Genetic variability in oilseed rape DH line population developed from F₁ hybrids obtained by crossing black-and yellow-seeded DH lines. I. yield and yield components

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Abstract The aims of this study were to estimate the diversity of doubled haploid population of winter oilseed rape (Brassica napus L.) in terms of yield, yield structure and seed colour, to determine the correlation between the studied traits and their heritability, and to select the best yellow-seeded genotypes. We studied 44 doubled haploids, obtained from F₁ hybrids of a cross between a black-seeded DH H₂-26 line and a yellow-seeded DH Z-114 line, as well as the parental forms. The greatest variation in DH line populations was observed for seed colour, seed yield and the number of pods per plant, while the smallest variability was obtained for thousand seed weight. Seed yield was positively correlated with the number of pods per plant and the number of seeds per pod, but negatively correlated with yellow seed colour. The broad-sense heritability coefficient was highest for seed colour and number of seeds per pod, and lowest for the number of pods per plant. When divided into 4 homogeneous groups according to seed colour, the genotypes differed significantly with respect to all the studied traits. A group of DH lines with black seed colour was characterized by the highest seed yield as well as highest thousand seed weight. The lowest yielding DH line group, that with yellow–brown seeds, had on average the highest number of seeds per pod and the lowest thousand seed weight. The best yellow-seeded lines gave significantly higher yields than the yellow-seeded parental line.

Keywords Brassica napus · DH line · Black seeds · Yellow seeds · Statistical analysis

Introduction

Since the introduction of double-low (00) varieties, oilseed rape (Brassica napus) has become an important source of high-quality oil, both for food and industrial purposes. It is one of the most cultivated oil plant which is a renewable raw material for production of liquid biofuels. Oilseed rape press cake, the by-product of oilseed rape oil processing, is a valuable high-protein feed for all classes of livestock in the poultry, swine, ruminant and even fish industries. However, the nutritive value of press cake or
The extraction meal of black-seeded oilseed rape is limited by the high content of fibre, which decreases the absorption of nutrients. Therefore, intensive research is being carried out into the breeding of oilseed rape with reduced fibre content (Relf-Eckstein et al. 2003). The source of this feature is yellow-seeded oilseed rape, which has a thin, transparent seed coat.

Yellow-seededness is a desirable trait in Brassica generally, because yellow seeds have less fibre, higher protein levels, and a higher oil content than black seeds (Katche et al. 2019). However, yellow-seededness does not exist naturally within species B. napus. Breeders have tried to develop yellow-seeded oilseed rape by transfer of this trait from related species, such as B. rapa, B. carinata and B. juncea (Liu and Gao 1987; Meng et al. 1998; Rahman 2001; Wang et al. 2011), or via resynthesis of B. napus from yellow-seeded B. rapa and B. oleracea (Chen et al. 1988; Wen et al. 2008). Mutagenesis can also be a source of yellow seed colour in oilseed rape (Bochkaryova and Gorlov 1999) and some spontaneous yellow-seeded mutants have been found in China (Liu 1992; Wu et al. 1999). However, the introduction of this trait to oilseed rape involves a reduction in both yield and agronomic performance. Thus, growth vigor and yield of yellow-seeded oilseed rape are not as good as in black-seeded oilseed rape (Zhang et al. 2007). Early research in Canada also indicated that yellow-seeded lines of B. napus, derived from interspecific crosses, had a low oil content, were highly susceptible to blackleg disease and were low yielding (Rakow et al. 2007). Therefore, yellow-seeded breeding materials required improvement by further crossing with high-yielding double-low quality black-seeded genotypes. The first Canadian true-breeding yellow-seeded line YN90-1016 was backcrossed several times with black-seeded, elite breeding lines, followed by reseletion of the yellow-seeded trait after each backcross. In this way, the high-yielding yellow-seeded line YN01-429 was developed (Rakow et al. 2011).

