



The critical period for yield and quality determination in canola (*Brassica napus* L.)

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ABSTRACT

Despite its global significance as an edible oil and biofuel, the critical period for yield determination in canola (edible oilseed rape – *Brassica napus* L.) has not been determined in the field. Field experiments were conducted at two contrasting sites in southern Australia where 100 °Cd shading periods (15% PAR transmitted) were applied from early vegetative growth until maturity to identify the developmental period when the crop was most sensitive to stress. Despite the significant difference between the two sites for yield in the unshaded control (450 g m⁻² in New South Wales, and 340 g m⁻² in South Australia), the critical period was consistent at both sites extending from 100 to 500 °Cd after the start of flowering (BBCH60), and centred 300 °Cd after BBCH60. Seed number (seed m⁻²) was reduced by an average of 48% in the critical period, generated in equal parts by reduced pod m⁻² in the early part of the period, and reduced seed pod⁻¹ in the latter part. Reduced seed number was partially compensated by an increase in seed size of 29%. These trends were similar on the branches and main stem. On the main stem, the timing of the critical period moved from earlier to later from lower to upper pods linked to the timing of their development. Seed oil content declined and protein content increased under shading in the critical period, while both oil and protein yield (kg m⁻²) were reduced by 40–50% and 30–40% respectively. The critical period is coincident with the greatest number of near-open buds and newly opened flowers, which are highly sensitive to assimilate supply for ovule development. Both pod abortion and restricted capacity for compensatory growth of surviving pods are consequences of assimilate restriction on developing ovules. Identification of the critical period provides a useful target for breeding and management strategies to maximize productivity.

1. Introduction

Canola (*Brassica napus* L.) or edible oilseed rape is the third most important oilseed produced globally with annual production increasing 2–4-fold in many of the major producing countries in the last 20 years (Kirkegaard et al., 2016). The rising world population and renewable energy policies are driving a surge in oilseed demand which is predicted to continue, and production may need to double by 2050 to satisfy these projections (Lu et al., 2011). The expansion of canola in most major producing countries from relatively reliable temperate growing areas in which it is well adapted, into more marginal and drier areas has combined with the predicted impacts of climate change to increase the future exposure of canola to abiotic stress such as temperature extremes and water deficit (Dreccer et al., 2018). As a result, there is an

increasing need to understand the effects of the intensity, timing and duration of stress on yield determination to target breeding and management strategies to maintain or increase canola productivity.

The critical period for yield determination is defined as the physiological stage in which abiotic stresses have the largest impact on yield determination (Robertson et al., 1934). Critical periods are typically determined using successive and discrete periods of shading to reduce the photosynthetic assimilates available for growth, mimicking the effects of abiotic stresses. The critical period for yield determination has been defined in this way for numerous crops including cereals (Fischer, 1985; Arisnabarreta and Miralles, 2008; Mahadevan et al., 2016), grain legumes (Sandana and Calderini, 2012; Lake and Sadras, 2014) and sunflower (Cantagallo et al., 1997). Yet despite its global importance as an oilseed crop, the critical period for canola has not

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been similarly determined. Previous studies have used either shading (Tayo and Morgan, 1979; Habekotte, 1993; Iglesias and Miralles, 2014; Labra et al., 2017) or defoliation and targeted irrigation (Tayo and Morgan, 1979; Zhang and Flottmann, 2018) to investigate source-sink relationships in canola and to investigate the plasticity of yield components. Defoliation and irrigation are likely to have confounding effects on yield (Lake and Sadras, 2014), and the shading experiments reported to date have used different intensity, timing and durations of shading. In most cases the shading extended for the entirety of the flowering period during which overlapping physiological processes including the growth and/or abortion of branches, flowers, pods and seeds are occurring simultaneously. Thus the existence of a discrete critical period most sensitive to stress, and the key physiological mechanisms involved remain unknown. The overall anthesis period which may last from 2 to 6 weeks in canola, is certainly considered to be a critical period for yield determination. Seed density (seed m^{-2}), the parameter most closely related to yield, is determined during anthesis (Diepenbrock, 2000; Iglesias and Miralles, 2014). Assimilate reduction in the period causes the most significant reductions in yield (Tayo and Morgan, 1975; Zhang and Flottmann, 2018), and the abortion rates of flowers, pods and seeds are highest during that period (Habekotte, 1993; Tayo and Morgan, 1979). However, the capacity for compensation in yield through increased seed weight, when seed number was reduced by shading at flowering, also varies from almost no change (e.g. 3% increase in seed weight in Zhang and Flottmann, 2018) to complete compensation (61% increase in seed weight, Labra et al., 2017). As a result of the extended flowering period in canola under Australian conditions (2–6 weeks), the overlapping yield-determining physiological processes during that period, and the plasticity in yield resulting from various compensatory processes, we sought insights from more discrete periods throughout the season in field-grown canola. Seed fill in canola commences after pod hulls have reached maximum size, and seed filling progresses with expansion of the seed coat with liquid endosperm, embryo growth and increasing oil content (Diepenbrock and Geisler, 1979). As a result, oil accumulates quite late in seed development so that assimilate reduction post-anthesis may be expected to reduce oil content. Fortescue and Turner (2007) found that excluding light from siliques from 2, 10 or 30 days after flowering had large effects on seeds per pod, but little impact on oil concentration. Labra et al. (2017) found no effect on seed oil or protein from reductions in the source-sink ratio during the entire flowering period, despite significant impacts on seed number and seed weight. This resulted from increases in both the rate and duration of the seed-filling period in plants shaded during flowering. The longer shading periods with overlapping physiological process and compensatory strategies make it difficult to determine from these studies whether specific critical periods for oil concentration may exist, and to what extent oil and protein content may be differentially affected. Given both seed oil and meal protein can affect the economic value of canola, the influence of stress timing on seed quality and oil yield are also of interest.

