



Flower formation and pod/flower ratio in canola (*Brassica napus* L.) affected by assimilates supply around flowering

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Abstract

An alternative means by which to examine the importance of assimilates supply to flower and pod formation is to analyze the relationships of leaf area index (LAI), above-ground dry matter (ADM), leaf area duration (LAD) and crop growth rate (CGR) around flowering with flower number and pod/flower ratio. For this objective, an experiment was conducted at Agricultural Research Station of Gonbad, Iran in 2005-2006 and 2006-2007. The experiment was a randomized complete block design arranged in split plot. Two cultivars of spring type canola (Hyola401 and RGS003) as subplots were grown at 5 sowing dates as main plots, spaced approximately 30 days apart, to obtain different environmental conditions and assimilates availability around flowering. The experiment was conducted at two conditions, i.e. supplemental irrigation and rainfed. In both main (MR) and branch (BR) racemes, flower number increased as LAI and ADM at the beginning of flowering increased. The reduction in flower number with reduction of LAI and ADM is evidence that canola plants can adjust to carbohydrates availability by altering the number of potential resource demanding sinks. Pod/flower ratio was quadratically related to ADM at the beginning of flowering. A significant positive linear relationship was found between LAD and CGR during flowering period and pod/flower ratio. Therefore, potential and actual pod number was related to cumulative dry matter production of the crop until the beginning of flowering and until the end of flowering, respectively.

Keywords: Canola; Flower; Pod; Dry matter; Assimilate supply.

Introduction

Counts of flowers and pods are useful to breeders and plant physiologists in understanding the reproductive efficiency of the crop (Coffelt et al., 1989). In canola, the main component of seed yield is the number of flowers that translate into pods (Angadi et al., 2000; Morrison and Stewart, 2002; Gan et al., 2004). So flower number and pod/flower ratio are very important factors determining canola seed yield. Determination of final flower and pod number is the net result of the processes of their initiation, achievement of a maximum number and pod abortion.

Canola usually produces nearly twice as many flowers than pods. Under typical conditions, canola differentiates more floral primordia than its photosynthetic capacity can support. McGregor (1981) reported that less than 45% of the flowers formed on *B. napus* cultivars produced pods. The ratio of pods/flowers in the study of Morrison and Stewart (2002) was 59% for *B. napus* cultivars. In wheat, Bindraban et al. (1998) reported about 20 kernels per unit crop dry matter, where significant differences occur among cultivars. The contribution of main and branch racemes in pod production depend on environmental conditions. Angadi et al. (2003) showed that under favorable growing conditions, secondary pods contributed 8-60% of the total pod number, but under stressful growing conditions, secondary pods contributed 6-38% of the total pod number. However, seed yield is the product of interaction between genotypes and environment (Liu and Herbert, 2000; Pahlavani et al., 2007). Under given locations, plant characteristics conducive to maximum seed yield are of interest to canola breeders (Chongo and McVetty, 2001). Plants that are best suited for high yield in highly productive environments should possess characters such as high assimilatory capacity that allows maximum pod production (Liu et al., 2005).

Although the relations of assimilates supply with seed number and seed yield were well studied in some species (Bindraban et al., 1998; Prystupa et al., 2004; Liu et al., 2005; Ruiz and Maddoni, 2006), less is known about the relations between assimilate supply around flowering with flower number and pod/flower ratio in canola. So as part of a broader project, flower production and pod/flower ratio were investigated as a function of assimilates supply around flowering, over a wide range of environmental conditions.

