



Original paper

Plasticity of seed weight compensates reductions in seed number of oilseed rape in response to shading at flowering



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ABSTRACT

Understanding the response of the number of seeds and seed weight to the availability of assimilates is crucial for designing breeding strategies aimed to increase seed and oil yield in oilseed rape. This study aims to answer the questions: i) do seed number and seed weight in oilseed rape differ in their plasticity in response to the availability of assimilates at flowering? and ii) how sensitive are oil and protein concentrations to the availability of assimilates during flowering?

A spring oilseed rape hybrid was sown in two field experiments and the treatments were combinations of i) two plant densities and ii) shading or no shading between the beginning and end of flowering. Seed yield was not affected by plant density or by shading. Lower plant density was compensated by an increase in seed number per plant, without effects on single-seed weight. However, the negative effect of shading during flowering on seed number per area was fully compensated by an increase in single-seed weight by 47–61%. The plasticity of single-seed weight observed in the present study of oilseed rape has never been reported for annual seed crops. Shading at flowering increased both the seed filling rate and the duration of the seed filling period at all positions in the canopy. We also observed that the reduction of the source-sink ratio at flowering increasing seed weight does not necessarily modify oil or protein concentrations. Thus, single-seed weight could be targeted to increase seed yield in oilseed rape without compromising oil content.

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1. Introduction

Food security will be challenged by the growth of the world's population, reaching 9.2 billion people in the next 50 years (United Nations, 2013). The “Green Revolution” improved the yield of energy-dense crops like cereals and oil species, allowing the increase in food calories, fats and proteins consumed by mankind (Khouri et al., 2014). Over the last 50 years, oilseed rape (*Brassica napus* L.), the source of one of the healthiest edible oils for human consumption (Momoh et al., 2004), has globally increased seed production, reaching 71 million tonnes in 2014 (FAOSTAT, 2015), partially powered by the rising demand for biofuels (Rondanini et al., 2012). Between the years 1991 and 2010 the oilseed yield progress in countries such as China, Canada, India, France and Germany, grew at annual rates in a range between 0.6 and 2% (see Kirkegaard et al., 2016). However, a stagnation has also been seen

in countries such as United Kingdom, Brazil, Finland, Sweden and the Czech Republic in recent years (Peltonen-Sainio et al., 2007a; Beddington, 2010; Rondanini et al., 2012). Therefore, new strategies are urgently needed to overcome such increasing leveling-off and to satisfy the growing demand for vegetable oil.

Seed yield is the product of the number of seeds and their average weight (Mitchell, 1970). Since the former is the yield component most associated with seed yield (Peltonen-Sainio et al., 2007b; Sadras and Slafer, 2012), past increase in seed yield has been mainly achieved by increasing the seed number per area (Fischer and Edmeades, 2010). However, modern genotypes of crops like sunflower (*Helianthus annuus*) are reaching seed numbers close to their saturation point from which further increase will not necessarily improve seed yield. Instead, it has been proposed that larger seeds with higher oil concentration, while maintaining seed number, could be a more effective strategy for improving seed and oil yield in oil crops (Pereira et al., 1999).

The time window during which seed number and single-seed weight are established are known to overlap around flowering, but to different degrees depending on the particular crop species

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(Calderini et al., 2001; Yang et al., 2009). During this period, plants allocate their assimilates to the reproductive organs setting the potential sink capacity (Andrade et al., 2005). Based on the assumption that “each organism has a critical stage in which their energy should be invested into maximizing their potential offspring”, Smith and Fretwell (1974) designed a theoretical model that distributes the available energy between size and number of offspring. Using this approach, Sadras (2007) analysed the balance between the seed yield components in grain crops, and hypothesized that seed number is directly related to assimilate availability during flowering, whereas seed weight or size can be considered constant. The plasticity in seed number and the stability of seed weight in response to the availability of assimilates at flowering have been demonstrated for several crop species, including wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), narrow-leafed lupin (*Lupinus angustifolius* L.) and pea (*Pisum sativum* L.) by manipulating the source-sink ratio (Fischer, 1985; Arisnabarreta and Miralles, 2008; Sandaña and Calderini, 2012), supporting the corollary of Sadras (2007). As a consequence, the plasticity of seed number and the conserved response of seed weight to the availability of resources have been assumed for oilseed rape (Diepenbrock, 2000; Gomez and Miralles, 2011). Nevertheless, quantitative evaluations of the sensitivity of yield components at flowering and the potential trade-off between seed number and single-seed weight have been scarcely assessed in oilseed rape (Tayo and Morgan, 1979), and have never been evaluated in field conditions.

