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PHENOTYPIC PLASTICITY IN SPRING OILSEED RAPE IN RESPONSE TO THINNING DURING THE GROWTH PERIOD

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Abstract

Spring oilseed rape varieties Bronowski and Orpal differed significantly in all characters measured after 12 weeks growth and at maturity. Thinning treatments significantly affected dry weight per plant, seed weight and pod number per plant, in both varieties, delayed thinning causing significant reductions in them. Seed number per pod, 1000-seed weight and harvest index were unaffected by the timing of the thinning treatments imposed. Under early thinning dry weight, seed weight and pod number per plant were greater than for the unthinned 20 plant per pot control. The response of the two varieties to the thinning treatments was similar.

Introduction

The expression of an individual genotype can be modified by different environments (Bradshaw, 1965). A common cause of environmental heterogeneity is variation in population density which affects the availability of nutrients, water and light for the growth of individual plants. Shortage of these resources caused by increased plant density can affect plant morphology (Khan & Bradshaw, 1976).

The effects of density on different plant characters in oilseed rape has been reported by several workers. Clarke & Simpson (1978) found that number of pods per plant and seed yield per unit area increased with increased plant density. Increasing plant density in spring oilseed rape caused a decrease in seed yield per plant (Degenhardt & Kondra, 1981) whereas Kondra (1975) and Degenhardt & Kondra (1981) found that 1000-seed weight was stable in spring oilseed rape. The above studies were made on plants grown and kept at constant density. However, the distance separating neighbouring plants (i.e. plant density) and their presence or absence during the plant growth cycle can profoundly affect the growth and development of individual plants (Ross & Harper, 1972).

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The stage at which competition is most intense is very important for optimising crop production. Hodgson & Blackman (1957) reported an experiment with *Vicia faba,* grown under close spacing in which they carried out thinning at different developmental stages. They found that the intensity of competition between plants even at relatively close spacing did not become marked enough to affect ultimate seed production until plants were at an advanced stage of vegetative growth, and it did not reach a maximum until the post flowering phase. Different characters of the plant showed differences in their response to thinning and some characters were little affected by it.

Spring and winter oilseed rape exhibit considerable phenotypic variation (Munir, 1982), and the experiment reported here was set up to assess the degree of phenotypic plasticity shown by spring oilseed rape in response to the removal of stress, by thinning plants in stands of a single fixed density at regular intervals during the growth period. The stage at which competition has its maximum effect on yield and yield components should thus be revealed, and also whether the extra space made available due to thinning is utilized. Finally, any differences should be apparent between varieties in their ability to utilize the space provided by thinning, i.e., it should be clear whether varieties differ in the extent of the plasticity of their phenotypes.

Materials and Methods

The experiment was carried out in greenhouse at the Department of Botany, University of Liverpool. The greenhouse was heated and kept at 25.5^{o}C. Natural day length was supplemented with artificial light to give 16 hours day length using 400 watt mercury vapour lamps. The experiment was set up on 9.12.80.

Two varieties of spring oilseed rape (*B. napus*) were used, Bronowski, released in Poland in 1955 and Orpal, released in France in 1978. Twenty plants were grown in a 17.5 cm plastic pot, from seed planted 3.5 cm apart in a hexagonal pattern, each seedling being equidistant from its immediate neighbours. The plants were grown in John Innes potting soil. Two to three seeds were placed at each position and seedlings were thinned to one plant per position after germination. The experiment consisted of three replications, each replication being a randomised block containing 15 pots of each variety.

