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Full Length Article

Delayed Planting Affects Seed Yield, Biomass Production, and Carbohydrate Allocation in Canola (*Brassica napus*)

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Abstract

Delayed planting causes substantial reduction in crop yield; however, information on physiological regulation of yield reduction is scarce. A field experiment was conducted using four planting dates as treatments, namely, early (September 15); optimal (September 25); late (October 25); and very late (November 15) in 2011 and 2012 to unravel the impact of delayed planting date on canola yield and physiological indexes, including tissue dry matter and carbohydrate profile partitioning. Optimal planting date was considered as a control. Results showed that canola seed yields on late and very late planting dates were severely decreased by 30% and 70%, respectively, compared with those on the optimal planting date because of a decrease in the number of branches and siliques per plant and seed weight. Delayed sowing reduced the inflorescence productivity due to less biomass from initial flowering. Inflorescence sugar profile including fructose, glucose, and sucrose showed more content on the late planting than that on the early and optimal planting date at 28 days after anthesis (DAA) (peak point) indicating they were possibly assigned to gain more biomass. However, starch content in the inflorescence on the early and optimal planting date was much higher than that in the late plantation at 28 DAA, indicating that the photoassimilates were mainly used as seed reserves such as lipids.

Key words: Biomass; Carbohydrate allocation; Planting date; Yield

Introduction

The sowing date of canola has been delayed in the production system in China. Main reasons were: 1, advancing or delaying of sowing and heading dates of rice in the rice-canola rotation system; 2, transplanting is being gradually replaced by direct seeding to reduce the cost of production in terms of less labor and omitting the period from seed sowing to transplanting. Although this delay on the sowing date of canola can alleviate seasonal contradiction between canola and rice production to some extent, late planting results in low canola yields (Chen *et al.*, 2005).

Studies have revealed that late planting can reduce yield of many crops (Chen *et al.*, 2005; Egli and Cornelius, 2009; Sindelar *et al.*, 2010). For example, López-Bellido *et al.* (2008) documented the reduction in chickpea yield as a result of delayed planting that could be strongly associated with decreased total dry matter production and leaf area duration index. Bauer *et al.* (2000) determined the relationship between fiber quality and canopy photosynthesis in cotton sown on different planting dates with the opinion that photosynthetic products, such as carbohydrates could influence fiber quality. However, they observed that difference in planting times did not affect the canopy photosynthesis (Bauer *et al.*, 2000). In addition, Gaudet *et al.* (2001) revealed that late seeded wheat contained lower concentration of highly polymerized fructan, resulting in reduced resistance to snow mold. These examples showed the physiological changes induced by late plantation in crop production. In canola, Chen *et al.* (2005) found that canola seeding from mid-April to mid-May led to 43% to 63% loss of seed yield. However, there is paucity in information about the mechanism regulating the reduction in yield of canola because of delayed sowing.

At flowering stage leaves of canola still manage to produce photoassimilates (Kandel and Kandel, 2011, Hua *et al.*, 2012). After the completion of flowering, senescence of most of the older leaves occurs, whereas, translocation of mobile nutrients such as nitrogen and potassium from the older leaves to developing siliques does happen at this stage (Joy *et al.*, 1967; Close and Beadle, 2006). Thus, shortened vegetative growth period as a result of delayed planting could reduce leaf biomass of canola that possibly leads to alteration in the production of carbohydrates in leaves and their translocation to other plant organs.

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Carbohydrates (sucrose and starch) are essential photosynthetic products, which are produced by green organs such as leaf and silique wall and directly associated with plant growth and biomass accumulation (Sairanen *et al.*, 2012). Ability of carbohydrate production by plant green tissues under various environments is distinct (Oleksyn *et al.*, 2000; Pettigrew, 2001). For example, Gaudet *et al.* (2001) reported that accumulation of highly polymerized fructan in wheat was a benefit of early seeding. However, fewer studies documented the carbohydrate production response to planting date in canola. Therefore, the objectives of our study were (1) to evaluate the impact of delayed planting on sugar profile allocation to various plant organs; (2) to analyze influence of the late planting on organs' biomass productivity; (3) to assess the impact of late planting dates on canola seed yield.

