Field Crops Research 122 (2011) 60–69

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Variability and regulation of the number of ovules, seeds and pods according to assimilate availability in winter oilseed rape (*Brassica napus* L.)

Xiujuan Wang[a,c], Amélie Mathieu[b], Paul-Henry Cournède[c], Jean-Michel Allirand[d], Alexandra Jullien[b], Philippe de Reffye[e], Bao Gui Zhang[a,*]

[a] Key Laboratory of Plant-Soil Interactions, College of Resources and Environmental Sciences, China Agricultural University, Beijing 100193, China
[b] AgroParisTech, UMR 1091 EGC, Thiverval-Grignon F-78850, France
[c] Ecole Centrale de Paris, Laboratory MAS, Chatenay-Malabry 92290, France
[d] INRA, UMR 1091 EGC, Thiverval, Grignon F-78850, France
[e] CIRAD, AMAP and INRIA, DigiPlante, Montpellier 34398, France

ARTICLE INFO

Article history:
Received 23 November 2010
Received in revised form 15 February 2011
Accepted 16 February 2011

Keywords:
Winter oilseed rape
Yield components
Assimilate availability
Architectural effect

ABSTRACT

The number of pods per plant and the number of seeds per pod are the most variable yield components in winter oilseed rape (WOSR). Both the number of ovules per pod and the potential for the ovule to develop into a mature seed may depend on pod position in the plant architecture and time of appearance. The complex developmental pattern of WOSR makes it difficult to analyse. The objectives of this study were to investigate the variability of the following yield components (a) ovules/pod, (b) seeds/pod, and (c) pods/axis in relation to two explanatory variables. These two variables include (1) flower and inflorescence position and (2) time of pod appearance, linked to the effect of assimilate availability.

Field experiments were conducted with the variety Mendel. Different trophic states were created by clipping the main stem or ramifications. The number and position of flowers that bloomed within the inflorescence were recorded based on observations every two to three days throughout the flowering season.

On the control plants, for the main stem we observed that the number of ovules per pod decreased for a few ranks and then tended to increase and again to decrease at the end. On ramification R1 and R4, the number of ovules increased at first, and then remained constant with the pod rank. Furthermore, the number of ovules per pod remained constant along the inflorescence on the other ramifications and increased with ramifications from top to bottom. The number of seeds per pod did not vary with the pod rank at the basal positions on inflorescences and decreased afterwards along the inflorescence. The clipping of the main stem or ramifications increased the number of ovules per pod, seeds per pod and pods per axis. The number of ovules and seeds per pod did not vary with the time of pod appearance for the pods located at normalised rank 0.01–0.1. However, the number of ovules and seeds per pod can be impacted by the time of pod appearance on the plant scale. Thus, our results indicate that the amount of available assimilates was the primary determinant of pod and seed production during the flowering period. The distribution of resources was significantly affected by both the positions of pods within an inflorescence and the position of inflorescences within a plant.

1. Introduction

Seed yield of oilseed rape is determined by several variables, including plant density, number of pods per plant, number of seeds per pod and individual seed weight (Diepenbrock, 2000). Large variations exist in the yield components of oilseed rape (Ozer et al., 1999; Malagoli et al., 2004; Tuncturk and Ciftci, 2007) among varieties and between plants of the same variety grown in the same field.

Winter oilseed rape (WOSR) has a complex developmental pattern. The inflorescences initiate acropetally but expand basipetally, and the flowers bloom acropetally along the inflorescence (Tittonel, 1990). The flowering ceases at approximately the same time on all inflorescences (Keiller and Morgan, 1988). Hence, this "double sense" gradient induces large differences in age and position of pods within the inflorescence/plant and thus in the pods' access to assimilates during their development (Tayo and Morgan, 1975).

The variation in number of pods and seeds highly depends on their access to assimilates (Lee and Bazzaz, 1982; Bawa and Webb,

* Corresponding author. Tel.: +86 10 6273 4425; fax: +86 10 6273 3596.
E-mail addresses: baogui.zhang@gmail.com, zhangbg@cau.edu.cn (B.G. Zhang).

0378-4290/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.fcr.2011.02.008

1984; Arathi et al., 1996, 1999). Tayo and Morgan (1979) have studied the impact of shading or leaf removal on the number of pods on the terminal inflorescence. They concluded that irrespective of the developmental stages over which shading took place, reductions in the number of pods occurred on the terminal inflorescences. The number of pods per plant was significantly reduced when the shading was applied at anthesis, although the reduction in the number of pods was partially compensated by an increase in the number of seeds per pod in the basal pods. Leaf removal treatments led to more severe reductions in the number of pods, pod yield and seed yield than the shading treatments. Furthermore, Pechan and Morgan (1985) found that defoliation on the terminal inflorescence at anthesis causes a significant reduction in the weight of pods per plant as a result of reducing the weight of the individual pods. These studies suggest that the supply of assimilates to the inflorescences from anthesis onwards is an important factor that contributes to the yield components in WOSR.

The assimilate availability for one organ depends both on the quantity of assimilates available at the whole plant level (Hocking and Pate, 1977) and on the competition with the other demanding organs (Harper et al., 1970; Robinson et al., 1980). These processes are subject to different constraints.

Plant architecture has a strong effect on assimilate partitioning among organs (Farrington and Pate, 1981). Flower position within one inflorescence and inflorescence position within the overall architecture of the plant are important factors affecting yield variation (Ellis and Sedgley, 1992; Brookes et al., 2010). However, within one inflorescence, flowers and seeds located close to the source of assimilates are more likely to survive (Nakamura, 1986; Thomson, 1989; Diggle, 1995; Guitian and Navarro, 1996; Medrano et al., 2000). This phenomenon is observed in many species (Berry and Calvo, 1991; Obeso, 1993). The number of reproductive structures that depend on the available resources also affects the allocation of assimilates between flowers or fruits located on different branches (Stephenson, 1981; Keiller and Morgan, 1988).

The course of fruit development in flowering plants includes periods of considerable overlap between growing fruits and seeds among inflorescences. This pattern of intense reproductive growth causes high demand within a short period of time. Thus, the timing of organ initiation and development regulates the partitioning of assimilates in the plant. Furthermore, senescence of the leaves during pod development decreases the assimilate supply, which controls the overlap in the growth of competing sinks and the relation between the photosynthetic source and sink (Bustan et al., 1995). As a result, early developed fruits and seeds receive more resources than those that develop later (Stephenson, 1980; Thomson, 1989; Guitian and Navarro, 1996).

In addition, pollination limitation could also lead to a variation in pods and seeds (Brunet and Charlesworth, 1995; Brookes et al., 2010). The magnitude of pollen limitation varies among flowers within an inflorescence, among inflorescences within a plant, and among plants within a season (Knight et al., 2005). The failure of seed production may be caused by either reduced pollen production or poor pollen quality (Berjano et al., 2006). However, we mainly focus on the factor of assimilate availability in this paper.

Based on the factors of variation discussed above, we analysed the yield elaboration in WOSR on both the pod scale and the whole plant scale, according to the position and time of pod development. Yield elaboration on the pod scale depends on the number of ovules. Fertilisation then influences the number of seeds per pod. Once the number of seeds is set, assimilate accumulation in the seed can lead to an increase in seed weight. At each stage, competition for assimilates results in a reduction in either the number or the weight of the organs. Thus, it is important to study the variations in yield components and the relationship between their variability and assimilate availability.

In this article, we studied the variability in the number of pods, ovules and seeds per pod within the plant architecture of WOSR. To investigate the effect of assimilate availability on these variables, we conducted field experiments in which some plant axes were clipped to induce a change in the demand of assimilates at the pod and axis levels. The number of pods, ovules and seeds per pod within the plant architecture were compared to the control plants. Our aim was to determine how pod positions in plant architecture, linked to local (or architectural) effects, and the time of pod appearance, influence the number of ovules and seeds per pod. The time of pod appearance is characteristic of plant ontogeny and potentially global resource availability (Mathieu et al., 2009).