Doubled-haploid (DH) technology has been successfully used in oilseed rape breeding for many years. DH lines are valued by breeders as an important source of genetic variation, providing excellent starting material for breeding new varieties. Moreover, for traits controlled by polygenic inheritance, DH technology requires significantly fewer genotypes, compared with early generations of hybrids produced by classical breeding. There are no heterozygotes, so there are no dominance effects, and no interactions of non-allelic heterozygous loci are observed (Szala et al. 2015). Therefore, it is easier to find an interesting genotype in DH line populations than in segregating populations, since the frequency of such a genotype among DHs is higher. This applies mainly to traits controlled by additive genes, especially recessive genes, and is thus particularly relevant to the inheritance of yellow seed colour in B. napus, which according to Rahman et al. (2010) is determined by three independent recessive genes.

The aim of this study was to estimate the diversity of DH population derived from F1 hybrids of crosses between black- and yellow-seeded DH lines, in terms of yield, yield components and seed colour. Important additional goals were to determine correlations between the studied traits and their heritability and to select the best-yielding yellow-seeded genotypes.

Materials and methods

Plant material

Forty-four DHs of winter oilseed rape obtained from F1 hybrids of crosses between the black-seeded DH H2-26 line and the yellow-seeded DH Z-114 line, and the parental lines, were used for this study. The yellow-seeded DH Z-114 line was derived from breeding materials with yellow seeds obtained at the Plant Breeding and Acclimatization Institute—National Research Institute in Poznan, Poland. The origin of these materials was a naturally occurring bright-seeded mutant and a Canadian spring line selected from segregating lines from a cross between B. napus × B. rapa (Bartkowiak-Broda et al. 2009).

The DH Z-114 line is characterized by excellent yellow seed colour, but low seed yield.

Experimental conditions

Forty-six genotypes were cultivated for 2 seasons to collect data on seed colour, yield and yield components including the number of branches, the number of pods per plant, the number of seeds per pod and the thousand seed weight. Field experiments, carried out in a randomized complete block design with four replications and a plot size of 1.2 m × 5.0 m, were conducted in the seasons 2016/2017 and 2017/2018 in...
a sandy loam soil at the Łagiewniki Experimental Station of Smolice Plant Breeding. The mean temperature for the growing season at the experimental site was 9.2 °C and 8.8 °C for the first and second year, respectively. Precipitation was 561.5 mm from August 2016 to July 2017 and 612.4 mm from August 2017 to July 2018. Approximately three weeks before harvesting, 5 plants were randomly selected from each plot to record data for number of branches and pods per plant. Twenty-five well-developed pods were taken from the middle of the main stems of each plant to measure the number of seeds per pod. Two months after harvest, the thousand seed weight was calculated as the average of five replicate samples from the mixed seeds of each plot. Seed colour was determined using a Color Flex spectrophotometer on a scale from 0 (black) to 5 (yellow) (Michalski 2009).

Methods of statistical analysis

The experimental data were analysed with uni-and multivariate statistical methods (Gomez and Gomez 1984; Morrison 1976). Analysis of variance, performed for six traits, allowed the designation of the statistical characteristics for all genotypes for each individual year. Broad-sense heritability (h²) was estimated according to Nyquist (1991) and Falconer and Mackay (1996). Two-factor analysis of variance for two years of trial data was carried out to test the hypotheses of no differences between genotypes or between years and the hypothesis of no genotype × year interaction. The relationships between traits were denoted by the correlation coefficients for all pairs of variables (quantitative traits), determined on the basis of mean values of genotypes for both years jointly. Using the procedure of Gabriel (1964), the studied genotypes were divided into homogeneous groups according to seed colour, after which the method of contrasts was used to compare the average value for traits between groups to examine the influence of seed colour on yield and its components in studied population. Moreover, each selected yellow-seeded DH line was compared and tested by the F-statistic with parental line DH Z-114 to identify DH lines with significantly better effects than the parental line for the studied traits.

To classify the DH lines in terms of six traits jointly, hierarchical clustering was performed by Ward’s method (1963) on the basis of Mahanalobis distance.

Results

Characteristics of trait variation

Combined analysis of variance revealed that genotype effects and year effects were highly significant (p < 0.01) for all traits (Table 1). Genotype × year interaction was also highly significant with the exception of number of branches. The values of mean squares in the analysis of variance indicated that environmental conditions have a greater influence on the yield, number of branches, number of pods and seed colour, and genetic variability in the number of seeds per pod and thousand seed weight.

