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The critical period for yield determination in oat (*Avena sativa* L.)

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ABSTRACT

Annual crops accommodate environmental variation through grain number, whereas grain weight is more stable. Grain number is determined in a species-specific window which has been established for many crops, but not for oat. Field trials were established at two sites in southern Australia and in one site in southern Chile where successive, single 14-d shading periods were applied from crop establishment to maturity to identify the developmental window when the crop is most responsive to stress. Three oat varieties were compared in Australia (Mitika, Williams and Wintaroo) and two in Chile (Mitika and Yallara). Unshaded controls yielded from 327 g m^{-2} in Australia to 747 g m^{-2} in Chile. The overall pattern of yield response to time of stress was similar to that of wheat; it spanned the period from stem elongation (GS31) to about 10 days after anthesis. In line with theory, most of the yield response was mediated through response in grain number; further, the two environments in Australia where reduction in grain number in response to stress shortly before anthesis was larger, individual grain weight increased with shading. Grains per panicle was more responsive to stress than panicles per m^2, in contrast to other cereals. The critical period is often assumed to be species-specific. However, our limited comparison of varieties suggests that there might also be varietal differences in oat. Interaction between time of shade and variety was significant for harvest index in all locations. Hence, we propose genotype-dependent response to time of stress is worth exploring.

1. Introduction

Oat is grown worldwide, with 60% of the world's production in Europe and 25% in the Americas. The Russian Federation and Canada are the largest producers of oat grain (FAOSTAT, 2016). Oat yield increased globally between 2003 and 2010, but acreage and production have declined (FAOSTAT, 2016). This is partially related to competition with other crops. For example, there are 310 oat varieties in the EU Plant Variety Database compared with over 1870 varieties of wheat (Marshall et al., 2013). In Australia, oat is currently grown over approximately 1.3 million ha producing about 1.5 million tonnes of grain and 850,000 t of export hay. In Chile, oat is the second largest temperate cereal after wheat, and has shown a stable acreage averaging 82,000 ha throughout the last 50 years, and increasing recently to 126,000 ha (ODEPA, 2014). Health benefits, such as lower blood cholesterol re-absorption, reduced risk of heart disease, and satiety (Ruxton and Derbyshire, 2008; Rasane et al., 2015) are drivers for increased demand for oat. High yield and quality are required for profitable oat crops, and these goals require filling major gaps in its physiology.

Defining the critical period for grain set and yield is important for both agronomy and breeding. Successful crop management seeks to avoid the coincidence of critical periods of vulnerability and prevalent abiotic stresses such as frost and heat (Kirkegaard and Hunt, 2011). Similarly, strategies to control biotic stresses (pest and diseases) require the knowledge of key phases for yield determination. Extending the duration of the critical period has been proposed as an avenue to breed high yielding varieties (Slafer et al., 2015) but this is not straightforward due to trade-offs with fruiting efficiency (Fischer, 2016) and overriding environmental influence (García et al., 2011).

Annual crops accommodate environmental variation through grain number, while grain weight is more stable (Sadras, 2007; Slafer et al., 2014). Grain number is determined in a species-specific window which has been established for wheat, barley, triticale, maize (Fischer, 1985; Savin and Slafer, 1991; Slafer et al., 1994; Arisnabarreta and Miralles, 2008; Estrada-Campuzano et al., 2008; Cerrudo et al., 2013), sunflower (Cantagallo et al., 1997), soybean, field pea, lupin, pea and chickpea (Board and Tan, 1995; Guilioni et al., 2003; Sandana and Calderini, 2012; Lake and Sadras, 2014). The curves relating yield and timing of stress for these crops have

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been compiled and compared (Calviño and Monzon, 2009; Sadras and Dreccer, 2015). Sadras and Dreccer (2015) highlighted the pre-flowering critical period in wheat and barley in contrast to the post-flowering critical period of grain legumes. While these patterns are robust, the critical period for grain set and yield is earlier in barley than in wheat, especially in two row barley (Arisnabarreta and Miralles, 2008), hence the risk in extrapolating between cereals.

The aim of this study was to determine the critical period for grain set and yield in oat. Common to previous studies on the critical period, where the aim was to measure the effect of timing rather than intensity of stress, we used shading to capture effects of common stresses such as drought and nitrogen deficiency mediated by reductions in photosynthesis (Fischer, 1985; Arisnabarreta and Miralles, 2008; Sandana and Calderini, 2012; Lake and Sadras, 2014).