Materials and Methods

The experiment was conducted at Agricultural Research Station of Gonbad, Golestan province, Iran (45 m a.s.l., 37° N, 55° E). The region is classified as a warm and semiarid Mediterranean climate. The soil was a fine, silty, mixed, thermic typic Calcixerol. Prior to sowing, soil samples were taken, and according to soil test data, P and K were preplant-incorporated to supply 50 kg P₂O₅ ha⁻¹ and 50 kg K₂O ha⁻¹ from triple super phosphate and potassium sulphate, respectively. N was applied at 75 kg N (as urea)/ha, that a third of this amount was applied preplant, a third of that was side-dressed at beginning of stem elongation and the rest at the beginning of flowering. The experiment was carried out over two conditions (supplemental irrigation and rainfed) and two years (2005-2006 and 2006-2007), in a randomized complete block design arranged in split plot with 3 replications. Two cultivars of spring canola (Hyola401, a hybrid cultivar and RGS003, an open pollinated one) as subplots were grown at 5 sowing dates as main plots. The sowing dates were 9 Nov., 6 Dec., 5 Jan., 4 Feb. and 6 Mar. in 2005-6 and 6 Nov., 6 Dec., 5 Jan., 4 Feb. and 6 Mar. in 2006-7, to have a wide range of environmental conditions and assimilates availability around flowering.

In supplemental irrigation conditions, plots were irrigated at the beginning of stem elongation, flowering and seed filling stages. Two days before irrigation times, soil samples were dried for 24 hours at 105 °C and weighed. Then Soil water content was measured and plots then irrigated to field capacity (Zhang et al., 1999). Plots were over planted and after seedling establishment, the plants were thinned to the desired spacing between plants of 5 cm (1000000 plant ha⁻¹). Each subplot consisted of eight five-meter long rows. Main plots and subplots were 2 and 0.4 m apart, respectively. A 3-m pathway separated replicates.

From each plot, above-ground dry matter and other necessary samples were taken from 10 plants of rows of 2 and 3. The plots were hand weeded during the season. Two days after the beginning of flowering, all of the flowers and buds (each main and branch racemes) were counted and recorded from 10 plants selected at random from within each plot. The plants were tagged and numbered, and at the physiological maturity the tagged plants were removed from the plot and the number of pods were counted (each main and branch racemes, separately). Flowering period was considered as the number of days between the beginning of flowering to the end of flowering. Phenological observations were made on a regular basis with the Harper and Berkenkamp (1975) growth stage key. From each plot, above-ground dry matter, LAI and other necessary samples were taken from 10 plants of rows of 2 and 3. The area of leaves (one side lamina) was measured using a leaf-area meter

(DIAS, Delta-T Devices). LAD was calculated by the equation as: $LAD = \frac{LAI_1 + LAI_2}{2(T_2 - T_1)}$.

Where LAI_1 and LAI_2 are the leaf area index between the beginning of seed filling and physiological maturity, and T is the day corresponding to LAI determination (Liu et al., 2005). CGR was calculated as the ratio of cumulative ADM during flowering period divided by the number of days during the period. The regression functions fitted to the data of each cultivar, over years and sowing dates, and significant relations (Table 1) were used (SAS, 1996). Because there was no significant difference between irrigation conditions (supplemental irrigation and rainfed) with respect to the coefficients of the functions, data of irrigation conditions were pooled, and used in regression analysis.

Table 1. Standard error for intercept (a) and slope (b), RMSE and significant level of linear functions.