2. Materials and methods

2.1. Plant material

WOSR is an annual plant with inflorescences of yellow flowers. Seeds are sown in the autumn and before winter, the plant develops a rosette of 10–15 leaves (Jullien et al., 2010). Stem extension begins with the return of the growing season in the spring. Flowering begins before stem extension has finished and continues for more than one month. The number of ramifications is pre-determined during the organ initiation early in the growth cycle in autumn. The meristem produces leaves, which bears axillary buds that can produce a ramification (Tittonel, 1990; Diepenbrock, 2000).

Flowering begins with the opening of the lowest bud on the main stem and continues upward with three to five or more flowers opening per day. Flowering at the base of the first secondary branch begins two to three days after the first flower opens on the main stem. Winter oilseed rape (*Brassica napus* L.) has entomophilous flowers that are capable of both self- and cross-pollination. Becker et al. (1992) found that depending on variety and weather, oilseed rape exhibits approximately 30% out-crossing. Insect mediated cross-pollination may be of only secondary importance for oilseed rape (Mesquida et al., 1988). The variety Mendel is self-compatible and mainly autogamous.

Following emergence of the leaves, internodes of the main stem begin to elongate. The expansion of the ramification is delayed compared to the main stem. Lateral inflorescences expand along the main stem from the top to the bottom. Flower emergence starts on the main inflorescence and develops basipetally to the lateral inflorescences (Tittonel, 1990), causing the basal and oldest ramifications to bear the youngest inflorescences. Pods are set once all of the leaves of the main stem have emerged. The first pods are initiated on the main stem and then on the ramifications from apical to basal. Within a ramification, pod setting remains acropetal (Jullien et al., 2010).

The inflorescences were numbered from top to bottom along the main stem. Thus the main stem is number R0 and the highest ramification is number R1. Flowers and pods on each inflorescence were recorded by their rank number starting from the base of the inflorescence (Fig. 1). On an inflorescence, pod number 1 is closest to the leaves and the main stem. The pods were gathered five by five to analyse the effect of pod rank on the number of ovules and seeds per pod. Because the length of inflorescences is different between plants, pod ranks were normalised for each inflorescence by dividing by the maximum rank on the inflorescence. This approach allows the conversion of the ranks of all of the inflorescences into a range between 0 and 1.

2.2. Experimental design and growing conditions

Field experiments were conducted in Grignon (Yvelines, France, 48.9°N, 1.9°E) at the National Institute for Agricultural Research

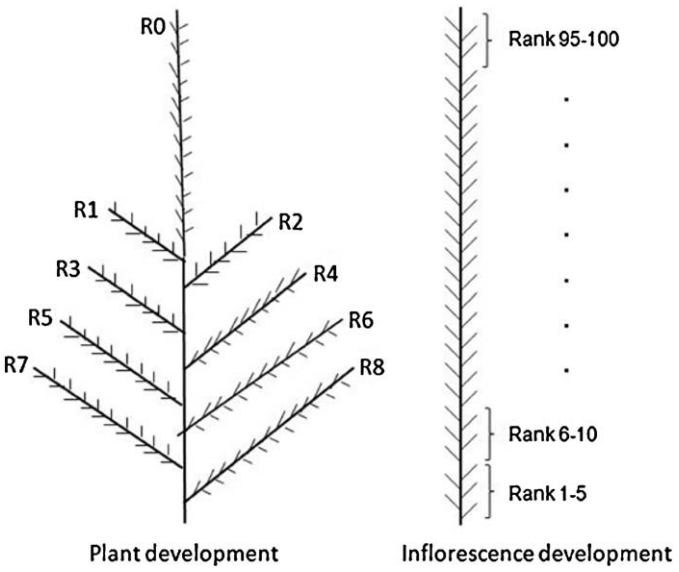

Fig. 1. Schematic diagram of winter oilseed rape. Plant development: the inflorescences initiate acropetally but expand basipetally. Flowering starts on the main stem (R0) and is followed by lateral inflorescences from top to bottom (basipetal). Inflorescence development: flowering and pod setting on the inflorescence occur from bottom to top (acropetal).

(INRA) during the growing seasons of 2008–2009. Seeds were sown on September 9th, 2008 at a density of 50 seeds per m^2. The experimental variety was Mendel. Plots were twenty rows, 0.30 m apart and 30 m long, and the plots were kept free of weeds, insects and diseases. The plants were harvested at the beginning of July.

2.3. Treatments and sampling

The demand of assimilates can be changed by clipping inflorescences. Thus, clipping treatments were conducted to investigate the effect of the competition for assimilates between inflorescences and at the plant level. Because the plants grow in the same field, we did not consider the difference in pollination conditions.

A total of 20 Mendel variety plants were randomly selected on the basis of similarity of their developmental stages in the field. Two treatments were administered: clipping ramifications (Treatment R-) or clipping the main stem (Treatment M-). Clipping was performed approximately in the 20th pod rank on the main stem. Ramifications were clipped when they emerged. The plants selected for the continuous observations were used as the control plants for the Mendel variety (Treatment CK). All of the treatments are shown in Table 1.

2.4. Measurements

2.4.1. Continuous observations

The plants on the field experimental site started to flower in mid-April, and the flowering season continued until mid-May. To investigate the effect of the position and appearance time of pods on the number of ovules and seeds per pod on the main stem and ramifications, 18 Mendel plants were randomly marked in mid-April, just before the flowering season. When the plants began to bloom, the numbers and positions of flowers that bloomed within inflorescences were recorded every two to three days throughout the flowering season from April 16th to May 18th. The positions and the times of appearance of the flowers and pods were recorded from the main stem (R0) and from the ramifications (R1, R4, R7, R9 and R11, see Fig. 1). Statistical analyses indicate that pod rank had no impact on the number of ovules (ANOVA, $F = 1.5$, df = 9, $P > 0.1$) and seeds (ANOVA, $F = 1.9$, df = 9, $P > 0.05$) for the pods located at normalised rank 0.01–0.1 of each inflorescence. Thus, to exclude the effect of pod rank, these pods were selected to analyse the effect of time of appearance.

2.4.2. Destructive measurements

Measurements began in mid-June when all of the flowers had developed into pods to ensure that the number of seeds and ovules could be measured in all of the pods of the inflorescences. For each plant, the number of pods per inflorescence and the number of seeds and aborted seeds per pod were carefully recorded according to the position of the pod (number of inflorescence and rank on the inflorescence). The number of ovules per pod was calculated as the sum of undeveloped ovules, aborted seeds and mature seeds per pod.

2.5. Statistical analysis

All statistical computations were conducted using R 2.11.1 (Copyright (C) 2010 the R Foundation for Statistical Computing).

2.5.1. Segmented regression

Segmented regression is a method of regression analysis in which the independent variable is partitioned into intervals and a separate line segment is fit to each interval. The boundaries between the segments are breakpoints. Segmented regression is regression analysis in which changes in the mean outcome levels and trends before and after an intervention are estimated (Wagner et al., 2002).

In our study, segmented regression was used to estimate the change in trend in pod rank before and after a breakpoint and the difference between the control and clipped plants. We created several variables to analyse the effect of pod rank and clipping treatment. A created variable is an artificial variable created to represent an attribute with two or more distinct levels.

Our experimental data showed that there are three segments on the main stem, and two segments on ramifications. Therefore, segmented regression with one or two breakpoints was used for ramifications and the main stem, respectively.

2.5.1.1. Segmented regression with one breakpoint. Segmented linear regression with two segments separated by a breakpoint can be useful to quantify an abrupt change in the response function (Y) of a varying influential factor (X).

$$Y = b_0 + b_1X + b_2T + e_t \quad (1)$$

X is the variable of pod rank; T is a created variable for before or after the breakpoint. T is coded 0 before the breakpoint and continuous

Table 1
Description of clipping treatments for the variety Mendel. R- denotes the treatment of clipping all of the ramifications; M- denotes the treatment of clipping the main stem and keeping all of the ramifications; CK denotes the control plants (no treatment). The '+' and the '–' represent keeping or removing main stem, respectively.

