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1 Floral bud damage compensation by branching and biomass 2 allocation in genotypes of *Brassica napus* with different architecture 3 and branching potential

4
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11 12 13 **Abstract**

14 Plant branching is a key process in the yield elaboration of winter oilseed rape (WOSR). It is also
15 involved in plant tolerance to flower damage because it allows the setting of new fertile
16 inflorescences. Here we characterize the changes in the branching and distribution of the number
17 of pods between primary and secondary inflorescences in response to floral bud clippings. Then
18 we investigate the impacts of the modifications in branching on the biomass allocation and its
19 consequence on the crop productivity (harvest index). These issues were addressed on plants
20 with contrasted architecture and branching potential, using three genotypes (Exocet, Pollen, and
21 Gamin) grown under two levels of nitrogen fertilization. Clipping treatments of increasing
22 intensities were applied to either inflorescences or flower buds.

23 We were able to show that restoration of the number of pods after clipping is the main lever for
24 the compensation. Genotypes presented different behaviors in branching and biomass allocation
25 as a function of clipping treatments. The number of fertile ramifications increased for the high
26 intensities of clipping. In particular, the growth of secondary ramifications carried by branches
27 developed before clipping has been observed. The proportions of yield and of number of pods
28 carried by these secondary axes increased and became almost equivalent to the proportion
29 carried by primary inflorescences. In terms of biomass allocation, variations have also been
30 evidenced in the relationship between pod dry mass on a given axis and the number of pods set,
31 while the shoot/root ratio was not modified. The harvest index presented different responses: it
32 decreased after flower buds clipping, while it was maintained after the clipping of the whole
33 inflorescences. The results are discussed relative to their implications regarding the identification
34 of interesting traits to be target in breeding programs in order to improve WOSR tolerance.

35 36 **Key words**

37 winter oilseed rape; *Brassica napus*; architecture; biomass allocation; harvest index; allometry;
38 plasticity; plant resilience.

39 40 **Introduction**

41 Branching is an important component of the yield of winter oilseed rape (WOSR - Lu *et al.*,
42 2011; Leterme, 1985; McGregor, 1980). The final architecture of the inflorescences and
43 subsequently of the yield depends on the ontogenetic dynamics of the apical and axillary
44 meristems giving rise to branches of increasing order, as has been described for different crops
45 and wild species by Moulia *et al.* (1999 a and b), Van Minnebruggen *et al.* (2014), and Park *et*
46 *al.* (2014). In the specific case of WOSR, floral initiation on the apical meristem occurs during

1 the winter between the mid-November and mid-January (Tittonnel, 1990). At the end of winter,
2 during plant bolting and stem elongation, and depending on the environment (and notably plant
3 density – Retuerto and Woodward, 2001) varying numbers of buds outgrow to produce fertile
4 branches. Flowering starts on the main inflorescence and propagates basipetally from the
5 youngest to the oldest branches of the plant (Jullien *et al.*, 2011). Generally final plant yield is
6 distributed between the apical inflorescence (approx. 10% to 20% - Leterme, 1985; Allirand *et*
7 *al.*, 2011) and lateral branches each bearing a terminal inflorescence (primary inflorescence) as
8 well as varying numbers of secondary branches with their own terminal inflorescence (secondary
9 inflorescences - Figure 1.A).

10 Branching is highly plastic as a function of genotype and environment (Pinet, 2010; Lei *et al.*,
11 2014; Van Minnebruggen *et al.*, 2014). The outgrowth of buds responds to different
12 environmental signals such as light quantity, light quality and nitrogen (Evers *et al.*, 2011; Lei *et*
13 *al.*, 2014; Furet *et al.*, 2014; Park *et al.* 2014). It is also governed by a complex hormonal
14 regulation (Janssen *et al.*, 2014) and requires the allocation of carbohydrates (Mason *et al.*,
15 2014). Thanks to its plasticity, branching is often involved in the response of plants to
16 environmental constraints, and notably to flower damage (Sadras, 1996; Tiffin, 2000). In WOSR,
17 floral bud damage may be due to pests (Lerin, 1987; Brandt and Lamb, 1994; Nilsson, 1994) or
18 environmental constraints (Morrison 1993; Lardon and Triboui-Blondel 1995; Annisa *et al.* 2013)
19 and can cause potentially dramatic yield losses. In particular, before flowering, WOSR plants
20 may undergo massive floral bud losses due to pollen stealing by pollen beetles (*Meligethes*
21 *aeneus* L – Lerin, 1987). Pollen beetles cause substantial and sometimes devastating damage
22 (yield reduction as high as 70% has been recorded – Nilsson, 1994).

23 Compensation is often achieved by the production of new floral buds more than by the increase
24 of seed weight (Williams and Free, 1979; Lerin, 1987; Tommey and Evans, 1992; Nilsson,
25 1994). Compensating floral buds may be produced on inflorescences carried by either existing or
26 new branches (Tatchell, 1983 and Nilsson, 1994). The setting of new branches and
27 inflorescences can compensate for floral bud losses but may also modify final biomass
28 partitioning within the plant. In particular, it may impact the ratio between seed weight and total
29 plant weight, the so-called Harvest Index (HI), which is an important criterion of crop
30 productivity. The interaction between the plasticity of the branching and the biomass re-
31 allocation is thus a component of plant tolerance to flower damage (Tiffin, 2000). We have
32 assumed that these interactions between architecture and morphogenesis may vary according to
33 genotype and environment. This variability can be used to identify traits, which could be targeted
34 in breeding programs in order to improve WOSR tolerance to flower damage.

35 The interaction between branching and biomass allocation was studied through the pruning of
36 inflorescences and branches by Bennett *et al.* (2012) for *Brassica napus*, *Brassica rapa*, and
37 *Arabidopsis thaliana*. Their results showed that morphogenesis controls the allocation of
38 biomass between vegetative and reproductive organs (Fig. 1.B). While their results focused on
39 the impact of the removing of lateral branches on the architecture of the apical inflorescence
40 (elongation, size of pods, seed weight), we proposed to extend this study and to evaluate (i) the
41 modification of both the global pattern of ramification and the yield distribution between
42 branches and (ii) the implications in terms of biomass allocation in response to different
43 intensities of inflorescence and floral bud pruning, with particular focus on WOSR. Our
44 hypotheses were (i) that an increased proportion of yield borne by secondary axes may result in
45 compensation, (ii) that at the scale of the axis, biomass allocation rules are conserved, and
46 particularly the allometric relationships between the number of pods and the pod yield, and (iii)

1 that at the plant scale an increase in biomass investment into structural tissues (new branches)
2 and a reduction in plant HI will be observed.

3 These issues were addressed on plants with contrasted architecture and branching potential,
4 using three genotypes (Exocet, Pollen, and Gamin) grown under two levels of nitrogen
5 fertilization. As concerns the use of a low nitrogen fertilization treatment, we hypothesized that
6 the plant ability to grow new branches and thus to compensate the floral damage will be lower.
7 Clipping treatments of increasing intensities were applied to either inflorescences or flower buds.
8
9

10 **Materials and Methods**

11 **1. Experimental design**

12 The experiments were carried out in 2007-2008 (Y1 - ClipInflo experiment) and 2008-2009 (Y2
13 – ClipFB experiment) in the Paris region of France (48.9°N, 1.9°E). The plants were grown
14 under field conditions. Seeds were sown on 4th Sept. 2007 and 7th Sept. 2008 at a density of 50
15 seeds.m⁻². We designed different combinations of variety and nitrogen fertilization (VN
16 combinations) in order to generate a broad range of dynamics of reproductive morphogenesis.
17 Three varieties with contrasting architectures were studied: Pollen, Exocet and Gamin. Pollen
18 and Exocet usually bear fewer axes than Gamin (6 to 9 axes *versus* 10 to 15 axes). Pollen and
19 Exocet present a standard height at harvest (1.80m) while Gamin is a half-dwarf variety (1.30m).
20 In addition, Pollen starts flowering earlier than Gamin and Exocet. Furthermore, Exocet is a
21 hybrid while Pollen and Gamin are inbred lines. Finally, Gamin produces more floral buds and
22 pods than Exocet and Pollen (approximately 1000 floral buds per plant for Gamin compared to
23 600 floral buds per plant for Pollen - Pinet, 2010). Two levels of nitrogen fertilization were used
24 as treatments: high (HN - 100 kg.ha⁻¹ on 1st Mar. 2008 for Y1 and 1st Mar. 2009 for Y2 and 40
25 kg.ha⁻¹ on 17th Mar. 2008 for Y1 and 50 kg.ha⁻¹ on 17th Mar. 2009 for Y2) and low (LN - 70
26 kg.ha⁻¹ on 17th Mar. 2008 for Y1 and 40 kg.ha⁻¹ on 17th Mar. 2009 for Y2). In Y1 (ClipInflo
27 experiment), four VN were used: Exocet, Pollen and Gamin with high nitrogen fertilization
28 (EHN, PHN, GHN respectively) and Exocet with low nitrogen fertilization (ELN). In Y2
29 (ClipFB experiment), six VN were used: Exocet, Pollen and Gamin with both high (EHN, GHN,
30 PHN, respectively) and low nitrogen fertilization (ELN, GLN, PLN, respectively). Soil
31 characteristics (water and nitrogen contents) were assessed for their similarity (data not shown).
32 Thus the individual plant is the replicate.
33
34