Relationships	a±Se	b±Se	RMSE	Significant level
Hyola401				
LAI at the BF and flower number in MR	6.1053±5.43	8.1838±1.37	5.47	***
LAI at the BF and flower number in BR	35.445±8.02	13.859±2.023	0.08	***
Dry matter at the BF and flower number in MR	11.77±2.26	0.0517±0.004	3.48	***
Dry matter at the BF and flower number in BR	52.90±5.74	0.0667±0.010	8.83	***
LAD during flowering and pod/flower ratio in MR	19.055±4.37	169.25±18.33	4.10	***
LAD during flowering and pod/flower ratio in BR	22.174±2.95	87.94±12.38	2.77	***
CGR during flowering and pod/flower ratio in MR	21.917±5.22	2.6706±0.370	9.16	***
CGR during flowering and pod/flower ratio in BR	19.537±3.44	1.772±0.244	6.03	***
RGS003				
LAI at the BF and flower number in MR	17.459±4.04	5.6699±1.04	3.73	***
LAI at the BF and flower number in BR	51.412±7.65	11.061±1.98	0.06	***
Dry matter at the BF and flower number in MR	17.47±3.32	0.0453±0.006	5.15	***
Dry matter at the BF and flower number in BR	63.97±5.90	0.0607±0.011	9.16	***
LAD during flowering and pod/flower ratio in MR	26.789±3.64	137.25±16.83	3.08	***
LAD during flowering and pod/flower ratio in BR	21.829±2.70	75.721±12.5	2.29	***
CGR during flowering and pod/flower ratio in MR	21.476±4.28	2.3117±0.322	7.43	***
CGR during flowering and pod/flower ratio in BR	16.527±3.46	1.399±0.260	5.99	***

MR= main racemes; BR= branch racemes; BF= beginning of flowering. *** Significant at 0.1% level of probability.

Results

There was a linear relationship between LAI at the beginning of flowering with flower number, explaining 66 and 62% of the variation of Hyola401 and RGS003 in MR (Figure 1 a and b), and 72 and 64% of the variation of Hyola401 and RGS003 in BR (Figure 1 c and

d), respectively. The slope of this relationship was more in Hyola401 (8.18 and 13.86 for MR and BR, respectively) than RGS003 (5.67 and 11.06 for MR and BR, respectively) (Figure 1 a, b, c and d), showing the greater response of Hyola401 than RGS003 to LAI at the beginning of flowering.

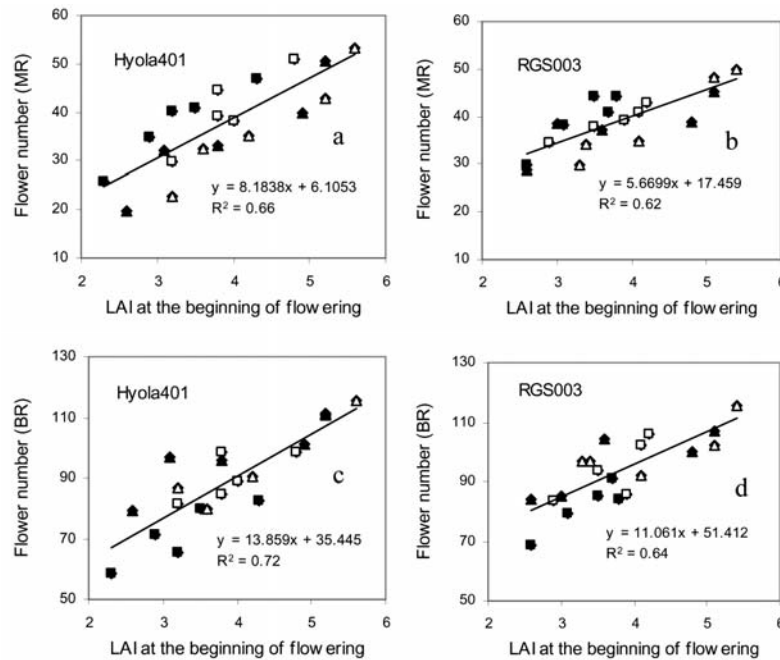


Figure 1. Relationship between LAI at the beginning of flowering and flower number in main (a and b), and branch (c and d) racemes. MR= main racemes; BR= branch racemes. (□) Irrigated condition in 2005-6; (■) Rainfed condition in 2005-6; (Δ) Irrigated condition in 2006-7; (▲) Rainfed condition in 2006-7. Each point is a mean of 10 plants and 3 replications.