Variety	Treatments	Main stem	Ramifications	Sample size (number of plants)
Mendel	R-	+	–	10
	M-	–	+	10
	CK	+	+	18

starting at 1 after the breakpoint; e_t is the random variation at rank X not explained by the model.

b_0 is the intercept of the line, b_1 is the slope before the breakpoint and b_2 is the change in the slope before and after the breakpoint (difference in the slopes of two segments).

2.5.1.2. Segmented regression with two breakpoints.

$$Y = b_0 + b_1X + b_2TA + b_3TB \quad (2)$$

X is pod rank from baseline; TA is a created variable for the first segment coded 0 before 1st breakpoint and starts at 1 after the breakpoint; TB is a created variable for the second segment coded 0 before 2nd breakpoint and starts at 1 after the 2nd breakpoint.

b_0 is the value of dependent variable at baseline; b_1 is the trend prior to the 1st breakpoint; b_2 is the change in trend after the 1st breakpoint; b_3 is the change in trend after the 2nd breakpoint.

2.5.1.3. Segmented regression between two groups with one breakpoint. A dummy variable is incorporated for group to analyse the change in slope after the breakpoint and between the control and clipped group.

$$Y = b_0 + b_1X + b_2T + b_3G + b_3GX + b_5GT \quad (3)$$

G is a created variable for groups, coded 0 for control plants and 1 for clipped plants; GX is a created variable for the control plants coded 0 before 1st breakpoint and starts at 1 after the breakpoint; GT is a created variable for the clipped plants coded 0 before the 1st breakpoint and starts at 1 after the breakpoint.

b_0 is the value of dependent variable at baseline; b_1 is the trend before the breakpoint; b_2 is the change in trend after the breakpoint; b_3 is the difference between the groups; b_4 is the difference between the groups in change in trend before the breakpoint; b_5 is the difference between the groups in change in trend after the breakpoint.

The t-test is used to test the significance of the individual coefficients in the equation. For example, if we are testing H_0: $b_i = 0$ and H_a: $b_i \neq 0$, then we consider the P-values to determine whether to reject or accept H_0. If the P-value is less than 0.05, then we reject H_0. The null being tested by this test is $b_i = 0$, which indicates that this variable is not related to Y.

2.5.2. Analysis of variance and the Tukey's HSD test

Analysis of variance (ANOVA) was performed to test the effect of ramification number on the number of ovules per pod, seeds per pod, total pods per axis and seeds per axis. Tukey's HSD (Honestly Significant Differences) multiple comparison tests were used when significant effects were encountered to determine which means were significantly different from one another.

Furthermore, the Kruskal–Wallis rank sum test was used to test the difference in the distributions of ovules and seeds per pod with times of pod appearance.

The F-test and Student's t-test were applied to evaluate the differences in the mean numbers of ovules, seeds per pod and pods per axis between control and clipped plants (Steel and Torrie, 1980).

3. Results

3.1. Number of ovules per pod

3.1.1. Effect of pod position and clipping treatments on the main stem

3.1.1.1. Effect of pod ranks. The segmented regression demonstrated that the number of ovules per pod differed significantly with the pod rank on the main stem in the control plants (coefficient b_1 in Eq. (2), $t = -2.2$, $P = 0.04$), but not in the clipped plants (coefficient b_1 in Eq. (2), $t = -1.6$, $P = 0.13$). The number of ovules per pod fluctuated along the main stem and decreased for a few ranks followed by a tendency to increase and then to decrease at the end of the stem.

3.1.1.2. Effect of clipping ramifications. Significant changes were present in trend (slope) before and after the 1st breakpoint (coefficient b_2 in Eq. (2), 0.19 ± 0.04 for CK, $t = 2.9$, $P < 0.05$ and 0.15 ± 0.09 for R-, $t = 2.3$, $P < 0.05$) and 2nd breakpoint (coefficient b_3 in Eq. (2), 0.85 ± 0.06 for CK, $t = -4.5$, $P < 0.001$ and 0.81 ± 0.06 for R-, $t = -2.5$, $P < 0.05$) in the control and clipped plants, as shown in Fig. 2.

The number of ovules per pod was significantly different in the second segment between the control and clipped plants (coefficient b_3 in Eq. (3), $t = 3.7$, $P < 0.001$), but not in the first and third segments. Because the 1st breakpoint was the location where clipping ramifications were performed, the result indicated that clipping ramifications did have an instant influence on the number of ovules per pod on the main stem.

The mean numbers of ovules on the main stem were larger in the clipped plants than in the control plants (t-test, $t = -7.4$, df = 379, $P < 0.001$). The total mean number of ovules per axis increased ranging from 1340 ± 334 (mean $\pm$ SD) to 1876 ± 455 (mean $\pm$ SD) in the control and clipped plants, respectively.

3.1.2. Effect of pod position and clipping treatments between inflorescences

3.1.2.1. Effect of pod ranks. Segmented regression indicated that the number of ovules per pod varied with the pod rank on ramifications R1 (coefficient b_1 in Eq. (1), $t = 3.4$, $P < 0.01$) and R4 ($t = 4.6$, $P < 0.001$) in the control plants, but not in the clipped plants (coefficient b_1 in Eq. (1), $t = -0.6$, $P = 0.58$ for R1 and $t = -0.3$, $P = 0.8$ for R4, respectively). The number of ovules per pod did not vary with the pod rank on ramifications R7, R9 and R11 (coefficient b_1 in Eq. (1), $P > 0.1$ for each ramification).

3.1.2.2. Effect of clipping the main stem. Significant differences were present in trend observed for the number of ovules per pod after the breakpoint in the control plants on ramifications R1 (coefficient b_2 in Eq. (1), $t = -4.1$, $P < 0.001$) and R4 ($t = -3.0$, $P < 0.05$), but not in the clipped plants (coefficient b_2 in Eq. (1), $t = 1.6$, $P = 0.14$ for R1 and $t = 0.5$, $P = 0.66$ for R4). The number of ovules per pod was somewhat small before the breakpoint, and then increased after the breakpoint for ramifications R1 and R4 (Fig. 2). However, segmented regression for ramifications R7, R9 and R11 indicated that there were no significant changes in the trend after the breakpoint in the control and clipped plants (coefficient b_1 in Eq. (1), $P > 0.01$ for ramifications R7, R9 and R11).

The mean number of ovules per pod was significantly higher in the clipped plants than in the control plants for the ramifications R1, R4, R7, R9 and R11 (Fig. 3, coefficient b_3 in Eq. (3), $P < 0.001$ for each ramification).

The measurements of the control plants (Treatment CK) suggested that the mean number of ovules per pod increased from R0 to R11 (30.8–33.8) between the ramifications from top to bottom (Tukey's HSD comparison test, $P < 0.001$, df = 5, $F = 10.7$, Table 2, CK).

3.1.3. Time of pod appearance

Along an inflorescence axis, pods appear acropetally, pods with higher ranks appear after pods with lower ranks. Furthermore, ramifications grow basipetally (from the top to the bottom along the main stem). A high correlation exists between pod position and time of appearance for each ramification (correlation coefficient is equal to 1 for each inflorescence on each plant).