35 **2. Clipping treatments**

36 Clipping was performed on individual inflorescences and data were recorded at the plant scale.
37 The plants were subjected to either inflorescence (ClipInflo) or to floral bud (ClipFB) clipping.
38 In ClipInflo, three intensities of inflorescence clippings were applied: no clipping (Control),
39 clipping of the terminal inflorescence (ClipI0) and clipping of the terminal inflorescence and the
40 four most apical inflorescences (ClipI4). Inflorescences were cut before flowering (level 55 on
41 the BBCH scale – Zadoks, 1974) at the axil of the leaf from which they originated. ClipInflo was
42 applied to four VN combinations: EHN, ELN, GHN and PHN. The ClipI0 treatment represented
43 from 5% (for EHN) to 10% (for ELN and PHN) of the total number of inflorescences in the
44 different VN combinations. For ClipI4 treatment, the percentage of clipped inflorescences
45 represented from 33% (GHN) to 50% (EHN) of the total number of inflorescences in the
46 different VN combinations.

In ClipFB, three intensities of floral bud clippings were carried out as follows: no clipping (Control), clipping of 50 floral buds on the main inflorescence and 20 floral buds on each of the four most apical inflorescences (ClipFB4), and clipping of all floral buds on the seven most apical inflorescences (ClipFB7). Clipping was applied before flowering (level 55 on the BBCH scale, on 17th Apr. 2009) to floral buds with a minimum diameter of 3×10^{-3} m in order to avoid damage to the meristems. ClipFB was carried out on 6 VN combinations: EHN, ELN, GHN, GLN, PHN and PLN. For ClipFB4, the percentage of clipped floral buds varied according to the VN combinations (from 23% for GHN to 60.5% for GLN). With ClipFB7, the percentage of clipped floral buds ranged from 67% (GHN) to 94% (PLN).

3. Measurements

In ClipInflo, the number of plants per treatment was five. At harvest (23rd May 2008), the number of fertile primary and secondary inflorescences per plant was counted, as was the total number of pods per primary axis (pooling the pods borne by primary and secondary inflorescences on a given primary axis). Each plant was divided into six compartments for dry weight measurements: the roots, the main stem, the vegetative parts (stem and leaves) of primary and secondary axes, the reproductive parts (pods) of primary and secondary axes. Each part was oven-dried (48 hours at 80 °C) and then weighed.

In ClipFB, for all VN and treatments, the number of pods and pod weight per plant as well as the number of primary axes and the dry matter by compartment were counted and measured on a sample of 10 or 13 plants. The number of pods and the pod weight per axis were measured on a sub-sample of 3 plants. In addition, on another subsample of three plants, and only for the Control and ClipFB7 treatments of GHN, GLN, PHN and PLN, the number of pods and the pod weight per axis as well as the number of secondary axes were measured and counted. Details of experiments are summarized in Table 1.

Table 1: Treatments and measurements carried out during the two years of the experiment. VN combinations correspond to the Variety and Nitrogen combinations. E, G and P mean Exocet, Gamin and Pollen varieties, respectively. HN and LN correspond to high and low nitrogen fertilizations. EHN: Exocet High Nitrogen, ELN: Exocet Low Nitrogen, GHN: Gamin High Nitrogen, GLN: Gamin Low Nitrogen, PHN: Pollen High Nitrogen, PLN: Pollen Low Nitrogen. Inflorescence clipping experiment (ClipInflo) corresponds to the clipping of the apical inflorescence (ClipI0) and to the clippings of the apical and the four most apical inflorescences (ClipI4). Bud clipping inflorescences (ClipFB) corresponds to the clippings of buds on each of the four most apical inflorescences (ClipFB4) and on the seven most apical inflorescences (ClipBF7). Compartments are the roots, the main stem, the vegetative parts (stem and leaves) and the reproductive parts (pods) of primary and secondary axes.

Years	Experiments	VN combinations	Clipping treatments	Size of the main sample			Size of the sub-sample	
				Number of pods and pod weight per plant	Number of primary axes	Dry matter by compartment	Number of pods and pod weight per axis	Number of secondary axes
Y1 2007- 2008	ClipInflo	EHN, ELN, GHN, PHN	Control	5	5	5	5	5
			ClipI0	5	5	5	5	5
			ClipI4	5	5	5	5	5
Y2 2008-	ClipFB	EHN, ELN	Control	10	10	10	3	0
			ClipFB4	10	10	10	3	0

2009

	ClipFB7	10	10	10	3	0
	Control	13	13	13	6	3
GHN, GLN	ClipFB4	10	10	10	3	0
	ClipFB7	13	13	13	6	3
	Control	13	13	13	6	3
PHN, PLN	ClipFB4	10	10	10	3	0
	ClipFB7	13	13	13	6	3

4. Data processing

4.1. Tolerance indices

Tolerance indices were calculated with respect to grain yield, number of pods and weight of a thousand pods. The index was calculated as the ratio between the value for an individual plant and the mean value of the control treatment of the corresponding VN combination (Agrawal *et al.*, 1999; Wise *et al.*, 2008).

4.2. Distribution of pods throughout plant architecture

In order to assess the distribution of pods throughout plant architecture, we defined the following four classes: pods carried by existing axes on either primary (Class1) or secondary inflorescences (Class2), and pods carried by new axes on either primary (Class 3) or secondary inflorescences (Class 4) (Figure 1.A). For each experiment and VN combination, the mean number of fertile primary axes for the Control treatment was calculated. Then, for each clipping treatments and each plant, the numbers of existing and new fertile primary axes were determined in comparison to the Control treatment: new fertile axes correspond to axes that are present in clipped plants and absent in the intact ones.

4.3. Biomass allocation

At the axis scale, biomass allocation between the number of pods and pod dry mass was assessed by fitting a mixed linear model between the logarithms of the two variables. The 'Plant' factor forms the random part; while the 'Clipping' and 'Pod dry mass' factors were considered as fixed factors of the mixed model (Bolker *et al.*, 2009). Assessment of the statistical significance of the 'Clipping' factor was made using F tests ($P < 0.05$). At the plant scale, the percentage in dry matter of each of the six compartments was calculated to determine the relative allocation between vegetative and reproductive organs on one hand and between first order and second order branches on the other hand. The ratio between shoot dry matter and root dry matter was also calculated. The harvest index was calculated ultimately from the ratio between the pod dry matter and the total aerial dry matter.

4.4. Statistical tests

4.3.1. Classification trees

In the first part of this paper, we used a tree-structured recursive partitioning method to describe the conditional distribution of the tolerance in grain yield given the status of two covariates that are the tolerances in terms of number of pods and of pod weight. A detailed explanation of the conditional inference tree method is given by Strobl *et al.* (2007) and Hothorn *et al.* (2006). Roughly, the algorithm works as follows: firstly, the global null hypothesis of independence between any of the input variables (here, the tolerance indices in number of pods and pod weight) and the response (the tolerance index in grain yield) is tested. The stop criterion is based on multiplicity adjusted p-values ("Bonferroni"). The criterion is maximized, *i.e.*, 1 - p-value is

1 used. A split is implemented when the criterion exceeds a threshold. For example, when the
2 threshold is equal to 0.95, the p-value must be smaller than 0.05 to split this node. Secondly, a
3 binary split in the selected input variable is implemented. These two steps are repeated until the
4 null hypothesis cannot be rejected, *i.e.* the criterion does not exceed the threshold. This statistical
5 approach ensures that the right sized tree is grown and that no pruning or cross-validation or
6 whatsoever is needed.