Materials and Methods

Crop Husbandry

The experiment was performed during the growth seasons in 2010–2011 and 2011–2012 at the experimental station of the Zhejiang Academy of Agricultural Sciences, Hangzhou, China. A new commercially available canola (*Brassica napus* L.) variety "Zheyou 50" with high oil content (50.1%) was utilized as the plant material. The soil type in the experimental station is loamy clay (loamy, mixed, and thermic Aeric Endoaquepts) and the crop previously planted in this area was rice. Before sowing, urea, calcium superphosphate, potassium oxide and borax were applied at the rate of 150, 375, 120, and 15 kg ha^{-1}, respectively as a basal fertilizer dose. Furthermore, urea at the rate of 75 kg ha^{-1} was applied as topdressing fertilizer at the end of January 2011 and 2012. Approximately five canola seeds were directly sown on soil in each shallow holes of plot (at a depth of approximately 3 cm). After one month, the seedlings were thinned into one plant. The field was not irrigated during the canola growth season because rainfall was sufficient in Hangzhou during this period (1041.7 and 1048.3 mm for the two growing seasons, respectively). Weeds were manually removed at seedling stage and aphids were wiped out by omethoate emulsion 0.06% (V/V) at flowering completion. The mean temperature and sunshine hours were shown in Fig. 1. The mean temperature from September to January almost linearly decreased but exhibited an opposite trend from January to May in the two growth seasons (Fig. 1). The temperature in January of the growth season in 2010–2011 was very low and almost reached 0°C. However, the variation in the mean temperature between the two growth seasons was negligible. In contrast to the temperature, the pattern of sunshine hours in the growth season of 2010–2011 was much longer than that in of the season 2011–2012 (Fig. 1). The two growth seasons obtained the shortest sunshine hours in January. However, sunshine hours were reduced by 50% in the growth season of 2011–2012 compared with the growth season of 2010–2011.

Experimental Design

Four planting dates namely, early (September 15); optimal (September 25); late (October 25); and very late (November 15), were selected to evaluate the effects of delayed planting on canola yield, biomass production, and carbohydrate allocation. The recommended optimal planting date was considered as the standard to compare the effects of different planting dates on agronomic and ecophysiological indexes. Experiment was carried out in randomized complete block design replicated three times with four planting date as experimental treatments. The plants were grown in plots (40 m in length), which space between rows was 0.35 m and that between plants was 0.2 m.

Yield and Yield Component Determination

Two type of sampling was done per plot per treatment; first at the initial flowering stage to analyze tissue biomass and carbohydrate contents and second at harvest maturity to determine yield and yield components. Twenty plants randomly selected from each plot were used to determine the yield components. Parameters defining yield components were number of branches per plant, siliques per plant, seeds per silique, and 1000-seed weight. The seed yield of each plant used to determine the yield components was added to the total seed yield of each plot.

Biomass Measurement

Five plants per plot per treatment were randomly chosen at flowering initiation stage. Sampling was done in the core area of subunit in a plot and then collected very carefully with a shovel to minimize root damage. Sampling was performed at an interval of one week. The plants were removed from the plot, tagged, and transported instantly to the laboratory. The plant roots were washed immediately to remove the soil. After cleaning, the plants were grouped according to different plant parts, including root, stem, leaf, and inflorescence (combination of buds, flowers, silique walls, and seeds). These tissues were initially exposed to 105°C for 30 min to stop cell metabolism. Then the temperature was adjusted to 75°C until the dry weigh kept in constant. The dry weight of the tissues was measured using a balance.

Carbohydrate Content Determination

The dried and weighed tissues were ground into powder by a pulverizer (Wenlin Dalin Machine Com. Ltd, China). The powder was then passed through a screen with a diameter of 0.5 mm. The powder was boiled in 30 mL of 800 mL L^{-1} ethanol for 30 min and then centrifuged at 10,000×*g* twice. After the sample was extracted, the powder was cooled to room temperature. The supernatant was added to 200 mg of

active charcoal to remove chlorophyll. The determination of the fructose, glucose, and sucrose contents was according to the method described by Hendrix (1993). Briefly, for glucose, a detection mixture containing glucose-6-phosphate dehydrogenase, hexokinase, phenazine methosulfate, ATP, $NADP^+$, and idonitrotetrazolium violet along with 20 µL sample aliquot was incubated at 37 °C for 15 min under dark condition. After incubation, mixture was determined at 492 nm using spectrophotometer (UV-2550, SHIMADZU, Japan). For fructose, another 10 µL of a solution including phosphoglucose isomerase was added in the previous glucose detection mixture. The mixture was also incubated at 37°C for 15 min under condition and then glucose content was determined at 492 nm. For sucrose, 83 unit of invertase was added to the fructose detection mixture and other operations were similar to fructose measurement. The pellet was retained for starch analysis. The starch in the pellets was digested with amyloglucosidase for 100 min at 55°C according to the protocol demonstrated by Hendrix (1993). The determination of starch content was then followed to glucose content measurement.

Statistics analysis

Statistical analysis was conducted using SPSS software for windows (version 11.0). Plant height, number of branches per plant, number of siliques per plant, seed number per silique, 1000-seed weight, and seed yield were examined for homogeneity using Bartlett's test; no significant difference was noted between the two growth seasons. Thus, the mean values of the two-year yield data were combined. The mean values of the tissue biomass, fructose, glucose, sucrose, and starch content between planting dates were compared using Fisher's least significant difference ($LSD_{=0.05}$) test.

