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Growth and development of sunflower fruits under shade during pre and early post-anthesis period

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Abstract

The effect of pre and post-anthesis shading (20% of incident radiation) on pericarp development, cotyledon cell number and seed growth dynamic of fruits from three positions in the capitulum (peripheral, mid and central) of two sunflower (*Helianthus annuus* L.) genotypes were studied at two locations.

Both shading treatments reduced pericarp weight, fruit volume and total yield per plant. Plants shaded during pre-anthesis maintained the number of filled fruits but reduced their individual weight and cotyledon cell number in the three positions on the capitulum. In contrast, post-anthesis shading reduced the number of filled fruits but their individual weight and cotyledon cell number were reduced only in the central fruits.

Sigmoidal functions were fitted to seed growth data to estimate the duration of lag phase, the seed growth rate (SGR) and the effective filling period (EFP). Pre-anthesis shading reduced EFP of peripheral fruits, SGR of mid fruits and SGR and EFP of central ones while post-anthesis shading increased the duration of the lag phase of mid and internal fruits.

The hierarchy of fruit growth between positions within the capitulum was not modified by shading treatments and it was associated with differences, among fruit positions, in cotyledons cells number (except between mid and central fruits in pre-anthesis shading) and SGR (except peripheral and mid fruits in post-anthesis shading).

SGR not only depended on the cotyledons cell number, which was fixed during the cell division phase of seed development, but it was also sensitive to environmental conditions during the linear phase of growth.

Keywords: *Helianthus annuus* L.; Cell number; Seed development; Shading; Sunflower; Yield components

1. Introduction

The fruit (grain) of the sunflower is formed by the pericarp (hull), which comprises between 20 and 25% of the fruit weight, and the kernel or seed (mostly embryo) where the largest proportion of lipids and dry matter is stored (Connor and Hall, 1997).

A developmental model of sunflower's seed can be defined by three sequential phases (Lindström et al., 2002). The initial phase (Phase I), up to 10 days after anthesis, includes fertilization, the period of active cell division and a slow increase of the dry weight. Here, the anatomy of the embryo structures are defined and the final number of embryo cells is fixed (Prokof'ev et al., 1985; Lindström et al., 2000). Also during this phase the pericarp completes its development (Villalobos et al., 1996; Connor and Hall, 1997; Lindström et al., 2000). Next follows an intermediate phase (Phase II), where there is an increase of cell volume and a rapid accumulation of dry matter in the seed. In the final phase (Phase III) maximum seed weight is achieved and the fruit reaches physiological maturity. A similar seed developmental model has been proposed for wheat (*Triticum aestivum* L.) (Wardlaw, 1970; Gao et al., 1993), corn (*Zea*

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mays L.) (Reddy and Daynard, 1983; Jones et al., 1996) and soybean (*Glycine max* (L.) Merr.) (Bills and Howell, 1963; Egli et al., 1981; Guldan and Brun, 1985).

In the sunflower capitulum, there is a developmental and growth gradient, which progresses from the fruits at the periphery towards those at its center. So, the effect of any environmental stress, while the reproductive development is in progress, will not be similar for the fruits at the different positions on the capitulum. For example, Yegappan et al. (1982) observed that water stress in post-anthesis reduced the weight of the central seeds and not that of the fruits at the capitulum periphery whereas Cantagallo et al. (2004) found that pre-anthesis shading only affected the weight of the fruits at the peripheral and mid positions on the capitulum.

The developmental status reached by the pericarp before anthesis could limit the subsequent seed growth and development and, consequently diminish the final fruit weight (Millet, 1986; Egli et al., 1987). Cantagallo et al. (2004) found in sunflower that the carpel weight at anthesis was related to the final weight of the fruit. Likewise, Scott et al. (1983) established, for barley (*Hordeum vulgare* L.) a positive relationship between the carpel size at anthesis and the final size of the caryopses. Also, the final size and shape of rice (*Oryza sativa* L.) (Murata and Matsushima, 1975) and soybean (Egli et al., 1987) seeds decreased when a physical restriction was imposed.

