

Source-sink manipulation in canola (*Brassica napus* L.) indicates that yield is source limited

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Abstract

Understanding the source-sink relationship and its influence on yield is critical in developing strategies for breeding and managing crops for high yield. The aim of this work was to determine whether the yield in canola when grown in high rainfall area is limited by the sink or source. Six canola cultivars were grown in field conditions and a series of experiments were conducted to manipulate the source-sink ratios in 2010 and 2011, including complete defoliation of individual plants and early canopy defoliation, partial removal of flowers and pods at full flowering, 60% reduction in incoming solar radiation for 5 weeks by shading from the first flower and during the pod-filling period, and supplemental irrigation during pod-filling. The defoliation and shading experiments reduced seed yield by 17-26% because the imposed treatments significantly reduced sources. The partial pod removal and shading during flowering increased mean seed weight (MSW) as the source available to the remaining seeds was increased. Supplemental irrigation increased yield by 10% without reducing MSW. The findings from all the experiments indicate that canola yield is predominantly limited by the source availability. Therefore agronomic management and breeding should be directed to increase source available to crop throughout the growing season.

Key words

Source-sink relation, shading, pod removal, defoliation, supplemental irrigation

Introduction

Sensitivity of crops to source and sink manipulation has been used to investigate the critical period for determining grain number and to evaluate whether the yield is limited by sink or source during the grain filling period. In determinate crops such as wheat and barley, grain number is determined by anthesis and has little overlap with determination of grain weight, and therefore little competition for assimilates between determining grain number and grain weight. Canola is an indeterminate crop with a strong overlap in flowering, stem growth, branch growth, pod setting, and grain setting which is extended beyond flowering (Iglesias and Miralles, 2014). This overlap inevitably causes a strong competition for assimilates by different plant organs. Furthermore, canola experiences a rapid decline in canopy photosynthesis during the pod-setting and seed filling period as leaves senesce (Mendham et al., 1981). The competition for assimilates and decline in canopy photosynthesis activity may lead to yield of canola and grain number being more sensitive to assimilate supply. Despite this difference between canola and cereals, source–sink manipulation studies have focused on determinate crops such as wheat and barley (Calderini et al., 2006; Zhang et al., 2010). There have been few studies on whether the yield of indeterminate crops such as canola is limited by sink or source and the impact of sink and source limitation on yield at different growth stages under field conditions (Palta et al., 2008; Sandana et al., 2009). In southern Australia, canola has become the third largest crop and plays a significant role as a break crop in farming system. Understanding the sensitivity of canola to source-sink manipulation on yield and seed number can provide physiological knowledge for breeders to target breeding and for agronomist to adopt management practices to maximise yield. The aim of this study was to evaluate the sensitivity of grain yield and yield components of canola to source and sink manipulation at different growth stages and explore the implication of the source-sink relations to breeding and agronomic management to maximize yield in southern Australia.

Materials and methods

Six open-pollinated and hybrid spring canola cultivars (*Brassica napus* L.) were sown on 20 May each year (2010 and 2011) at Kojonup, Western Australia and grown under well fertilised conditions. A randomized split-plot experimental design was used to conduct defoliation at individual plant and canopy levels, partial pod removal at full flowering, shading at flowering and at the beginning of pod filling, and supplemental irrigation at pod filling. The genotypes were assigned in whole plot and the treatments in subplot. The

treatments were replicated 4 times each year. The plot size was 20 m by 1.54 m. The complete defoliation and partial pod removal experiments were conducted in individual plants (3 plants per plot) at full flowering. Canopy defoliation was also conducted at canopy (an area of 5 m by 1.8 m) levels at the 8 leaves stage. Shading at flowering was imposed for 5 weeks on an area of 2 m by 1.8 m using horticultural shade cloth when the first flower appeared. Shading at pod filling was imposed from the end of flowering (10% flowers remaining) to maturity. Shading reduced the photosynthetic active radiation by 60%. For supplemental irrigation treatment, 60 mm of water was applied to six genotypes in a micro plot consisting of an area of 1.8 m by 2 m within the whole plot. For the individual plant defoliation and pod removal experiments, individual plants were harvested. For early canopy defoliation, shading, and irrigation experiments, plant samples were harvested from an area of 0.54 m². All samples were dried to determine yield and yield components. A split-plot ANOVA was performed to evaluate the impact of treatment on biomass, yield, harvest index, and yield components and the interaction between genotype and the treatments. Genotype was assigned in the whole plot and the treatments in the subplot. The means were compared using the LSD of the means, calculated from standard errors of the difference of the means using corresponding degrees of freedom.