Results

Seed Yield and Yield Components

Delay in planting significantly affected plant height. Reduction in height by 9.9% and 28.3% in plants were observed in plots with late and very late planting dates compared with that of the optimal planting date (Table 1). This result indicated that a late plantation is not beneficial for canola growth and development. In addition, the dwarf plant exhibited poor performance of agronomic traits (Table 1). For example, few branches and siliques per plant as well as less seeds per pod were observed in late planted canola plants (Table 1). Poor performance of yield components directly resulted in significantly lower seed yield, exhibiting average reduction of 26.4% and 67.9% in the late and very late sown plants, respectively, compared with those of the early sown plots (Table 1).

Biomass Accumulation

Root biomass was the least on very late planting date and maintained a relatively stable value during the whole reproductive growth stage, which was below 4 g plant^{-1} (Fig. 2). However, plant root on early and optimal planting dates exhibited a growing state for the increasing biomass from 0 DAA (initial flowering stage) and the maximum root biomass of the optimal planting date treatment (21 DAA in both growth seasons) was 5.2 and 3.8 fold higher, respectively, than that on the very late planting date (Fig. 2). The stem grew rapidly before 21 DAA and grew slowly thereafter in all planting dates. The difference in stem biomass between the early/optimal and the late/very late planting date was very large during the entire reproductive growth stage (Fig. 2). The maximum stem biomass on the late and very late planting dates was averagely 49.9% and 25.3% of the optimal planting date (Fig. 2). The canola plants' leaves directly entered senescence stage because of early planting, in which a decreasing leaf biomass was observed on the early planting date. Although the leaf biomass on optimal, late, and very late planting dates increased initially, the range of this increase differed. Leaf biomass decreased rapidly from 14 DAA on all planting

Table 1: Comparison of yield and yield components of canola among different planting dates (early, optimal, late, and very late planting date) in 2011 and 2012. Mean values of the traits were combined due to the non significant difference between two years after homogeneity analysis

Plant dates	Plant height (cm)	Number of branches per plant	Number of siliques per plant	Number of seeds per silique	1000-seed weight (g)	Seed yield (kg ha^{-1})
Early (Sep 15)	185.3 a	10.5 a	359.2 a	23.3 a	4.66 a	3485 a
Optimal (Sep 25)	181.8 b	10.4 a	333.7 b	22.8 a	4.56 b	3609 a
Late (Oct 25)	166.9 c	7.1 b	230.2 c	20.5 b	4.19c	2564 b
Very late(Nov 15)	132.9 d	5.5 c	98.8 d	17.7 c	3.89 d	1117 c
Homogeneity	0.646^{NS}	0.761^{NS}	1.884^{NS}	0.601^{NS}	0.515^{NS}	1.263^{NS}
F value	679***	122***	354***	81***	234***	376***

NS indicates not significant; *** indicates significant at α=0.001; Different lowercase letters in the same column show a significant difference at P≤0.05 using Duncan's test at a probability of 0.05

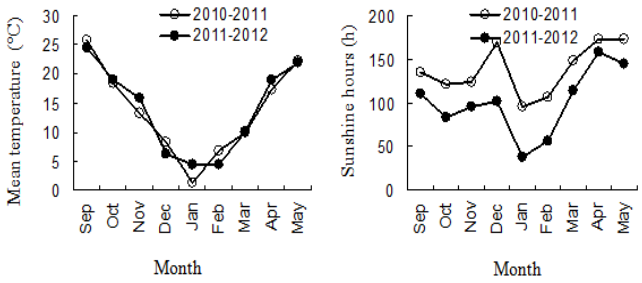

Fig. 1: Mean temperature and sunshine hours from September to May during 2010-2011 and 2011-2012 two growth seasons

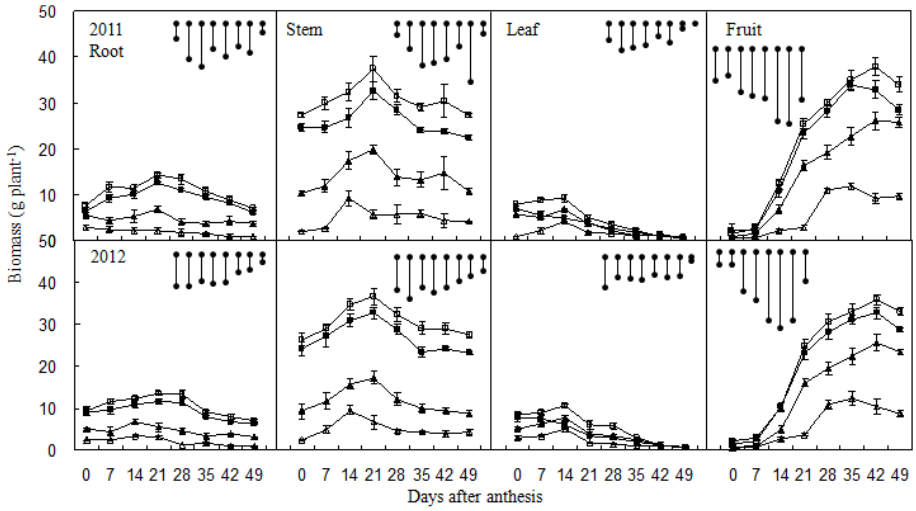

Fig. 2: Biomass accumulation in the root, stem, leaf, and inflorescence from 0, 7, 14, 21, 28, 35, 42, and 49 days after anthesis during 2011 and 2012 on early (Sep 15), optimal (Sep 25), late (Oct 25), and very late (Nov 15) planting dates. Error bars indicate standard error of mean. Vertical bars with solid circle indicate $LSD_{0.05}$ at each developmental stage