Coefficients of variation for all traits were higher for the DH line population than for parental lines (Table 2). The highest variation in the DH line population was observed for seed colour. The variability of this trait was higher in the first year (CV = 64.5%) than in the second year of the study (CV = 53.9%). A wide range of variability among the studied DH lines was also found for seed yield and the number of pods per plant, while the lowest variability was obtained for thousand seed weight. This feature also turned out to be the most constant, as its coefficient of variation for parental forms was low and fluctuated around 2-3%, depending on the year and parental line. On the other hand, the highest variability for parental lines was recorded for seed yield for the DH Z-114 line (CV = 12.6% and CV = 15.2% in the first and second year, respectively) and for the number of pods per plant for DH H₂-26 in the first year of the experiment (CV = 12.5). Complete results (mean values for all monitored traits for individual genotypes and both years) were presented in the Supplementary Table S1.

The broad-sense heritability coefficient was highest for seed colour and number of seeds per pod, and the smallest for number of pods per plant.

Correlation between yield, yield components and seed colour

The correlation coefficients between the traits are given in Table 3. In the DH line population, the seed yield was positively correlated with the number of pods per plant (r = 0.56**) and the number of seeds per pod (r = 0.37**), but was negatively correlated with the yellow colour of seeds (r = -0.34**), meaning
that lines with dark-coloured seeds produced a higher yield than light-seeded lines. Furthermore, yellow seed colour was positively correlated with the number of seeds per pod (r = 0.39**) and negatively correlated with thousand seed weight (r = -0.47**), so those lines with a light seed colour were characterized by a larger number of smaller seeds in each pod compared with black-seeded lines.

The studied genotypes were divided into homogeneous groups according to seed colour (Table 4). Based on the first-year results, the DH lines (included both parental lines) were divided into four significantly different groups, and based on the second-year results, the DH lines (included both parental lines) were divided into six significantly different groups. The partition into homogeneous groups based on the average value of the seed colour from two years revealed four statistically significantly different groups named as yellow, yellow–brown, brown and black. Group 1, categorised by yellow seed colour, consisted of six DH lines and parental line DH Z-114; group 2, with a yellow–brown seed colour, consisted
of 12 DH lines; group 3, categorised by brown seed colour, consisted of 11 DH lines; and group 4, with a black seed colour, consisted of 15 DH lines and parental line DH H2-26 (Fig. 1). The contrasts were used to compare the average values for traits between the homogeneous groups to examine the influence of seed colour on yield and yield components (Table 5). The groups of lines differed significantly with respect to all the studied traits. Group 4, representing DH lines with a black seed colour, was characterized by both the highest seed yield as well as the highest thousand seed weight. In contrast, DH lines with yellow–brown seeds

### Table 3 Correlation coefficients among studied traits

| Trait | 1  | 2  | 3  | 4  | 5   | 6   |
|-------|----|----|----|----|-----|-----|
| Yield | 1  |    |    |    |     |     |
| Number of branches per plant | 0.06 | 1  |    |    |     |     |
| Number of pods per plant     | 0.56** | 0.23* | 1  |    |     |     |
| Number of seeds per pod      | 0.37** | 0.04 | -0.21* | 1  |     |     |
| Thousand seed weight         | -0.03 | -0.10 | 0.06 | -0.61** | 1  |     |
| Seed colour                  | -0.34** | -0.13 | -0.27* | 0.39** | -0.47** | 1  |