Results

Defoliation caused significant reduction in all yield components except MSW with no interaction between genotype and the treatment. It reduced biomass per plant by 33% ($P < 0.001$), HI by 11% ($P < 0.001$), and yield by 33% (Fig. 1). The yield reduction was attributed to 26% ($P < 0.001$) fewer pods per plant, and 19% ($P < 0.001$) fewer seeds per pod rather than MSW (no change). Defoliation at the vegetative stage reduced biomass by 17% but increased HI by 7%. It reduced yield by 11% as a result of reduced pods m⁻² rather than any effect on the number of seeds per pod and MSW (Fig. 1). The partial pod removal reduced biomass per plant by 24% ($P < 0.001$), HI by 14% ($P < 0.001$), resulting in a loss of yield per plant of 24% ($P < 0.001$) (Fig. 1). The removal of pods reduced the number of pods per plant from 133 to 80 while the number of seeds per pod remained the same, resulting in a 40% reduction in seeds per plant. This potentially increased the resource available to the remaining pods by 40%. In response to the increased source availability, MSW was significantly increased by 10% ($P < 0.001$) for all cultivars.

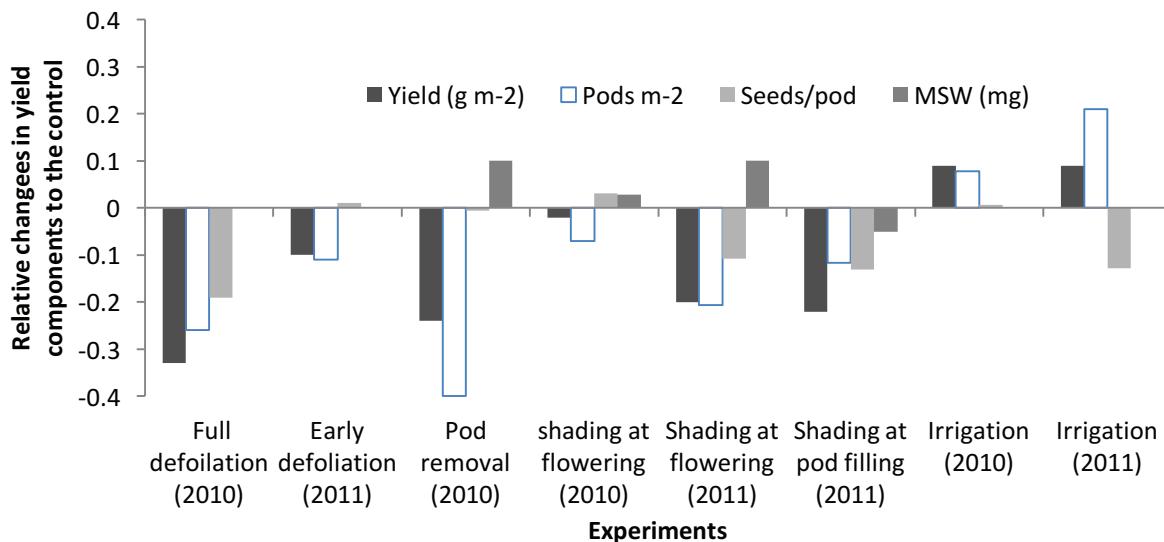


Fig.1 Relative changes in yield, pods m⁻², seed per pod, and mean seed weight (MSW) compared to the control treatment as a result of defoliation, partial pod removal, shading and supplemental irrigation in 2010 and 2011.

The effect of shading at flowering on yield and yield components differed between 2010 and 2011 (Fig. 2). In the extremely dry season of 2010, shading did not affect the number of pods m⁻², seeds per pod, and MSW, resulting in only 4% decrease in seeds m⁻² and no yield difference (Fig. 2). In contrast, shading at flowering reduced pods m⁻² by 21% ($P < 0.01$) and seeds per pod by 11% ($P < 0.01$) in 2011 (Fig. 1), resulting in a 29% ($P < 0.01$) reduction in sink size (seeds m⁻²). In response to the reduced sink size, MSW increased by 10%. Shading at flowering reduced yield from 353 g m⁻² to 269 g m⁻² (Fig. 2). Shading at pod-filling led to a similar reduction in yield to shading at flowering, but their effect on yield components were different. It reduced seeds per pod by a similar percentage (11%) but pods m⁻² by a smaller percentage (12%) than

shading at flowering. However, MSW was 5% ($P < 0.05$) lower than the control despite the reduced seeds m^{-2} . Over all, shading at pod-filling reduced biomass from 1035 g m^{-2} to 806 g m^{-2} and yield from 353 g m^{-2} to 261 g m^{-2} (Fig. 2a).

The additional 60 mm water supplied through irrigation increased yield by 9% ($P < 0.05$) (Fig. 2b), mainly from increased pod number ($P < 0.05$) in 2010 and 21% ($P < 0.01$) in 2011 (Fig. 1). It did not affect seeds per pod in 2010 but reduced seeds per pod by 13% as the number of pods increased in 2011 (Fig. 1). Overall, it increased sink size by 8% in 2010 and a 17% in 2011 as the number of pods m^{-2} increased. MSW was not affected by irrigation in both years (Fig. 1).