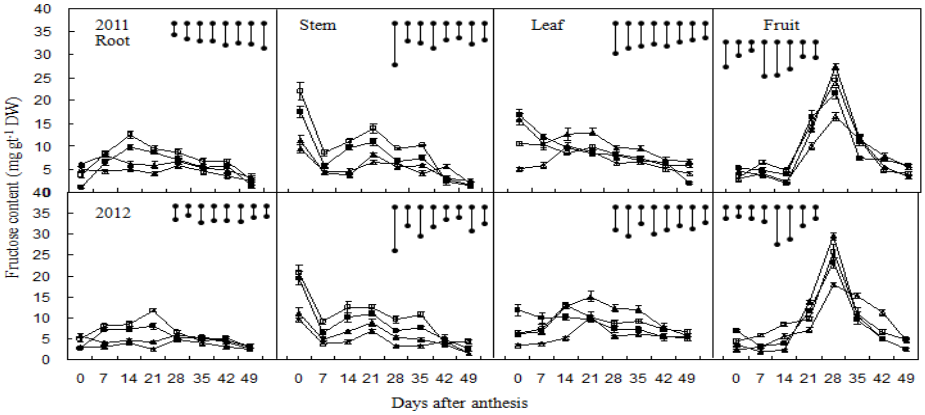

Fig. 3: Dynamic of fructose content in the root, stem, leaf, and inflorescence from 0, 7, 14, 21, 28, 35, 42, and 49 days after anthesis during 2011 and 2012 on early (Sep 15), optimal (Sep 25), late (Oct 25), and very late (Nov 15) planting dates. Error bars indicate standard error of mean. Vertical bars with solid circle indicate $LSD_{0.05}$ at each developmental stage

dates (Fig. 2). At 14 DAA, the leaf biomass on the optimal planting date averagely increased by 27.0% and 53.6% compared with that on late and very late planting dates. Reproductive organ growth was rapid after 7 DAA on the four planting dates, but such growth slightly decreased during maturation because of dehydration. The difference in inflorescence biomass became evident between the early/optimal planting date and the late/very late planting date from 21 DAA. A significant difference in inflorescence biomass between the early and optimal planting dates was noted at the late seed and pod developmental stage (Fig. 2). The maximum inflorescence biomass (42 DAA) on the optimal planting date was higher than that on the early, late, and very late planting dates with 10.9%, 31.1%, and 68.9% in 2011; and 8.7%, 28.6% and 65.7% in 2012, respectively.

Fructose Content

The root fructose content on early and optimal planting dates differed from that on the late and very late planting dates at the early reproductive growth stage (Fig. 3). A significantly higher amount of fructose content was observed on early and optimal planting dates at 14 and 21 DAA in 2011 and 2012, respectively, compared with that on late and very late planting dates (Fig. 3). The stem fructose content at the initial flowering stage was very high on the four planting dates but dropped drastically at 7 DAA compared with 0 DAA (Fig. 3). On the four planting dates, the highest stem fructose content was obtained on the optimal planting date and then on the early planting date. At 0 DAA, the stem fructose contents on late and very late