We report two field experiments in diverse environments in southern Australia in which successive 100°Cd shading treatments were used to determine the critical period for yield determination in field-grown spring canola. The components of yield, its distribution on the plant, and the impact on seed quality (oil and protein) were also assessed.

2. Material and methods

2.1. Sites and experimental design

Field experiments were carried out in 2016 at two sites in south-eastern Australia: 25 km north of Wagga Wagga ($-34.96; 147.31$) in southern New South Wales (NSW); and Riverton in South Australia ($-34.12; 138.76$). The Wagga Wagga site was located on a deep acid loam Kandosol soil (Isbell, 2002) in the equi-seasonal rainfall zone of

southern NSW with average annual rainfall of 546 mm and growing season rainfall (April to October) of 332 mm. The Riverton site was located on an acidic loamy clay Chromosol in the winter-dominant Mediterranean environment of South Australia with average annual rainfall of 527 mm, and average growing season rainfall of 461 mm. Canola followed crops of wheat and faba-bean in the previous two seasons, and the sites were elevated in the landscape to reduce the risk of damaging frost. In Australia, spring canola is sown in autumn (fall) and grows vegetatively through the mild winter to flower in early spring, and is harvested in late spring or early summer (Kirkegaard et al., 2016). At both sites, the spring hybrid variety Pioneer® 44Y89 (CL) which has a phenology type described as fast-mid development in Australia, was used in the experiments, and was sown on 2nd and 3rd of May at Wagga Wagga and Riverton, respectively, in plots 4 m to 6 m in length and comprising 6 rows spaced 0.25 m apart. The crops were managed using recommended agronomy to manage weeds, pests and diseases and were fertilised to avoid nutrient limitations to growth. At Wagga Wagga the crops were fertilised at sowing with 11 kg N ha^{-1} and 23 kg P ha^{-1} as mono-ammonium phosphate with the seed and 100 kg N ha^{-1} broadcast as urea pre-sowing, and top-dressed with 100 kg N ha^{-1} as urea on 8 June (stem elongation). Soil mineral N measured prior to sowing (1.2 m) was 133 kg N ha^{-1} . At Riverton the crops were fertilised at sowing with $18 \text{ kg ha}^{-1} \text{ N}$ and $20 \text{ kg ha}^{-1} \text{ P}$ as di-ammonium phosphate with the seed and top-dressed on 30 June and 21 July with 41 kg N ha^{-1} with liquid urea and ammonium sulphate. Soil mineral N measured prior to sowing was 124 kg N ha^{-1} .

The effect of timing of stress was quantified using unshaded controls and consecutive, single shading events applied for a targeted $\sim 100^\circ\text{Cd}$ which varied from 6 to 13 days duration as temperature changed through the season (Fischer, 1985; Arisnabaretta and Miralles, 2008; Lake and Sadras, 2014; Mahadevan et al., 2016). The shading treatments commenced around 30 days after sowing (das) at Wagga Wagga and 48 das at Riverton which corresponded to the 4–6 leaf stage at both sites and continued to physiological maturity resulting in 15 shade timings treatments at Wagga Wagga and 14 at Riverton. In effect, the earliest shading period at Riverton was absent. Treatments were arranged in a randomised complete block design at each site with four blocks, and the shaded areas ($2 \text{ m} \times 3 \text{ m}$ Wagga Wagga; $2 \text{ m} \times 1.5 \text{ m}$ Riverton) were established within the randomised plots in each block. The number of shade treatments required (up to 15) was estimated from long-term temperature data at the sites. Shading was applied with stabilised nylon net set onto steel frames that were mobile, and adjustable so that the height could be adjusted as the crop grew to keep the top of the net 50 cm above the crop canopy. The southern end was kept partially open to ensure temperature and humidity was similar to the outside while minimising light entry. The reduction in incoming photosynthetically active radiation was 85% at both sites.

2.2. Plant measurements and data analysis

Crop phenology in the unshaded control treatments was recorded weekly using the BBCH development code (Meier, 2001) and was also monitored in the shaded treatments to determine if any significant differences were observed as a result of the transient shading. The start of flowering was taken as the point when 50% of plants had one open flower (BBCH60), and this was used as the point of origin for the consideration of the timing of the critical period. The end of flowering corresponded to BBCH69. The phenology was recorded in thermal time ($^\circ\text{Cd}$), using a base temperature of 0°C , and defined as SUM (Average Daily $T - 0^\circ\text{C}$ base temperature). The mid-point of each shading period calculated in $^\circ\text{Cd}$ was used with reference to this point of origin to estimate the critical period. Bordered quadrats comprising the central 4 rows (1 m^2) were sampled from each shaded area of the plots at maturity and oven dried to determine seed yield and yield components. Shoot biomass, yield, harvest index, pod number, seeds per pod, seed number, and individual seed size were determined. A subsample of seed

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