7 8 **4.3.2. Mann–Whitney tests**

9 Due to the small sample sizes, the branching and biomass allocation variables did not meet the
10 assumptions of normality so that their responsiveness to the clipping treatments was examined
11 using Mann–Whitney tests (Sokal and Rohlf, 1995).

12 13 **4.3.3. Software**

14 Statistical treatments were performed using the statistical program R.

15
16 For the sake of legibility and to lighten the manuscript, not all the VN are presented in the
17 figures. When the results concerns both experiments, only the common VN are presented (EHN,
18 ELN, GHN and PHN). The other VN combinations are shown in the SI. However, in the specific
19 cases when the two experiments or the VN combinations show difference in the magnitude of the
20 responses, the results of all the VN combinations are presented.

21 22 23 **Results**

24 25 **What were the respective contributions of the number of pods and of the pod weight to the** 26 **plant compensation?**

27 In the two experiments, the tolerance in terms of number of pods is the covariate showing the
28 strongest association with the tolerance in grain yield. This result highlighted the key role of the
29 production of new pods in WOSR compensation in response to flower damage (Figure 2). When
30 considering both experiments, compensation in seed yield was observed in most of the plants
31 (71% for ClipInflo, 73% for ClipFB). Tolerance indices in the number of pods of 77%
32 (ClipInflo) and 104% (ClipFB) were enough to compensate with respect to seed yield. Below
33 these thresholds, different patterns were observed according to clipping treatments and that
34 corresponds to different combinations of tolerance indices for the number of pods and the pod
35 weight. For ClipFB, a minimal tolerance index of 72% in the number of pods is necessary, below
36 this value no compensation in the seed yield was observed. Between 72% and 104%, a tolerance
37 index of 95% with respect to the pod weight was necessary to compensate in seed yield. For
38 ClipInflo, for a tolerance index below 77% for the number of pods, a tolerance index of at least
39 115% (overcompensation) with respect to the pod weight was necessary to compensate in seed
40 yield. No threshold in the tolerance index of the number of pods was detected below which there
41 was no possible compensation in seed yield (whatever the compensation in the pod weight). It is
42 although noteworthy that 53% of the plants under ClipInflo overcompensated *i.e.* had a tolerance
43 index higher than one.

44 No significant difference in the tolerance in seed yield was observed according neither to
45 genotype nor to nitrogen. Only ELN had a noteworthy low tolerance in seed yield (0.69 on
46 average over ClipFB4, ClipFB7, ClipI0, and ClipI4) but the difference with the Control was not
47 significant due to an important range of variation.

1
2 **Was there any modification in plant branching in response to the clipping treatments?**

3 A global upward trend in the number of fertile primary axes has been observed in response to
4 floral bud clipping of increasing intensities (ClipFB, Figure 3.A). This increase was significant
5 for plants under ClipFB4 PHN (+1.5, $P<0.05$), and PLN (+1, $P<0.05$) as well as for ClipFB7
6 GHN (+1, $P<0.05$), GLN (+3, $P<0.05$), and PHN (+3, $P<0.05$). In parallel, the number of fertile
7 secondary axes per plant increased significantly for plants of GHN, GLN, PHN, and PLN in
8 response to ClipBF7 (+ 8, + 16, +11 with $P<0.1$ and + 5 inflorescences with $P<0.15$, respectively
9 - Figure 3.B).

10 The clipping of the apical inflorescence (ClipI0) did not modify significantly the number of
11 fertile primary axes (except for EHN where 4 new basal fertile axes were observed, $P<0.05$, –
12 Figure 4.A). The intensive clipping (ClipI4) reduced by 4 the final number of fertile primary
13 axes, *i.e.* no new fertile primary axis was produced to compensate the initial loss (Figure 4.A).
14 The interquartile range of the number of fertile secondary axes was dramatically more variable
15 compared to primary axes (except for ELN for which the number of secondary axes was very
16 low). Increase in the number of fertile secondary axes was significant for EHN (+ 23
17 inflorescences in Clip I0 and +12 in inflorescences ClipI4) and ELN (+4 inflorescences – Figure
18 4.B).

19
20 **How far do these new axes modify plant yield architecture?**

21 During both experiments, we observed a shift in pod yield distribution from the primary to the
22 secondary inflorescences. For ClipFB, secondary inflorescences carried 2.6% of yield in control
23 plants. This proportion increased significantly in response to ClipFB4 (17%, $P<0.05$) and to
24 ClipFB7 (43%, $P<0.05$). For plants of ClipInflo, the same observation was made with 26% of
25 yield carried by secondary inflorescences in the control plants, compared to 25.4% (pv=ns) and
26 42.5% ($P<0.05$) in ClipI0 and ClipI4 treatments.

27 For the sake of clarity, only the data concerning the topology of distribution of pods in ClipFB
28 are presented here in Figure 5 (see Figure 1 in SI for ClipInflo). The distribution of pods was
29 modified for some VN of ClipFB4: EHN, GLN, PHN and PLN had a reduced proportion of pods
30 on the primary inflorescences of respectively -17%, -12%, -56%, and -60%. The ranges of
31 variation of the box plot were also increased compared to Control. These decreases were
32 compensated by both an increase in the proportion of pods carried by the secondary
33 inflorescences and the appearance of some new axes. The appearance of new axes was observed
34 for EHN, GLN, PHN, and PLN even if this was more important for PHN (+2%) and PLN
35 (+14.5%).

36 The modifications observed in the plants under ClipFB4 were amplified in the plants under
37 ClipFB7: the decrease in the proportion of pods carried by the primary inflorescence was all the
38 most important and concerned all the VN: EHN (-41%), ELN (-29%), GHN (-51%), GLN (-
39 43%), PHN (-87%), PLN (-56%) compared to Control. In the same manner the proportion of
40 pods carried by the secondary inflorescences increased for all VN (+40%, +23%, +48%, +36%,
41 +54%, +49% for ELN, GHN, GLN, PHN and PLN, respectively), and the appearance of new
42 primary and secondary axes were observed for GHN, GLN and PHN (+3%, + 7%, +13.3% for
43 GHN, GLN, PHN on new primary inflorescences and +18.5% for PHN on new secondary
44 inflorescences). The differences in the response of the different VN to ClipFB are coherent with
45 the results obtained on the number of axes (Figure 3): plants of Gamin and Pollen were more
46 reactive to clipping than plants of Exocet in response to ClipFB.

47

1 In the Control of ClipInflo (Figure 1 in SI), the primary inflorescences produced the most
2 important share of pods on the plant (from 66.5% for GHN to 94.5% for ELN), except for PHN
3 (54%). It is also noteworthy that the production of pods on secondary inflorescences was much
4 higher than in ClipFB experiment in three out of four VN (EHN, GHN, PHN).
5 In response to ClipI0, the proportion of pods carried by the primary inflorescence decreased only
6 for plants under EHN (-45%). For the three other VN combinations, the production of pods on
7 primary and secondary inflorescences on existing axes remained constant but with a higher range
8 of variability. Pods carried by primary and secondary inflorescences on new axes (Class 3 and
9 Class 4, respectively) were of less importance, except for EHN with 15% and 11% of the total
10 number of pods carried by primary and secondary inflorescences, respectively.
11 In response to ClipI4, part of pods produced by primary inflorescences on existing axes
12 decreased (-39% for EHN, -18% for ELN, -29% for GHN, -10% for PHN compared to Control).
13 Pods carried by secondary inflorescences on existing primary axes accounted for a higher share
14 for the four VN combinations (+25.5%, +16.5%, +22%, +8.5% for EHN, ELN, GHN and PHN,
15 respectively). There was no pod carried by primary and secondary inflorescences on new axes.
16 Concerning the differences between genotypes behaviors under ClipInflo, Exocet was more
17 reactive than Gamin and Pollen. This is coherent with results obtained on the number of axes
18 (Figure 4) but different from results obtained for plants under ClipFB.