A central objective of oilseed rape breeders is to improve oil yield (Labana et al., 2013). The biosynthesis of fatty acids and other components like proteins takes place during the seed filling period (Diepenbrock and Geisler, 1979). Therefore, variations in the rate and length of this phase may affect both seed weight and seed oil concentration. In maize (*Zea mays* L.), seed weight decreased and, on the contrary, the proportion of oil and protein concentration increased in response to lower source-sink ratio during flowering (Jia et al., 2011). Because seed filling and fatty acid synthesis occur simultaneously, a potential trade-off between seed weight and oil concentration deserves special attention (Pereira et al., 1999). Several studies have addressed the effect of the availability of assimilates on oil concentration during seed filling in oilseed rape (Fortescue and Turner, 2007; Iglesias and Miralles, 2014; Rondanini et al., 2014); however, these effects have not been assessed when changes in the source-sink ratio occur at flowering.

Since it has been well established that there is a dynamic interaction between source and sink (Calderini et al., 2001; Asseng et al., 2016; Shi et al., 2016), unravelling the response of yield components to the availability of assimilates during flowering will provide important cues to increase seed and oil production. Therefore, this study aims to answer the following questions: i) do seed number and single-seed weight differ in their plasticity in response to the availability of assimilates at flowering in oilseed rape? and ii) how sensitive are oil and protein concentrations to the availability of assimilates during flowering? To address these questions, we quantified the variations in seed number, seed weight, oil and protein concentrations in response to reduction in incoming photosynthetically active radiation (PAR_{inc}) during flowering (Fig. 1) under two contrasting plant densities and in two different growing seasons.

2. Materials and methods

2.1. Experimental set-up and treatments

Spring oilseed rape cv. ‘Solar CL’ (NPZ-Lembke, Germany) was sown in two field experiments (Fig. 1) carried out at the Estación Experimental Agropecuaria Austral in Valdivia (39°47’S., 73°14’W.), Chile, in a Duric Hapludand soil.

In Experiment 1 (Exp. 1) plants were sown on September 4, 2014 at two plant densities (40 and 80 plants m^{-2}) and two source-sink treatments (full sunlight and plots shaded by a black net intercepting 70% of the incident PAR between beginning of flowering [BBCH 61] and end of flowering [BBCH 69], i.e., during 19 days). The treatments were arranged in a split-plot block design with three replicates, where plant population was assigned to main plots and source-sink treatments to sub-plots. Their effects were tested on oilseed rape plants sown in plots of 2×4 m size of 11 rows at 0.175 m apart.

Experiment 2 (Exp. 2) was sown on September 28th 2015 at two plant densities (30 and 45 plants m^{-2}) and two source-sink treatments (the same as in Exp. 1 except for the duration of shading, which was 28 days). The plot size and experimental design were the same as in Exp. 1. Since plant densities used in Exp. 1 (40 and 80 plants m^{-2}) did not affect seed yield, for Exp. 2 lower densities were used (30 and 45 plants m^{-2}).

2.2. Experimental management and weather data

In both experiments plots were fertilized at sowing with phosphorus (150 kg ha^{-1} of $Ca(H_2PO_4)_2$) and potassium (100 kg ha^{-1} of $K_2SO_4 \cdot MgSO_4$). Nitrogen fertilization (50% NO_3 and 50% NH_4) was split into two applications: 80 kg N ha^{-1} five days after plants emerged (BBCH 10) and 80 kg N ha^{-1} when the fifth internode was expanded (BBCH 35). Plots were irrigated weekly to complement rainfall and to avoid water shortages until harvest in both growing seasons. To keep plants free of biotic stresses, weeds were periodically removed by hand, while diseases and insects were prevented with fungicides or insecticides at the rates recommended by their manufacturers. In Exps. 1 and 2 the shading nets were kept open on the south side to facilitate free air circulation and access for pollinators.

Weather data (maximum and minimum air temperatures and incident solar radiation) were recorded at 30 min intervals from sowing until harvest at the meteorological station of Universidad Austral de Chile (<https://centrocbb.cl/clima/indexData.php>) located at 5 km of the experiment. Air temperature under the nets was on average less than 1 °C lower than in controls as was shown in previous experiments at the Estación Experimental Agropecuaria Austral (Sandaña et al., 2009).

2.3. Light environment at flowering stage

Seven days after the beginning of flowering (BBCH 65), light intercepted by the canopy ($IPAR$) was calculated as the difference between incident (PAR_{inc}) and transmitted (PAR_{trans}) light recorded by a 1 m long LI-191 R quantum line sensor (LI-COR Inc., Lincoln, NE, USA). To estimate PAR_{inc} , the sensor was held 10 cm above the canopy, while for PAR_{trans} the line sensor was held at 100 cm of height (corresponding at the bottom of the main raceme), at 75 cm of height (corresponding at the bottom of the first branch), 50 cm (corresponding at the bottom of the 6th branch), and at ground level. At the same stage, and similar to PAR, measurements of R:FR were performed 10 cm above the canopy, at 100, 75, 50 cm of plant height and at ground level, using the Skye SKR 110 Red/Far Red sensor (Skye Instruments Ltd, Llandrindod Wells, UK). Both PAR and R:FR measurements were made at noon during sunny days. R:FR measurements were done with the sensor facing parallel to the soil surface oriented to the north, south, east and west, which allowed the light scattered by neighbouring plants to reach the sensor. The average of the four values was used for further analysis.

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