



# Vegetative plasticity and floral branching compensate low plant density in modern spring rapeseed



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## ABSTRACT

Sunlight is a crucial environmental factor for photosynthesis. Plant density affects both quality and quantity at light penetration into the canopy. The effects of plant density on the expression of photomorphogenic traits in cultivated spring rapeseed (*Brassica napus* L.), and their consequences on seed production per unit area are unknown. The aims of this work were to: i) analyze the magnitude of shade avoidance responses to plant densities in five spring rapeseed genotypes, ii) describe the dynamics of floral branching in response to genotype and plant density, and iii) study yield and its components and seed quality in field-cultivated plants with contrasting plant densities (15 and 240 pl m<sup>-2</sup>). Rosette diameter was the main attribute of vegetative plasticity modified by plant density, without significant changes in petiole length. Plant density changed the relationship between intercepted solar radiation (ISR) and red/far red ratio (R/FR) during crop development, but at flowering all densities reached ISR = 95% and R/FR ratio < 0.1. From flowering to maturity, the lower the plant density, the lower the R/FR, associated to increased silique area by a promotion of floral branching. Growth dynamics of floral branches at first, second and third orders were strongly affected by plant density and genotype. Seed yield per plant could be described by a negative power-law function as a function of plant density at harvest, exhibiting a high reproductive plasticity capable of compensating grain yield per unit area. Fruiting efficiency per plant was around 100–160 seeds g<sup>-1</sup>, regardless of plant density. Seed oil and protein content were not responsive to plant density. We concluded that plant density could be reduced without significant penalty for seed production per area, because short-cycle spring rapeseed genotypes expressed a strong vegetative and reproductive plasticity at individual level when plants were grown under well-watered and fertilized conditions.

## 1. Introduction

Sunlight is a crucial environmental factor for photosynthesis. Additionally, the capacity of the crop to capture radiation throughout the crop cycle is closely associated with biomass production at harvest, and thereby with the magnitude of seed yield. Light quality is also relevant because it serves as a sensory cue for the adjustment of plant growth and development. A precise early signal of competition is the reduction of red/far red ratio (R/FR) as a direct consequence of the presence of neighboring plants whose leaves efficiently absorb red and blue photons and transmit or reflect far-red and green photons (Ballaré

et al., 1990). Plants perceive the low R/FR ratios principally through the phytochrome B photoreceptor, which promotes the shade avoidance syndrome (SAS), a set of physiological responses that increases the elongation of vegetative structures such as stems and petioles, accelerates flowering, and reduces the number and size of seeds (Smith and Whitelam, 1997). When plant density increases, the reduction of photosynthetically active radiation (PAR) transmitted and blue photons detected by cryptochrome 1 photoreceptor partially induce overlapping SAS signaling pathways (Keller et al., 2011).

Adaptive plasticity due to SAS is well documented in natural populations (Dudley and Schmitt, 1995; Botto and Smith, 2002; Botto,

*Abbreviations:* R/FR ratio, red/far red ratio; ISR, intercepted solar radiation; LAI, leaf area index; DAE, days after emergence; DAF, days after flowering; SAS, shade avoidance syndrome; SEM, standard error of mean

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2015). At high plant density, SAS confers an important advantage for asymmetric competition because it allows plants to capture more radiation and increase growth rate (Schmitt and Wulff, 1993; Casal, 2013). Several grain crops display strong plasticity as part of SAS (Carriedo et al., 2016). Rapeseed genotypes show strong photomorphogenic responses to low R/FR ratios in vegetative and reproductive phases both as individual plants cultivated in pots or in the field under natural radiation. Rondanini et al. (2014) demonstrated that low irradiance after flowering was relevant to reduce rapeseed seed yield, but an increase of the R/FR ratio partially alleviated yield reductions.

Crop population density modifies available resources per individual plant, and the ability to use these resources depends on plant strategies that induce vegetative and reproductive plasticity. Consequently, plant plasticity has important implications for sustaining crop productivity. For example, intra-specific competition in maize produced early plant hierarchies with dominant and dominated plants, affecting productivity per unit area (Maddonni and Otegui, 2006; Pagano and Maddonni, 2007). In winter rapeseed genotypes, an increase in canopy density caused a reduction in the number of rapeseed adult plants due to a self-thinning effect, achieving maximum yields at an intermediate plant density of 50–60  $\text{pl m}^{-2}$  (Leach et al., 1999; Roques and Berry, 2016). Interestingly, in spring rapeseed genotypes, the reduction of plant densities had no significant negative effects on seed yield per unit area, as was observed for plant densities from 100 to 40  $\text{pl m}^{-2}$  (McGregor, 1987; Angadi et al., 2003) and 40 to 20  $\text{pl m}^{-2}$  (Brill et al., 2016). However, lower plant density from 15 to 5  $\text{pl m}^{-2}$  (out of the agronomic range) significantly reduced crop productivity in winter rapeseed genotypes (Zhang et al., 2012; Wang et al., 2015; Brill et al., 2016). These results suggest that there is a physiological limit to the capacity of plant plasticity to compensate seed yield at low densities.

It is noteworthy that the degree of plasticity expressed at different densities depends on the trait considered. For example, in rapeseed, seed size and oil content are conservative and stable reproductive traits without variations across a wide range of growing conditions (Gomez and Miralles, 2011), but the number of siliques and the number of grains per plant are plastic traits that increase at low densities (Angadi et al., 2003; Harker et al., 2015). The response of floral branching dynamics to plant density has not been previously measured during rapeseed crop development. Although it is well established that rapeseed plant plasticity increases seed production per plant at low densities, the effects of plant density on the expression of photomorphogenic traits and their consequences on seed production per unit area are absolutely unknown.

The aims of this study were to i) analyze the magnitude of some SAS responses to plant densities in five spring rapeseed genotypes, ii) describe the responses of the dynamics of floral branching to genotype and to plant density, and iii) study yield and its components and seed quality in crops cultivated in the field at contrasting plant densities (from 15 to 240  $\text{pl m}^{-2}$ ), under non-limiting conditions of water, nutrient, and biotic constraints.

