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Source-sink manipulations indicate seed yield in canola is limited by source availability

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ABSTRACT

In canola, strong competition for assimilates from the overlapping of structural and reproductive growth can lead canola yield to be limited by source availability during seed filling. In this study, we tested this hypothesis by manipulating source-sink relationships in a series of experiments (i) shading during flowering and during seed filling, (ii) partial removal of flowers and pods of individual plants, (iii) defoliation at the vegetative stage and after full flowering, and (iv) supplemental irrigation during seed filling. Shading (60% of incoming radiation reduction) during flowering reduced the number of pods and seeds (sink) but increased mean seed weight (MSW), resulting in 24% yield loss. Shading during seed-filling reduced MSW as well as the number of pods and seeds per area and, causing 26% yield reduction compared to the control. Partial pod removal and full defoliation at full flowering decreased pods per plant and reduced yield by10–40%. Defoliation during the vegetative stage reduced yield by 11%. Supplemental irrigation increased yield by 10% without any impact on MSW. However, these manipulations simultaneously either reduced or increased the sink size (seeds m^{-2}) while altering the source availability. If the manipulated plants were assumed to have a similar sink size to the control, shading would have decreased MSW by 16–22%. Similarly, the full defoliation after full flowering decreased MSW by 27% and the defoliation at the vegetative stage by 11%. On the contrary, supplemental irrigation would have increased MSW by 8–21%. The decrease in MSW in the downward-manipulation of source availability and the increase in MSW in the upward-manipulation of source availability indicate that canola yield was driven by source availability during seed filling period. However, yield reduction from shading at flowering indicates that yield could be limited by sink size established during flowering. Therefore, agronomic management and future breeding should be directed to increase assimilates available to the crop from flowering onwards.

1. Introduction

Canola is Australia's third most important crop after wheat and barley (Kirkegaard et al., 2016) and has become one of the most important break crops for the wheat-based farming system (Zhang et al., 2016). A quantitative understanding of the extent to which source or sink limit yield and how this changes during development is crucial to improving yield of canola. The final grain yield of a crop can be considered as the outcome of the balance between the supply of carbohydrate (source) and the capacity of grains to accumulate available carbohydrates (sink). Sensitivity of the crop to source and sink manipulation has been used to investigate the critical period for determining grain number (Fischer, 1985; Keiller and Morgan, 1988) and to evaluate whether the yield is limited by sink or source during the grain filling period (Habekotte, 1993; Iglesias and Miralles, 2014). Understanding the sensitivity of the crop to source-sink manipulation on yield and seed number can provide physiological knowledge for agronomist to adopt adequate management practices to achieve higher yield and for breeders to select for particular traits (Magari and Kang, 1993; Foulkes et al., 2007; Zhang et al., 2010).

In determinate crops, such as wheat and barley, grain number (sink size) is determined by the completion of anthesis and seed weight is determined during the seed filling period (after anthesis). These two processes have little overlap, and thus there is little competition for assimilates between determining grain number and seed weight (Hay and Kirby, 1991; Slafer and Savin, 1994). This distinct separation of two processes enables yield limitation by source and sink to be determined relatively easily based on the change in mean seed weight (MSW) to a manipulation altering the source-sink ratio. Majority of the source-sink manipulation studies concluded that the yield is limited mainly by sink rather than source in wheat and barley (Borras et al., 2004; Calderini et al., 2006; Ruuska et al., 2006; Foulkes et al., 2007; Zhang et al., 2010).

In contrast, indeterminate crops, such as canola, are much more

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complex because they have a strong overlap in flowering, stem and branch growth, pod setting and development, and seed filling. In canola, for example, basal nodes are already at the pod setting and seed filling when upper nodes are reaching flowering, and the crop continues to grow stems and branches (Tayo and Morgan, 1975; Iglesias and Miralles, 2014). This overlap inevitably results in a strong competition for sources by different plant organs (Tayo and Morgan, 1979) and make it less straightforward to determine whether yield in canola is limited by source availability or sink capacity. Furthermore, canola experiences a rapid decline in canopy photosynthesis activity during the pod-setting and seed filling period as leaves senesce (Allen and Morgan, 1975; Mendham et al., 1981), and flowers shade the canopy (Rao et al., 1991). This competition and decline in canopy photosynthesis activity may lead to yield and seed number being more sensitive to assimilate supply (source) during the seed filling period. Despite this significant difference, there have been few studies on whether the yield of canola is limited by sink or source and on how sink and source limitation affect yield at different growth stages. In a controlled environment, variations in yield in oilseed rape (*Brassica napus* L.) have been shown to be linked with the source availability from flowering onwards and the strength of pods and seeds as sink to draw on the supply of source (Tayo and Morgan, 1979). Pruning axillary branches increased the source-sink ratio of canola and produced larger embryos and heavier seeds, but the exclusion of light from the developing pods and seeds for their entire growth period significantly reduced seed number per pod (Fortescue and Turner, 2007). The individual plants in a controlled environment can experience different light and water environment compared to those in a canopy under the field condition, and therefore such conclusions might not be directly extrapolated to field conditions. In field conditions, shading at flowering onwards reduced sink size (pod and seed density), reduced pod density and yield because pod and seed set and development depends on the availability of photosynthates (Habekotte, 1993). In contrast, Labra et al. (2017) observed that seed yield was not affected by shading during flowering because an increase in single-seed weight fully compensated for the effect of reduced seed number. Defoliation at the vegetative stage was reported to have no impact on yield in canola as long as it is done before budding stage (Kirkegaard et al., 2012). Iglesias and Miralles (2014) found that shading during seed filling decreased MSW while pod removal increased MSW. These experiments concluded that oilseed rape is either source-limited or source and sink co-limited during the seed filling period. However, the manipulations in the above studies changed the source availability and sink size at the same time and therefore the effect of source and sink manipulation on yield were intermixed and not separated.