The mean number of ovules per pod for the pods located at randomized rank 0.01–0.1 did not differ significantly according to the

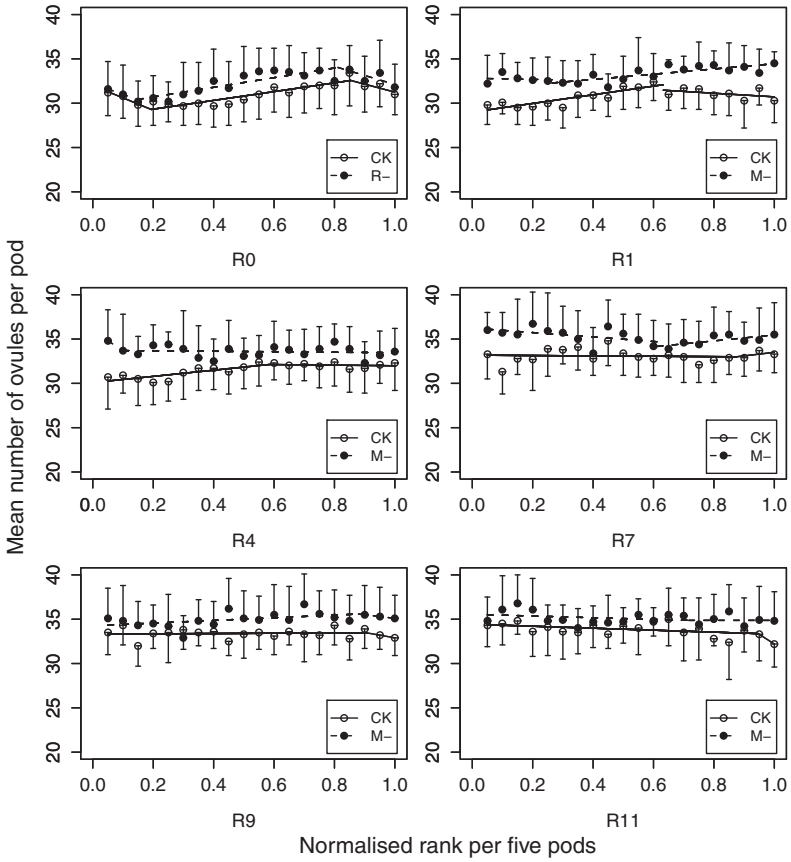

Fig. 2. Mean number of ovules per pod along the inflorescence on the main stem R0 and the ramifications R1, R4, R7, R9 and R11 (variety: Mendel). Dots and circles represent mean number of ovules per pod for the control (CK) and clipped (R-) plants, respectively. Vertical bars represent standard deviations. Fit lines using segmented regression are shown.

time of pod appearance for inflorescences R0, R1, R4, R7, R9 and R11 (ANOVA, $F < 1$, $P > 0.1$ for each ramification). Therefore, the time of pod appearance had no influence on the number of ovules per pod for these pods.

The distributions of the number of ovules per pod tended to shift towards greater values with the time of pod appearance on the inflorescences R0, R1 and R4 (Kruskal–Wallis rank sum test, R0: $\chi^2 = 88.5$, df = 8, $P < 0.001$; R1: $\chi^2 = 43.6$, df = 6, $P < 0.001$ and R4: $\chi^2 = 25.9$, df = 5, $P < 0.001$). However, it had no significant difference on ramifications R7, R9 and R11 (Kruskal–Wallis rank sum test, R7: $\chi^2 = 7.9$, df = 6, $P = 0.25$; R9: $\chi^2 = 3.9$, df = 5, $P = 0.56$; R11: $\chi^2 = 9.2$, df = 6, $P = 0.17$) (Fig. 4A).

3.2. Number of seeds per pod

3.2.1. Effect of pod position and clipping treatments on the main stem

3.2.1.1. Effect of pod ranks. The segmented regression demonstrated that the number of seeds per pod remained constant before the 2nd breakpoint (0.77 ± 0.04, coefficient b_1 in Eq. (1), $t = -1.2$, $P > 0.1$) and decreased significantly after that point with rank on the main stem in the control plants (coefficient b_1 in Eq. (1), Fig. 3, R0, $t = -2.8$, $P < 0.05$). However, the number of seeds per pod did not show a significant difference before and after the 2nd breakpoint (0.6 ± 0.04, coefficient b_1 in Eq. (1), $t = -0.5$, $P = 0.64$) with the pod rank in the clipped plants.

Table 2
Effect of clipping main stem treatment (M-) on the number of ovules and seeds per pod on ramifications R0, R1, R4, R7, R9 and R11 compared to the clipped plants (CK). Values are mean ± SD. Values with different superscripts (within a column) differ significantly using the Tukey's HSD test at $P < 0.05$.

No. ramification	Mean number of ovules per pod ± SD		Mean number of seeds per pod ± SD	
	CK	M-	CK	M-
R0	30.9 ± 2.7^{a}		24.2 ± 6.8^{b}	
R1	30.7 ± 2.6^{a}	33.1 ± 2.4^{a}	22.4 ± 7.1^{a}	26.0 ± 7.6^{ab}
R4	31.6 ± 2.5^{b}	33.7 ± 2.7^{a}	21.4 ± 8.1^{a}	27.3 ± 6.7^{ab}
R7	33.1 ± 2.5^{bc}	35.2 ± 3.1^{b}	21.7 ± 9.2^{a}	24.3 ± 9.2^{b}
R9	33.4 ± 2.2^{bc}	35.0 ± 3.0^{b}	21.0 ± 9.8^{a}	23.8 ± 8.8^{bc}
R11	33.8 ± 2.7^{bc}	35.0 ± 2.7^{b}	24.4 ± 8.8^{b}	21.7 ± 9.0^{c}
df	5	4	5	4
F	10.7	11.7	89.8	23.9
P-value	***	***	***	***
CK vs. M-	df = 1, $F = 32.7$, $P < 0.001$		df = 1, $F = 672.7$, $P < 0.001$	

*** $P < 0.001$.

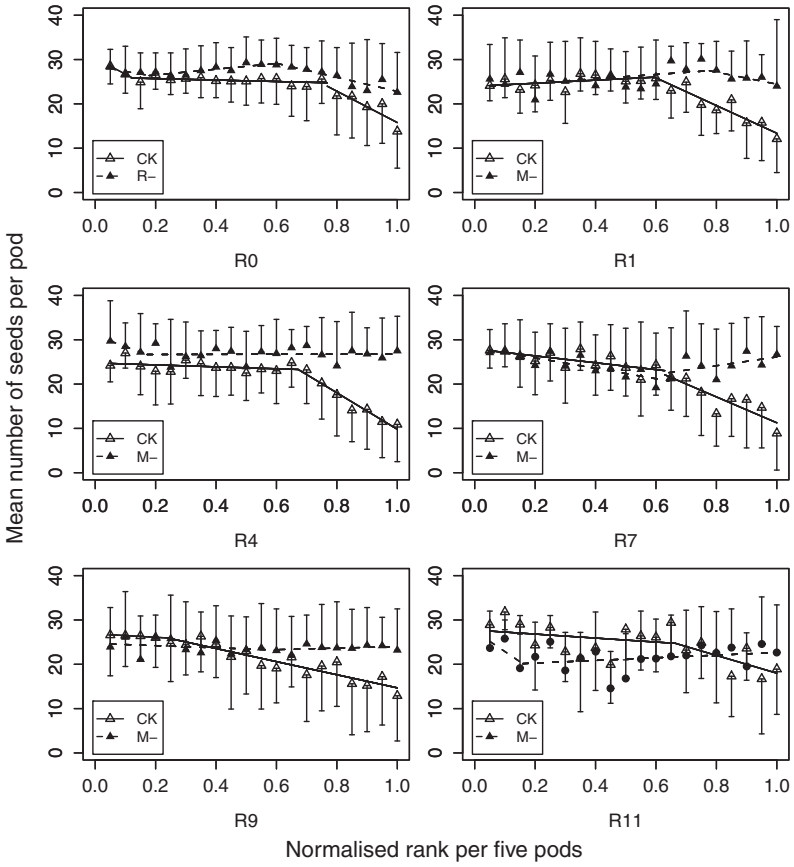

Fig. 3. Comparison of the mean number of seeds per pod on the main stem R0 and the ramifications R1, R4, R7, R9 and R11 (variety: Mendel). Triangles and empty triangles represent the number of seeds per pod for the control (CK) and clipped main stem (M-) plants, respectively. Vertical bars represent standard deviations. Fit lines using segmented regression are shown.

3.2.1.2. Effect of clipping ramifications. Segmented regression indicated that no significant changes in trend (slope) existed before and after the 1st breakpoint on the main stem in the control (coefficient b_2 in Eq. (2), 0.12 ± 0.05, $t = 1.1$, $P = 0.29$) and clipped plants (0.18 ± 0.07, $t = 0.9$, $P = 0.39$). However, the changes in trend before and after the 2nd breakpoint were significant in the control (coefficient b_3 in Eq. (2), $t = -6.6$, $P < 0.001$) and clipped plants (coefficient b_3 in Eq. (2), $t = -4.1$, $P < 0.05$). Therefore, the change in the number of seeds per pod in the distal pods was larger than in the basal pods. This result indicated that the effect of clipping ramifications on the number of seeds per pod depended on the position of pods within the main stem.