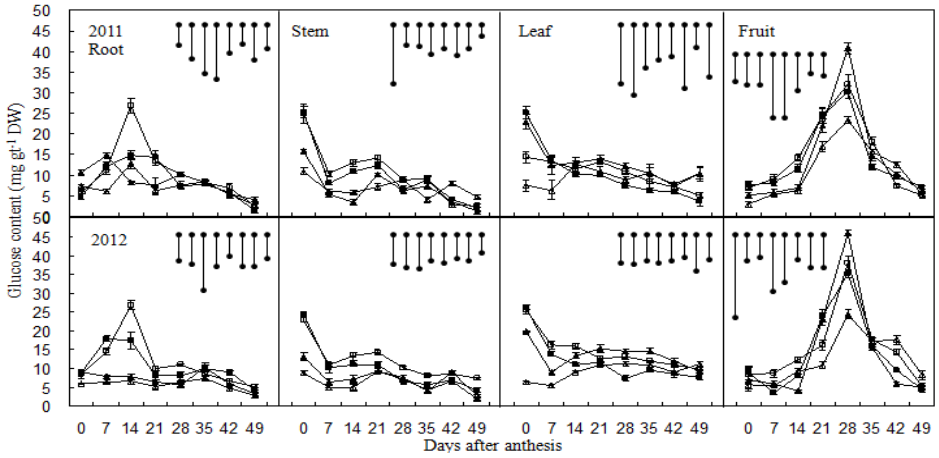

Fig. 4: Dynamic of glucose content in the root, stem, leaf, and inflorescence from 0, 7, 14, 21, 28, 35, 42, and 49 days after anthesis during 2011 and 2012 on early (Sep 15), optimal (Sep 25), late (Oct 25), and very late (Nov 15) planting dates. Error bars indicate standard error of mean. Vertical bars with solid circle indicate $LSD_{0.05}$ at each developmental stage

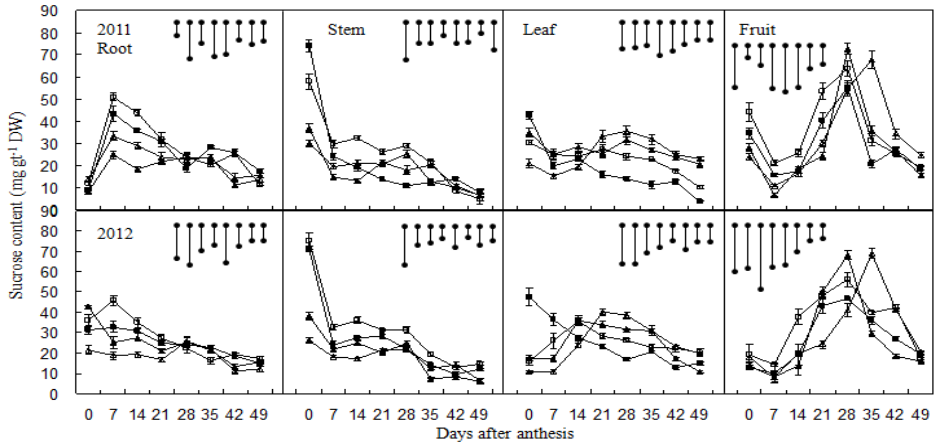

Fig. 5: Dynamic of sucrose content in the root, stem, leaf, and inflorescence from 0, 7, 14, 21, 28, 35, 42, and 49 days after anthesis during 2011 and 2012 on early (Sep 15), optimal (Sep 25), late (Oct 25), and very late (Nov 15) planting dates. Error bars indicate standard error of mean. Vertical bars with solid circle indicate $LSD_{0.05}$ at each developmental stage

planting dates were averagely reduced by 47.2% and 55.6%, respectively, compared with those on the optimal planting date (Fig. 3). The leaf fructose content on the early planting date exhibited a decreasing trend in both growth seasons. The leaf fructose content increased initially until 21 DAA and then decreased in optimal plating date in 2012 and in delayed planting date, including late/very late planting date in both the growth seasons. This result suggested that the pattern of fructose accumulation in the leaves was altered when planting date was delayed. The leaf fructose contents at 21 DAA on late planting date were averagely 35.9%, 28.3%, and 32.9% higher than on early, optimal, and very late planting dates in both growth seasons (Fig. 3). The fructose content of inflorescence before 14 DAA was low but increased thereafter. The peak value of fructose content was gained at 28 DAA on all planting dates. The highest fructose content of inflorescence was observed on the late planting date but not on the optimal planting date. The fructose contents on early, optimal, and very late planting dates were reduced on average by 21.4%, 11.8%, and 39.8%, respectively, at 28 DAA compared with those on the late planting date (Fig. 3).

Glucose Content

Root glucose content on the optimal planting date reached the peak value at 14 DAA and was significantly higher with an average of 49.6%, 69.9%, and 63.6% than that on the early, late and very late planting dates, respectively (Fig. 4). The stem glucose content at 0 DAA on early and optimal planting dates was the highest during the reproductive growth stage. However, their difference was not significant.