*significant at the level $\alpha = 0.05$

**significant at the level $\alpha = 0.01$

### Table 4 Partition of DH lines on homogeneous groups according to seed colour

| Season | Group | Mean* | Number | Genotypes                                      |
|--------|-------|-------|--------|------------------------------------------------|
| 2016/  | 1     | 3.80  | 7      | DH-7, DH-16, DH-19, DH-26, DH-31, DH-38, Z-114 |
| 17     | 2     | 2.74  | 12     | DH-2, DH-3, DH-10, DH-18, DH-20, DH-28, DH-30, DH-33, DH-34, DH-35, DH-37, DH-40 |
| 3      | 1.98  | 11    |        | DH-6, DH-8, DH-9, DH-11, DH-22, DH-23, DH-25, DH-27, DH-32, DH-36, DH-41 |
| 4      | 0.47  | 16    |        | DH-1, DH-4, DH-5, DH-12, DH-13, DH-14, DH-15, DH-17, DH-21, DH-24, DH-29, DH-39, DH-42, DH-43, DH-44, H2-26 |
| 2017/  | 1     | 4.48  | 7      | DH-16, DH-19, DH-23, DH-26, DH-30, DH-35, Z-114 |
| 18     | 2     | 3.59  | 11     | DH-2, DH-7, DH-9, DH-20, DH-27, DH-28, DH-31, DH-33, DH-37, DH-38, DH-40 |
| 3      | 3.15  | 8     |        | DH-3, DH-6, DH-8, DH-11, DH-18, DH-22, DH-25, DH-34, |
| 4      | 2.58  | 4     |        | DH-10, DH-32, DH-36, DH-41 |
| 5      | 1.29  | 2     |        | DH-12, DH-29 |
| 6      | 0.75  | 14    |        | DH-1, DH-4, DH-5, DH-13, DH-14, DH-15, DH-17, DH-21, DH-24, DH-39, DH-42, DH-43, DH-44, H2-26 |

*Mean represents the mean value of seed colour as determined spectrophotometrically on a scale from 0 (black) to 5 (yellow)
(group 2) showed the lowest yields. These lines had the highest average number of seeds per pod and the lowest average thousand seed weight.

For the 4 homogeneous groups, correlations between seed yield and seed yield components were calculated (Table 6). The relationship between the yield and the number of pods per plant expressed as correlation coefficients in all groups was similar (from 0.49 to 0.56**), but for the yellow-seeded lines (group 1) this was not significant due to the small sample size of this group. In group 2 (yellow–brown seeds) and group 4 (black seeds), the number of seeds per pod played an important role in seed yield formation, giving correlation coefficients of $r = 0.44^*$ and $r = 0.73^{**}$, respectively. In groups 1, 2 and 3, thousand seed weight was not significantly correlated with seed yield, while in group 4 (black seeds) the correlation was highly significant but negatively correlated ($r = -0.47^{**}$).

![Fig. 1 Seeds of parental lines and four DH lines representing four homogeneous groups in terms of colour](image)

**Table 5** Estimates of the contrasts between homogenous groups separated on the basis of seed colour for yield and yield components

| Contrast between groups | Yield (dt ha$^{-1}$) | Number of branches per plant | Number of pods per plant | Number of seeds per pod | Thousand seed weight (g) |
|-------------------------|----------------------|-------------------------------|--------------------------|-------------------------|--------------------------|
| 1—2                     | 2.07**               | − 0.34*                      | 12.43                    | − 0.73                  | 0.08*                    |
| 1—3                     | 0.67                 | − 0.19                       | − 0.70                   | 1.93**                  | − 0.45**                 |
| 1—4                     | − 2.46**             | − 0.39**                     | − 2.72                   | 2.86**                  | − 0.63**                 |
| 2—3                     | − 1.40*              | 0.15                         | − 13.13*                 | 2.66**                  | − 0.53**                 |
| 2—4                     | − 5.00**             | 0.05                         | − 15.44**                | 4.17**                  | − 0.77**                 |
| 3—4                     | − 3.60**             | − 0.10                       | − 2.31                   | 1.50**                  | − 0.25**                 |
| Mean                    | 31.32                | 6.46                         | 185.62                   | 19.11                   | 5.47                     |

*Significant at the level $\alpha = 0.05$

**Significant at the level $\alpha = 0.01$

**Table 6** Correlation coefficients between yield and its components in homogenous groups

| Group          | No of branches per plant | No of pods per plant | No of seeds per pod | Thousand seed weight |
|----------------|--------------------------|----------------------|---------------------|----------------------|
| 1—yellow       | − 0.17                   | 0.49                 | 0.30                | − 0.10               |
| 2—yellow-brown | 0.15                     | 0.56**               | 0.44*               | 0.14                 |
| 3—brown        | 0.02                     | 0.54**               | 0.37                | 0.33                 |
| 4—black        | 0.09                     | 0.55**               | 0.73**              | − 0.47**             |

*Significant at the level $\alpha = 0.05$

**Significant at the level $\alpha = 0.01$
Selection of the best-yielding yellow-seeded lines

Table 7 shows a comparison of yellow-seeded lines with the parental line DH Z-114. Of the six lines compared, four lines gave significantly higher yields than the yellow-seeded parental line. The highest yielding line DH-26 had a significantly larger number of branches per plant, number of pods per plant and thousand seed weight than parental line DH Z-114.

