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SCIENCE DIRECT®
Field Crops Research 96 (2006) 48–62
Field Crops Research
www.elsevier.com/locate/fcr

Responses of sunflower yield and grain quality to alternating day/night high temperature regimes during grain filling: Effects of timing, duration and intensity of exposure to stress

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Received 19 February 2005; accepted 20 May 2005

Abstract

In order to quantify the effects, at different stages during grain filling, of alternating day/night high temperature regimes on sunflower grain yield and quality, heads were exposed to high temperatures during 7 or 6 days starting either 10–12 days after anthesis (daa, HT1), 18 daa (HT2) or 24 daa (HT3). Also, heads were exposed to high temperatures for periods of 2, 4 or 6 days in each of HT1 and HT2. Temperatures covered a range of mean daily grain temperature of 20–40 °C and peak grain temperatures (i.e., those prevailing during the central 5 h of the daylight period) of 26–45 °C. High temperature stress for periods of 4 days or longer produced significant ($p < 0.05$) reductions in grain yield and grain quality. Early (HT1) exposure to stress reduced yield by 6%/°C above a mean grain temperature threshold of 29 °C; later (HT2 + HT3) exposures reduced yield by 4%/°C above a threshold of 33 °C. These reductions in yield were attributable to reductions in unit grain weight at all positions (periphery, intermediate, central) on the head, and an increase in the proportion of very small (10–30 mg) grains, termed half-full (HF) grains in this paper. In both full and HF grains, stress in either HT1 or HT2 reduced final pericarp weight, associated with fewer number of cell layers and thinner cell walls in the schlerenchyma. High temperatures reduced both the rate and duration of oil deposition in the grain, with the greatest effects being found with early (HT1) exposures. The unsaturation (oleic acid/linoleic acid) ratio of oil from mature grain was altered only when exposure to heat stress overlapped with the cessation of deposition of storage lipids. The effects of duration and intensity of heat stress on relative (to control) grain yield and oil content could be reasonably summarized using a linear response to cumulative hourly heat load calculated with a base temperature of 30 °C. We conclude that: (i) 4 days of alternating day/night temperatures resulting in mean daily grain temperatures of >30 °C can reduce sunflower grain yield and quality; (ii) the magnitude of these effects is strongly dependent on the timing of exposure and their nature on the grain growth processes active at the time of stress; and (iii) an hourly heat load (base = 30 °C) provides a useful integrative estimator of the effects of exposure to heat stress on grain yield and oil content for a given phase of grain filling.

Keywords: Helianthus annuus; High temperature stress; Grain weight; Pericarp; Oil; Fatty acid; Unsaturation ratio

1. Introduction

The temperature of some plant organs can exceed air temperature, particularly if they are exposed to direct sunlight, reflect poorly and/or do not dissipate heat easily through transpiration (Lewis and Nobel, 1977). Ploschuk and Hall (1995) found that grain temperatures in sunflower could be up to 5 °C warmer than air temperature during much of the daylight period on sunny days, in spite of the fact that heads were partially shaded by the upper leaves of the canopy. These observations suggest that sunflower grains could often be exposed to stressful high temperatures during part of the day on sunny days in both temperate and subtropical areas. Current tendencies towards increasing temperature, associated with global change (Easterling et al., 1997) might also increase the frequency of episodes of high temperature in warmer climates (Wheeler et al., 2000).

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0378-4290/$ – see front matter
doi:10.1016/j.fcr.2005.05.006

Exposure to a few hours per day of high temperature during grain filling are enough to affect the unit grain weight and grain quality in wheat (Tashiro and Wardlaw, 1990; Stone and Nicolas, 1995; Wardlaw et al., 2002) and barley (Savin and Nicolas, 1996; Wallwork et al., 1998; Passarella et al., 2002). Exposure of sunflower capitulae to constant temperatures >34 °C during 7 days reduced grain size and quality (Rondanini et al., 2003). A more precise definition of the thermal conditions that can evoke reductions in grain yield and quality in sunflower requires the use of alternating day/night temperatures (i.e., a regime closer to that operating under natural conditions) and an exploration of the number of days of exposure required to produce an effect.

