



# Maternal environment and dormancy in sunflower: The effect of temperature during fruit development



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## ABSTRACT

A rapid and uniform germination in the field is an important requirement for commercial hybrid sunflower seed. Persistence of dormancy after harvest can negatively affect this aspect of seed quality, and seed lots with some degree of dormancy cannot be commercialized. Seed dormancy intensity and duration can vary greatly among sunflower genotypes, but it is also subject to strong interactions with the maternal environment. In this paper we report results of investigations into the effect of temperature during sunflower fruit development on the level of dormancy after harvest. After conducting controlled (greenhouse) and field experiments (sowing dates and plastic tents), we found that higher temperatures during later stages of achene development significantly increased the level of dormancy at harvest and its persistence during storage. The impact of the maternal (thermal) environment on embryo and coat-imposed dormancy was also investigated. Results showed that although maturation under warmer environments reduced embryo dormancy, this effect was overcompensated for by the enhancement of inhibition imposed by the pericarp and the seed coat. In addition, the results obtained suggest that observed changes in dormancy in response to the maternal environment could be at least partially explained by changes in achene and/or embryo sensitivity to ABA. Results presented here should be useful when choosing a proper environment for the production of hybrid sunflower seed of high quality, avoiding high temperatures during later stages of fruit development.

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## 1. Introduction

At harvest, sunflower fruits (achenes) are usually dormant and germinate poorly (Cseresnyes, 1979; Corbineau et al., 1990). Depending on the genotype and the maternal and storage environments, this dormant state can last for a few weeks or several months (Brunick, 2007). Because hybrid seed destined for sowing cannot be processed and commercialized until germination standards are met, a prolonged dormancy is a problem for the seed industry committed to provide in a timely fashion F1 hybrid seed

either for local or counter season markets (Maiti et al., 2006). In addition, industrial costs related to proper seed storage increase.

Mechanisms involved in seed dormancy are determined genetically and this is therefore a heritable trait, but its intensity at harvest and its maintenance afterwards can also be modulated by the maternal environment (Finch-Savage and Leubner-Metzger, 2006). Studies performed in several species indicate that the environmental conditions explored during seed or fruit development and maturation (hereafter, just fruit development) can affect the dormancy level of harvested seeds or fruits (Fenner, 1991). Even though several environmental factors (*i.e.* day length, radiation, water and nutrient availability) have been shown to affect the level of dormancy at harvest, there is strong agreement on the dominant effect of ambient temperature during development on the regulation of seed dormancy at harvest (Benech-Arnold, 2004). The effect of the maternal thermal environment on seed dormancy has been

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studied in many species, and increases in the average temperature during seed development are usually associated with lower levels of dormancy (Fenner, 1991). Examples of this response are winter cereals: low temperatures during grain development result in higher grain dormancy in wheat (Black et al., 1987; Nakamura et al., 2011) and barley (Rodríguez et al., 2001, 2015). However, there are almost no reports regarding the possible effect of the thermal environment explored by sunflower fruits during development on their dormancy level at harvest. Indeed, one previous preliminary study by Fonseca (2000) suggested that the effect of temperature on seed dormancy might be opposite in sunflower to that observed in winter cereals. Even though commercial sunflower seed production takes place in different regions and thermal environments, the precise effect of temperature has not been explored properly under controlled (e.g., greenhouse) or field conditions.

According to the classification proposed by Baskin and Baskin (2004), sunflower achenes display physiological dormancy. The various structures that make up the sunflower achene contribute to dormancy, and their relative contribution varies during fruit development. The embryo is surrounded by a single layer of living endospermatic cells intimately coalesced with the seed coat which is dead at maturity, forming the true sunflower “seed” (Seiler, 1997; Szemruch et al., 2014). This “seed” is further enclosed by the pericarp, forming the fruit. All these structures surrounding the embryo are referred to as “envelopes” in this study. At early stages of fruit development, dormancy is imposed mainly by the envelopes and the embryos germinate readily if they are isolated and incubated in water (Le Page-Degivry and Garelo, 1992; Corbineau et al., 1990). As development progresses, the dormancy level of the embryo increases gradually until it reaches a maximum at about 20–22 days after anthesis (DAA). During later developmental stages, embryo dormancy decreases gradually and achene dormancy is mostly due to the envelopes. At harvest maturity, the embryo usually presents low or intermediate levels of dormancy, whereas the achenes are deeply dormant as a result of strong “envelope-imposed” dormancy. Dormancy imposed by the envelopes at harvest maturity usually persists for some time, and may require several weeks or months of dry storage to disappear completely (Corbineau et al., 1990; Bianco et al., 1994). Although several reports have focused on the contribution of the embryo and the seed envelopes to the level of dormancy in sunflower fruits, information is lacking on how these components might be affected by the maternal (thermal) environment. In addition, it is not understood how each of the different structures composing the envelopes (endospermatic layer, seed coat and pericarp) may contribute to dormancy.