For other crops there is evidence that final seed size is a function of the number of cells present in cotyledons or endosperm (Egli, 1998; Lemontey et al., 2000). During the development of seeds, the increase in cell volume is limited, so the final seed size and the capacity to accumulate dry matter in the seminal tissue will be determined by the number of cells present in the cotyledons or endosperm (Egli, 1998). It has been found that environmental factors such as supra-optimal temperatures in corn (Jones et al., 1985) and water or light stress in wheat (Wardlaw, 1970; Brocklehurst, 1977), which affected the cell division process in the seed by reducing the final number of embryo or endosperm cells, resulted in seeds with a lower weight. In soybean, the reduction in the source-sink ratio by shading or defoliation during the initial development of the seed resulted in a smaller number of cotyledon cells and a lower final seed weight (Egli et al., 1989).

There is little work relating the effects of environmental factors or agronomic practices on the cell division process in the embryo and subsequent seed growth of sunflower (Karyagina et al., 1999). In the present study, the effect of shade during the pre-anthesis and early post-anthesis periods on the pericarp development, cotyledon cell dynamics and seed growth was analyzed in fruits from three positions in the capitulum.

2. Materials and methods

2.1. Plant material

2.1.1. Experiment I

Two commercial sunflower genotypes, Dekasol (DK) 3900 and DK4030 (Monsanto®, Argentina), were sown on November 29, 2001 at the Experimental Station INTA Balcarce, Argentina (Lat. S 37°45′; Long. W 58°18′). The soil was a Typic Argiudol (Soil Survey Staff, 1999). Plant density was adjusted to 5.6 plants m^{-2}. The crop was managed according to the recommended conventional agronomical practices (Pereyra and Farizo, 1981). Weeds and insects were adequately controlled. Environmental conditions during crop growth kept soil water content above 50% of field capacity.

The phenology referred to here corresponds to that defined by Schneiter and Miller (1981). The treatments consisted of two shading periods: one applied pre-anthesis (Pre-A), for 14 days from reproductive stage R2; the other in early post-anthesis (Post-A), for 14 days from full anthesis (stage R5.10) and a control treatment (Con) (Fig. 1a). When each treatment started, plants at the appropriate growth stage (R2 or R5.10) were identified and marked.

Pre-A shading started at R2 and finished 14 days later at R4 stage. At R2 the inflorescence is surrounded by bracts, the first internode below the base of the inflorescence elongates 0.5–2.0 cm above the nearest leaf (Schneiter and Miller, 1981). At this moment all the disc florets were differentiated. Peripheral, mid and internal ovaries averaged 0.7, 0.4 and 0.2 mm long, respectively. At R4 the inflorescence begins to open and the ray flowers become

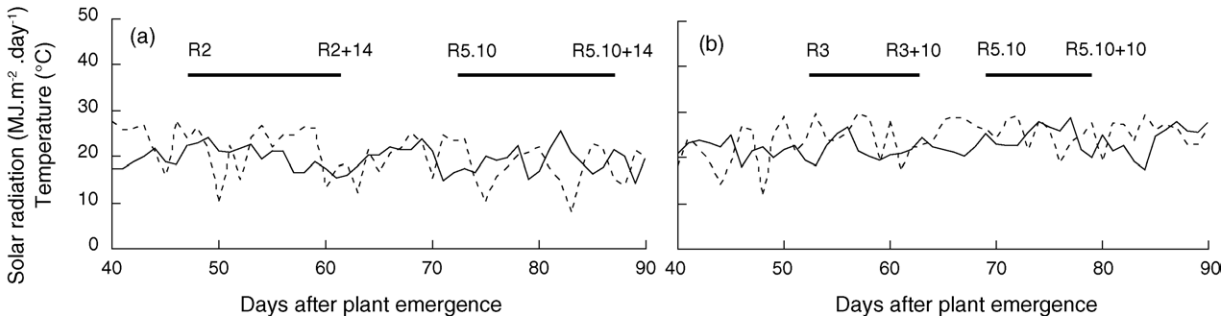

Fig. 1. Timing of shading treatments and mean daily solar radiation (MJ m^{-2} day^{-1} - - -) and temperature (°C; —) for each location. (a) Experiment I: Balcarce (Lat, S 37°45′; Long, W 58°18′); (b) Experiment II: Bahía Blanca (Lat, S 38°45′; Long, W 62°11′). Horizontal bars over the line graphs indicate the intervals of time when shading was applied. R2, R3 and R5.10 note reproductive stages of sunflower development as described by Schneiter and Miller (1981).