The number of seeds per pod did differ significantly before and after the 2nd breakpoint (coefficient b_3 in Eq. (3), $t = 3.8$, $P < 0.001$), but not for the 1st breakpoint (coefficient b_3 in Eq. (2), $t = -0.2$, $P > 0.1$) between the control and clipped plants. Clipping ramifications did have a significant effect on the number of seeds per pod (Fig. 3, R0).

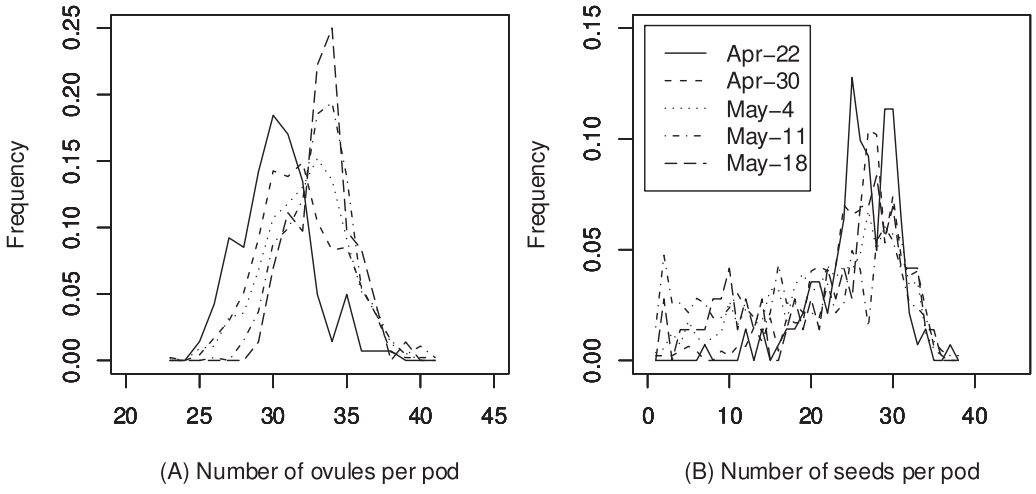

Fig. 4. Frequency distributions of the number of ovules per pod (A) and seeds per pod (B) on the main stem and ramifications for each measurement date (variety: Mendel).

Table 3
Effect of clipping main stem treatment (M-) on the total number of pods per axis and seeds per axis on ramifications R0, R1, R4, R7, R9 and R11 for clipped plants and control plants. Values are mean ± SD. Values with different superscripts (within a column) differ significantly using the Tukey's HSD test at $P < 0.05$.

No. ramification	Mean total number of seeds per axis ± SD		Mean total number of pods per axis ± SD	
	CK	M-	CK	M-
R0	1062.3 ± 703^{a}		43.9 ± 11^{a}	
R1	475 ± 29^{b}	611 ± 65	21.2 ± 4.7^{b}	23.9 ± 5.3^{b}
R4	471 ± 42^{b}	720 ± 60	22.1 ± 6.5^{b}	26.7 ± 5.4^{b}
R7	543 ± 36^{b}	735 ± 66	25.1 ± 5.9^{b}	27.4 ± 6.2^{b}
R9	496 ± 49^{b}	713 ± 37	23.6 ± 4.4^{b}	30.0 ± 6.9^{b}
R11	633 ± 90^{b}	766 ± 128	26.0 ± 8.1^{b}	35.3 ± 8.7^{c}
Total number per plant	4912 ± 194	4927 ± 51	150 ± 2	144 ± 4
df	5	4	5	4
F	23.3	0.69	23.3	3.24
P-value	***	ns	***	*
CK vs. M-	df = 1, $F = 26.9$, $P < 0.001$		df = 1, $F = 16$, $P = 0.0001$	

ns, not significant.
* $P < 0.05$.
*** $P < 0.001$.

The mean numbers of seeds per axis were larger in the clipped plants (*t*-test, $t = 2.9$, df = 386, $P < 0.05$). An increase in the total number of seeds per axis was present, ranging from 1054 ± 282 (mean ± SD) to 1568 ± 398 (mean ± SD) in the control and clipped plants, respectively.

3.2.2. Effect of pod position and clipping treatments between inflorescences

3.2.2.1. Effect of pod ranks. The mean number of seeds per pod did not differ significantly in pods before breakpoints for each ramification on the control plants (coefficient b_1 in Eq. (1), breakpoint: R1: 0.6 ± 0.04, $t = -0.8$, $P = 0.44$; R4: 0.67 ± 0.03, $t = -1.9$, $P = 0.08$; R7: 0.63 ± 0.08, $t = -0.9$, $P = 0.4$; R9: 0.24 ± 0.17, $t = -1.1$, $P = 0.2$ and R11: 0.66 ± 0.2, $t = -1.7$, $P = 0.12$). However, significant decreases were present in the number of seeds per pod with rank after the breakpoints for each ramification in the control plants (coefficient b_2 in Eq. (1), $P < 0.001$ for each ramification). The number of seeds per pod did not vary significantly with the pod rank in the clipped plants (coefficient b_2 in Eq. (1), $P > 0.1$ for each ramification). The number of seeds per pod tended to decline with higher pod rank, but the decline was more severe along the inflorescence for ramifications R1, R4 and R7 (Fig. 3, coefficient b_2 in Eq. (1), $P < 0.05$ for each ramification). Furthermore, as shown in Fig. 3, a large variability was present in the number of seeds per pod along the inflorescence on ramification R11.

3.2.2.2. Effect of clipping the main stem. Clipping the main stem did not significantly influence the number of seeds per pod before breakpoints on ramifications R1, R7, R9 and R11 (coefficient b_3 in Eq. (3), $P > 0.1$ for each ramification), but it had an impact on the ramification R4 (coefficient b_3 in Eq. (3), $t = 3.6$, $P = 0.001$). The differences in the number of seeds per pod were significant between the control and clipped plants after breakpoints for ramifications R1, R4, R7 and R9 (coefficient b_3 in Eq. (3), $P < 0.001$ for each ramification). Thus, the results indicated that clipping the main stem had a greater influence on the number of seeds per pod on the upper ramifications than on the lower ramifications.

The mean number of seeds per pod on the main stem and on ramification R11 was higher than on ramifications R1, R4, R7 and R9 in the control plants. However, the mean number of seeds per pod decreased with ramifications from top to bottom in the clipped plants (Table 2).

The mean total number of seeds per ramification increased ($F = 26.9$, df = 1, $P < 0.005$, ANOVA, Table 3) in the clipped plants compared to the control plants. However, the total number of seeds per plant was not different (mean ± SD, CK: 4912 ± 194 and M-: 4927 ± 51, *t*-test, $t = -0.72$, df = 9, $P = 0.5$).

3.2.3. Time of pod appearance

The mean number of seeds per pod for the pods located at randomized rank 0.01–0.1 did not differ significantly according to the time of pod appearance for inflorescences R0, R1, R4, R7, R9 and R11 (ANOVA, $F < 1$, $P > 0.1$ for each ramification). Therefore, the time of pod appearance had no influence on the number of seeds per pod for the first pods.

The distributions of the number of seeds per pod showed a statistically significant difference with the time of pod appearance for inflorescences except R11 (Kruskal–Wallis rank sum test, R0: $\chi^2 = 51.3$, df = 8, $P < 0.001$; R1: $\chi^2 = 32.5$, df = 6, $P < 0.001$; R4: $\chi^2 = 27.1$, df = 5, $P < 0.001$; R7: $\chi^2 = 34.7$, df = 6, $P < 0.001$; R9: $\chi^2 = 43.1$, df = 5, $P < 0.001$; R11: $\chi^2 = 4.9$, df = 6, $P = 0.55$). At the end of the flowering time, more pods with a small number of seeds were present (Fig. 4B).