In both main and branch racemes, flower number had positive relationship with ADM at the beginning of flowering (Figure 2). In MR, the linear relationship between ADM at the beginning of flowering and flower number explained 90 and 74% of the variation of Hyola401 and RGS003, respectively (Figure 2 a and b). The slope of this relationship was 0.0517 in Hyola401 and 0.0453 in RGS003, showing that for an each $g\ m^{-2}$ increase in ADM at the beginning of flowering, flower number of Hyola401 and RGS003 increased 0.0517 and 0.0453 per MR, respectively (Figure 2 a and b), indicating more response of flower number to ADM at the beginning of flowering in Hyola401. Also, there was a linear positive relationship between ADM at the beginning of flowering and flower number per BR, explaining 70 and 61% of the variation of Hyola401 and RGS003, respectively (Figure 1 c and d). This relationship explained a greater proportion of the variation of the data in Hyola401 than RGS003. For an each $g\ m^{-2}$ increase in ADM at the beginning of flowering, flower number of Hyola401 and RGS003 increased 0.0667 and 0.0607 per BR, respectively (Figure 1 c and d).

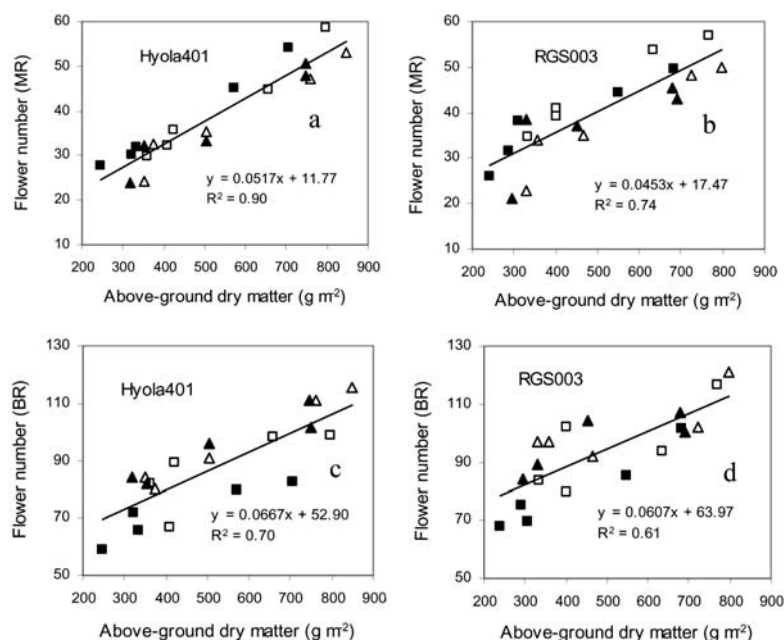


Figure 2. Relationship between above-ground dry matter at the beginning of flowering and flower number in main (a and b), and branch (c and d) racemes. MR= main racemes; BR= branch racemes. (□) Irrigated condition in 2005-6; (■) Rainfed condition in 2005-6; (△) Irrigated condition in 2006-7; (▲) Rainfed condition in 2006-7. Each point is a mean of 10 plants and 3 replications.

In both cultivars, pod/flower ratio was quadratically related to ADM at the beginning of flowering (Figure 3). In MR, the quadratic relationship between ADM at the beginning of flowering and Pod/flower ratio explained 74 and 80% of the variation of Hyola401 and RGS003, respectively (Figure 3 a and b). Also, in BR, the quadratic relationship between ADM at the beginning of flowering and Pod/flower ratio explained 75 and 81% of the variation of Hyola401 and RGS003, respectively (Figure 3 c and d).