Plant hormones have been shown to play a pivotal role in regulating the germination response and the expression of physiological dormancy in many different species (Finch-Savage and Leubner-Metzger, 2006). There is considerable evidence that the plant hormone abscisic acid (ABA) is a positive regulator of both the induction and maintenance of dormancy (Bewley, 1997). It has been shown that, in general, the transition from a high to a low dormancy level is accompanied by a reduction in embryo or seed sensitivity to the inhibitory effect of ABA (Finch-Savage and Leubner-Metzger, 2006). Sensitivity to ABA may vary depending on environmental conditions that prevailed during seed development. Examples of this type of response have been reported for *Sorghum bicolor*, in which certain environmental conditions during grain filling, such as water or nutrient availability, were associated with changes in embryo sensitivity to ABA that corresponded with the resulting dormancy level (Benech-Arnold et al., 1991, 1995). In sunflower, it is still unknown whether the effects of the environmental conditions during fruit development on the level of dormancy are mediated or not by differences in achene sensitivity to ABA.

Therefore, the aims of the present work were: (1) to investigate the effect of the thermal environment to which sunflower plants are

exposed during fruit development under both controlled (greenhouse) and field conditions on the level of dormancy of the mature fruits; (2) to evaluate if the observed effect of the thermal environment on achene dormancy is related to changes in embryo and/or coat imposed dormancy; (3) to explore if the effects of the maternal (thermal) environment on fruit dormancy level are related to changes in embryo or achene responsiveness to ABA.

## 2. Materials and methods

Different experimental systems were used to explore a variety of thermal conditions during fruit development. In Experiment I, plants were cultivated in pots in the field and at full anthesis (R-5.9 according to Schneider and Müller (1981)) some plants were transferred into a warm greenhouse until harvest time, while control plants remained in the field nearby. In Experiment II, trials were sown in the field on three different dates between early and late spring. In the third experimental system (Experiments III and IV), polyethylene tents (and their corresponding controls) were used to increase the temperature of the air surrounding the plants cultivated in the field; in this case, tents were applied during most of the fruit development phase (Experiment III) or during each of two halves of fruit development (Experiment IV). Experiment I was carried out during 2001–2002, Experiments II and III during 2008–2009 and Experiment IV during 2009–2010.

### 2.1. Plant materials and sites of the experiments

Plant material used in Experiment I was HA342, an inbred line with high oleic acid content. Plants were cultivated during late spring and summer at the Facultad de Agronomía, Universidad de Buenos Aires, Argentina (34°25'S, 58°25'W). In field experiments (Exp. II, III and IV) two different sunflower inbred lines (female and male) were grown together in the field. The F1 hybrid grain, the main focus of our work, was obtained following the same practices as in the process of commercial hybrid seed production. The experiments were conducted at Fontezuela, Buenos Aires, Argentina (33°53'S, 60°27'W).

### 2.2. Growth conditions in Experiment I

Thirty sunflower plants were cultivated individually in 50 l plastic pots. Plants were fertilized and watered manually, and fungicides and insecticides were applied whenever necessary. Soil mixture included natural top soil and sand (2:1) for optimal drainage. Plants (21 in total) that reached the R-5.1 stage (according to the scale proposed by Schneider and Müller (1981)) on the same day were selected for the experiment. At R-5.9 stage, six plants were transferred to a warm greenhouse and 15 plants were kept in the field (together with remaining plants which were kept as border plants). The greenhouse was approximately 60 m<sup>3</sup> in volume and temperature was set at 32 °C. Temperature above this limit was prevented by forcing external air through wet straw cooling pads. Meteorological data (temperature, radiation and relative humidity) inside and outside the greenhouse was recorded hourly in a weather station (Campbell Scientific Inc., USA). At harvest (60 days after R-5.1; plants had already passed the R-9 stage) heads were threshed manually and achenes from the outer two-thirds of the head were collected separately and used in germination tests (as described in Section 2.4). After harvest achenes were stored dry in paper bags and kept in a chamber at 15 °C. For germination tests, achenes from different plants were pooled to obtain experimental units. For the “field” treatment, plants were assigned randomly to three groups of five plants each, and these three pools were treated as experimental units. For the “greenhouse” treatment, achenes

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