The number of aborted ovules corresponds to the difference between the number of ovules and the number of seeds in a pod. This number of aborted ovules was related to the number of flowers per square meter in the field. The higher the number of flowers in the field was, the smaller the number of aborted ovules per pod (Fig. 5). The total number of aborted ovules was large at the beginning then remained constant and increased with the time at the

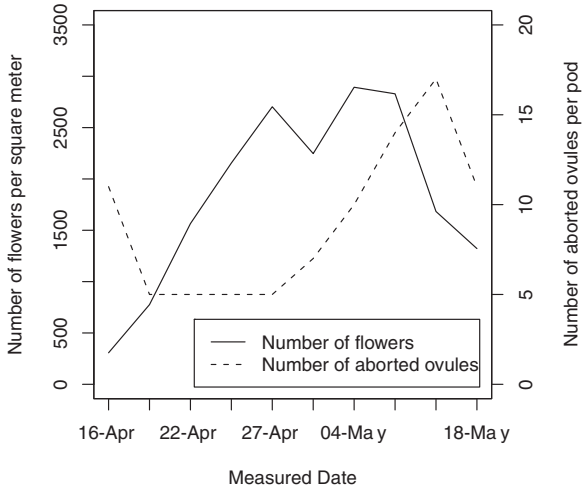

Fig. 5. Number of flowers in the field per square meter and number of aborted ovules per pod during the flowering period.

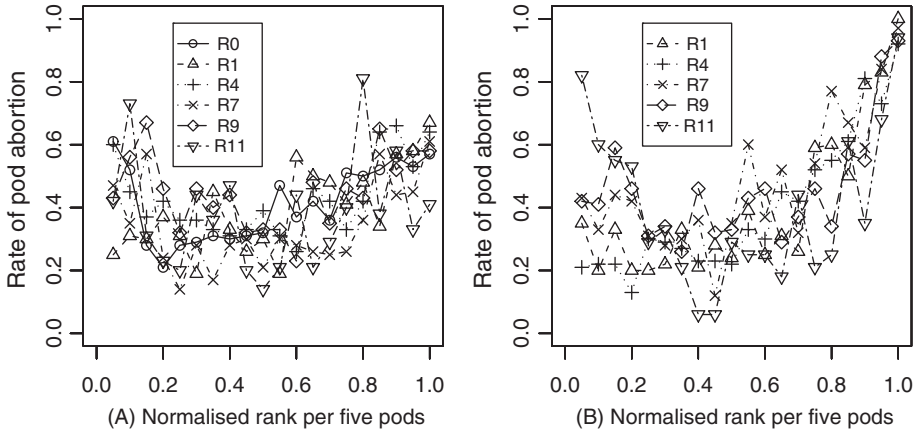

Fig. 6. Rate of pod abortion according to the normalised rank on inflorescences R0, R1, R4, R7, R9 and R11 (variety: Mendel).

end of flowering. Therefore, the time of pod appearance influences the number of seeds per pod in pods appears earlier or later during the flowering period.

3.3. Number of pods

3.3.1. Effect of pod ranks

The number of pods per inflorescence depends on the number of developed pods and aborted pods, which can be described by the ratio of the number of aborted pods to the total number of pods at each pod rank (pod abortion). This ratio was large at the basal position, then remained constant and increased with the pod rank along the inflorescence (Fig. 6) in the control (CK) and clipped plants (M-).

3.3.2. Effect of clipping treatment

The rate of pod abortion was not significantly different between inflorescences in the control ($F = 1.65$, df = 5, $P = 0.15$) and clipped plants ($F = 0.6$, df = 4, $P = 0.66$) (Fig. 6). Furthermore, the pod abortion rate did not differ significantly between the control and clipped plants ($F = 1.2$, df = 1, $P = 0.28$). All pods aborted at the end of inflorescence on the clipped plants.

Ramification clipping induced a significant increase in the number of pods on the main stem (t-test, $t = -3.1$, df = 17, $P < 0.01$), with an average of 58 ± 13 (mean $\pm$ SD) pods in the plants with clipped ramifications compared to 44 ± 11 (mean $\pm$ SD) pods in the control plants.

Furthermore, the mean total number of pods per axis also increased compared to the control plants (ANOVA, $F = 16$, df = 1, $P < 0.0001$, Table 2). The plants with clipped main stems had an average increase of 5 pods for each ramification compared to the control plants. However, the mean total number of pods per plant was not significantly different (t-test, $t = -0.12$, $d = 8$, $P = 0.3$) between the control (CK: 144 ± 4 (mean $\pm$ SD); R0, R1, R4, R7 and R11) and clipped plants (M-: 150 ± 2 (mean $\pm$ SD); R1, R4, R7 and R11, Table 3).

The mean total number of pods per axis was larger on the main stem than on ramifications and did not differ significantly among ramifications (Tukey's HSD test, $P < 0.01$, Table 3).

4. Discussion

In this study, WOSR plants varied in both intra-inflorescence and inter-inflorescence yield components. Pod position and time of pod appearance, related to assimilate availability, had effects on yield components in varying degrees (Table 4). For any treatment, the number of ovules and seeds per pod can be increased for each axis. The implications of these results are considered below.

4.1. Pod position

Plant architecture plays an important role in the number of ovules per pod, seeds per pod and pods per axis (Ortiz et al., 2009; Brookes et al., 2010).

The number of ovules per pod differed between two axes. On the main stem, the number of ovules per pod was large at the basal positions followed by small numbers, then increased along the inflorescence but decreased at the distal positions. Furthermore, the number of ovules per pod was small at the beginning of ramifications R1 and R4. This difference could be due to the complex developmental patterns of inflorescences in WOSR. Ramifications are initiated from the bottom to the top, however, the expansion of ramifications occurs in the inverse order of their initiation and is delayed compared to the main stem. The duration between initiation and expansion is longer for basal ramifications than for upper ramifications. As a result, initiated pods on the basal ramifications have a longer developmental period, which could explain the greater number of ovules per pod in the lower ramifications.

Table 4
Variation of yield components of winter oilseed rape with different factors: R11 according to time of pod appearance.

Factors	Number of ovules per pod	Number of seeds per pod	Number of pods per axis
Pod rank	a	b	NA
Ramification position	+	+	ns
Clipping ramifications (R-)	+	+	+
Clipping main stem (M-)	+	+	+
Time of pod appearance	ns	c	ND

'a' represents first decrease, then increase and decrease again. 'b' represents first remain constant, and then decrease. 'c' represents the time of pod appearance had effect on the number of seeds per pod. '+' and '−' represent 'increase' or 'decrease' with the factors, respectively. 'ns' represents not significant. 'NA' not appropriate. 'ND' no data to analyse.

The pod rank appeared to be the major determinant of the number of seeds per pod within one inflorescence. The decreasing pattern observed could be due to a limited access to assimilate because they have been depleted or intercepted by more proximal pods along the stem (Stephenson, 1981; Lee, 1988; Brookes et al., 2010). This result indicates the importance of the pod position because the farther the pod is from the leaves, the smaller its number of seeds (Pate and Farrington, 1981). The interception of assimilates by proximal pods could explain why the number of seeds per pod in distal pods did not vary with the pod rank in the clipped plants, as the competition for assimilates is assumed to be lower for these plants.

The distribution of the number of seeds in the plant architecture is more complex. The main stem had larger number of seeds per pod than the ramifications, this might be due to the apical dominance effects (Ruiz de Clavijo, 1995). Apical dominance is an inhibitory influence exerted by the main stem on the development of axillary inflorescences and is best demonstrated via main stem removal (Cline, 1997). If the main stem is clipped, then apical dominance is released and one or more of these lower lateral inflorescences begins to grow out. This phenomenon can explain why the main stem had more pods than the ramifications and why the main stem had a slower decrease in the number of seeds per pod according to the rank than the ramifications. Furthermore, the main stem flowers earlier and has a competitive advantage over the ramifications as the supply of assimilates is higher during main stem growth (Pate and Farrington, 1981). Also, at the end of the flowering period, the competition for assimilates increased as leaf area decreased, the number of pods increased and the pod canopy created deep shade (Mendham et al., 1981).