There were two sets of thinning treatments where the number of plants per pot was reduced from 20 to 10, and two controls in which the number of plants per pot remained at 20 and 10 throughout. In set 1, thinning took place at 2, 4, 6, 8 and 10 weeks from germination and the plants which remained after thinning were harvested and their dry weights measured after 12 weeks growth. In set 2, thinning took place 2, 4, 6, 8, and 10 weeks from germination as in set 1, but additional thinning was carried out 12, 14 and 16 weeks from germination. The plants remaining after thinning in set 2 were harvested at maturity on 8.5.81, 18 weeks from germination and their dry weights measured. Thinning was carried out by cutting plants at soil level in alternate rows leaving 10 plants per pot. All harvested plants were oven dried at 38°C for seven days and dry weights recorded. In addition to data for plant dry weight, set 2 plants were used to provide data for number of pods per plant, seed weight per plant, seed number per pod and 1000-seed weight. To avoid pod shattering the plants were harvested when the majority of pods were ripe. This meant that some of the pods were still green and it was noticed at seed collection that in some pods seeds were not fully developed. However, since the number of unripe pods did not differ between varieties, they would have minimal effect on the data and its interpretation. Seed was separated by hand and a sample of up to 400 seeds taken from each plant to determine 1000-seed weight. For most of the plants all seeds were counted and number of seeds per pod and 1000-seed weight determined. For those plants which had more than 400 seeds, seed number per pod was determined from seed weight per plant, pod number per plant, and 1000-seed weight, obtained from the 400 seed sample. Harvest index was calculated by dividing seed weight per plant by dry weight per plant.

Analyses of variance were carried out on the data for all characters at both harvests. Simple correlation coefficients between the characters at maturity were also calculated.

Results

Data for the two varieties for mean dry weight per plant after 12 weeks growth, thinned to 50% density at 2, 4, 6, 8 and 10 weeks, are given in Table 1. The differences for dry weight per plant due to thinning are significant ($P < 0.05$). It can be seen that, as the time of thinning is delayed, there is a corresponding decrease in mean plant dry weight. Orpal accumulates significantly more dry matter per plant during the 12 weeks growth than Bronowski ($P < 0.05$).

Data for dry weight per plant, seed weight per plant, pod number per plant, seed number per pod, and 1000-seed weight at maturity, and harvest index, are given in Table 2 and analyses of variance for these characters are summarised in Table 3. These data show that differences due to thinning treatments for dry weight per plant, seed weight per plant and pod number per plant are significant ($P < 0.05$), whereas seed number per pod, 1000-seed weight and harvest index are not significantly affected by thinninng. This suggests that, measured by their effect on mature plant characters, later thinnings cause significant reductions in dry weight per plant, seed weight per plant and pod number per plant ($P < 0.05$). No significant effects of later thinnings were found, however, for seed number per pod, 1000-seed weight or harvest index, these features of plant growth remaining stable regardless of the time of thinning.

Table 1. Dry weight per plant for Bronowski and Orpal spring oilseed rape harvested 12 weeks after germination.

	Weeks after germination					
Variety	2	4	6	8	10	Mean
Bronowski	1.23	0.85	1.89	0.78	0.78	1.11b
Orpal	2.14	2.37	1.18	1.21	1.10	1.60a
Mean	1.69a	1.61a	1.54a	1.00b	0.94b	

LSD at p = 0.05 between
Variety (V) = 0.32
Treatment (T) = 0.51
V x T interaction = 0.71
Mean values in a row or a column with the same letter are not significantly different at $p \leq 0.05$.

When compared with the 20 plants per pot control, early thinning allowed an increase in dry weight per plant, seed weight per plant, and pod number per plant. No similar increase as a consequence of early thinning was, however, found for seed number per plant, 1000-seed weight or harvest index.

Orpal again is superior to Bronowski at Harvest 2 (Table 2) in dry weight per plant, seed weight per plant, pod number per plant 1000-seed weight and harvest index. However, Bronowski had a significantly greater number of seeds per pod than Orpal. No significant variety treatment interaction was found at maturity, thinning affecting both varieties in the same way.

Correlations between yield components and their level of significance are given in Table 4. Significant positive correlations ($p < 0.001$) were found between dry weight per plant, seed weight per plant and pod number per plant. Correlations of dry weight per plant with 1000-seed weight and harvest index were positive and significant ($p < 0.01$ and $p < 0.05$ respectively). Seed weight per plant was positively and significantly correlated ($p < 0.001$) with pod number per plant, 1000-seed weight and harvest index. The correlations of pod number with 1000-seed weight ($p < 0.05$) and harvest index ($p < 0.001$) were positive and significant. Seed number per pod and 1000-seed weight were negatively and significantly correlated ($p < 0.01$). Harvest index was positively correlated with seed number per pod and with 1000-seed weight ($p < 0.05$).