In this study, we hypothesize that source or sink limitation in canola depends on the growth stage, namely that yield is driven by source availability during seed filling while it can be limited by the established sink size during flowering. If the yield of canola is limited by source availability rather than sink capacity, then any manipulation of source-sink ratio downwards would reduce MSW, yield and vice versa, provided the sink size (grain number) remains relatively similar between the control and manipulations. In this study, we manipulated source and sink size by shading the crop at different growth stages, partial removal of the sink, and providing additional sources by supplemental irrigation to investigate the responses of grain yield and yield components to the source- and sink-manipulations. We aimed to determine whether canola seed yield is limited by the availability of photosynthetic assimilate (source) or by the sink size at different growth stages and explore the implication of the source-sink relations to agronomic management and breeding to maximize yield in southern Australia.

2. Materials and methods

Six spring canola cultivars (*Brassica napus* L.) were selected for this source-sink relationship study. The cultivars included open-pollinated and hybrid triazine tolerant (TT), imidazolinone tolerance (IT) and conventional canola (CT) canola, representing the current canola varieties grown in Australia. The experiments were conducted in 2010 and 2011 near Kojonup, Western Australia. The year 2010 was a warm and extremely dry season with the growing season rainfall at 20% percentile (1 in 5 years) while 2011 was slightly above-average rainfall year (Zhang and Flottmann, 2016a). The crop was sown to achieve 40 plants m^{-2} by adjusting seeding rates according to thousand seed weight and the germination rate. Using a randomized split-plot experimental design, we conducted the following experiments: (i) shading during flowering and during seed filling, (ii) partial removal of flowers and pods of individual plants, (iii) defoliation at the vegetative stage and after full flowering, and (iv) supplemental irrigation during seed filling in 2010 and 2011 (Table 1). The genotype was assigned to whole plot and the treatments to the subplot. The treatments were replicated four times each year. The plot size was 20 m by 1.54 m. In both years, the crop was managed under close to the optimum agronomic conditions by supplying with 150 kg N ha^{-1} split as 20 kg N ha^{-1} at sowing, 50 kg N ha^{-1} at 4–6 leaf stage, and 50 kg N ha^{-1} at budding to flowering. The initial soil available N in the 0–120 cm soil profile at sowing was at 120 kg/ha in 2010 and 2011. Therefore it was assumed that N was not limiting.

Table 1
Information about experiments.

Experiment	Year	Treatment scale	No of genotypes*	Length of stress (days)
Shading at flowering	2010, 2011	Canopy-scale/ Micro plot	6	35
Shading during seed filling	2011	Canopy-scale/ Micro plot	6	45
Defoliation	2010	Individual plants *in situ*	6	
	2011	Canopy-scale/ Micro plot	6	
Flower and pod removal	2011	Individual plants *in situ*	6	
Supplemental irrigation	2010, 2011	Canopy-scale/ Micro plot	6	

* The six genotypes are CB Jardee, Hyola 50, Hyola 751, Pioneer 46Y78, Thunder, and Tornado.

2.1. Defoliation, partial flower and pod removal experiments

In 2010, nine plants with similar plant height, number of branches, and stem diameter at 30 cm height above the ground at flowering were tagged in each plot. Three plants were used as the control treatment, three as defoliation treatment, and three as partial flower and pod removal. The three plants used for treatments were randomly selected from the nine plants. For the defoliation treatment, all leaves on the three plants were removed by hand at the base of petiole, and the defoliated plants remained in situ within the crop canopy. After plants passed full flowering and pods appeared in about 2/3 of the main raceme, 50% of pods and remaining flowers on raceme and branches were cut off using a pair of scissors. At maturity, the three plants from each treatment were harvested separately for biomass, harvest index, yield, and yield components.

In 2011, a separate defoliation experiment was conducted during the vegetative stage. The defoliation treatment was imposed on six cultivars at 5 m length at one end of 20 m main plot by removal of all leaves before the bud visible stage using a whip-snipper. At maturity, plant samples from an area of 0.54 m^{-2} quadrat (5 rows of 0.5 m) were harvested from each defoliated and control plots for biomass, yield and harvest index measurement and a separate three randomly selected