The clipping treatments induced significant variations in the number of ovules, seeds and pods in the plants. The number of ovules increased in pods that emerged immediately after the clipping, regardless of which axis was clipped (main stem: M- or ramifications: R-). Ramification clippings were performed approximately in the rank 20th on the main stem, and the number of ovules and seeds per pod increased from normalised rank 0.2 compared to the control plants. This variety appears to have a quick response to the loss of organs, resulting in the fast production of new reproductive organs (Wright and Meagher, 2003). Furthermore, the number of pods significantly increased on the main stem in the clipped plants.

The effect of clipping treatments was also observed upon clipping the main stem plants. The number of ovules per pod in ramifications R1 and R4 did not vary with the pod rank in the clipped plants. The number of ovules per pod was also larger in all of the ramifications in the clipped plants compared to the control plants. The number of seeds per pod did not decrease with higher pod rank on the main stem and ramifications in the clipped plants.

The total number of seeds and pods per axis did not show any significant difference between the control and clipped plants. We can conclude that a full compensation of the yield loss might occur for the clipped plants due to the potential for architectural development that is not fully expressed in control conditions. Furthermore, a large variability on the ramification R11 in the control and clipped plants was present, which could be due to assimilate availability. Most of the pods in the plant stopped growing, so the competition for assimilates should be smaller at the end of reproductive stage.

When clipping the main stem or ramifications, the demand for assimilate and thus the trophic pressure in the entire plant decreases. Plants subjected to clipping treatments developed more pods and more seeds per pod than control plants that were not subjected to clippings. These results are similar to other researches in which fruit production in late opening flowers has been increased experimentally by removing early opening flowers or stigmas (Ehrlen, 1993; Lehtila and Syrjanen, 1995). Hiei and Ohara (2002) indicated that main stem clipping enhances the performance of lateral branches in *Melampyrum japonicum*, as more ovules and more seeds per pod as well as more pods in ramifications were obtained.

4.2. Time of pod appearance

Pods develop acropetally within one inflorescence. Thus, the early developed pods have a competitive advantage over later formed pods. Therefore, the early pods could produce the larger numbers of seeds per pod. Flowering on the later developing secondary inflorescences may continue for some time after the main stem has finished flowering. Older pods at the base of these flowering inflorescences are well developed, while new flowers are still being initiated at the tips. Thus, the number of seeds that develop in each pod and in each inflorescence will be influenced by resource availability.

The data analysis reveals that the time of pod appearance had no influence on the number of ovules and seeds per pod for the pods located at normalised rank 0.01–0.1. However, it had impact on the number of ovules and seeds on the whole plant. The number of ovules per pod increased with the time of pod appearance on the main stem and ramifications R1 and R4. The number of aborted ovules was large at the beginning, then decreased and remained constant, but increased with the time of pod appearance. This results in the variation in the number of seeds. This pattern of ovule abortion is correlated inversely with the number of flowers in the fields. Few flowers open at the beginning of the flowering and only on the main stem. The number of ovule abortions progressively increases while flowers appear on all of the ramifications. Finally, most flowers become pods and inflorescences gradually stop growing, which results in a lower number of flowers in the field at the end of the reproductive period and, hence, a reduced amount of pollen grains for late flowers. This reduced pollen count corresponds to the variation of pollen quantity and quality during the flowering period, for example, the inefficient pollinator (Berjano et al., 2006), and thus leads to different pollination conditions, which can affect negatively the fertilization process and the abortion of seeds (Brunet and Charlesworth, 1995; Brookes et al., 2010). Furthermore, the variation of aborted ovules could be a cause of the variation of the rate of pod abortion with the pod rank. Because the survival of pods depends on the number of seeds per pod (Ganeshaiah et al., 1986). Plant architecture could also induce differences in the ability of a flower to be pollinated. The density of pollen might vary at different locations in the WOSR canopy (McCartney and Lacey, 1991).

In addition, a correlation exists between the position of a pod and its date of emergence in the plant, but these two factors are difficult to differentiate. However, we know that the ratio of supply of assimilates to demand decreases with time during the reproductive period (Jullien et al., 2010). Furthermore, the number of seeds per pod was smaller for the latest developed pods, which is in accordance with the hypothesis that resource availability is an important factor in ovule abortion.

Our study focuses primarily on the effect of assimilate availability on yield components. However, pollination also influences the yield. To study the impact of the pollination of the yield components, a probabilistic model has been developed to simulate the distributions of the number of ovules and seeds per pod. The model can also be used to simulate the distribution of the number of pollen grains (Wang et al., 2009). This model allows us to estimate the distribution parameters of the number of pollen grains per stigma and discuss the effect of pollination deficit on the number of seeds per pod. We found that most pods can obtain enough pollen grains to fertilise the ovules. Lack of pollen may occur at the beginning and the end of the flowering period, which is consistent with the results in this study.

In conclusion, our results indicate that in WOSR, the amount of available assimilates was the primary determinant of pod and seed production during the period of flowering and pod setting. The distribution of resources was significantly affected both by the position of a pod within inflorescences, and by the position of the inflorescences within a plant. Basally positioned pods had a distinct advantage in acquiring resources due to their greater proximity and earlier development time. Increases in pod rank and ramification position affect appearing time, which can be observed through the change in assimilate availability on the entire plant. The results from this study help further the understanding of the variation in yield components of oilseed rape.

Acknowledgements

We thank the involved technical staff from INRA-EGC and Pauline Eymeri for their kind assistance on experiments. This work was partly supported by the Chinese Ministry of Science and technology via the Project 2006AA10A303-1 and the China Scholarship Council (CSC), which provides the PhD scholarship of Xiujuan Wang.

References

Arathi, H.S., Ganeshaiah, K.N., Shaanker, R.U., Hegde, S.G., 1999. Seed abortion in *Pongamia pinnata* (Fabaceae). Am. J. Bot. 86, 659–662.

Arathi, H.S., Ganeshaiah, K.N., Uma Shaanker, R., Hegde, S.G., 1996. Factors affecting embryo abortion in *Syzygium cuminii* (L.) Skeels (Myrtaceae). Int. J. Plant Sci. 157, 49–52.

Bawa, K.S., Webb, C.J., 1984. Flower, fruit and seed abortion in tropical forest trees: implications for the evolution of paternal and maternal reproductive patterns. Am. J. Bot., 71.

Becker, H.C., Damgaard, C., Karlsson, B., 1992. Environmental variation for outcrossing rate in rapeseed (*Brassica napus*). Theor. Appl. Genet. 84, 303–306.

Berjano, R., de Vega, C., Arista, M., Ortiz, P.L., Talavera, S., 2006. A multi-year study of factors affecting fruit production in *Aristolochia paucinervis* (Aristolochiaceae). Am. J. Bot. 93, 599–606.

Berry, P.E., Calvo, R.N., 1991. Pollinator limitation and position dependent fruit set in the high Andean orchid *Myrosmodes cochleare* (Orchidaceae). Plant Syst. Evol. 174, 93–101.

Brookes, R.H., Jesson, L.K., Burd, M., 2010. Reproductive investment within inflorescences of *Stylidium armeria* varies with the strength of early resource commitment. Ann. Bot. (Lond.) 105, 697–705.

Brunet, J., Charlesworth, D., 1995. Floral sex allocation in sequentially blooming plants. Evolution 49, 70–79.

Bustan, A., Erner, Y., Goldschmidt, E.E., 1995. Interactions between developing citrus fruits and their supportive vascular system. Ann. Bot. (Lond.) 76, 657–666.

Cline, M.G., 1997. Concepts and terminology of apical dominance. Am. J. Bot. 84, 1064.

Diepenbrock, W., 2000. Yield analysis of winter oilseed rape (*Brassica napus* L.): a review. Field Crops Res. 67, 35–49.

Diggle, P.K., 1995. Architectural effects and the interpretation of patterns of fruit and seed development. Annu. Rev. Ecol. Syst. 26, 531–552.

Ehrlen, J., 1993. Ultimate functions of non-fruiting flowers in *Lathyrus vernus*. Oikos 68, 45–52.

Ellis, M.F., Sedgley, M., 1992. Floral morphology and breeding system of three species of *eucalyptus*, section *Bisectaria* (Myrtaceae). Aust. J. Bot. 40, 249–262.