Table 2. **Total dry weight per plant and its components at maturity (Harvest 2).**

Thinning, weeks from germination	Dry weight per plant (g)			Seed weight per plant (g)			Pod number per plant			Seed number per pod			1000-seed weight (g)			Harvest index		
	Bronowski	Orpal	Mean	Bronowski	Orpal	Mean	Bronowski	Orpal	Mean	Bronowski	Orpal	Mean	Bronowski	Orpal	Mean	Bronowski	Orpal	Mean
(10 plants control)	3.20	4.12	3.66ab	0.77	1.21	0.99ab	19.00	2.433	21.67ab	14.13	11.89	13.01	2.81	4.023.41		0.24	0 29	0.26
2	3.15	5.48	4.31a	0.84	1.62	1.23a	19.00	30.00	24.50a	19.64	11.70	15.67	2.42	4.58	3.50	0.26	0.31	0.28
4	2.48	3.67	3.11abc	0.72	1.02	0.87abc	14.79	20.67	17.73abc	14.24	11.67	12.96	2.83	4.23	3.53	0.25	0.26	0 26
6	2.88	2.71	2.79bc	0.79	0.72	0.75bc	18.00	16.00	17.00abc	15.06	11.43	13.24	2.89	3.62	3.25	0.27	0 25	0 26
8	3.02	3.57	3.30abc	0.76	0.93	0.85abc	17.67	20.67	19.17abc	15.18	11.24	13.21	2.68	4 08	3.38	0.24	0.28	0.26
10	2.20	2.35	2.27c	0.40	0.65	0.53c	9.67	12.67	11.17c	14.39	12.50	13.44	3.22	3.92	3.57	0 20	0.28	0 24
12	3.02	2.45	2.73bc	0.76	0.69	0.72bc	20.33	15.67	18.00abc	12.68	11.23	11.95	2.82	3.90	3.36	0.25	0.28	0 27
14	1.72	2.81	2.27c	0.34	0.73	0.54bc	8.00	14.00	11.00c	14.67	12.76	13.76	3.18	4.02	3.60	0.20	0 27	0.23
16	1.67	2.41	2.04c	0.36	0.63	0.49c	10.00	12.67	11.33c	10.76	12.33	11.54	3.00	3.89	3.44	0.20	0.25	0.22
No thinning (20 plants control)	1.89	2.87	2.38bc	0.36	0.82	0.59bc	9.33	16.33	12.83c	12.08	11.67	11.87	3.22	3.86	3.54	0 19	0 27	0 23
Variety mean	2.52b	3.25a		0.61b	0.90a		14.58b	18.30a		14.29a	11.84b		2.91b	4.01a		0.23b	0.27a	
LSD at p = 0.05 between																		
Variety (V) mean			0.62		0.20			3.55			1.33			0.25			0 03	
Treatment (T) mean			1.38		0.45			7.94			NS			NS			NS	
T x V mean			NS		NS			NS			NS			NS			NS	

Trait means having the same letter in a column or variety means in a row are not significantly different.

Table 3. Analyses of variance of the effects of thinning treatments on plant characters at maturity.

Item	d.f.	Plant character: Dry wt. per plant	Seed wt. per plant	Pod no. per plant	Seed no. per pod	1000-seed weight	Harvest index
Treatment (T)	9	2.54*	2.27*	2.95**	1.31	0.33	0.71
Varieties (V)	1	5.84*	8.69**	4.58*	14.22***	84.86***	8.36**
T x V	9	0.73	0.66	0.67	1.47	1.50	0.42
Error	37						

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Discussion

The time at which plant number per pot was reduced by thinning from 20 to 10 had a significant effect upon dry weight produced after 12 weeks growth (Table 1). Thinning effects on mature plant dry weight, seed weight and pod number were also significant (Table 3). Earlier thinning gave greater responses, reflected in higher values for these characters compared with delayed thinning treatments and with the unthinned 20 plant per pot control (Table 2). Increase in these characters showed that plants successfully exploited the space made available to them by removal of the thinned plants, the enhanced growth of the remaining plants compensating for the removal of the thinned individuals. Plant density is known to affect dry weight and seed weight in oilseed rape (Clarke & Simpson, 1978; Degenhardt & Kondra, 1981). These observations were made on plants sown and maintained at a single density, whereas in the present study plant density was changed during the course of the experiment. This will therefore reveal the dynamic nature of the response of the oilseed rape plant to density change. The data from this experiment clearly show that different plant characters respond to the thinning treatments imposed at different times (growth stages) and in different ways, confirming the data of Khan & Bradshaw (1976) in *Linum*.