19
20 **How is biomass allocation modified in response to these changes in pod distribution and**
21 **yield architecture?**

22
23 **Allocation at the branch scale.**

24 The relationship between pod dry mass and number of pods, respectively, was analyzed
25 separately for ClipFB and ClipInflo and for the primary (Figure 6 and Figure 2 in SI) and
26 secondary (Figure 3 in SI) inflorescences. A slow-down in the increase in the number of pods
27 above a certain pod dry mass was observed for the primary inflorescences of ClipInflo for some
28 VN combinations and clipping intensities (Figure 6-B). Above this threshold, biomass will be
29 allocated to existing pods to increase their weight instead than to the meristem to produce new
30 pods what is a shift in the biomass allocation. The number of pods increased linearly with pod
31 dry mass in secondary inflorescences indicating no slow-down in the number of pods for ClipFB
32 and ClipInflo (Figure 3 in SI). The mixed linear model fitted to data (after logarithmic
33 transformation) showed significant variation in the slopes and the intercepts for 17 of the 40
34 combinations of VN and clipping treatments of ClipFB and ClipInflo. The main effect of the
35 clipping treatments was a shift in the x-axis that concerned an increase in pod dry mass, which
36 was between 60% and 100%. In comparison, significant variations detected in the slopes ranged
37 from 26% to 53%, which is much smaller.

38
39 **Shoot/root**

40 Under ClipInflo, similar variations in the shoot/root ratio were found with all the treatments, *i.e.*
41 a global upward trend with increasing clippings but that was not significant. This result is
42 illustrated for the two experiments for EHN, ELN, GHN and PHN in Table 2. Under ClipFB, the
43 results were more variable and no significant variation was identified. The shoot/root ratio
44 tended to increase in line with clipping intensity under ClipInflo for the VN of high nitrogen
45 treatment (EHN, GHN and PHN). The shoot/root was higher under high nitrogen treatment
46 (EHN) than under low nitrogen treatment (ELN) in ClipInflo and ClipFB, which is a classic
47 response by the shoot/root ratio to N starvation.

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Harvest index

The harvest index values measured for the two clipping treatments are presented for all the VN combinations (Table 3). Results indicate a difference between the two clipping treatments in terms of crop competitiveness. For ClipFB, the harvest index decreased significantly for all the VN

Table 2. Shoot:root ratio ($\text{g}\cdot\text{g}^{-1}$) for the EHN, ELN, GHN and PHN combinations of ClipInflo and ClipFB experiments. Data in the table indicate the median value with minimum and maximum in brackets. Mann-Whitney tests were used to assess the significance of the results.

VN	Control	ClipFB4	ClipFB7
EHN	12.74 [2.15 - 19.52]	13.39 [2.61 - 21.23]	17.17 [2.56 - 22.02]
ELN	10.56 [2.65 - 14.5]	8.84 [2.86 - 13.46]	9.97 [2.85 - 14.34]
GHN	11.95 [2.15 - 17.58]	10.25 [2.3 - 16.02]	10.98 [2.5 - 18.94]
GLN	9.5 [2.011 - 13.11]	8.32 [2.4 - 12.38]	8.71 [2.72 - 13.53]
PHN	12.38 [2.38 - 17.54]	11.3 [2.47 - 18.34]	13.86 [2.6 - 17.86]
PLN	7.8 [2.32 - 10.59]	8.65 [2.85 - 13.28]	8.39 [2.9 - 12.16]
VN	Control	ClipI0	ClipI4
EHN	15.86 [13.79 - 19.63]	16.66 [12.0 - 20.18]	17.19 [13.76 - 19.90]
ELN	9.31 [7.80 - 12.72]	10.97 [9.03 - 12.91]	10.13 [7.13 - 13.34]
GHN	11.33 [11.14 - 16.5]	12.33 [10.7 - 14.87]	10.94 [8.47 - 12.0]
PHN	14.83 [10.75 - 17]	13.1 [10.9 - 17.24]	15.47 [11.85 - 17.8]

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12
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14
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Table 3. Harvest index for all the VN combinations of ClipInflo (EHN, ELN, GHN and PHN) and ClipFB (EHN, ELN, GHN, GLN, PHN, PLN) experiments. Data in the table indicate the median value with minimum and maximum in brackets. *** indicates significant difference at $P<0.05$ using Mann-Whitney tests.

VN	Control	ClipFB4	ClipFB7
EHN	0.64 [0.61 - 0.69]	0.58 *** [0.51 - 0.63]	0.56 *** [0.48 - 0.59]
ELN	0.62 [0.54 - 0.64]	0.57 *** [0.46 - 0.59]	0.56 *** [0.52 - 0.69]
GHN	0.68 [0.57 - 0.70]	0.65 *** [0.55 - 0.68]	0.60 *** [0.51 - 0.62]
GLN	0.65 [0.62 - 0.69]	0.60 *** [0.52 - 0.62]	0.56 *** [0.52 - 0.61]
PHN	0.67 [0.55 - 0.72]	0.62 *** [0.59 - 0.64]	0.58 *** [0.50 - 0.60]

PLN	0.64 [0.59 – 0.7]	0.55 *** [0.52 – 0.59]	0.58 *** [0.45 – 0.59]
VN	Control	ClipI0	ClipI4
EHN	0.56 [0.55 – 0.58]	0.56 [0.51 – 0.59]	0.56 [0.51 – 0.67]
ELN	0.58 [0.49 – 0.73]	0.54 [0.51 – 0.57]	0.52 [0.50 – 0.56]
GHN	0.55 [0.49 – 0.63]	0.65 *** [0.60 – 0.67]	0.64 [0.57 – 0.66]
PHN	0.53 [0.53 – 0.58]	0.54 [0.50 – 0.57]	0.55 [0.53 – 0.57]

1 combinations (-9% for ClipFB4 and -13% for ClipFB7). This decrease in the harvest index
2 resulted from the significant increase in the aerial vegetative biomass (except for ClipFB4 and
3 ClipFB7 ELN and ClipFB4 GHN), while pod dry mass was not affected (ClipFB4 GLN;
4 ClipFB7 GHN, GLN, PHN), decreased (ClipFB4 EHN, ELN, GHN; ClipFB7 EHN, ELN, PLN)
5 or increased (ClipFB4 PHN, PLN). The increase in vegetative biomass could be related to the
6 production of new secondary axes.
7 For ClipInfo, the harvest index was not modified by the clipping treatments, except for ClipI0
8 GHN for which it increased. Aerial vegetative biomass was not modified by the clipping
9 treatment for the four VN (data not shown). Consequently, the variations in the harvest index
10 were closely related to variations in pod dry mass. This was specifically the case for GHN for
11 which the increase in the harvest index was related to a marked increase in pod dry mass
12 (tolerance in pod yield is equal to 1.32).

13
14

15 Discussion

16

17 We have shown that flower damage modifies yield architecture and its components. In particular
18 we were able to show that restoration of the number of pods is the main lever for the
19 compensation in yield. New pods were mainly set on primary inflorescences or on new
20 secondary inflorescences carried by existing primary branches. Newly produced primary
21 branches with fertile pods were observed for the highest clipping intensities. The different
22 clipping treatments reduced the predominance of the primary inflorescences compared to
23 secondary inflorescences (from 90% for the Control to 50% for the most severe cutting
24 treatment). In the specific case of inflorescence clipping, a high share of overcompensation was
25 observed what is a classic response by the rapeseed to the suppression of apical dominance.
26 These results were consistent with those obtained by Williams and Free (1979), Lerin (1987)
27 and Nilsson (1994) who had already evidenced the importance of the number of pods for the
28 compensation. Tommey and Evans (1992) also demonstrated that floral bud clippings on primary
29 axes increased the yield carried by the remaining intact primary axes. However they did not
30 describe the spatial distribution of these new pods.

