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Assessment of the critical period for the effect of intercepted solar radiation on sunflower oil fatty acid composition

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ABSTRACT

The fatty acid composition of sunflower (*Helianthus annuus* L.) oil closely depends on the environmental conditions during grain filling. Temperature and solar radiation are the main environmental factors driving oil fatty acid composition. Minimum night temperature and intercepted solar radiation per plant (ISR) during grain filling independently affect oleic acid percentage of traditional sunflower oil. Critical period for temperature effect on this trait has been shown to be placed between 100 and 300 °C day after flowering (°Cd af). The period of maximal sensitivity of fatty acid composition to ISR remains unknown. The aim of the present work was to identify the time window of high sensitivity (critical period) of fatty acid composition to ISR of sunflower oil. For this, ISR was modified by shading (50% or 80%) or thinning (50%) field grown sunflower hybrid DK3820 during different periods of grain filling. The timing of maximal sensitivity of fatty acid composition to source variations during post flowering periods was explored and analyzed by two widely used approaches: (i) evaluation of the relative oleic acid percentage under short shading treatments in relation to the control and (ii) window-pane analysis of the response of oleic acid percentage to ISR. The first approach generated differing estimates of the critical period depending on the level of radiation reduction. Using the second approach, a developmental interval during which oleic acid was most sensitive to ISR regardless of the radiation level was determined. The critical period began at 350 °Cd af and ended at 450 °Cd af. The critical period for radiation effect on oleic acid concentration differed from that of the radiation effect on grain weight and oil concentration and from the critical period for temperature effect on oil fatty acid composition. Different critical periods for different traits and specific environmental factors are indicative of the complexity of the interaction between environmental conditions and grain growth and oil synthesis dynamics.

1. Introduction

The quality and potential uses of vegetable oils are determined by their fatty acid composition. Sunflower oil is one of the most widely used vegetable oils because of its nutritional and industrial attributes. Sunflower oil quality is often considered in terms of oleic acid content, as this is nowadays the preferred fatty acid for both edible purposes and biodiesel production (Mensink et al., 2003; Marvey, 2008). Environmental factors have a decisive influence on sunflower oil quality (Roche et al., 2006; Izquierdo et al., 2006, 2009). It has long been known that temperature is the main factor affecting the proportion of oleic acid in the oil of traditional sunflower cultivars (Canvin, 1965). Additionally, increasing intercepted solar radiation per plant (ISR) during grain filling has been shown to increase oleic acid percentage in several crop species (Izquierdo et al., 2009; Zuil et al., 2012). In sunflower, differences in oleic acid relative concentration driven by this factor could be higher than 10 percentage points (Izquierdo et al., 2009). This effect on oleic acid percentage has been correlated with a decrease in linoleic acid concentration, with no significant changes in saturated fatty acids concentration (Izquierdo et al., 2009; Echarte et al., 2010). Intercepted solar radiation per plant and mean or minimum night temperature during grain filling independently affected oleic acid percentage of the oil of traditional sunflower (Echarte et al., 2010), soybean and maize (Zuil et al., 2012). The additive effect of temperature and radiation on fatty acid composition implies that these environmental factors affect oleic acid percentage through different mechanisms (Salisbury and Ross, 1992). In agreement with this observation, it has been shown that minimum night temperature affects oleic acid desaturation process through regulation of oleate desaturase activity (Izquierdo et al., 2006; Rolletschek et al., 2007) while intercepted solar radiation changes oleic/linoleic

Abbreviations: ISR, intercepted solar radiation per plant; PAR, photosynthetically active radiation; °Cd af, °C day after flowering.

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ratio through regulation of post flowering assimilates availability to the grains (Echarte et al., 2012).

Particular phases during plant development are more relevant for the determination of grain composition traits. Several authors have explored critical periods for the determination of grain number and grain weight in several species (Fischer, 1975; Savin and Slafer, 1991; Arisnabarreta and Miralles, 2008; Kiniry and Ritchie, 1985; Jiang and Egli, 1993; Kantolic et al., 2007).

Empirical relationships between grain composition traits and environmental conditions can be incorporated into simulation models to reflect interactions between environmental signals and physiological processes. The plant phenology, the non linearity of response of biochemical and physiological processes, as well as the erratic nature of climatic events often add to models predictions high degree of unexpected variability, which makes the output difficult to interpret. The critical period of a given trait is a modeling tool that helps to improve the accuracy of crop models predictions (Pereyra-Irujo and Aguirrezábal, 2007). Furthermore, the knowledge of many critical periods has been helpful for understanding the mechanisms underlying plant responses to environmental factors (e.g. Pleite et al., 2008).

In sunflower, critical periods for the effect of solar radiation on grain number (Cantagallo et al., 2004), grain weight and oil concentration (Aguirrezábal et al., 2003) have been found. These traits and the fatty acid composition of the oil have been shown to be more sensitive to heat stress during particular periods of grain filling (Rondanini et al., 2003, 2006). A critical period for fatty acid composition response to moderate minimum night temperature for sunflower oil has also been determined (Izquierdo et al., 2006). By contrast, the period of maximal sensitivity of oil composition to ISR throughout grain filling remains unknown. Since temperature and radiation affect fatty acid composition through different mechanisms (Echarte et al., 2012), critical periods for the effect of both factors on fatty acid composition could be different.