A significant positive relationship was found between LAD during flowering period and pod/flower ratio in both cultivars (Figure 4). The relationship between LAD during flowering period and pod/flower ratio explained 83 and 79% of the variation of Hyola401 and RGS003 in MR (Figure 4 a and b), and 74 and 68% of the variation of Hyola401 and RGS003 in BR (Figure 4 c and d), respectively. In both main and branch racemes, the relationship showed a greater proportion of the variation of the data in Hyola401 than RGS003. Also, in both main and branch racemes, the slope of this relationship was more in Hyola401 than RGS003, showing that for an each 0.1 unit increase in LAD during flowering period, pod/flower ratio of Hyola401 and RGS003 increased 16.9 and 13.7% (169 and 137% increase for an each unit) in MR (Figure 4 a and b), and 8.8 and 7.6% (88 and 76% increase for an each unit) in BR (Figure 4 c and d), respectively. This indicated more response of pod/flower ratio to LAD during flowering period in Hyola401 than RGS003.

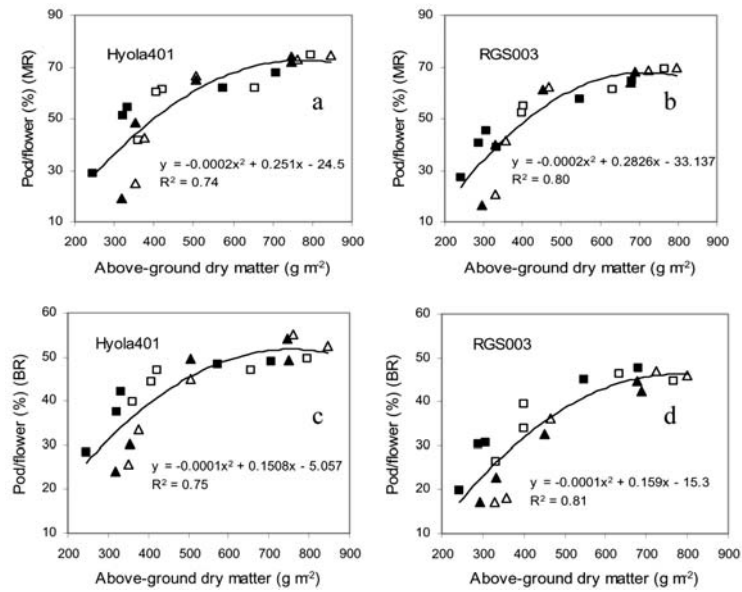


Figure 3. Relationship between above-ground dry matter at the beginning of flowering and pod/flower ratio in main (a and b), and branch (c and d) racemes. MR= main racemes; BR= branch racemes. (□) Irrigated condition in 2005-6; (■) Rainfed condition in 2005-6; (Δ) Irrigated condition in 2006-7; (▲) Rainfed condition in 2006-7. Each point is a mean of 10 plants and 3 replications.

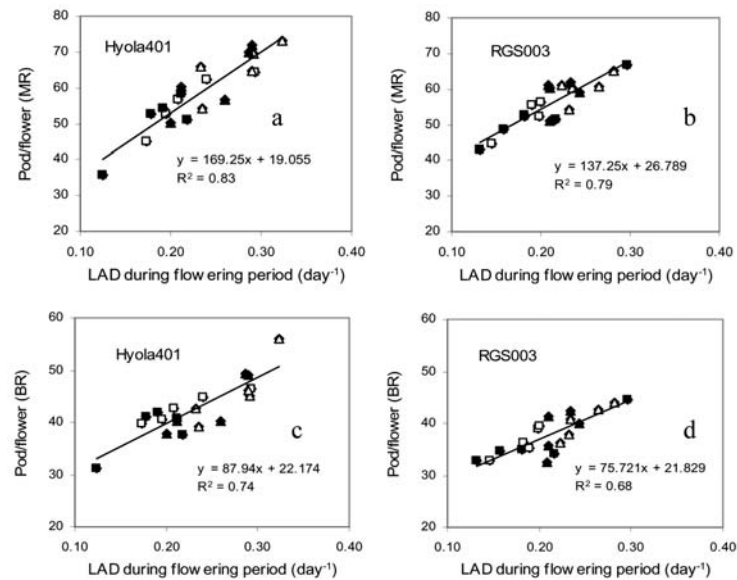


Figure 4. Relationship between LAD during flowering period and pod/flower ratio in main (a and b), and branch (c and d) racemes. MR= main racemes; BR= branch racemes. (□) Irrigated condition in 2005-6; (■) Rainfed condition in 2005-6; (Δ) Irrigated condition in 2006-7; (▲) Rainfed condition in 2006-7. Each point is a mean of 10 plants and 3 replications.