31

32 Two factors, the variety and the nitrogen fertilization, were defined to generate a wide range of
33 branching potential. With regards to nitrogen, we were expecting different responses in
34 branching and compensation for the high and low nitrogen fertilization because nitrogen
35 deficiency is known to reduce the branching. Indeed it can be assumed that the ability of a plant
36 to produce new inflorescences is related to both its architecture and nutritional status prior to

1 clipping (Gruntman *et al.*, 2011). A hypothesis to explain the lack of effect of the nitrogen
2 treatment, is that the floral bud damage were not drastic enough to induce the growth of primary
3 axes and thus to observe contrasted behavior between low and high nitrogen fertilization.
4 We identified common trends in the changes of branching and biomass allocation over the VN
5 combinations. The VN showed differences in the magnitude of the responses that are difficult to
6 interpret because of the inter-plant variability. However VN responses seemed to vary according
7 to clipping treatments. Both inflorescence and bud clippings were performed to simulate the
8 reproductive damage that are commonly observed in WOSR crops. Frost event can lead to apical
9 meristems losses in small plants. Cabbage stem flea beetles can also damage the apical
10 meristems when feeding in the main stem in some occasions. However inflorescence losses are
11 less frequent than bud losses caused by the numerous flights of pollen beetles on WOSR crops.
12 When only the flower buds were removed (ClipFB), Pollen and Gamin were more reactive in
13 terms of branching than Exocet. When the whole inflorescences were removed (ClipInflo), VN
14 responses were different with Exocet being the most reactive genotype. However we failed to
15 identify statistically significant relationship between the intensity of the responses in branching,
16 biomass allocation, and the plant compensation. It is difficult to link directly a number of
17 branches to tolerance. Plasticity may better be assessed through the rate of response or the
18 precocity in the response. This needs dynamic characterization of the morphogenesis with non-
19 destructive measurements on plants (*e.g.*: dynamics of the number of branches or numbers of
20 pods; Pinet, 2010).
21 Result obtained with the allometry relationships between the pods dry mass and number of pods
22 illustrates the kind of trait we could define and provide for breeding programs. Our results
23 indicate that there is a slow-down in the increase in the number of pods above a certain dry mass
24 allocated to the pods for the primary inflorescences. Above this threshold, supplemental biomass
25 will be affected to pod weight and not to the production of new pods. This threshold in pod dry
26 mass has been observed for the primary inflorescences of ClipInflo but not for the secondary
27 inflorescences under ClipInflo or with ClipFB. This shift in the biomass allocation could be
28 explained by the competition between growing pods and the meristem that produces new pods.
29 In secondary inflorescences, the number of pods increases linearly with pod dry mass indicating
30 no competition between the production of new pods and the filling of existing pods. An increase
31 in the slope of this relation has been detected in 13 combinations of VN and clipping treatments
32 (among the 17 combinations of VN and clipping treatments with significant variation in the slope
33 and/or the intercept). This increase could be linked to a capacity to produce a larger number of
34 pods per unit of dry mass in response to clipping and might also correspond to a transient
35 response by the plant to cutting and biomass reallocation. Since results evidenced that number of
36 pods is the main lever for compensation (Figure 2), the number of pods produced per gram of
37 pod dry mass could thus be an interesting trait to target for the selection of tolerant genotypes.
38
39 As regards with biomass allocation within the plant, the global trend upward in the shoot/root
40 ratio in response to clipping treatments, while not significant, was suggestive of biomass
41 reallocation from root compartment to aerial parts of the plant. This assumption is consistent
42 with the functional equilibrium hypothesis: the dry matter distribution between root and shoot is
43 regulated by equilibrium between root activity and shoot activity (Brouwer and De Wit, 1969).
44 Thus, the production of new inflorescences and pods may have been supported by the biomass
45 remobilization from roots to shoots. Change in biomass allocation from roots to shoots was also
46 identified as a trait implied in the compensation of floral damage of annual wild species
47 (common groundsel - Obseo and Grubb, 1994; coast tarweed - Gonzales *et al.* 2008; Carolina

1 horsenettle - Wise and Cummins, 2006). However, other plant compartments could contribute to
2 biomass supply to the inflorescences and the pods. In our study, data did not enable a detailed
3 exploration of biomass reallocation from the stems and leaves based on variations in leaf mass
4 per area that are highly variable and decrease during plant bolting and branching (Jullien *et al.*,
5 2009). Similarly, it was not possible to evaluate adaptations regarding the number of seeds per
6 pod, even though these have been shown to change in line with the source/sink ratio (Wang *et*
7 *al.*, 2011).

8
9 The harvest index is an integrated final criterion to assess the balance of the biomass allocation
10 between pods and the rest of the plant (except the root compartment). In our study it was either
11 maintained (for inflorescence cutting) or decreased (for floral bud clipping). The decrease in
12 harvest index can be related to the cost in biomass for the production of new axes and
13 inflorescences that bear the new pods. In the case of inflorescence clipping, the harvest index
14 was not affected because initial flower stalk was also clipped and did not grow out avoiding
15 assimilates investment in a non-productive axis. The new axes are replacement after a kind of
16 reset of the axis. On the contrary, in the case of floral bud clipping, only the buds have been cut
17 and initial flower stalk has been maintained. The compensative inflorescences are in addition.
18 The cost of the production of axes on the global sources/sink ratio of the plant has been
19 evaluated by a modeling approach by Jullien *et al.* (2012) and Pinet (2010). Simulations show
20 that the plant bolting and the elongation of the ramification induce a dramatic decrease in the
21 sources/sink ratio largely prior seed filling. In the case of flower damage, simulations show that
22 the sources/sink ratio increases temporarily because of the loss of sink organs. However, a quick
23 return to normal value of the sources/sink ratio is observed following the growth of new sink
24 organs (axes and pods).

25
26 Our study explores the interactions between morphogenesis and biomass distribution shown in
27 the conceptual diagram of Figure 1 in the case of flower damage in WOSR. A next step could be
28 to focus on the change in the distribution of biomass after clipping and the ability of the plant to
29 reuse this biomass to produce new pods. This may provide new traits to be target in breeding
30 programs in order to improve WOSR tolerance to floral bud damage.

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36

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38 39 **Figure legends**

40
41 Figure 1. (A) Topology of the aerial parts of a WOSR plant. Left: topology before floral bud
42 damage, right: after floral bud damage newly formed pods may be located on either existing
43 inflorescences or on new inflorescences. New inflorescences may be carried by existing primary
44 axes (1) or by new ones (2,3). (B) Diagram of the interaction between branching pattern and
45 biomass allocation.

46 Figure 2. Classification trees based on tolerance indices of seed yield, number of pods and pod
47 weight. (A) ClipFB, (B) ClipInflo.

48 Figure 3. Number of fertile primary (A) and secondary (B) axes per plant in ClipFB experiment
49 for EHN, ELN, GHN, GLN, PHN and PLN. *** 0.05 / * 0.15 using Mann-Whitney tests. The
50 meanings of the acronyms of the VN combinations are detailed in Table 1.

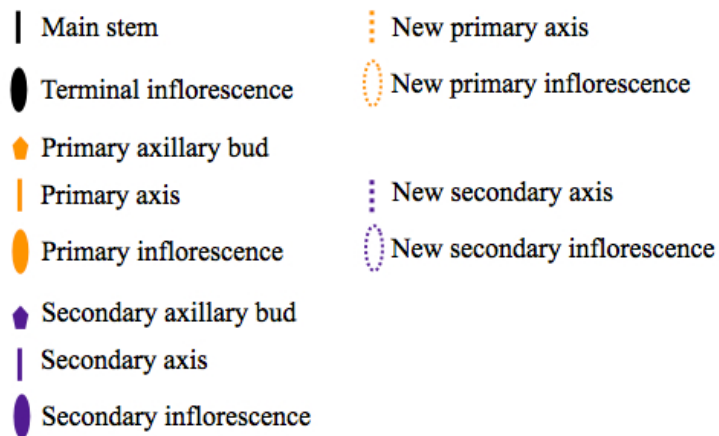
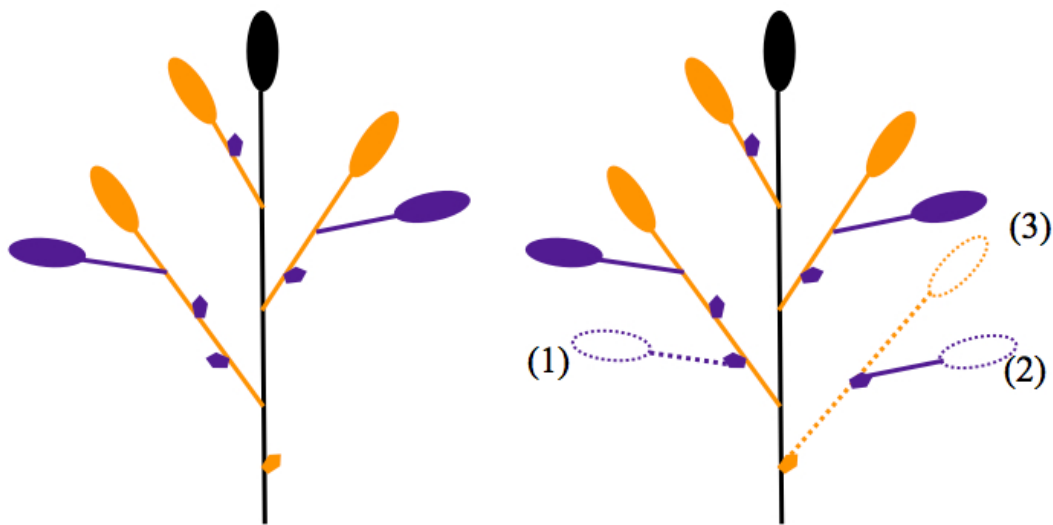
51 Figure 4. Number of fertile primary (A) and secondary (B) axes per plant in ClipInflo experiment
52 for EHN, ELN, GHN and PHN. *** 0.05 / * 0.15 using Mann-Whitney tests. The meanings of
53 the acronyms of the VN combinations are detailed in Table 1.