Different methods of experimental analysis have been used in order to elucidate these critical periods. These methods are usually based on the application of short treatments during different periods throughout the crop cycle. In many research works, the critical period is determined by evaluating the effect of these short treatments in relation to control values. The main limitation of this method of analysis is that the determined critical period depends on the treatment duration and moment of application (Cantagallo et al., 1997; Arisnabarreta and Miralles, 2008; Sandaña and Calderini, 2012). Alternatively, window-pane analysis allows determining critical periods that do not depend on the treatments. This method of analysis consists of relating a given trait to an environmental factor during time windows of different length and different starting time in order to find the period exhibiting the strongest relationship between trait response and factor (e.g. Aguirrezábal et al., 2003; Izquierdo et al., 2006).

The aim of the present work was to identify the key time window for fatty acid composition response to ISR of sunflower oil. For this, the timing and/or the sensitivity of fatty acid composition to source variations during various post flowering periods has been explored and analyzed by two widely used approaches: (i) evaluation of the dependence of the effect of short duration shading treatments on the moment in which they were imposed and (ii) window-pane analysis of the response of oleic acid percentage to ISR. The combination of both approaches allowed us to precisely assess the period during which fatty acid composition is most sensitive to solar radiation. Dynamics of grain filling and fatty acid composition empirically supports the statistically determined critical period and shed some light on the mechanisms underlying fatty acid response to environmental conditions during grain filling.

2. Materials and methods

Sunflower (*Helianthus annuus* L., hybrid DK3820) was grown in the field at the Unidad Integrada Balcarce INTA-FCA (37° S, 58° W) Balcarce-Argentina. Soil was a Typical Argiudoll. Experiments were performed during growing seasons 2008–2009 (Exp. 1) and 2010–2011 (Exp. 2). Seeds were planted on November 6th, 2008 and November 19th, 2010, for Exps. 1 and 2, respectively. Treatments were arranged in a randomized complete block design with three replicates. Experimental units were six rows six meters long spaced at 0.7 m. Plant population density at sowing was 6.5 plants m^{-2}. Crops were grown under optimal nutrient and water conditions. Soil fertility in all experiments was enough to attain maximum yields for sunflower crops grown under non-limiting water conditions (yield > 5000 kg ha^{-1}; Sosa et al., 1999; Andrade et al., 2000). Soil water content was measured every 5–7 days by the Time Domain Reflectometry method, with a moisture measuring system (Trase System, Model 6050X1, Soilmoisture Equipment Corp., Santa Barbara, CA, USA). Irrigation was applied to maintain soil water above 40% available water in the first 0.60 m of the soil profile during the entire growing season. Pests, diseases and weeds were adequately controlled. At flowering, pollination bags (Delnet, Rosario, Argentina) were used to prevent cross-pollination. Flowering of a plant was defined by the appearance of stamens in all florets from the outer whorl of the capitulum (R5.1 stage, Schneiter and Miller, 1981). Flowering of an experimental unit was considered to have occurred when 95% of the plants had reached R5.1 stage. Plants were self-pollinated manually.

Treatments meant to vary ISR during different periods of the grain filling were applied when inner flowers of 95% of the plants had been pollinated (three days after R6, Schneiter and Miller, 1981), and ended at physiological maturity. Since treatments were applied after grain set, grain number did not differ among treatments. Physiological maturity was reached at 615 °Cd af and 590 °Cd af in Exp. 1 and Exp. 2, respectively (base temperature = 6 °C). Treatments consisted of shading (Sh) and thinning (Th) whose starting and ending thermal time (°Cd af) are depicted in Table 1. Long term treatments (Th A, $Sh_{80\%}$ A and $Sh_{50\%}$ A) were applied during the whole grain filling period. Shading treatments were achieved by placing a uniform, black, synthetic, and neutral mesh cloth above the canopy of the two central rows (Dosio et al., 2000; Izquierdo et al., 2008). Shades reduced incident solar radiation by 80% (Exp. 1 and Exp. 2) or 50% (Exp. 2). Thinning treatments were performed by eliminating alternate plants in the row in order to get 50% (3.3 plant m^{-2}) of the original crop population density. Untreated sunflower plots served as control.

To estimate physiological maturity, 15 grains from rows 4 to 19 of three capitula were harvested twice a week during grain filling. To explore grain filling dynamics, 12 grains of rows 6–8 were excised in the same way. Grain removal was repeated on the same plant as long as total removal did not exceed 5% of average final capitulum grain number. Grains were oven-dried at 60 °C and weighed. Physiological maturity was determined as the time when average dry weight per grain did not further increase (Aguirrezábal et al., 2003).

2.1. Sample processing and chemical analysis

Once physiological maturity was reached, ten capitula were sampled from the two central rows of each plot and oven-dried with circulating air at 60 °C. Grains between rings 4 and 19 of the capitulum were manually separated in order to determine fatty acid composition of grains set at a similar date and therefore, exposed to similar environmental conditions (Izquierdo et al., 2002). Only non-empty grains (kernel occupying at least 20% of the internal volume of the hull) were considered in sample analyses. Oil extraction