## 2. Materials and methods

### 2.1. Experimental

Four experiments were carried out under field conditions between 2011 and 2015 at the School of Agriculture, University of Buenos Aires (34°35'S, 58°29'W), using five commercial spring rapeseed genotypes, including 3 hybrids (Hyola 61 and Hyola 830 from Advanta Seeds; and Solar CL from Al High Tech), and 2 open-pollinated varieties (Bioaureo 2486 from Nuseed; and SRM 2836 from Sursem). Crops were hand-sown on a silty clay loam classified as Vertic Argiudoll according to the USDA taxonomy, in  $2 \times 1.5$  m plots, with rows spaced at 0.2 m. Sowing dates ranged from May to July. Five weeks after sowing, plots were manually thinned to the target plant density, at densities from 15 to

240  $\text{pl m}^{-2}$ , using 60  $\text{pl m}^{-2}$  in all experiments as reference plant density. In Exp. 1, Hyola 61 was sown on July 8, 2011 at 60, 120 and 240  $\text{pl m}^{-2}$ . In Exp. 2, Hyola 61 was sown on May 8, 2012 at 15, 30 and 60  $\text{pl m}^{-2}$ . In Exp. 3, Hyola 61 and SRM 2836 were sown on June 30, 2014 at 15 and 60  $\text{pl m}^{-2}$ . In Exp. 4, Bioaureo 2486, Hyola 830 and Solar CL were sown on May 14, 2015 at 15 and 60  $\text{pl m}^{-2}$ . Natural rainfall was complemented by drip irrigation to avoid water stress. Plots were fertilized (at sowing and at six leaf stage) with 10  $\text{g N m}^{-2}$ , 2  $\text{g P m}^{-2}$ , and 1.5  $\text{g S m}^{-2}$  (IPNI 2015). Pests and diseases were chemically controlled, and weeds were mechanically controlled. Temperature and solar radiation varied greatly among years (Fig. S1). In the most productive years, the seed yield was  $> 400 \text{ g m}^{-2}$  (Exp. 1 and 4) and in the least productive years the seed yield was  $< 200 \text{ g m}^{-2}$  (Exp. 2 and 3).

### 2.2. Measurements

Phenological stages of emergence, rosette, stem elongation, visible floral bud, first flowering (first open flower), and maturity were recorded when 50% of the plants reached each stage according to Arnould (1989). Vegetative measurements throughout the crop cycle included plant height, petiole length, length and width of the last fully expanded leaf, and rosette horizontal diameter. Reproductive measurements included length of main floral raceme, number of floral branches, and number of siliques. First flowering was registered on September 27, 2011 (Exp. 1), August 23, 2012 (Exp. 2); September 20 and 24, 2014 for Hyola 61 and SRM 2836, respectively (Exp.3), August 12, 23 and September 14, 2015 for Bioaureo 2486, Solar CL and Hyola 830, respectively (Exp.4). In Exp. 2, leaf area index was measured at first flowering on plants from 1-m row of each plot, using a LI-3100C area meter (LI-COR Inc., Lincoln, NE). Dynamics of floral branching was determined on 18 plants per treatment, tagged at first flowering in the main floral raceme. The appearance of first, second and third order axillary branches (with an open flower) was recorded twice a week (Pinet et al., 2015), and the number of fertile branches (with at least one filled silique) was recorded at harvest. R, FR, and PAR ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) were measured using a four-channel SKR 1850A sensor (Skye Instruments Ltd., Powys, UK) attached to a LI-1400 datalogger (LI-COR Inc., Lincoln, NE). Canopy intercepted solar radiation (ISR) was measured at noon on clear days using a 1-m long linear radiometer (Cava-Rad, Cava devices, Buenos Aires, Argentina). Cumulative ISR for the whole crop cycle (from emergence to maturity) was also calculated according to Rondanini et al. (2014). Local mean daily temperature ( $^{\circ}\text{C}$ ) and daily global incident irradiance ( $\text{MJ m}^{-2} \text{ day}^{-1}$ ) were obtained from a National Weather Service station located 200 m from the experiments.

At crop maturity, 0.9  $\text{m}^2$  from the three central rows of each plot were harvested and above-ground biomass separated into stalk, seed and chaff, dried in a forced-air oven at 70  $^{\circ}\text{C}$  for 72 h, and weighed. Plant density at harvest was also determined and compared to target plant density. Observed plant density at harvest was lower than target plant density, especially for the range of higher densities of 120 and 240  $\text{pl m}^{-2}$  (reflecting about  $-20\%$  of self-thinning). Seed yield (on a dry basis) was expressed both on area ( $\text{g m}^{-2}$ ) and plant basis ( $\text{g pl}^{-1}$ ) and its components were determined. Thousand seed weight was estimated from three 200 seed aliquots. Fruiting efficiency was calculated as the seed number produced by unit of non-seed reproductive biomass, in a way similar to that used for wheat by González et al. (2014). Seed oil content (on a dry basis) was determined by Soxhlet extraction (method 1.122 from IUPAC, 1992) and seed protein content by micro-Kjeldahl (Nelson and Sommer 1973). Oil and protein content were expressed both as percentage of dry matter (g per 100 g of grain) and in equivalent energy basis, assuming 9 kcal per gram of oil and 4 kcal per gram of protein (Penning de Vries and van Laar, 1982). In addition, seed yield was expressed in an energy basis ( $\text{kcal m}^{-2}$ ).

### 2.3. Statistical analysis

Experiments were arranged in a completely randomized design with three replicates for each genotype per plant density treatment, except for Exp. 3, which had six replicates. The experimental unit was the individual plot ( $2 \times 1.5$  m). For each experiment, means of treatments were separated with ANOVA and Tukey's test at 5% level of significance. To compare genotypes across experiments, relative seed yield for each value was calculated as the proportion of seed yield reached at  $60 \text{ pl m}^{-2}$  (as this plant density was used in all experiments), to which a value of 100 was assigned. Simple linear regression and negative power-law function ( $y = ax^{-b}$ ) models were fitted to data. Angular transformation was applied to percentages. Statistical packages used were INFOSTAT ([www.infostat.com.ar](http://www.infostat.com.ar)) and Graph Pad Prism ([www.graphpad.com](http://www.graphpad.com)).

## 3. Results

### 3.1. Vegetative plasticity benefits light interception in low plant density

Plant density modified the relationship between ISR and R/FR during crop development, especially in the range from 15 to  $60 \text{ pl m}^{-2}$  (Fig. 1). At visible floral bud stage, the lowest plant density ( $15 \text{ pl m}^{-2}$ ) had 50% ISR and 0.8 R/FR, whereas higher plant density (30 and  $60 \text{ pl m}^{-2}$ ) increased ISR reaching values of 90–95% and reduced R/FR down to values of 0.2–0.3 (Fig. 1). However, at flowering stage all densities achieved values of 95% for ISR and  $< 0.1$  for R/FR ratio. After flowering, dynamics of ISR and R/FR were different depending on the densities. Thus, at the fruiting and maturity stages, ISR remained high for all densities due to the interception by the green siliques. Nevertheless, R/FR ratio at maturity increased up to 0.4, 0.5, and 1.0 for plant densities of 15, 30 and  $60 \text{ pl m}^{-2}$ , respectively (Fig. 1). Low R/FR ratio at low plant density was associated with a canopy formed by a dense layer of green siliques due to greater floral branching (see Section 3.2 below). For the high density range, from 60 to  $240 \text{ pl m}^{-2}$ , no significant differences were observed between plant densities in both R/FR ratios (increasing from 0.04 at flowering to 0.67 at maturity) and ISR (decreasing from 98 at flowering to 90% at maturity).