As expected, there was a linear relationship between CGR during flowering period and pod/flower ratio in both cultivars (Figure 5), explaining 74% of the variation of the cultivars in MR (Figure 5 a and b), and 75 and 62% of the variation of Hyola401 and RGS003 in BR (Figure 5 c and d), respectively. For an each $\text{g m}^{-2} \text{day}^{-1}$ increase in CGR during flowering period, pod/flower ratio of Hyola401 and RGS003 increased 2.67 and 2.31% in MR (Figure 5 a and b), and 1.77 and 1.40% in BR (Figure 5 c and d), respectively, indicating more response of pod/flower ratio to CGR during flowering period in Hyola401 than RGS003.

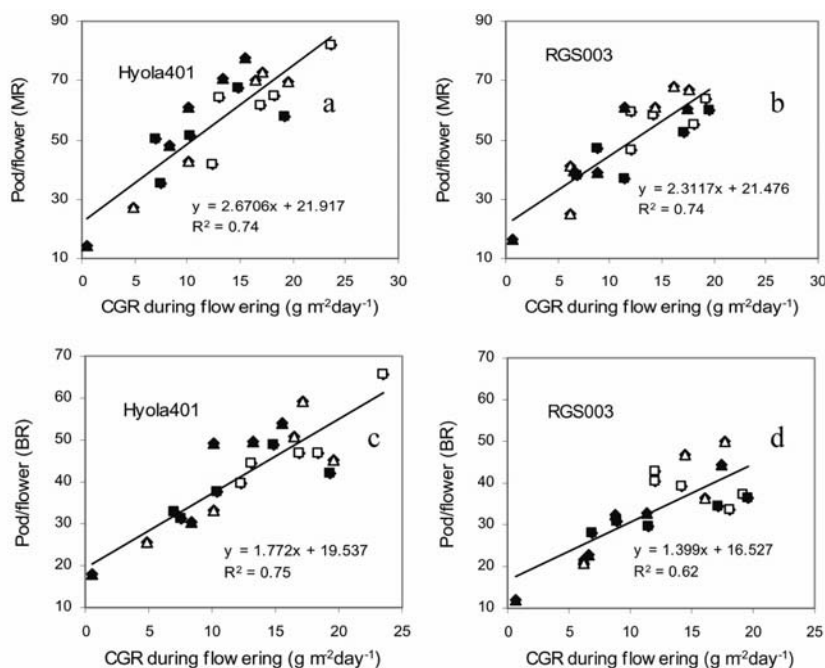


Figure 5. Relationship between CGR during flowering period and pod/flower ratio in main (a and b), and branch (c and d) racemes. MR= main racemes; BR= branch racemes. (□) Irrigated condition in 2005-6; (■) Rainfed condition in 2005-6; (△) Irrigated condition in 2006-7; (▲) Rainfed condition in 2006-7. Each point is a mean of 10 plants and 3 replications.

Discussion

This study is an agreement with what is well established in the literature (Evert, 1996; Chongo and McVetty, 2001; Prystupa et al., 2004; Liu et al., 2005; Gunasekera et al., 2006; Akram-Ghaderi and Soltani, 2007). In the present study, flower number increased as LAI and ADM at the beginning of flowering increased (Figures 1 and 2). Also, pod/flower ratio increased as LAD and CGR during flowering period increased (Figures 4 and 5). This implies that agronomic management and environmental conditions that increased LAI and ADM at the beginning of flowering, and increased LAD and CGR during flowering period, increased flower number and pod/flower ratio of canola plants. The reduction in flower

number with reduction of LAI and ADM at the beginning of flowering (Figures 1 and 2) in this study is evidence that canola plants can adjust to carbohydrates availability by altering the number of potential resource demanding sinks. In both cultivars, the higher number of flowers per MR and BR produced at the higher amount of LAI and ADM (Figures 1 and 2) did not translate into more pods (Figure 3), indicating that in the higher level of LAI and ADM around flowering, assimilate supply at the beginning of flowering wasn't a limiting factor to increase pod formation.