The weight of seed produced by an oilseed rape plant is the product of three yield components; number of seed bearing pods, number of seeds produced per pod and individual seed weight, usually expressed as 1000-seed weight. Pod number per plant is the main determinant of seed yield and exhibits a high degree of phenotypic plasticity, being considerably affected by environment (Olsson, 1960; Thurling, 1974b; Clarke & Simpson, 1978). In contrast, seed number per pod and 1000-seed weight in *B. napus* are relatively less plastic (Olsson, 1960; Thurling, 1974b) and tend therefore to be characteristic of a particular variety.

The ability of the component parts of the oilseed rape plant to respond to the thinning treatments imposed i.e., their phenotypic plasticity, can be related to the growth cycle of the plant. After the seedling stage dry matter accumulation takes place at a rapid rate. Flowering normally begins some 7 to 10 weeks from germination, and at this point leaf area index and crop growth rate reach maxima (Allen & Morgan, 1975; Major, 1977). After flowering, total plant dry weight continues to increase and crop growth is still high even though leaf area is declining rapidly. Inanaga, Kumura & Murata (1979) have shown from studies of photosynthesis and respiration in oilseed rape, that whilst leaves are the major photosynthetic organs until flowering, once flowering begins, photosynthesis by pods becomes increasingly important in contributing to the production of dry matter in both pods and seeds. Although pod photosynthesis makes a major contribution to pod and seed development, the role of leaves, in contributing to yield by way of flower bud formation (Thurling, 1974b) cannot be overlooked. This is confirmed by the $^{14}CO_2$ assimilation experiments of Brar & Thies (1977) and of Major & Charnetski (1977) who have shown that photosynthates from the upper leaves and the stem are received by pods. Leaves, thus, have an important function in determining, through flower bud formation, the number and sizes of pods (Tayo, 1974; Clarke & Simpson, 1978). Thurling (1974a) also observed that growth in *B. napus* prior to anthesis had a much greater in-

Table 4. Correlation coefficients between yield and yield components.

	Seed wt. per plant	Pod no. per plant	Seed no. per pod	1000-seed wt.	Harvest index
Dry weight per plant	0.95***	0.94***	0.13	0.41**	0.32
Seed weight per plant		0.95***	0.19	0.43***	0.59***
Pod number per plant			0.08	0.29*	0.50***
Seed number per pod				0.40**	0.28*
1000-seed weight					0.26*

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

fluence on seed yield than post anthesis growth. Clarke (1978) found in oilseed rape that leaf removal at the start of flowering had a very pronounced effect on seed yield and yield components due to a reduction in the number of pods as a consequence of leaf removal at anthesis. He argued that this was due to a reduction in the supply of assimilates to pods at that time.

High correlations between dry weight, seed weight and pod number per plant suggest that early growth, i.e. dry matter accumulation leads to the production of greater number of pods which is the main factor controlling seed yield per plant. The absence of any significant correlation between pod number per plant and seed number per pod suggests that the number of pods per plant does not adversely affect the number of seeds per pod and the pods themselves support the seeds within them. The negative correlation between seed number and 1000-seed weight is the product of a fixed assimilate pool being distributed to a number of seeds, during the development of which competition may develop so that compensation of one against the other takes place, resulting in a negative correlation between seed weight and number.

The lack of any variety treatment interaction at maturity shows that both Bronowski and Orpal respond to thinning in the same way, both having the ability to utilise to a certain extent the extra resources made available to them by thinning during the early growth period. The data show that seed number per pod, 1000-seed weight and harvest index are unaffected by changed environment, but they do differ between varieties. In contrast, plant dry weight, seed weight per plant, and pod number per plant are affected both by plant density, and by the thinning treatments imposed, and hence are highly plastic components of yield in *B. napus.*

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