ISR dynamics was not affected across the broad range of plant densities of  $30\text{--}240 \text{ pl m}^{-2}$  (Fig. 2, see Exp. 1 and 2). By contrast, very low plant density of  $15 \text{ pl m}^{-2}$  delayed the capture of radiation during the vegetative and early reproductive stages (i.e., rosette and visible floral bud stages). Maximum ISR was mainly reached around flowering (Fig. 2). A particular case was observed in Exp.3 for Hyola 61 and SRM 2836 genotypes. Both genotypes reached their first flowering with only 40–60% ISR (Fig. 2) due to the late sowing date and the short crop cycle (i.e., 80 days at flowering for Exp. 3 compared to 90–120 days at flowering for other experiments). Despite the differences observed in

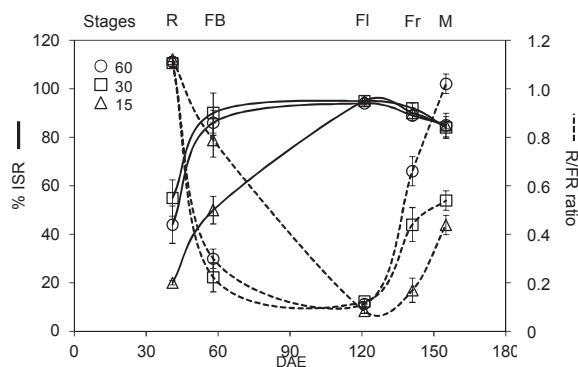


Fig. 1. Dynamics of intercepted solar radiation (% ISR) and R/FR ratio at the bottom of canopy of Hyola 61 spring rapeseed at contrasting plant densities ( $15, 30$  and  $60 \text{ pl m}^{-2}$ ). Crop stages of rosette (R), visible floral bud (FB), first flowering (FI), full fruiting (Fr), and crop maturity (M) are indicated. Data are from Exp. 2. Vertical bars shown  $\pm 1$  SEM.

ISR, comparing the lowest density with the others, cumulative ISR through the entire crop cycle was only slightly reduced at low plant density. For example, in Exp. 1 cumulative ISR was reduced from  $1380 \text{ MJ m}^{-2}$  at  $240 \text{ pl m}^{-2}$  to  $1300 \text{ MJ m}^{-2}$  for at  $60 \text{ pl m}^{-2}$  ( $-6\%$ ), while the reduction was about  $-8\%$  from 60 to  $15 \text{ pl m}^{-2}$  in Exp. 2 (data not shown).

In terms of plant morphology, rosette diameter was the main attribute of vegetative plasticity modified at low density, without significant changes in petiole length (Table 1). Genotypic differences in vegetative plasticity were observed early during plant development. Hyola 61 showed higher vegetative plasticity than SRM 2836 at 58 days after emergence (DAE, Exp. 3, Table 1). For pooled data from Hyola 61 in Exps. 1–3, a negative power-law function was fitted to the relative diameter of rosette measured at 58–59 DAE (relative to the value of  $60 \text{ pl m}^{-2}$  from each experiment) as a function of plant density (Fig. 3). Rosette diameter increased up to 30% at densities lower than  $60 \text{ pl m}^{-2}$ , and decreased up to 17% when densities were higher than  $60 \text{ pl m}^{-2}$  (Fig. 3).

No effect of plant density on phenological development was evident at crop level in any experiment. LAI at flowering (measured for Exp. 2) was about 3 for plant densities between 15 and  $60 \text{ pl m}^{-2}$ , with a leaf area per plant from  $2000$  to  $500 \text{ cm}^2 \text{ pl}^{-1}$ , respectively (data not shown).

### 3.2. Reproductive plasticity is associated with floral branching and reproductive biomass allocation

Reproductive biomass allocated in floral branches was significantly affected by genotype and plant density (Table 2). Although seed and chaff biomass from main raceme was not affected by plant density, for floral branches both traits were significantly ( $p < 0.01$ ) increased as density was reduced (Table 2). Thus, the ratio between seed allocated to branches and to the main raceme rose from 2.3 to 5.8 in Hyola 61, and from 1.4 to 3.5 in SRM 2386, when plant density decreased from 60 to  $15 \text{ pl m}^{-2}$  (Table 2). Fruiting efficiency per whole plant was around 154 and 157 seeds  $\text{g}^{-1}$  for Hyola 61, and 113 and 107 grains  $\text{g}^{-1}$ , for SRM 2836 at low and high density, respectively, without significant differences between plant densities. A similar response of floral branching and fruiting efficiency to plant density was observed for the three genotypes in Exp. 4 (data not shown).

To achieve a better understanding of inflorescence development at different plant densities in the rapeseed crop, the number of floral branches of different orders after flowering at 15 and  $60 \text{ pl m}^{-2}$  in Hyola 61 and SRM 2836 cultivars was analyzed (Fig. 4). Dynamics of floral branches of first, second and third orders were strongly affected by plant density and genotype (Fig. 4). High density reduced the number of branches, the most susceptible being the highest levels of floral branch (third order), followed by the second branch order. At low plant density, final number of floral branches for the first, second and third order were 5:6:2 and 5:3:1 for Hyola 61 and SRM2836, respectively; and this was reduced to 4:1:1 and 4:0:0 at high density, respectively (Fig. 4).

### 3.3. Seed yield per unit area at low plant density is compensated by seed yield per plant

Seed yield per plant, seed number per plant and above-ground biomass were reduced by increasing plant density in all experiments (Table 3). By contrast, thousand seed weight was not affected by genotype, plant density, or their interaction (Table 3). Interestingly, the high plasticity of rapeseed crop compensated the changes in plant density by adjustments at individual plant level. In fact, seed yield per unit area was not significantly affected by plant density in any experiment (Table 4). Genotypic differences were significant in Exp. 3 but not in Exp. 4, without significant interaction between genotype and plant density in any case (Table 4). Seed number per unit area