Multivariate evaluation of the similarity of the DH lines

Based on the Mahalanobis distance of the DH lines, a dendrogram of similarities between genotypes with respect to the yield, yield components and colour was created (Fig. 2). The cluster analysis showed that the genotypes could be placed into two main groups: a group comprising 16 black-seeded lines and a group of 30 lines with yellow, yellow–brown and brown seed colour.

Discussion

In this analysis, the greatest variability in DH population was observed for seed colour. This was caused by obtaining recombinants with very different seed colour, ranging from yellow through yellow–brown and dark-brown to black. Although seed colour is a complex quantitative trait that is strongly influenced by environment (Snowdon et al. 2007), and in the present study year effect and genotype × year interaction were also highly significant for this trait, seed colour proved to be highly heritable.

Among the studied traits of the seed yield components, the highest variability was found for the number of pods per plant. According to many authors (Marjanović-Jeromela et al. 2007; Ahmadi and Bahrani

Table 7 Comparison of the yellow-seeded DH lines with parental line Z-114

| Line  | Yield (dt ha⁻¹) | Number of branches per plant | Number of pods per plant | Number of seeds per pod | Thousand seed weight (g) | Seed colour |
|-------|----------------|-----------------------------|--------------------------|------------------------|--------------------------|------------|
| DH-7  | 0.99           | 1.70**                      | 33.12                    | −1.86                  | −0.21                    | 3.78       |
| DH-16 | 4.49*          | 1.11*                       | 35.40                    | −1.48                  | −0.36**                  | 3.93       |
| DH-19 | 6.43**         | 0.88                        | 75.12**                  | −3.76**                | 0.38**                   | 4.18       |
| DH-26 | 11.50**        | 1.05*                       | 57.13**                  | −0.23                  | 0.32**                   | 4.33       |
| DH-30 | 8.39**         | 0.05                        | 18.55                    | 1.39                   | 0.27*                    | 3.68       |
| DH-31 | 2.19           | 0.78                        | 52.99*                   | −3.49**                | 0.75**                   | 3.65       |
| Z-114 | 25.75          | 5.41                        | 143.00                   | 21.65                  | 4.96                     | 4.52       |

*Significant at the level α = 0.05
**Significant at the level α = 0.01
2009; Ahmadi 2010; Sadat et al. 2010; Rameeh 2011), the number of pods per plant is the trait most modified by environmental influences, but simultaneously it is also the most important factor for seed yield. In the presented study, this trait was also the most highly correlated with seed yield. On the other hand, a low value for the correlation coefficient between the yield and the number of pods on the plant in oilseed rape was obtained by Özer et al. (1999), Marinković et al. (2003) and Ghodrati et al. (2011). Some of these authors even observed a negative relationship between these traits. The predominant influence of environmental factors on the number of pods per plant is demonstrated by the low value of heritability coefficient obtained on the basis of experiments. Similar results were presented by Ali et al. (2003), Marinković et al. (2003) and Sharafzadeh et al. (2015), whereas Sadat et al. (2010), Zare and Sharafzadeh (2012) and Rameeh (2015) showed that the number of pods per plant is highly heritable. The lowest variability was observed for thousand seed weight. It was almost exclusively caused by genetic factors, as indicated by the low values of coefficients of variation for the parental forms. Also, the high value of the broad-sense heritability coefficient shows that the phenotype for this trait is largely determined by genotype. Thousand seed weight turned out to be the least variable feature among the yield-forming components, but it did not generally affect the level of yield. The correlation coefficient for the group of black-seeded lines even indicated a negative effect of thousand seed weight on yield. This limits the usefulness of thousand seed weight as a reliable selection criterion for yield, contrary to the suggestions of Engqvist and Becker (1993), who considered this trait a good selection factor. On the other hand, many authors reported such a correlation (Özer et al. 1999; Marjanović-Jeromela et al. 2007; Ahmadi and Bahrani 2009). However, Başalma (2008), Azadgoleh et al. (2009) and Rameeh (2011) did not obtain a significant positive correlation between thousand seed weight and yield. Interesting results were obtained by Sadat et al. (2010) who observed genetic variability, inheritance and relationships between yield and its components in three oilseed rape cultivars and their offspring in the next two generations. In the F2 generation they found a significant positive correlation between yield and thousand seed weight, while in the F3 generation the correlation, although not significant, was clearly negative.

