in the dark, conditions in which their water content was around 7% on the dry weight basis. This value brings the cytoplasm to a highly viscous state, in which no metabolism can occur (Buitink and Leprince, 2004), and the transcriptional machinery is unlikely to work (Chahtane et al., 2016), although some local molecular relaxation may still take place (Ballesteros and Walters, 2019). Therefore, the increase in thermotolerance during storage illustrates a case of cryptic genetic variation (Paaby and Rockman, 2014). Interestingly, this cryptic variation was found to be plastic because the parental heat before harvest decreased the propensity

to induce thermodormancy in H10-205 during dry storage (Fig. 5D). Since breeding research or seed production could impose to store the seed lots before testing their germination potential, the issue of cryptic genetic variability due to dry storage needs to be addressed. Oxidation in the dry state is thought to release dormancy, as shown by the accelerated after-ripening under high pressure of oxygen in *Arabidopsis* (Chahtane et al., 2016; Buijs et al., 2018). Also, oxidation during long-term storage is hypothesized to induce a progressive increase in phyA-controlled germination in *Arabidopsis* (Kim et al., 2019). However, alternative hypotheses exist, such as temperature-dependent changes in epigenetic marks that could occur during seed maturation and control the response to heat during imbibition (reviewed in Auge et al., 2017; Iwasaki et al., 2022) or, more speculatively, during storage.

Primary dormancy varied according to the temperature during tomato seed development (Fig. 6) as shown previously for several other crops and wild species (Springthorpe and Penfield, 2015; Coughlan et al., 2017; Finch-Savage and Footitt, 2017; Awan et al., 2018). We show that the susceptibility of seeds to become thermoinhibited or thermodormant relies on the parental temperature, a phenomenon that has only been described so far in Brassicaceae and lettuce (Contreras et al., 2009; Coughlan et al., 2017; Awan et al., 2018). In these species, cool temperatures increase primary dormancy and the propensity to induce secondary dormancy. Similarly, in tomatoes, warm sub-optimal temperatures led to decreased primary dormancy and a propensity to induce thermodormancy (Fig. 6, Supplementary Fig. S5). We did not test cold temperatures below 20°C during the culture as they are less relevant for tomato seed production. Most of the effects on germination response to heat were detected when fruits were exposed to daily temperatures of 32°C, which is above the optimal temperature range but still below 35°C at which stress symptoms are detected (Bineau et al., 2021). Also, the amplitude of these effects varied according to the genotype. For one genotype, H10-107, thermodormancy was lost in favour of thermotolerance when heat occurred during maturation (Fig. 6), suggesting the loss or repression of the germination arrest mechanism during imbibition at 35°C. However, for most of the genotypes, the proportion of thermoinhibited seeds increased with increasing temperature at the expense of thermodormancy (Fig. 6, Supplementary Fig. S7), implying that thermoinhibition is a safeguard to avoid germination under unfavourable heat during imbibition. The parental temperature affected thermodormancy more than the genetic effect (Table 1, Supplementary Table S1), a finding consistent with data obtained from experiments using different maternally supplied nutrients on germination at 35°C (Geshnizjani et al., 2020). The genotype effect and the interactions between the genotype and the heat sum before and after flowering were equally important (Table 1). So far, heat sums have not been taken into account to explain the maternal temperature effect on seed dormancy.

It is understood that the parental effect on seed behaviour during germination represents a form of transgenerational phenotypic plasticity (Auge et al., 2017; Iwasaki et al., 2022; Authier et al., 2023). It allows the mother plant to adapt the phenotype of its progeny to different environments, thereby improving their fitness. During tomato domestication, the diversification of fruit aspects and palatability, together with the adaptation to environmental conditions, occurred simultaneously with a strong reduction in genetic diversity (Blanca et al., 2015; Pascual et al., 2015). The transgenerational plasticity of germination responses

to heat environments could still be detected in our genetic material obtained from the MAGIC population using non-stressful parental conditions as recently shown for *Arabidopsis* (Authier et al., 2023). The MAGIC population was obtained from crosses between four parents from *S. lycopersicum* var. *lycopersicum*, the domesticated species, and four parents of *S. lycopersicum* var. *cerasiforme*, which is phylogenetically positioned between *S. pimpinillifolium* and the domesticated group (Blanca et al., 2015). Thus, the control of transgenerational plasticity highlighted here was not lost during the domestication process, even if environmental conditions throughout the life cycle that were used were not necessarily those encountered in the native regions of both groups. Thus, the MAGIC population offers a gene reservoir for the potential adaptation of cultivated tomatoes in relation to climate change and will help decipher how the signalling pathways differentially regulate germination phenology in response to heat.

Supplementary material. To view supplementary material for this article, please visit: <https://doi.org/10.1017/S0960258524000217>.

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