1 Figure 5. Pods distribution between different axes of the plant for ClipFB. Control (A), ClipFB4
2 (B) and ClipFB7 (C). Grey boxplots correspond to pods of primary inflorescences carried by
3 existing primary axes. Green boxplots correspond to pods of secondary inflorescences carried by
4 existing primary axes. Blue boxplots correspond to pods of primary inflorescences carried by
5 new primary axes. Purple boxplots correspond to pods of secondary inflorescences carried by
6 new primary axes. Results are expressed as a percentage of the total number of pods. The
7 meanings of the acronyms of the VN combinations are detailed in Table 1.

8 Figure 6. Relationship between the number of pods and the total pod dry mass on the primary
9 inflorescences for EHN, ELN, GHN and PHN of ClipFB (A) and ClipInflo (B). Black, green and
10 purple dots correspond to Control, ClipFB4 and ClipFB7 treatments, respectively. Black, red and
11 blue dots correspond to Control, ClipI0 and ClipI4 treatments, respectively. The meanings of the
12 acronyms of the VN combinations are detailed in Table 1. Linear mixed-models were used to
13 assess the significance of the results.

Figure 1.JPEG

(A)



(B)

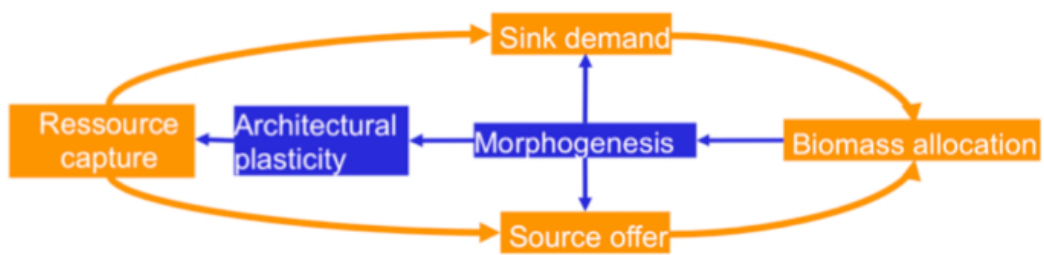


Figure 2.JPEG

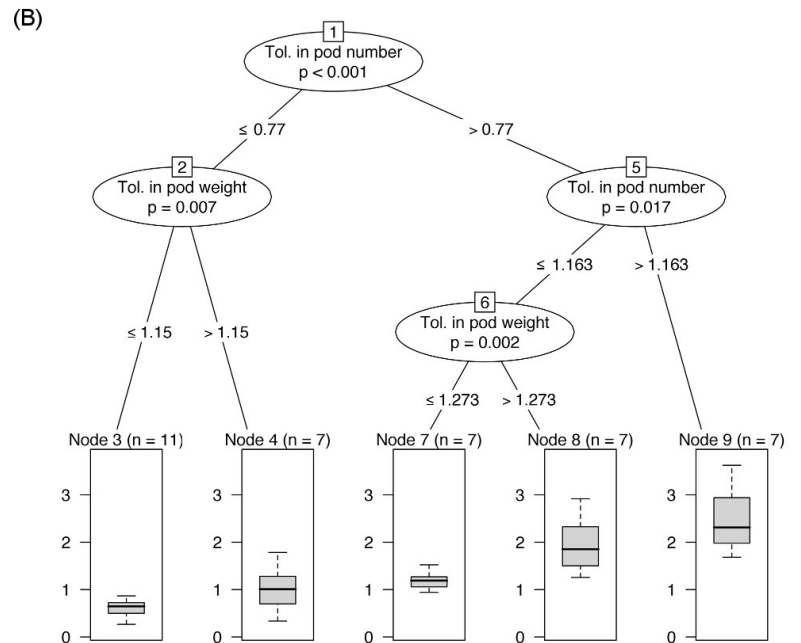
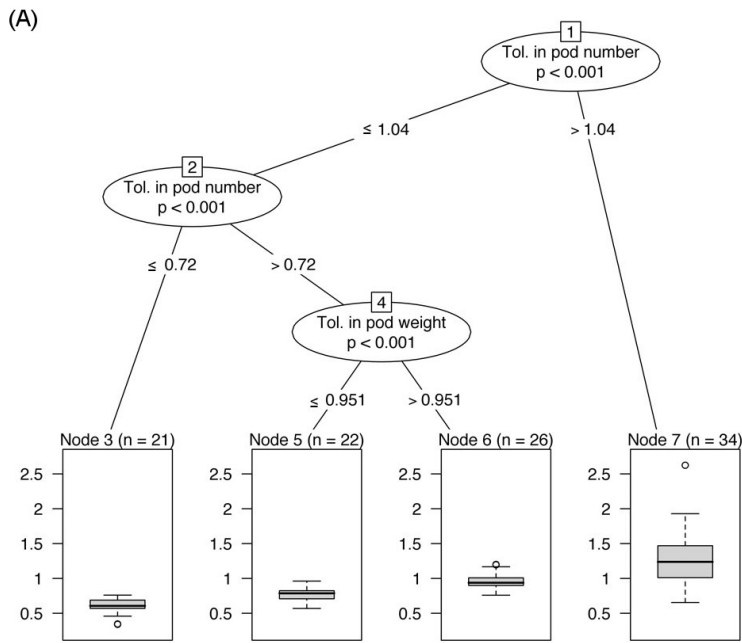