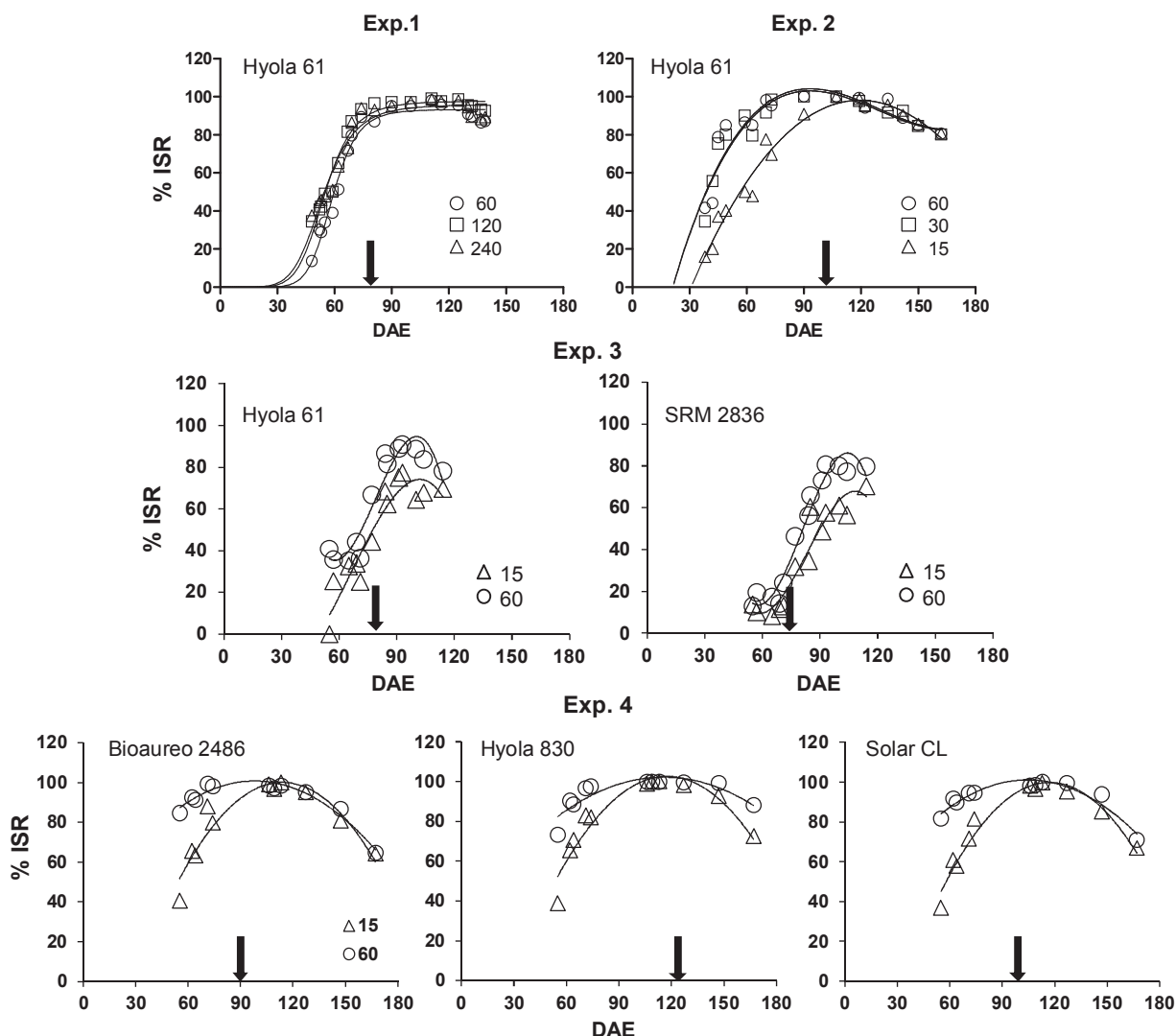


Fig. 2. Dynamics of the intercepted solar radiation (% ISR) during days after emergence (DAE) of spring rapeseed genotypes growing at contrasting plant density from Exp. 1–4. Black arrows indicate timing of first flowering. Non-linear functions fitted to data are shown.

**Table 1**  
Effects of plant density (PD) on petiole length, and rosette diameter at 58–59 days after emergence (DAE) for rapeseed genotypes from Exp. 1–3. Percentage change in rosette diameter with respect to 60 pl m<sup>-2</sup> is shown in brackets.

Exp.	Genotype	PD (pl m <sup>-2</sup> )	Petiole length (mm)	Diameter rosette (mm)	
1	Hyola 61	60	49 a	195 a	
		120	51 a	187 a	(-4%)
		240	61 a	162 a	(-17%)
		p-value	0.519	0.380	
2	Hyola 61	15	69 a	351 a	(+27%)
		30	80 a	348 ab	(+25%)
		60	86 a	277 c	
		p-value	0.266	0.020	
3	Hyola 61	15	42 ab	223 a	(+39%)
		60	38 b	160 b	
	SRM 2836	15	53 ab	253 a	(+10%)
		60	56 a	229 ab	
		p-value	0.046	0.018	

For each experiment, means followed by different letters within a column indicate significant differences for Tukey's test. P-values are also shown.

mimicked the response observed in seed yield. Above-ground biomass per unit area did not significantly vary among plant densities (Table 4). Harvest index was not affected by plant density in Hyola61 in Exp. 1

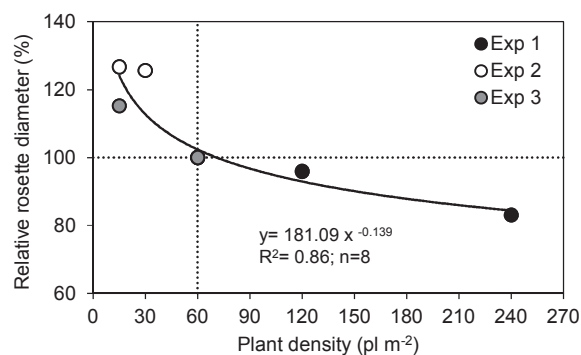


Fig. 3. Relationship between the relative rosette diameter measured at 58–59 DAE and plant density for Hyola 61 spring rapeseed from Exp. 1–3. Rosette size data are relativized to values for 60 pl m<sup>-2</sup> of each experiment (dotted lines). A negative power-law function fitted to pooled data is shown.

and 2 (from 15 to 240 pl m<sup>-2</sup>) but increased significantly when plants were cultivated at 60 pl m<sup>-2</sup> compared to 15 pl m<sup>-2</sup> in Exp. 3. In the same experiment, Hyola 61 showed higher harvest indices than SRM 2836 (Table 4).

Seed yield per plant was significantly associated with plant density at harvest, and a negative power-law function, specific for each

**Table 2**

Effects of plant density (PD), genotype (G) and their interaction on the biomass allocated in the main floral raceme and floral branches, discriminating between seed and chaff (non-seed reproductive biomass) of spring rapeseed genotypes. Data are from Exp. 3.

Genotype	PD	Main floral raceme		Floral branches		Seed from branches/ main raceme ratio	
		(pl m <sup>-2</sup> )	seed (g pl <sup>-1</sup> )	chaff (g pl <sup>-1</sup> )	seed (g pl <sup>-1</sup> )		chaff (g pl <sup>-1</sup> )
Hyola 61	15		1.34 a	1.80 a	7.84 a	16.92 a	5.8 a
	60		1.32 a	1.72 a	3.10 bc	7.30 b	2.3bc
SRM 2836	15		1.68 a	2.12 a	5.88 ab	16.88 a	3.5ab
	60		1.68 a	1.80 a	2.32 c	7.18 b	1.4 c
p-value	G		0.009	0.187	0.073	0.952	0.047
	PD		0.935	0.187	< 0.001	< 0.001	< 0.001
	G x PD		0.935	0.424	0.426	0.975	0.574

Means followed by different letters within a column indicate significant differences for Tukey's test. P-values are also shown.

experiment and genotype, could be fitted to the relationship (Fig. 5). No significant relationship was observed when seed yield per unit area was contrasted to the range of plant density (Fig. 5). Since reproductive plasticity was variable across genotypes and experimental conditions, seed yield per unit area and seed yield per plant were calculated relative to data from 60 pl m<sup>-2</sup> and plotted against plant density at harvest in order to fit the pooled data from the four experiments with a single function. Relative seed yield per plant was fitted by negative power-law function ( $R^2 = 0.90$ ;  $n = 60$ ) confirming the huge reproductive plasticity per plant observed at very low plant densities between 15 and 30 pl m<sup>-2</sup>. By contrast, there was no relationship between relative seed yield per unit area and plant density (Fig. 6).