Farrington, P., Pate, J.S., 1981. Fruit set in *Lupinus angustifolius* Cv, Unicrop. I. Phenology and growth during flowering and early fruiting. Aust. J. Plant Physiol. 8, 293–305.

Ganeshaiah, K.N., Shaanker, R.U., Shivashankar, G., 1986. Stigmatic inhibition of pollen grain germination-its implication for frequency distribution of seed number-important. Oecologia (Berl.) 70, 568–572.

Guitian, J., Navarro, L., 1996. Allocation of reproductive resources within inflorescences of *Petrocoptis grandiflora* (*Caryophyllaceae*). Can. J. Bot. 74, 1482–1486.

Harper, J.L., Lovell, P.H., Moore, K.G., 1970. The shapes and sizes of seeds. Annu. Rev. Ecol. Syst. 1, 327–356.

Hiei, K., Ohara, M., 2002. Variation in fruit- and seed set among and within inflorescences of Melampyrum roseum var. japonicum (Scrophulariaceae). Plant Species Biol. 17, 13–23.

Hocking, P.J., Pate, J.S., 1977. Mobilization of minerals to developing seeds of legumes. Ann. Bot. (Lond.) 41, 1259–1278.

Jullien, A., Mathieu, A., Allirand, J.-M., Pinet, A., de Reffye, P., Cournede, P.H., Ney, B., 2010. Characterization of the interactions between architecture and source-sink relationships in winter oilseed rape (*Brassica napus*) using the GreenLab model. Ann. Bot. (Lond.), doi:10.1093/aob/MCQ205, http://www.aob.oxfordjournals.org.

Keiller, D.R., Morgan, D.G., 1988. Distribuiton of carbon-labelled assimilates in flowering plants of oilseed rape (*Brassica napus* L.). J. Agric. Sci. 111, 347–355.

Knight, T.M., Steets, J.A., Vamosi, J.C., Mazer, S.J., Burd, M., Campbell, D.R., Dudash, M.R., Johnston, M.O., Mitchell, R.J., Ashman, T.L., 2005. Pollen limitation of plant reproduction: pattern and process. Annu. Rev. Ecol. Evol. Syst. 36, 467–497.

Lee, T.D., 1988. Patterns of fruit and seed production. In: Lovett, J.D., Lovett, D.L. (Eds.), Plant Reproductive Ecology: Patterns and Strategies. Oxford University Press, New York, NY, USA, pp. 179–202.

Lee, T.D., Bazzaz, F.A., 1982. Regulation of fruit and seed production in an annual legume, *Cassia fasciculata*. Ecology 63, 1363–1373.

Lehtila, K., Syrjanen, K., 1995. Compensatory responses of two Melampyrum species after damage. Funct. Ecol. 9, 511–517.

Malagoli, P., Laine, P., Le Deunff, E., Rossato, L., Ney, B., Ourry, A., 2004. Modeling nitrogen uptake in oilseed rape cv. capitol during a growth cycle using influx kinetics of root nitrate transport systems and field experimental data. Plant Physiol. 134, 388–400.

Mathieu, A., Cournède, P.H., Letort, V., Barthélémy, D., de Reffye, P., 2009. A dynamic model of plant growth with interactions between development and functional mechanisms to study plant structural plasticity related to trophic competition. Ann. Bot. (Lond.) 103, 1173–1186.

McCartney, H.A., Lacey, M.E., 1991. Wind dispersal of pollen from crops of oilseed rape (*Brassica napus* L.). J. Aerosol. Sci. 22, 467–477.

Medrano, M., Guitian, P., Guitian, J., 2000. Patterns of fruit and seed set within inflorescences of *Pancratium maritimum* (Amaryllidaceae): nonuniform pollination, resource limitation, or architectural effects? Am. J. Bot. 87, 493–501.

Mendham, N.J., Shipway, P.A., Scott, R.K., 1981. The effects of delayed sowing and weather on growth, development and yield of winter oil-seed rape (*Brassica napus*). J. Agric. Sci. 96, 389–416.

Mesquida, J., Renard, M., Pierre, J.S., 1988. Rapeseed (*Brassica napus* L.) productivity: the effect of honeybees (*Apis mellifera* L.) and different pollination conditions in cage and field tests. Apidologie 19, 51–72.

Nakamura, R.R., 1986. Maternal investment and fruit abortion in *Phaseolus vulgaris*. Am. J. Bot. 73, 1049–1057.

Obeso, J.R., 1993. Does defoliation affect reproductive output in herbaceous perennials and woody plants in different ways? Funct. Ecol. 7, 150–155.

Ortiz, P.L., Berjano, R., Talavera, M., Arista, M., 2009. The role of resources and architecture in modeling floral variability for the monoecious amphicarpic *Emex spinosa* (Polygonaceae). Am. J. Bot. 96, 2062–2073.

Ozer, H., Oral, E., Dogru, U., 1999. Relationships between yield and yield components on currently improved spring rapeseed cultivars. Turk. J. Agric. For. 23, 603–607.

Pate, J.S., Farrington, P., 1981. Fruit set in *Lupinus angustifolius* Cv. Unicrop. II. Assimilate flow during flowering and early fruiting. Aust. J. Plant Physiol. 8, 307–318.

Pechan, P.A., Morgan, D.G., 1985. Defoliation and its effects on pod and seed development in Oil seed rape (*Brassica napus* L.). J. Exp. Bot. 36, 458–468.

Robinson, M., Harav, I., Halevy, A.H., Plaut, Z., 1980. Distribution of assimilates from various source leaves during the development of *Gladiolus grandiflorus*. Ann. Bot. (Lond.) 45, 113–122.

Ruiz de Clavijo, E., 1995. The ecological significance of fruit heteromorphism in the amphicarpic species *Catananche lutea* (Asteraceae). Int. J. Plant Sci. 156, 824–833.

Steel, R.G.D., Torrie, J.H., 1980. Analysis of Covariance. Principles and Procedures of Statistics: A Biometrical Approach, 2nd ed. McGraw-Hill, New York, pp. 401–437.

Stephenson, A.G., 1980. Fruit set, herbivory, fruit reduction and fruiting strategy of *Catalpa speciosa* (Bignoniaceae). Ecology 61, 57–64.

Stephenson, A.G., 1981. Flower and fruit abortion: proximate causes and ultimate functions. Annu. Rev. Ecol. Syst. 12, 253–279.

Tayo, T.O., Morgan, D.G., 1975. Quantitative analysis of the growth, development and distribution of yield in oil-seed rape (*Brassica napus* L.). J. Agric. Sci. 85, 103–110.

Tayo, T.O., Morgan, D.G., 1979. Factors influencing flower and pod development in oil-seed rape (*Brassica napus* L.). J. Agric. Sci. 92, 363–373.

Thomson, J.D., 1989. Deployment of ovules and pollen among flowers within inflorescences. Evol. Trend Plant 3, 65–68.

Tittonel, E.D., 1990. Evènements liés à l'évolution florale chez le colza *Brassica napus* L. var Oleifera Metzg. Thèse de doctorat thesis. Université Paris 6, Paris.

Tuncturk, M., Ciftci, V., 2007. Relationships between yield and some yield components in rapeseed (*Brassica napus* SSP. *Oleifera* L.) cultivars by using correlation and path analysis. Pak. J. Bot. 39, 81–84.

Wagner, A., Soumerai, K.S., Zhang, B., Ross-Degnan, F.D., 2002. Segmented regression analysis of interrupted time series studies in medication use research. J. Clin. Pharm. Ther. 27, 299–309.

Wang, X.J., Mathieu, A., Cournède, P.H., Allirand, J.M., Jullien, A., de Reffye, P., Zhang, B.G., 2009. Stochastic models in floral biology and application to the study of oilseed rape fertility. In: Li, B.-G., Jaeger, M., Guo, Y. (Eds.), International Symposium on Plant Growth Modeling, Simulation, Visualization and Applications (PMA09). IEEE Computer Society, Beijing, China, pp. 175–182.

Wright, J.W., Meagher, T.R., 2003. Pollination and seed predation drive flowering phenology in *Silene Latifolia* (Caryophyllaceae). Ecology 84, 2062–2073.