Figure 3.JPEG

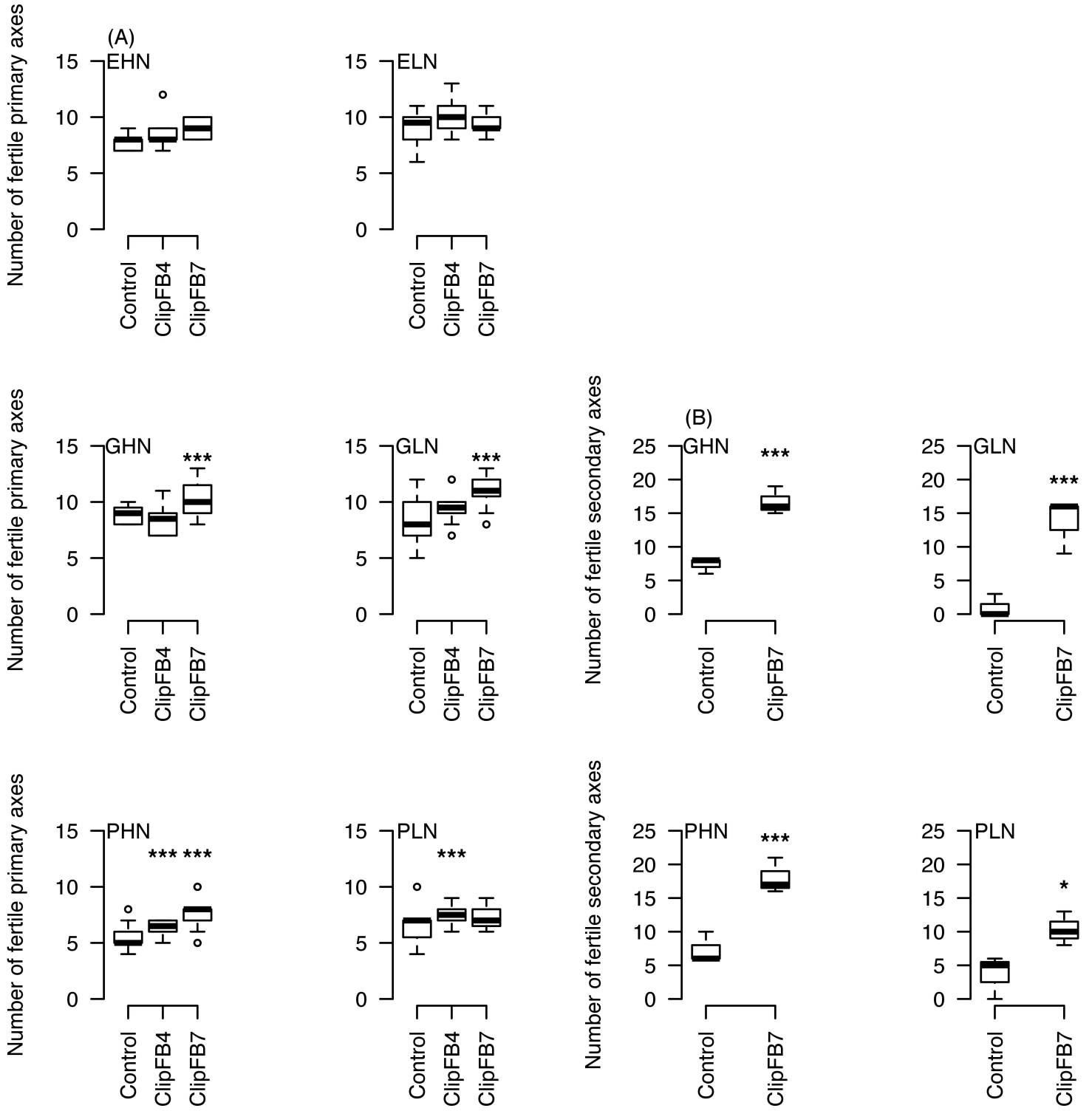


Figure 4.JPEG

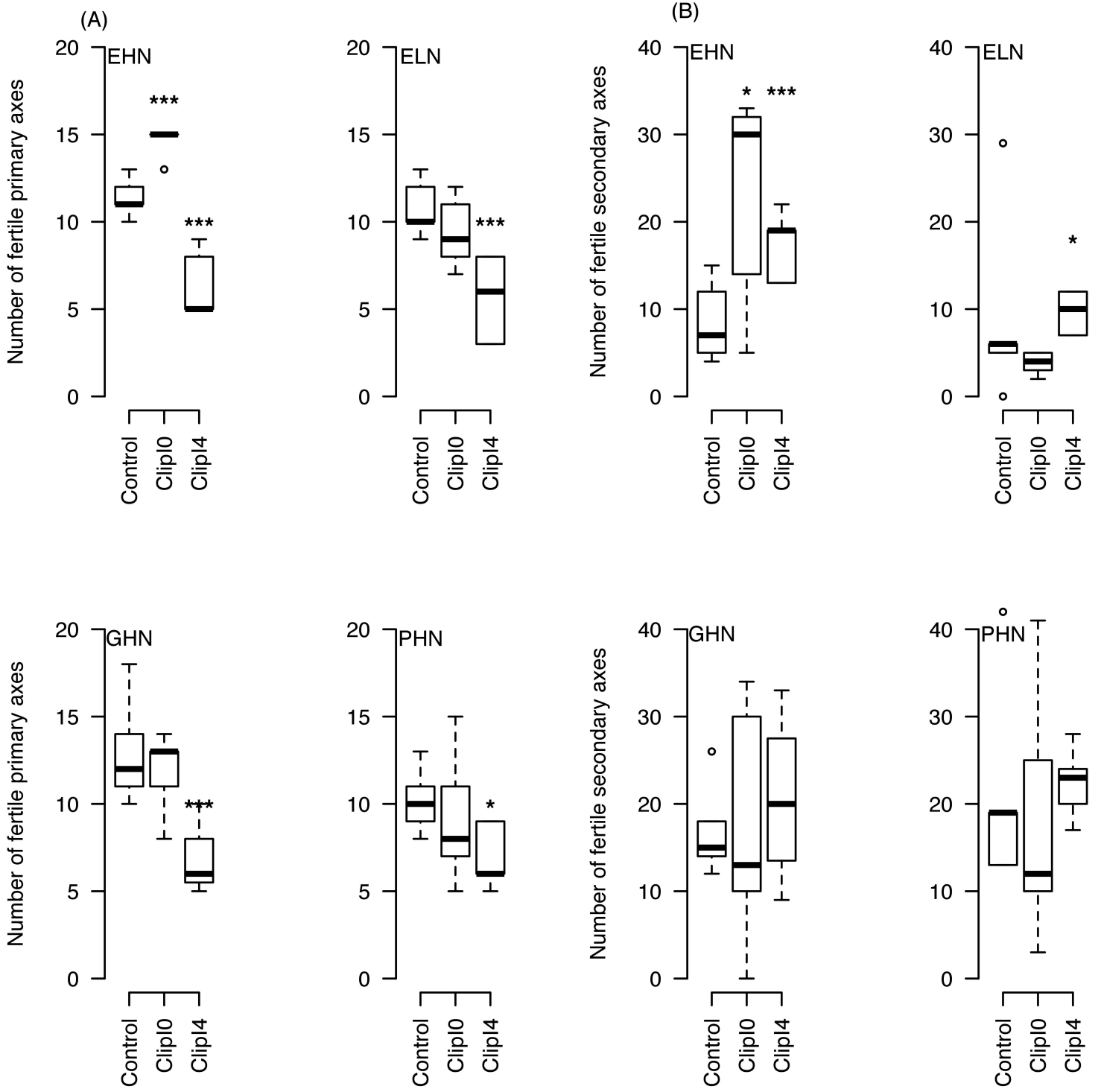


Figure 5.JPEG