### 3.4. Seed oil and protein are not responsive to plant density

Seed oil and protein content varied among genotypes and experiments, but no significant tendencies of seed quality and plant density were observed (Table 5). Oil yield per unit area (g oil m<sup>-2</sup>) was not affected by genotype or plant density (Table 5). Genotype effects on protein yield per unit area were significant only in Exp. 3 (Table 5). A negative relationship between seed oil content and seed protein content was observed when the data of all experiments were pooled, with a significant slope of  $-1.3$ , demonstrating that seed oil was reduced more than proportionally as seed protein increased (Fig. 7). The same trend was observed for the variables expressed in an energy basis (Fig. 7) with a slope of  $-3.03$ , which reflect the oil-to-protein energy ratio (i.e., 9:4 kcal, is equivalent to multiplying the slope  $-1.3$  in term of dry matter by the oil-to-protein energy ratio = 2.25). No significant relationship was observed between seed oil content and seed yield (per area or per plant), and no relationship emerged when were expressed in an energy basis (Fig. 7). The same trend was observed for seed protein content and seed yield (data not shown).

## 4. Discussion

### 4.1. Vegetative plasticity modifies canopy light capture

Spring rapeseed genotypes, grown at contrasting plant densities under field conditions without abiotic or biotic restrictions, exhibited a high vegetative, as well as reproductive plasticity per plant, modifying canopy light capture and R/FR ratio. Also, a self-thinning effect was observed, as the number of plants at harvest was around 20% lower than target plant density, at high plant densities between 120 and 240 pl m<sup>-2</sup>. A similar self-thinning effect has also been reported for winter oilseed rape, with reductions of 16% and 30% for densities between 150 and 250 pl m<sup>-2</sup>, respectively (Leach et al., 1999), and reductions of 25% and 50% for densities between 20 and 200 pl m<sup>-2</sup>, respectively (Roques and Berry 2016).

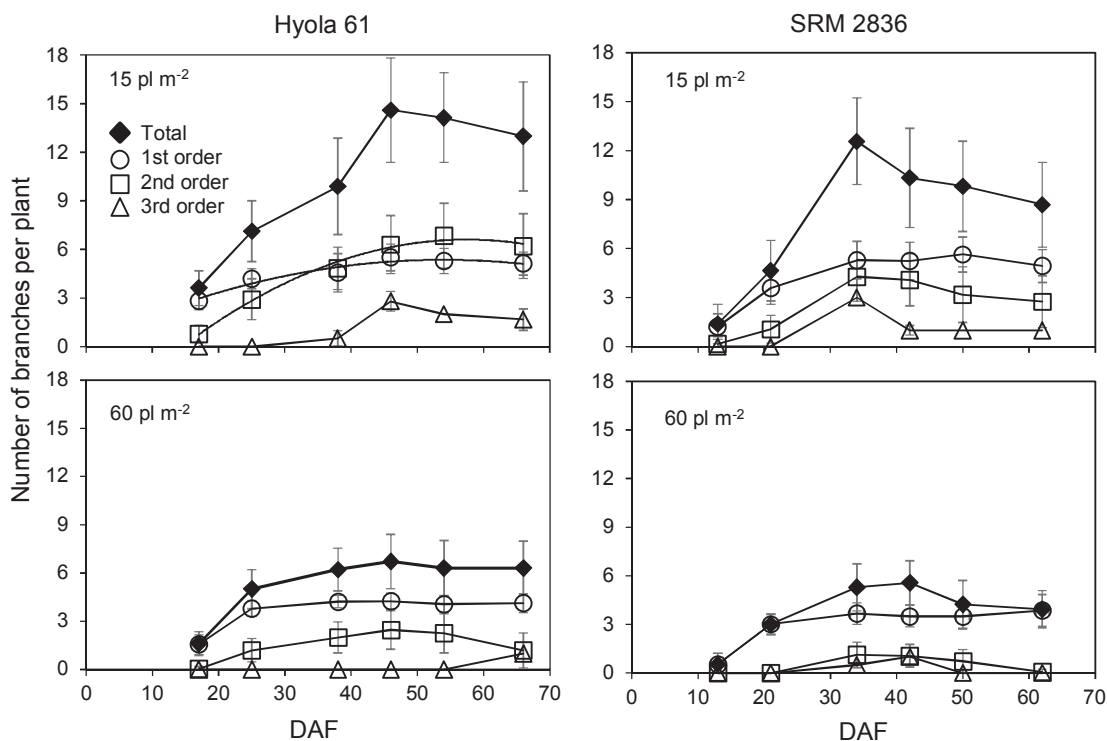


Fig. 4. Dynamics of appearance of primary, secondary and third order floral branches during days after first flowering (DAF) for spring rapeseed genotypes Hyola 61 (left panels) and SRM 2836 (right panels) growing at contrasting plant density of 15 and 60 pl m<sup>-2</sup>. Data are from Exp. 3. Vertical bars shown  $\pm$  1 SEM.



**Table 3**

Effects of plant density (PD), genotype (G) and their interaction on seed yield per plant, seed number per plant, above-ground biomass per plant, and thousand seed weight of spring rapeseed. Data are from Exps. 1–4.

Exp.	Genotypes	PD (pl m <sup>-2</sup> )	Seed yield (g pl <sup>-1</sup> )	Seed number (10 <sup>3</sup> pl <sup>-1</sup> )	Thousand seed weight (g)	Above-ground biomass (g pl <sup>-1</sup> )
1	Hyola 61	60	8.1 a	2.59 a	3.13 a	23.71 a
		120	3.4 b	1.05 b	3.16 a	10.48 b
		240	2.2 b	0.67 b	3.23 a	6.98 b
	p-value	PD	0.002	0.002	0.733	0.004
2	Hyola 61	15	19.1 a	5.78 a	3.33 a	72.24 a
		30	11.6 ab	3.66 ab	3.27 a	43.96 ab
		60	3.7 b	1.08 b	3.46 a	12.25 b
	p-value	PD	0.023	0.039	0.807	0.011
3	Hyola 61	15	9.6 a	2.88 a	3.13 a	29.09 a
		60	4.5 bc	1.41 bc	3.19 a	12.63 b
	SRM 2836	15	6.6 b	2.14 ab	3.10 a	24.89 a
		60	3.0 c	0.96 c	3.20 a	9.72 b
	p-value	G	0.003	0.004	0.905	0.111
		PD	< 0.001	< 0.001	0.310	< 0.001
G x PD		0.375	0.453	0.835	0.754	
4	Bioaureo 2486	15	24.5 a	7.71 a	3.18 a	na
		60	6.8 b	2.20 c	3.11 a	–
	Hyola 830	15	20.3 a	4.50 bc	3.17 a	–
		60	7.9 b	1.94 c	3.02 a	–
	Solar CL	15	14.7 ab	6.11 ab	3.30 a	–
		60	5.9 b	2.18 c	3.61 a	–
	p-value	G	0.096	0.024	0.125	–
		PD	< 0.001	< 0.001	0.831	–
		G x PD	0.197	0.055	0.393	–

For each experiment, means followed by different letters within a column indicate significant differences for Tukey's test. P-values are also shown. na: data not available.