The positive relationship between spike dry weight at anthesis and the number of fertile florets produced per unit land area has been reported in a number of different cases (Slafer and Andrade, 1993; Gonzalez et al., 2003). In wheat, assimilates supply between terminal spikelet initiation to anthesis determine the magnitude of floret mortality and hence the final number of floret primordial that will be fertile at anthesis (Kirby, 1988).

As pointed out by Habekotte (1993), in this study, potential and actual pod number were related to cumulative dry matter production of the crop until the beginning of flowering and until the end of flowering respectively, i.e. to total assimilate availability over that period. This emphasizes that the contribution of assimilates supply (LAI, LAD, ADM and CGR around flowering) were very significant source for flower and pod formation. In canola, pod density appears to be fully determined just after the end of flowering (Habekotte, 1993). So environmental conditions during flowering period is of great importance in pod formation. The amount of vegetative growth and the weather conditions (temperature, rainfall and radiation) during flowering period determine the magnitude of buds and flowers and hence the final pod number. However, flowering is the critical period to accumulate dry matter. Hocking et al. (1997) reported that about 50% of the dry matter content of the mature canola plants accumulated during flowering period. Maximum dry matter for leaves occurred at the start of flowering, and for stems at the end of flowering (Hocking et al., 1997). Therefore, LAD and CGR during flowering are very important factors to determine pod number and hence seed yield. The increased pod/flower ratio due to greater LAD and greater CGR during flowering period observed in the present study (Figures 4 and 5) supports the idea that the number of flowers that translate into pods depends upon the amount of assimilates supply (Miralles et al., 2003; Gonzalez et al., 2003). In both main and branch racemes, LAD and CGR during flowering period was fairly well related with pod/flower ratio (Figures 4 and 5), indicating that pod/flower ratio was driven by availability of carbohydrates during this phase. In wheat, Abbate et al. (1997) showed CGR around anthesis to be linearly related to kernel number per unit area.

Canola yield can be given as the product between total dry matter and harvest index, which is the integrated product of plant number per unit land area, pod number per plant, seed number per pod, and seed weight. The present study shows that optimum environmental conditions around flowering, as such we can see in early sowing dates, not only accumulated more ADM at the beginning of flowering and flowering period but also produced more flowers and pods per unit land area than that of late sowing dates (some data not shown). However, in the Mediterranean type conditions of Gonbad area, higher ADM around flowering is important, as resulted in an increased number of flowers and pods, and hence seed number per unit land area and seed yield. This result in part agrees with Specht et al. (1986) who stated that achieving a high total dry matter through adequate vegetative growth is an essential prerequisite for high reproductive growth and a high seed yield in soybean.

Conclusion

Under warm and semiarid Mediterranean conditions, like Gonbad area, optimum sowing dates and supplemental irrigation could be very good management options to coincide the critical period of flowering with favorable conditions. In this study, higher LAI and LAD in early sowing dates and supplemental irrigation probably increased the interception of solar radiation, and thus a greater CO₂-fixing ability of the canola plants resulted in accumulation of more assimilates. These results indicated that rapid leaf formation and expansion, and delayed leaf senescence are the characteristics of high-yielding varieties, in the Mediterranean type conditions of Gonbad area. In this study, a great proportion of the variation in flower number and pod/flower ratio were related to assimilate supply around flowering. Potential and actual pod number was related to cumulative dry matter production of the crop until the beginning and end of flowering, respectively.

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