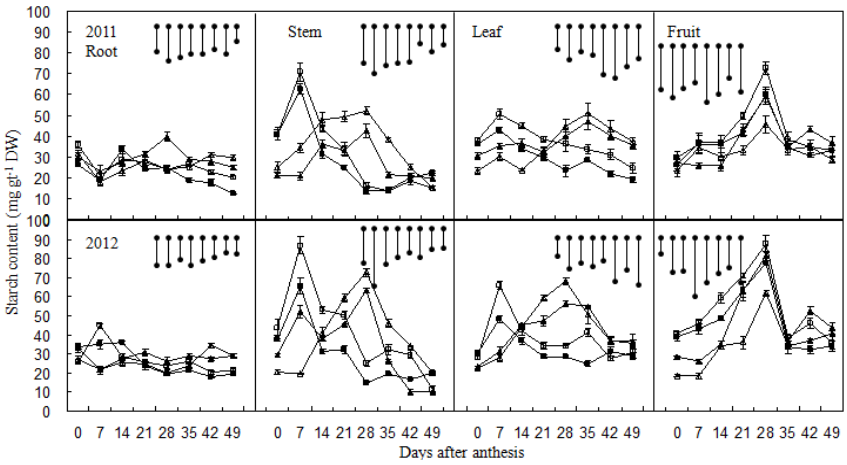

Fig. 6: Dynamic of starch content in the root, stem, leaf, and f inflorescence from 0, 7, 14, 21, 28, 35, 42, and 49 days after anthesis during 2011 and 2012 on early (Sep 15), optimal (Sep 25), late (Oct 25), and very late (Nov 15) planting dates. Error bars indicate standard error of mean. Vertical bars with solid circle indicate $LSD_{0.05}$ at each developmental stage

Stem glucose content on late and very late planting dates was averagely decreased by 39.1% and 58.6% at the initial flowering stage compared with that on the optimal planting date (Fig. 4). For leaf glucose content, early and optimal planting dates showed a decreasing trend in the two growth seasons. Similar to leaf fructose content, leaf glucose content on late and very late planting dates increased from 7 DAA, indicating that leaf senescence was delayed when late sowing was done. Thus, leaf glucose content on the late planting date was higher than that on early and optimal planting dates from 28 to 35 DAA. For instance, leaf glucose content on the late planting date was averagely 40.7% and 17.9% higher than that on early and optimal planting dates at 28 DAA (Fig. 4). Inflorescence glucose content increased very quickly after two weeks of the initial flowering on different planting dates. Glucose content on late planting date was markedly higher than that on the other dates when the highest amounts were obtained at 28 DAA (Fig. 4). No significant difference in inflorescence glucose content was observed between early and optimal planting dates at 28 DAA. However, the inflorescence glucose content on the very late planting date treatment was the lowest, in which the content was 42.7% and 47.0% less than that on the late planting date in two years, respectively (Fig. 4).

Sucrose Content

The differences in root sucrose content on early, optimal, late, and very late planting dates were significant before 21 DAA in both the years (Fig. 5). Root sucrose content on the optimal planting date was markedly higher than that on the other three planting dates except 0 DAA. At 7 and 14 DAA, the root sucrose content in the optimal planting date was averagely 21.5%, 47.8%, and 46.8% in 2011 and 15.0%, 39.6%, and 39.6% in 2012, higher than that on early, late, and very late planting dates, respectively (Fig. 5). Stem sucrose content exhibited a decreasing trend from the initial flowering stage. Similar to stem fructose and glucose contents, sucrose content was the highest at the initial flowering stage. Stem sucrose content on the optimal planting date treatment was markedly higher than that on the other three planting dates from 7 to 35 DAA (Fig. 5). Leaf sucrose content under early planting date treatment was decreasing from initial flowering stage (Fig. 5). However, sucrose content on the optimal planting date increased initially at the early reproductive growth stage and then decreased. In contrast, the trend was changed in the dynamics of leaf sucrose accumulation occurred on the late and very late planting dates. From 21 DAA, leaf sucrose content on late and very late planting dates increased rapidly. In particular, leaf sucrose content on the very late planting date was higher than that on the other three planting dates, which was averagely 47.2%, 58.5%, and 49.3% higher than that on the early planting date and 23.7%, 32.0% and 28.0% higher than that on the optimal planting date at 21, 28, and 35 DAA, respectively (Fig. 5). Fruit sucrose content was also modified on late and very late planting dates. At the early reproductive growth stage, higher inflorescence sucrose content was obtained in the optimal planting date. However, the peak value of inflorescence sucrose content was observed at 28 DAA on the late planting date. The inflorescence sucrose content was averagely increased by 27.9% and 15.0% on the late planting date compared with that on early and optimal planting date at 28 DAA, respectively (Fig. 5). The maximum inflorescence sucrose content on the very late planting date drifted to 35 DAA, which was one week later than that of the three planting dates. Furthermore, inflorescence succrose content on the very late planting date almost reached the maximum amount on the late planting date (Fig. 5).