The growth patterns of the components of the sunflower grain are shifted in time, so that the growth of the pericarp precedes that of the embryo, and the latter is well under way before storage lipids begin to accumulate (Connor and Hall, 1997). The relationship between the patterns for each component can vary between genotypes (Mantese, 2001) and cessation of storage lipid accumulation can occur either before or very close to grain physiological maturity. Because of these temporal shifts and their variation between genotypes, the outcome of an exposure to high temperature stress is likely to vary as a function of the degree of overlap between the active growth processes and the exposure to high temperature. Previous work on sunflower (Rondanini et al., 2003) used the inbred line HA89, in which oil deposition ceases 3–5 days before physiological maturity. It is therefore of interest to compare these responses with those of high oil content hybrids in which oil deposition does not cease until very close to physiological maturity. Differences of this nature could also impact on oil quality (i.e., ratio of oleic to linoleic acid), as this variable did not respond to early exposures to stress in HA89, but showed alterations in response to exposures during mid- and late-grain filling. There is also some uncertainty about the effects of high temperature on the growth of the pericarp. Constant high temperatures during about two thirds of the grain-filling period reduced pericarp weight (Chimenti et al., 2001), but exposures of 7 days to constant high temperature in early grain filling did not (Rondanini et al., 2003).

In this work we exposed the heads of plants of high oil content sunflower hybrids to high alternating day/night temperatures in up to three separate phases during the grain-filling period. Duration of the exposure varied across the four experiments between 2 and 7 days, and our main objectives were to: (i) quantify the changes produced by exposure to stress on yield and its components; (ii) determine the duration and intensity of exposure to stress required to evoke a response; and (iii) relate observed responses to the patterns of growth of the components of the grain (hull, kernel and oil) and the determinants of grain oil content and quality.

2. Materials and methods

2.1. Growth conditions and heat stress treatments

Four experiments were performed at the Facultad de Agronomía, Universidad de Buenos Aires (34°35′S) during the summers of 2001–2004. In Exps. 1 and 2, four alternating day/night high temperature regimes lasting either 7 (Exp. 1) or 6 days (Exp. 2) were applied in each of three separate phases of grain-filling (HT1–HT3, Table 1). In Exps. 3 and 4, three different alternating day/night high

Table 1
Summary description of environmental conditions prior to flowering and during grain filling in Exps. 1 to 4, together with information on crop development, and timing, duration and number of levels of high temperature stresses applied

	Exp. 1	Exp. 2	Exp. 3	Exp. 4
Genotype	Paraíso 20	Paraíso 30	Paraíso 30	Paraíso 30
Pericarp colour	Black striped	White striped	White striped	White striped
Sowing date (S)	24 January 2001	2 January 2002	23 November 2002	27 November 2003
Days to flowering (F)	52	55	74	63
Average mean temperature (°C) S–F	26.2	24.9	24.6	23.4
Average PAR (mol m^{-2} d^{-1}) S–F	37.5	42.4	39.3	38.1
Duration of temperature treatments (days)	7	6	2, 4 and 6	2, 4 and 6
Number of temperature treatments	4	4	3	3
Beginning of treatments (daa: days after anthesis)				
HT1	10	12	12	12
HT2	18	18	18	18
HT3	26	24	–	–
Physiological maturity (PM) for controls (daa)	31	29	30	34
Average mean temperature (°C) F–PM (for controls)	23.6	22.3	21.5	22.0
Average PAR (mol m^{-2} d^{-1}) F–PM	12.9	11.2	16.6	16.1
Grain yield (g/plant) for controls				
HT1	42.2	73.1	75.5	63.4
HT2	38.0	69.2	78.3	60.9
HT3	42.3	70.0	–	–

Values for grain yield of control plants are mean values for each timing of stress in a given experiment.