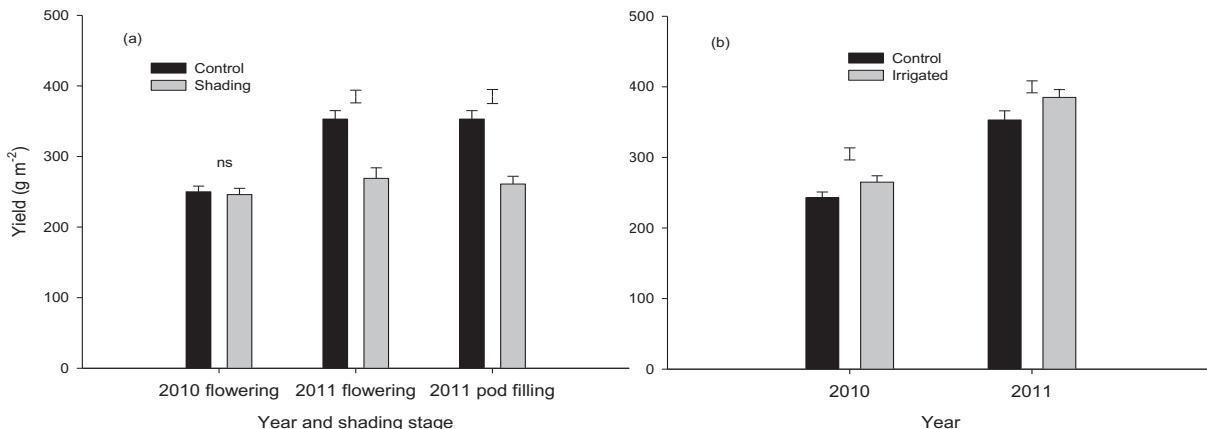


Fig 2. The effect of (a) shading at flowering and at podding on seed yield of canola in 2010 and 2011 and (b) supplemental irrigation of 60 mm at the end of flowering/beginning of pod filling in 2010 and 2011. The bars above the means indicate standard error and the lsd at $P = 5\%$ is shown between the bars.

Discussion

Altering the source-sink ratio either up or down provides evidence for our hypothesis that canola yield is more source- than sink-limited in the high-rainfall zone of southern Australia. When the shaded crop at flowering returned to the normal radiation level at the end of flowering, the crop appeared to have an abundant source available to the reduced number of seeds and resulted in significant increase in MSW. The increase in MSW in response to reduced sink size by shading at flowering and to the increased source by partial pod removal supports the source limitation hypothesis. Supplemental irrigation at the beginning of pod filling prolonged the flowering period, allowed more flowers to become viable pods and increased sink size by increasing the number of pods. In response to the increased sink, MSW did not decrease compared with the control. This further supports our conclusion that the control crop was under a source limitation. On the other hand, the lower MSW observed in the shaded crop at the pod filling stage indicates that assimilate supply was limiting even under the reduced sink size. Our conclusion under field condition is in agreement with the findings for individual plants in winter type oilseed rape under controlled environment conditions (Tayo and Morgan, 1979).

In contrast with many studies in determinate crops, this study showed that when the source was manipulated by shading, defoliation or supplemental irrigation, sink (seeds m^{-2}) was significantly modified (either reduced or increased) at the same time. This complicates the interpretation of results of source-sink manipulation, making source-sink relationships in canola much more complex than in the determinate crops such as wheat and barley. It is commonly assumed that seed filling was source-limited otherwise sink-limited if the magnitude of seed weight change was significant in the source-sink manipulation experiments (Borras et al., 2004). In our study, there was no significant difference in MSW between defoliation and the control, between supplemental irrigation and the control, and a small difference between shading at pod filling and the control. However, this lack of difference in MSW needs to be interpreted with care because the treatments significantly modified sink size (seeds m^{-2}), ranging from 23-40% fewer seeds m^{-2} mainly from the reduced pods m^{-2} . If the number of pods remained the same as in the control, MSW would have decreased by 11-27% by reducing the source supply. This indicates the canola crop could have been much more source-limited than indicated by the change of MSW.

The response of canola to the source-sink manipulation is in contrast to many studies in wheat in which yield was rarely source-limited (Borras et al., 2004; Calderini et al., 2006). The difference between canola and wheat could be related to assimilate supply between the two crops and to the competition for assimilates between plant organs. In wheat, the current photosynthetic assimilates contribute to 60-70% of yield and the stored water soluble carbohydrates (WSC) in stem and leaf sheath can provide 30-40% of yield (Foulkes et al., 2007). The reduction in assimilates from shading during the grain filling period can be almost fully compensated for by the stored WSC in stems under moderate source reduction, resulting in insignificant yield reduction (Zhang et al., 2010). For canola, the current photosynthetic assimilates contributed about 90% of seed yield and the contribution of stored water soluble carbohydrates to yield was around 10-12% (Habekotte, 1993). The reduction in assimilates to seeds under shading during pod-filling might have been significantly greater than the stored WSC and could not be compensated for by a relatively small amount of the stored WSC. In addition, during pod development and seed filling, the indeterminate feature of canola competes for assimilates to grow pods, stems, branches, and at the same time to fill seeds; resulting in high demand for assimilates. Therefore, it is unlikely that assimilate supply can meet all demands and therefore yield of canola is source-limited during the seed filling stage.

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