Starch Content

Root starch content among early, optimal, late, and very late planting dates was not significant during most of the early reproductive growth stage. However, root starch contents on late and very late planting dates were significantly higher than those on early and optimal planting dates during late seed developmental stage (42 and 49 DAA, respectively). Root starch contents on early and optimal planting dates were averagely decreased by 44.9% and 33.6% at 42 DAA and 45.6% and 29.0% at 49 DAA, respectively, compared with those on the very late planting date (Fig. 6). In contrast to other types of carbohydrates, starch in the stem exhibited a distinct accumulation pattern that was apparently affected by different planting dates. The peak of the stem starch content was divided into two groups. One group was observed on early and optimal planting dates, in which the maximum amounts were observed at 7 DAA with an average increment of 43.4%, 57.4%, 55.2%, and 64.4%, respectively, compared with those on late and very late planting dates (Fig. 6). The other group was observed on late and very late planting dates, in which the highest amount was obtained at 28 DAA. Stem starch content at 28 DAA on the very late planting date was averagely 76.5%, 67.0%, and 15.8% higher than that on early, optimal, and late planting dates, respectively (Fig. 6). Leaf starch content on different planting dates exhibited a similar trend to the stem (Fig. 6). The leaf starch contents on early and optimal planting dates were increased in the first week and then kept decreasing. The leaf content on the optimal date was significantly higher than that on the early planting date at most of the reproductive growth stage because of early leaf senescence that occurred as a result of early planting. On late and very late planting dates, leaf starch contents were lower than those on early and optimal planting dates at early reproductive growth stage. However, leaf starch contents on late and very late planting dates were markedly higher than those on early and optimal planting date at 35 DAA in 2011 and 28 DAA in 2012. At 35 DAA, the very late planting date had an average increment of 44.5%, 34.1%, and 8.0% while that increased by 58.6%, 49.7%, and 17.3% at 28 DAA compared with those on early, optimal, and late planting dates respectively (Fig. 6). Kinetics of the inflorescence starch content was similar to fructose, glucose, and sucrose contents on the four planting dates. However, the main difference was that the inflorescence starch content on the optimal planting date was significantly higher than that on the other treatments. On the optimal planting date, inflorescence starch content was averagely 14.4%, 12.9%, and 33.3% higher than that on early, late, and very planting dates at 28 DAA, respectively (Fig. 6).

Discussion

For most crops, a delayed planting date can significantly reduce plant yield and quality (Bauer *et al.*, 2000; López-Bellido *et al.*, 2008; Robinson *et al.*, 2009). In the current study, reduction of yield was due to decreased number of siliques per plant, seeds per sililique and seed weight when planting date was delayed (Table 1). One of the reasons for silique reduction is decreased of branching (Table 1). Kelley (2001) reported that late planting can significantly reduce number of heads in wheat. Branching is an intricate trait, which is affected by many environmental cues, such as phytochrome, phytohormones (i.e. strigolactone), nutrition conditions (i.e. nitrogen supplement) (Aguilar-Martínez *et al.*, 2007; Zhang *et al.*, 2007; Ferguson and Beveridge, 2009; Hayward *et al.*, 2009; Finlayson *et al.*, 2010; Zhu and Kranz, 2012; Dun *et al.*, 2013). Delayed planting possibly shortened the growth period of canola that might affect axillary bud differentiation and therein the reduction of branches. However, the pattern and amount of gene expression or the level of internal phytohormones regulating axillary bud differentiation on the late planting date were unknown. Delay in planting date could cause inefficient photo-assimilates production in plants that might lead to overall less amount of nutrient supply from source (leaf, stem, roots) to sink (seeds) (Schiltz *et al.*, 2005). As a result, accumulation of seed biomass was markedly reduced on the late planting date. In contrary, heavier seed weight was observed in plants with early planting date.

In this study, it is clearly shown that planting dates significantly affected the biomass production that varies from organ to organ in plants. Moreover, the differences observed in different planting dates could be attributed to meteorological variations (such as temperature, sunlight etc.). Although winter canola has low temperature tolerance to some extent, extremely low temperatures can also cause damage if combined with other adverse agronomic practices, for example, an inappropriate planting date. Early planting date triggers an early onset of organ senescence because high temperature at the seedling stage can accelerate organ genesis and differentiation (Fig. 1) (Yin *et al.*, 1997; Thingneas *et al.*, 2003). As a result, leaf biomass on the early planting date was decreasing, whereas leaf biomass on the other three treatments increased before the end of flowering (Fig. 2) (Jochum *et al.*, 2007; Zhao *et al.*, 2007). In contrast to early planting date, plants meet relatively low temperature when canola planting date was delayed. In the present study, the difference in mean temperature between October and November was approximately 5°C. Thus, low temperature after germination can slow the seedling growth rate on all planting dates (Marsh, 1992; Vandelook and Van Assche, 2008). In addition to this initial low temperature after late planting, the whole plant organ biomass accumulation was significantly reduced because of a further decrease in the mean temperature and interval of plant biomass accumulation before January (Figs. 1 and 2). However, the impact of low temperature on plant biomass accumulation in delayed sown canola was much more profound than that in early planting date, because most of

leaves were not differentiated when canola suffered low temperature stress. Moreover, low temperature is also required for the vernalization and induction of flowering in winter type canola (Ferreira *et al.*, 1995; Fowler *et al.*, 1996; Robertson *et al.*, 1996; Mahfoozi *et al.*, 2001; Zhao *et al.*, 2007a). Consequently, all of the canola plants promptly reached to reproductive phase (initially budding) once the temperature became suitable for budding as the mean temperature increased after January. Thereafter, the amount of plant biomass including root, leaf, and stem were reflected by early vegetative growth status before flowering. Nielsen *et al.* (2002) reported that late planting caused a reduction of 144 growing degree days, resulted in reduced corn yield and suggested that it could be compensated by early maturing genotypes.