The number of seeds per pod is considered by a number of authors to be the least variable component of yield (Öztürk 2010; Zare and Sharafzadeh 2012). In contrast, Ali et al. (2003) and Sadat et al. (2010) reported both high variability and low heritability of this trait. Chen et al. (2011) observed that seeds per pod and seed weight are pod development traits, and that pod development is influenced by many abiotic factors such as temperature, light and nutrients. The marked impact of environmental conditions on these traits was also mentioned by Radoyev et al. (2008) and Shi et al. (2009). In the present study the number of seeds per pod was clearly influenced by the environment, as indicated by the coefficients of variation for the genetically stable parental lines, which were higher for the number of seeds per pod than for thousand seed weight. The number of seeds per pod as a yield component contributed significantly to yield.

In many genetic experiments, inheritance and correlations between yield and yield components depend on the environment and the plant material under investigation, which might explain the ambiguous results obtained by researchers. Despite this ambiguity, such correlations are of interest to breeders because a trait which is correlated with the main breeding goal can be used for indirect selection. However, the results we report in this paper indicate the difficulty of effective selection for high yielding genotypes based on yield components only. The number of pods per plant, which had the most significant effect on seed yield, had average heritability, while the most heritable yield component, the number of seeds per pod, was much less well correlated with yield.

There were significant differences between homogeneous colour groups in terms of yield and its components, especially thousand seed weight and seed yield. Although the seed yield was negatively correlated with light seed colour, as shown by the correlation coefficients for the DH population, lines with yellow–brown seed colour gave a lower yield than lines with yellow seeds. Moreover, all yellow-seeded DH lines produced a higher yield than the yellow-seeded parent, the DH Z-114 line, including four DH lines that yielded significantly higher at significance level $\alpha = 0.01$. The groups also differed in the significance of the correlation between yield and its
components, especially the number of seeds per pod and thousand seed weight. A highly significant correlation relationship between yield and these yield components was only observed for black-seeded lines. The above result indicates that selection of yellow-seeded lines based on yield components may not be very effective. In order to select yellow-seeded lines with higher yields, the contrast method can be used. Using this method, four yellow-seeded DH lines that were significantly higher yielding than the yellow-seeded maternal line were selected.

Clustering analysis on the basis of yield and yield components can be used for a multidimensional evaluation of genotypes from different geographic origins or from advanced breeding lines and cultivars (Jankulovska et al. 2014; Rameeh 2015). Such a clustering of genotypes enables them to be comprehensively assessed for practical use in plant breeding. However, the occurrence of negative correlations between traits that are important for the agronomic value of oilseed rape makes it difficult to identify the most valuable genotypes. A dendrogram of similarities was also unable to reveal the group of genotypes with the greatest agronomic value.

**Conclusion**

The use of DH technology has made it possible to obtain a population of DH lines characterized by high diversity in terms of the studied traits. Six yellow-seeded DH lines obtained in the population gave higher yields than the yellow-seeded parental line, including four DH lines with significantly higher yields. The best line, DH-26, as well as giving a higher yield, was characterized by a significantly higher number of branches per plant, number of pods per plant and thousand seed weight in comparison to the yellow-seeded maternal line.

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**Date availability** All critical data supporting the conclusions of this manuscript will be made available by the authors, without undue reservation, to any qualified researcher.

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