**Table 4**

Effects of plant density (PD), genotype (G) and their interaction on seed yield per area, seed number per area, above-ground biomass per area, harvest index, seed oil, and seed protein content of spring rapeseed. Data are from Exps. 1–4.

Exp.	Genotypes	PD (pl m <sup>-2</sup> )	Seed yield (g m <sup>-2</sup> )	Seed number (10 <sup>3</sup> m <sup>-2</sup> )	Above-ground biomass (g m <sup>-2</sup> )	Harvest Index
1	Hyola 61	60	493.0 a	157.3 a	1439.3 a	0.34 a
		120	449.1 a	140.7 a	1389.0 a	0.32 a
		240	404.0 a	125.4 a	1305.6 a	0.31 a
	p-value	PD	0.569	0.406	0.851	0.072
2	Hyola 61	15	294.5 a	89.3 a	1113.3 a	0.26 a
		30	264.7 a	82.0 a	998.4 a	0.26 a
		60	165.7 a	48.1 a	540.2 a	0.31 a
	p-value	PD	0.058	0.227	0.072	0.052
3	Hyola 61	15	165.2	52.7ab	533.0 a	0.32 a
		60	192.4 a	60.5 a	541.8 a	0.36 a
	SRM 2836	15	133.4 b	43.2 b	498.7 a	0.27 b
		60	158.9	49.5ab	500.1 a	0.32 ab
	p-value	G	0.017	0.027	0.409	0.001
		PD	0.056	0.116	0.912	0.040
G x PD		0.915	0.855	0.938	0.610	
4	Bioaureo 2486	15	576.2 a	181.7 a	na	–
		60	397.3 a	127.9 a	–	–
	Hyola 830	15	531.4 a	112.5 a	–	–
		60	451.1 a	113.0 a	–	–
	Solar CL	15	368.5 a	160.6 a	–	–
		60	344.5 a	125.0 a	–	–
	p-value	G	0.105	0.065	–	–
		PD	0.103	0.074	–	–
		G x PD	0.511	0.283	–	–

For each experiment, means followed by different letters within a column indicate significant differences for Tukey's test. P-values are also shown. na: data not available.

R/FR ratio changed during crop development for rapeseed canopies at contrasting plant density (Fig. 1). Before flowering the pattern of light environment was similar in all densities tested: the increase of ISR was associated with reduction in the R/FR ratio. Similar relationships between ISR and R/FR were reported by Evers et al. (2006) who demonstrated that a rise of light intercepted during wheat development is accompanied by an exponential decline in R/FR ratio at wheat plant densities ranging between 100 and 500 pl m<sup>-2</sup> (see Fig. 1 in Evers et al., 2006).

Vegetative plasticity per plant was due to an adjustment in the rosette diameter, which in lower density crops maintained ISR at canopy level, with only a slight decrease (< 8%) in accumulated solar radiation over the whole crop cycle. This permitted crops to reach the beginning of flowering with maximum intercepted solar radiation, regardless of plant density and genotype (Fig. 2). Assuming that the critical period for grain yield determination in rapeseed occurs during the post flowering stages (Habekotté 1997; Diepenbrock, 2000; Rondanini et al., 2013), vegetative plasticity allowed crops to reach that critical period with maximum radiation capture (90–95% ISR) at canopy level, through the adjustment of rosette size. Thus, under well-watered and fertilized growing conditions, there seems to be no limit to the expression of vegetative plasticity in modern short-cycle spring rapeseed, even at plant density as low as 15 pl m<sup>-2</sup>.

After flowering R/FR ratio was modified by plant density in a different way from that from emergence to flowering. Plasticity in rapeseed after flowering was related to floral branching, which was strongly promoted by low plant density (Fig. 4) and took place until late crop development, when R/FR ratio increased sharply (from 0.4 at flowering to 0.6 and 1.0 at maturity for low and high plant density, respectively, Exp. 3). High floral branching was also observed in isolated plants with low R/FR ratio of 0.36 (Rondanini et al., 2014). In contrast, plasticity in wheat is related to tillering. Evers et al. (2006) found that tillering ceased under specific light conditions within the canopy, independent of plant density, and to a lesser extent independent of light intensity. These authors suggested that cessation of tillering is induced when the fraction of PAR intercepted by the canopy exceeds a specific threshold