Despite numerous reports on the negative effect of late planting on crop yield and quality, the associated physiological mechanism(s) was relatively less investigated. Carbohydrate is an important photosynthetic product, and most of the plant biomass is transformed from this product (Engels, 1994; Pizarro and Bisigato, 2010). Our result showed that the allocation pattern of carbohydrate was evidently altered in the stem, leaf, and inflorescence on different planting dates (Figs. 3 to 6). On the late planting date, the peak of leaf biomass and carbohydrates, including fructose, glucose, sucrose, and starch were produced on a later date than the early and optimal planting date, revealing the delayed leaf development and carbohydrate metabolism. Synthesized carbohydrates in the leaf via photosynthesis should be transported to other organs for utilization (Mason and Maskell, 1928; Hammond *et al.*, 1984). At initial flowering, very high content of these carbohydrates except starch was observed in the stem. The phenomenon was possibly caused by the transient deposition of carbohydrate in this tissue from the leaves combined with its own photosynthesis and very low flowers and buds biomass (Hua *et al.*, 2012). Moreover, sufficient carbohydrates could support stem consumption during the elongation and widening. The utilization was indicated by gaining the maximum stem biomass at the middle reproductive growth stage (Fig. 2; Garcia *et al.*, 2001; Slewinski, 2012). The stem starch content on early and optimal planting dates was similar to other carbohydrates except at the initial flowering point, suggesting the timely transformation of starch for these planting dates to other chemical compounds, such as lignin and cellulose or transported to developing siliques and seeds (Sauter and Kende, 1992; Studer *et al.*, 2011). Evidence in *Arabidopsis* suggested that starch turnover may determine the capacity to synthesize lignins. Further, sugars function as a source of carbon skeleton and signal to enhance the synthesis of lignins (Stafford, 1967; Rogers *et al.*, 2005). In this context, the stem should be lignified as soon as possible because of the rapidly increasing inflorescence biomass. To support the weight of increasing siliques and seed biomass, a solid stalk is necessary. Given the increasing temperature from the initial flowering, late development in the leaf resulted in advantageous carbohydrate production ability. However, the smaller biomass of the stem and inflorescence is a big restriction for its transformation into corresponding biomass on the late and very late planting dates. This result suggested that plant biomass accumulation before the initial flowering stage is more important than that after the flowering for obtaining the eventual biomass. As for silique and seed, their developments are essential issues for reproductive growth in canola. Silique and seed development also requires utilization of large quantitative of carbohydrates (King *et al.*, 1997; Fallahi *et al.*, 2008). At flowering stage, the development of leaves is indirectly proportional to silique/seed (Fig. 2, Hua *et al.*, 2012), thereby indicating that the photoassimilates in the leaves were transferred to the developing tissues during senescence. At reproductive phase, silique walls became the source, whereas the seeds were the sink for the synthesis of storage compounds. The inference has been proved by the result that inflorescence carbohydrate content in the four planting dates reached their climax at 28 DAA, whereas leaf carbohydrate content occupied a small fraction at this point. This opinion was in accordance with previous investigations (Gammelvind *et al.*, 1996). Noticeably, the peak value of the carbohydrate content in inflorescence was not ranked the first on early or optimal planting dates except for the starch content. Although both sucrose and starch are two important photosynthetic products, their functions are not totally the same despite of their redundant function in some metabolic processes (Huber and Israel, 1982; Stitt *et al.*, 1984; Goldshcmidt and Huber, 1992; Geigenberger, 2003; Coneva *et al.*, 2012). On the late planting date, regardless of the same phenomenon, such as seed reserve synthesis, the late organ development led to the reduce uptake of carbohydrate for biomass accumulation. Different from sucrose, fructose, and glucose, starch almost disappeared in the mature seeds and transformed into lipids during seed development (Hills, 2004; Andriotis *et al.*, 2010). Thus, the developmental rhythm was modified on the late and very late planting dates from tissue carbohydrate accumulation and partitioning.

In conclusion, the results indicated that lower seed yield and inferior performance of the seed yield component were observed on the late planted crop. Reduction of branches, silique numbers, and seed weight led to decrease in seed yield as planting date delayed. Decreasing temperature and sunshine hours during vegetative growth before flowering initiation on the late planting, resulting in less assimilate production in roots, stem, and inflorescence and thereafter accumulation in seeds. Partitioning of carbohydrate was altered in the leaf due to development lag on the late planting date. The sugars, including sucrose, fructose, and glucose, in the inflorescence were beneficial for biomass accumulation on the late planting date, whereas starch took advantages for storage (i.e., lipids) biosynthesis.

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