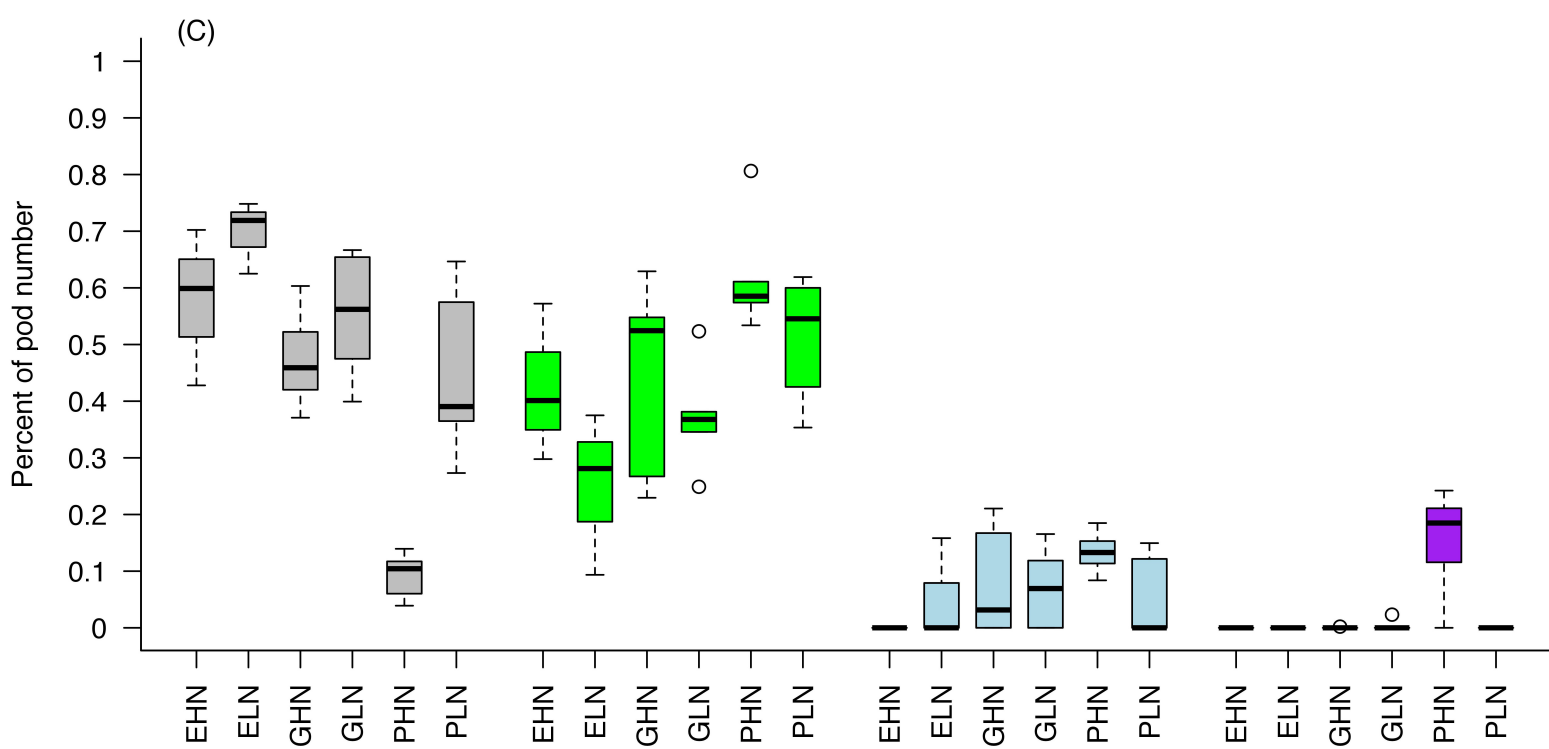
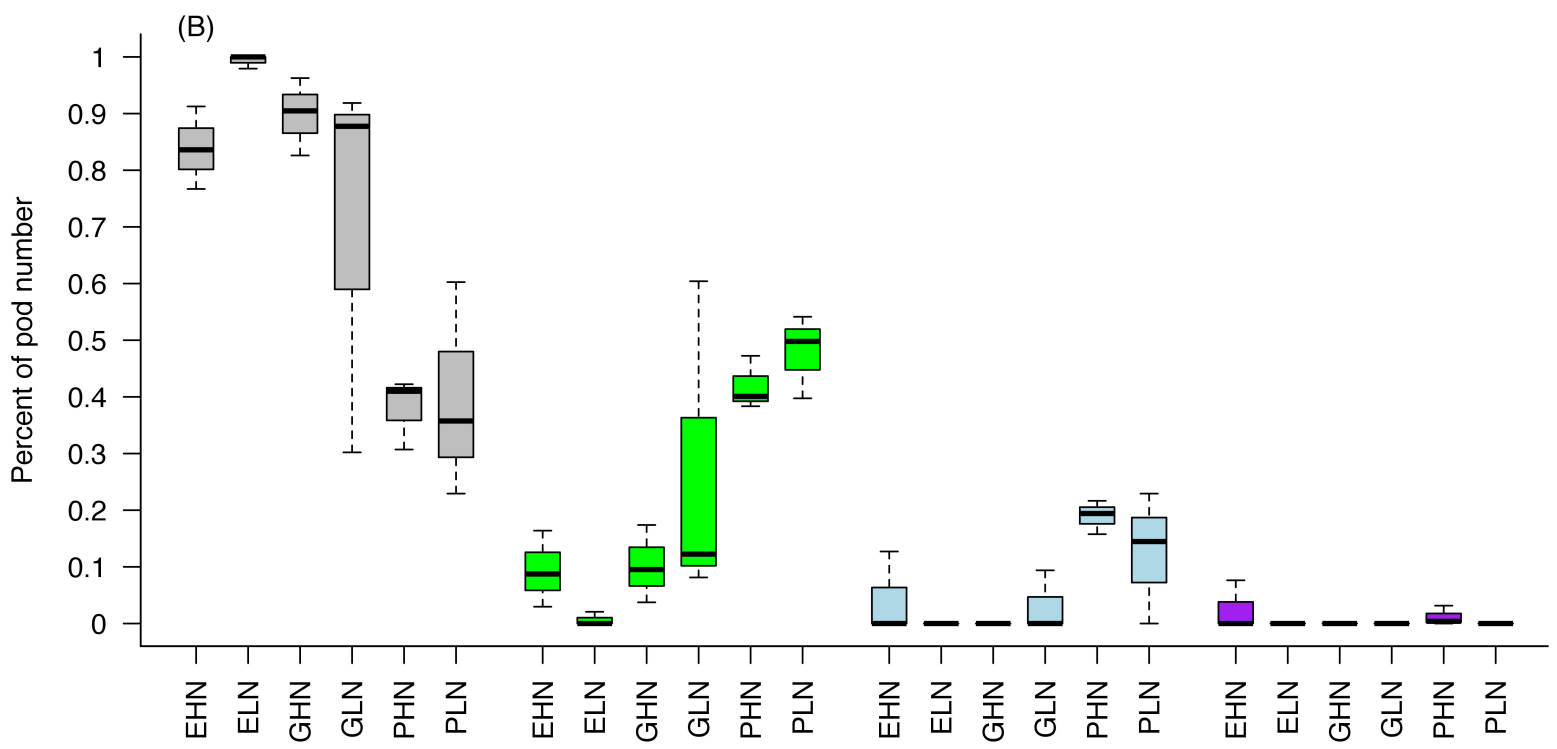
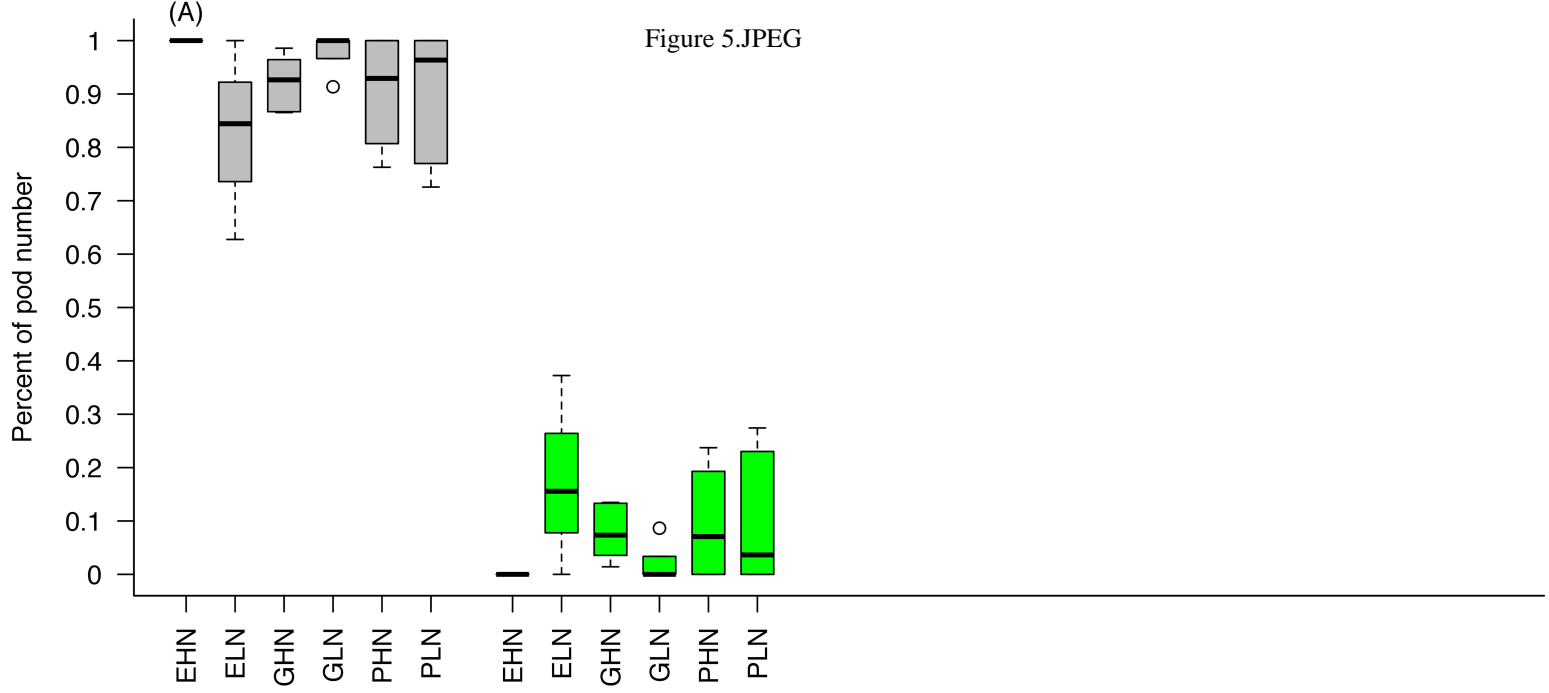


Figure 6.JPEG