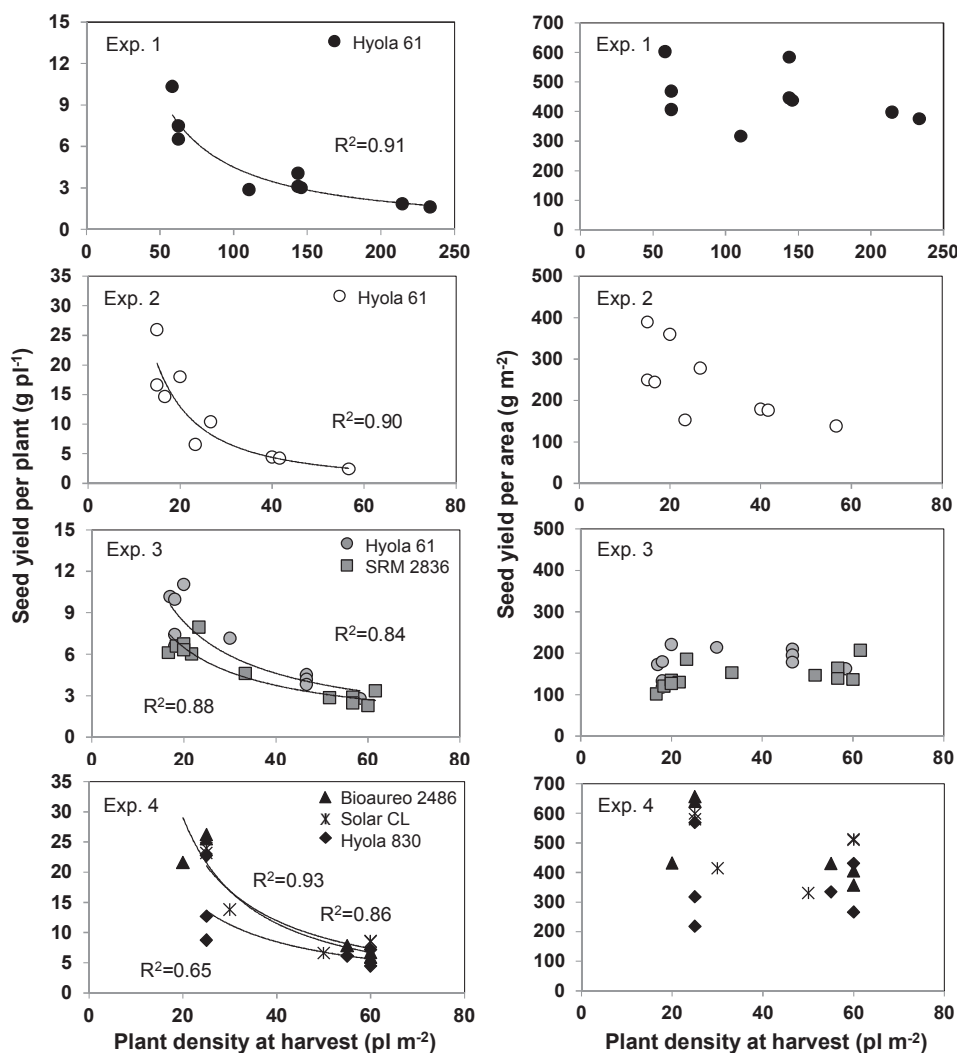


Fig. 5. Seed yield per plant (left panels) and seed yield per area (right panels) as a function of plant density at harvest for spring rapeseed genotypes from Exps. 1–4. Note the different scales on the axis for different experiments. Negative power-law functions fitted to data are shown.

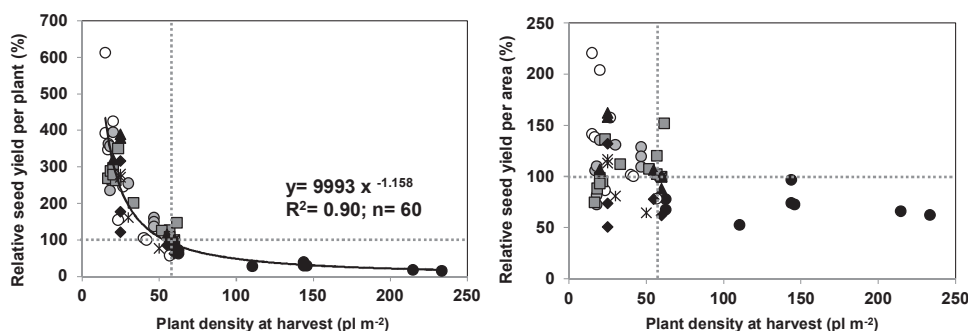


Fig. 6. Relative seed yield per plant (left panel) and relative seed yield per area (right panel) as a function of plant density at harvest for spring rapeseed genotypes from Exps. 1–4. Seed yield data are relativized to values for 60 pl m<sup>-2</sup> of each experiment (dotted lines). A negative power-law function fitted to pooled data is shown. Code symbols as in Fig. 5.

(0.40–0.45) and R/FR ratio drops below 0.35–0.40 (Evers et al., 2006). Such thresholds of ISR and R/FR ratio for expressing plasticity in wheat (i.e. tillering) were not found in spring rapeseed for expressing floral branching plasticity. A clearer connection between the rate of branching and changes of light quality after flowering need to be determined for rapeseed.

Contrary to the general dynamics of radiation capture described by Diepenbrock and Grosse (1995) and Diepenbrock (2000) for winter rapeseed, a gap in radiation capture after flowering was not observed in our experiments at any plant density (Fig. 2). It is possible that the lack of a gap in ISR after flowering was associated with the fact that green siliques grew fast enough to compensate for leaf senescence. Other authors demonstrated the high efficiency of siliques in capturing solar

radiation (Singal et al., 1987) and a broad range of radiation-use efficiency for rapeseed crops (Berry and Spink 2006). From about two weeks after full flowering, the total carbon fixation by silique hulls exceeded that of leaves, because siliques were exposed to higher radiation than leaves (Gammelvind et al., 1996). Closer to crop maturity, low plant density had lower R/FR ratio than high plant density, associated with slow leaf senescence and higher silique area due to increased branching. These observations agree with a high leaf senescence caused by low R/FR ratio applied from early development in isolated plants (Rondanini et al., 2014), and the extension of photosynthetic surface through high branching (Brunel-Muguet et al., 2013).

**Table 5**  
Effects of plant density (PD), genotype (G) and their interaction on seed oil and protein content, oil yield and protein yield of spring rapeseed. Data are from Exps. 1–4.

Exp.	Genotypes	PD (pl m <sup>-2</sup> )	Seed oil (%)	Seed protein (%)	Oil yield (g oil m <sup>-2</sup> )	Protein yield (g protein m <sup>-2</sup> )
1	Hyola 61	60	42.2 a	22.9 a	208.0 a	113.3 a
		120	40.7 a	23.5 a	182.8 a	106.3 a
		240	41.0 a	24.0 a	165.6 a	97.0 a
	p-value	PD	0.672	0.745	0.445	0.796
2	Hyola 61	15	39.5 ab	21.8 ab	116.3 a	64.2 a
		30	37.7 b	23.3 a	99.8 a	61.7 a
		60	41.7 a	20.4 b	69.1 a	33.8 a
	p-value	PD	0.028	0.040	0.266	0.087
3	Hyola 61	15	44.6 a	19.5 a	73.7 ab	32.2 a
		60	44.6 a	19.6 ab	85.8 a	37.7 a
		SRM 2836	15	45.9 a	20.6 a	61.2 b
	60	47.0 a	19.3 a	74.7 ab	30.7 a	
	p-value	G	0.035	0.539	0.056	0.039
	PD	0.517	0.295	0.053	0.118	
G x PD	0.487	0.263	0.969	0.673		
4	Bioaureo 2486	15	51.2 a	15.5 c	295.0 a	89.3 a
		60	50.3 a	16.0 bc	199.8 a	63.6 a
	Hyola 830	15	45.9 ab	18.8 ab	243.9 a	99.9 a
		60	43.6 b	20.4 a	196.7 a	92.0 a
	Solar CL	15	47.7 ab	17.3 bc	175.8 a	63.7 a
		60	47.0 ab	18.4 ab	161.9 a	63.4 a
	p-value	G	0.001	< 0.001	0.064	0.239
	PD	0.219	0.052	0.089	0.216	
G x PD	0.771	0.620	0.567	0.405		

For each experiment, means followed by different letters within a column indicate significant differences for Tukey's test.