2. Material and methods

2.1. Crops and treatments

Field experiments were carried out in three locations: Pinery (34° 19′S, 138° 29′E) and Turretfield (34° 32′S, 138° 50′E) in Australia, and the experimental station of Universidad Austral de Chile, Valdivia (39° 47′S, 73° 14′E) in Chile. At Pinery and Turretfield, crops were sown on 28th May 2013 and 6th June 2014, respectively, in plots comprising of five rows, 3.2 m long at a spacing of 0.21 m. In Valdivia sowing date was 5th July 2014 and plots comprised of five rows, 1.5 m long at a spacing of 0.15 m. Crops were fertilised at sowing with 22 kg N ha^{-1} and 55 kg P_2O_5 ha^{-1} (120 kg ha^{-1} of diammonium phosphate) in Australia and 300 kg N ha^{-1} (split in two halves; at sowing and beginning of tillering), 100 kg P_2O_5 ha^{-1} and 150 kg K_2O ha^{-1} in Chile. Three varieties, Mitika, Williams and Wintaroo, where grown in Australia and, two varieties, Mitika and Yallara, were grown in Valdivia. All are grain varieties, except Wintaroo, a hay variety. Mitika is a dwarf type, and the remaining varieties are medium height to tall.

The effect of timing of stress was quantified using unshaded controls and consecutive, single shading events applied for two weeks, starting two (Pinery) or three weeks (Turretfield, Valdivia) after sowing (Fischer, 1985; Arisnabarreta and Miralles, 2008; Sandana and Calderini, 2012; Lake and Sadras, 2014). Treatments were laid out in a split plot design with varieties as main plots and time of shading as sub-plots, with four (Pinery and Turretfield) or three replicates (Valdivia). Shading was applied with UV stabilised black nylon net set on PVC frames of 1 × 1.3 m (Australia) or wood frames (Chile); the height of the shade net was gradually increased as required to maintain it at 20 cm above the crop. The reduction in the incoming photosynthetically active radiation (PAR) during a shading treatment was 94% in Pinery and Turretfield and 80% in Valdivia.

2.2. Measurements and data analysis

Crop phenology in unshaded controls was recorded fortnightly using Zadoks scale (Zadoks et al., 1974). Samples of 0.32 m^2 (Australia) and 0.15 m^2 (Chile) were collected from the centre of the shaded portion in the plots at maturity and oven dried to determine yield and its components. Shoot biomass, yield, harvest index, grain number, and individual grain weight were determined at all the three environments; number of panicles per m^2, number of grains per panicle and screenings were determined only in Australia. Screenings is the percentage of grains on a weight basis, that pass through a 2 mm screen and are generally discarded before milling. Yield, shoot biomass, individual grain weight, number of panicles, and screenings were determined directly, and the other components were derived from these primary traits.

Data were analysed in two complementary ways. First, analysis of variance was performed for each experiment to test the effect of timing of shading, variety and their interaction on yield and its components. Fisher's PSLD was used to test for differences between the shaded treatments and the unshaded controls at $P \leq 0.05$. Second, yield and its components were expressed as a ratio between shaded and unshaded control for each timing of shading. Ratios were then plotted against the mid-point of the shading periods using a phenological scale for controls and spline curves fitted by eye as in Sandana and Calderini (2012). Thermal time (°Cd) was calculated using daily mean temperature and a base temperature of 0 °C (López-Castañeda and Richards, 1994). Temperature was derived from the nearest available meteorological station for each site.

3. Results

3.1. Growing conditions and crop phenology

Fig. 1 summarises the weather during the experiments. Pinery and Turretfield had similar weather with higher incidence of radiation, higher temperature and higher evaporative demand than Valdivia. The highest temperature during the growing season was 38 °C in Pinery, 41 °C in Turretfield and 30 °C in Valdivia. Rainfall tracked reference evapotranspiration until flowering at Pinery and Turretfield and ceased thereafter, characteristic of Mediterranean-type environments. Seasonal rainfall was 257 mm at Pinery and 252 mm at Turretfield. The rainfall was always above reference evapotranspiration in Valdivia, which received 654 mm during the growing season.

The crop duration for all three environments ranged from 168 to 175 days (Fig. 1). In Australia, Mitika was three days earlier than Williams and 11 days earlier than Wintaroo to GS60. In Chile, Mitika and Yallara had similar phenological patterns (Fig. 1).

3.2. Yield of unshaded control and response to time of stress

Associated with milder temperature and wetter conditions (Fig. 1), yield of controls in Valdivia almost doubled the yield of controls in Pinery; variation in yield among environments was primarily related to grain number (Table 1). Mitika was the highest yielding variety in all the three sites; it out-yielded Wintaroo by 17–45% in Australia, and it out-yielded Yallara by 28% in Chile.

Table 2 summarises the ANOVA of grain yield and yield components. Both variety and time of shading affected yield and most yield components in all three environments. Of interest, interactions indicate variety-dependent response to time of shading and were significant for yield, grain number, grain weight and screenings at Pinery, grains per panicle at both Pinery and Turretfield, and harvest index in all three environments (Table 2). Yield was related to grain number, biomass and harvest index and independent of grain weight across the experiments (Table 3). Grain number related more closely to grains per panicle than to panicles per m^{-2} (Table 3).

3.3. Critical period of yield determination

Fig. 2 shows the effect of timing of stress on yield, grain number and grain weight in relation to crop development, and Fig. 3 shows the effect of timing of stress on the components of grain number per m^2 and screenings. The sensitivity window for yield spanned from stem elongation to approximately 300 °Cd after anthesis. Yield response to time of stress was related to the response of grain number and independent of grain weight. Furthermore, in the Australian