#### 4.2. Reproductive plasticity compensates for seed yield per unit area without affecting seed oil content

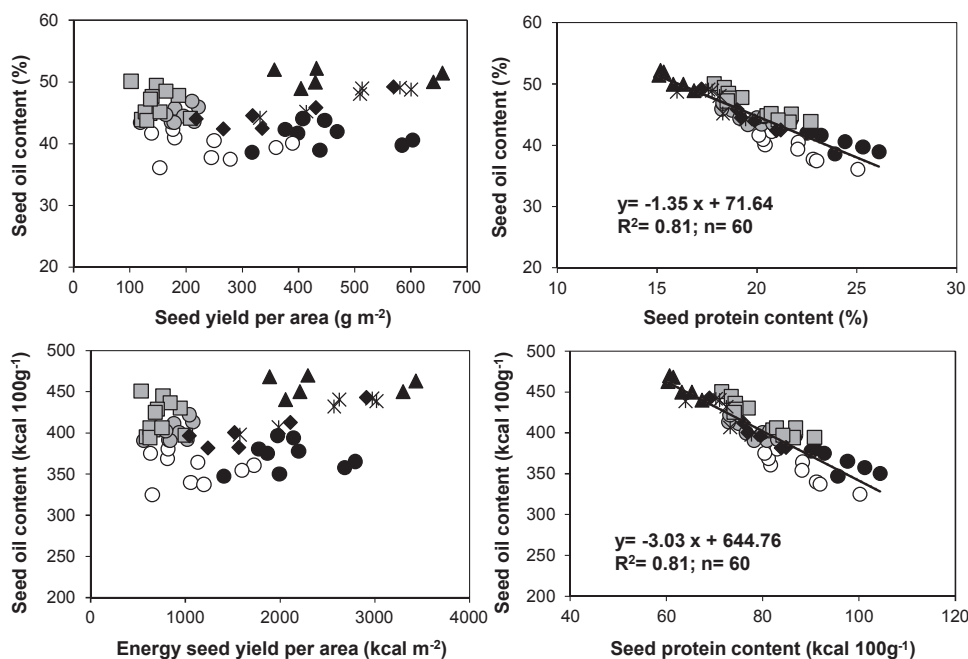
Reproductive plasticity in rapeseed in our experiments was mainly caused by floral branching, and this important trait varied with the genotype and plant density. The branching response to plant density has been previously measured at harvest time (Leach et al., 1999; Angadi et al., 2003; Zhang et al., 2012), but this is the first report on branching dynamics during crop development. Dynamics of appearance

of floral branches per plant peaked at 30 or 40 days after flowering, for SRM 2836 and Hyola 61 genotypes, respectively, especially due to the contribution of second and third order branches (Fig. 4). Interestingly, final number of branches was reduced by half in both genotypes as plant density increased four times (from 15 to 60 pl m<sup>-2</sup>). Reproductive plasticity related to floral branching was also observed in other determinate crops, as soybean (Board and Kahlon, 2013; Agudamu et al., 2016) and field pea (Spies et al., 2010) whereas branch number was insensitive to plant density in chickpea genotypes for short-season environments (Siddique et al., 1984; Gan et al., 2006).

Changes in the branching and distribution of the number of siliques between primary and secondary inflorescences have recently been described in response to clipping of the floral bud which simulates floral bud damage naturally caused by frost or pests (Pinet et al., 2015). These authors found that restoration of the number of siliques after clipping was the main process for the compensation, as the number of fertile ramifications (mainly secondary ones) increased at the high intensities of clipping. The proportions of yield and of number of siliques carried by these secondary axes increased and became almost equivalent to the proportion carried by primary inflorescences (Pinet et al., 2015). Similarly, in the present work, seed biomass provided by floral branches, in relation to those provided by the main raceme, increased 1.5 times when plant density was reduced (Table 2), highlighting the importance of floral branching as a trait of reproductive plasticity.

The biomass allocation to seed and chaff (non-seed reproductive biomass) was higher in the main floral raceme than in floral branches, regardless of genotype and plant density. Only 1.1–1.3 g of chaff was associated with 1 g of seed from the main floral raceme, whereas this value rose to 2.2–3.1 in floral branches (Table 2), demonstrating that branches were less efficient in producing seeds per unit of invested chaff. In addition, fruiting efficiency for spring rapeseed ranged between 100 and 160 seeds per gram of chaff biomass across genotype and plant density. Such values of fruiting efficiency were similar to those found for modern wheat cultivars, i.e. 60–140 seeds g<sup>-1</sup> (Ferrante et al., 2012).

Seed yield per plant could be described by a negative power-law function as a function of plant density at harvest over the range of 15–240 pl m<sup>-2</sup> (Fig. 6) with a high reproductive plasticity which maintained grain yield per unit area. All experimental data were well fitted ( $R^2 = 0.90$ ) with a unique function when relative seed yield per plant was used (relative to seed yield observed at 60 pl m<sup>-2</sup> plant



**Fig. 7.** Relationships between seed oil content and seed yield per area (left panels), and between seed oil and protein content (right panels) expressed both in a dry matter and an energy basis, for spring rapeseed genotypes growing at contrasting plant density from Exps. 1–4. Linear regressions fitted to data are also shown. Code symbols as in Fig. 5.



density of each experiment). The important compensation at individual plant level when crop was sown at very low densities, determined that such adjustment per plant caused no significant effects of plant density on seed yield per unit area. Additionally, its numerical components (seed number per area and thousand seed weight), and its physiological components (above-ground biomass per unit area, and harvest index) did not show significant differences among plant densities. These findings agree with Angadi et al. (2003) who did not observe plant density effects on seed yield per area in the range of 20–80 pl m<sup>-2</sup> in an experimental year with good water supply. Also, they partially agree with Leach et al. (1999) who observed maximum seed yield per area at 50–60 pl m<sup>-2</sup> and decreasing seed productivity when density was over 150 pl m<sup>-2</sup> in winter rapeseed. A similar response was observed by Roques and Berry (2016) but adjusting linear plus exponential curves, and economic optimum densities ranged from 7 to 180 pl m<sup>-2</sup>, with a median of 32 pl m<sup>-2</sup> in Western Australia (French et al., 2016). Others reported slightly detrimental effects of very low plant density (around 20 pl m<sup>-2</sup>) on seed yield per area, ranging from -4 to -10% depending on year and spatial arrangement (Wang et al., 2015; Gan et al., 2016).

Plant density did not affect seed oil content, as this trait was mainly affected by genotype and environmental conditions in each experiment (Fig. 7). The negative relationship between seed oil and protein, with a slope of -1.3, indicates a greater sensitivity of oil synthesis to genotypic and environmental factors than that of protein, similar to the finding by Peltonen-Sainio et al. (2011). The same is true when oil, protein and seed yield are expressed in an energy basis. The lack of negative relationship between grain yield and oil content supports the idea that there is no trade-off between seed productivity and grain quality (Gomez and Miralles, 2011; Rondanini et al., 2014). Also, no dilution of seed protein content at high grain yield was observed, supporting the idea that genetic improvement focused on seed grain yield and seed grain number does not necessarily reduce grain size or quality in rapeseed.

In summary, under good water and nutrient conditions without biotic constraints, plant density could be reduced without excessive penalty on seed production per area owing to the expression of vegetative and reproductive plasticity per plant in short-cycle spring rapeseed genotypes. SAS responses to low plant density are associated with the adjustment of rosette diameter, whereas reproductive plasticity is related to floral branching, mainly the promotion of branches of second and third order. These findings could be useful to design management practices relevant to avoid unnecessary re-sowing of rapeseed crops that are moderately affected by frost, hail or pests, and crops evidencing failures at emergence. However, other important agronomic aspects of low plant density need to be evaluated, such as poor competition with weeds at early crop stages, and the lack of synchronization of silique development and crop maturity in relation to the hierarchy of branching.

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