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ORIGINAL PAPER

Heritability, genetic advance and sequential path analysis of oil yield and related traits in spring oilseed rape genotypes

Hossein Zeinalzadeh-Tabrizi**Department of Horticulture and Agronomy
Kyrgyz-Turkish Manas University, Bishkek, Kyrgyzstan**

Abstract

The efficiency of crop breeding programs is largely driven by the availability of genetic diversity and the inheritance of desirable traits. Heritability, genetic advance and sequential path analysis were assessed in 26 spring oilseed rape genotypes in a randomized complete block design with three replicates over two crop years 2018-2020 at the experimental field of Moghan Agricultural Research Station, Parsabad, Iran. Several morpho-physiological characteristics were recorded during the experiments. Genetic characteristics, heritability, and genetic advance in oilseed rape genotypes were estimated using the restricted maximum likelihood (REML)/Best Unbiased Linear Prediction (BLUP) method. Significant variations between oilseed rape genotypes were found for all characteristics investigated. This study found greater PCV values than GCV, showing that the environment influenced these traits. Broad-sense heritability ranged from low (8.81% for SPAD) to moderately high (79.09% for SW). The heritability estimate was moderately high for FC, PH, FPH, BN, PL, PT, SNP, SW, and OY. High heritability and genetic advance for OY were also observed in this research. SW, BN, and OY had moderately high heritability in the broad sense with high genetic advance as a percentage of the mean (GAM), demonstrating the existence of additive genes that regulate these characteristics and, thus, selection will be effective in crop improvement. Conventional path analysis showed that several traits, especially those with significant direct effects on OY exhibited substantial collinearity. Sequential path analysis revealed that SY, FP, and SW showed the most significant direct effects on OY. It can be concluded that SW and PL with high broad-sense heritability and GAM are good traits for indirect selection in the breeding program for spring oilseed rape genotypes.

Keyword: BLUP, correlation, direct effect, path analysis, REML, stepwise regression

INTRODUCTION

The study of genetic diversity of traits and the relationship between yield and its components is one of the interests of breeders in implementing a successful breeding program. Oilseed rape (*Brassica napus* L.) is one of the world's most important oilseeds. Its seeds contain more than 40% oil, and the rest of the meal is rich in protein, and after soybeans, it is the world's most important source of edible oil (Seymour et al. 2012). In Iran, the area under oilseed rape cultivation in the crop year 2019-2020 was more than 160 thousand hectares with an average yield of 2105 kg ha⁻¹ and 340 thousand tons of seed yield (Anonymous 2020), which is less than the world average yield. One of the primary objectives of oilseed rape breeding is to increase crop productivity per unit area.

Any breeding program's success is dependent on knowledge of effective key traits, genetic control system, how these traits are inherited, and environmental factors that influence their occurrence (Chaghakaboodi et al. 2012). Seed yield in oilseed rape depends on the genetic capacity of the variety, climatic conditions, soil type, and crop management. It is important to predict and accurately estimate the genetic effects of individuals in order to select them for plant breeding programs (da Costa et al. 2002), which ultimately leads to maximum genetic advance (Furlani et al. 2005). The study of yield and its components in oilseed rape by different researchers has shown that the number of pods per plant (Ali et al. 2002, Marjanović-Jeromela et al. 2011, Zare, Sharafzadeh 2012, Ismaili et al. 2016, Rameeh 2016), number of pods in the main stem (Aytaç et al. 2008, Nasim et al. 2013, Rameeh 2015), number of seeds per pod (Ul-Hasan et al. 2014), 1000-seed weight (Bayat et al. 2008, Sharafi et al. 2018), plant height (Zebarjadi et al. 2011, Sandhu et al. 2017), oil content (Baradaran et al. 2007, Rabiee et al. 2012) and harvest index (Tiwari et al. 2017), play a significant role in oilseed rape seed and oil yield.

Accurate prediction of genetic values of genotypes is of particular importance in plant breeding (da Costa et al. 2002). Henderson (1975) proposed the best linear unbiased prediction (BLUP) approach of mixed linear models for random prediction of genetic values. Also, Patterson and Thompson (1971) proposed the REML (Restricted Maximum Likelihood) method, an ideal procedure for estimating variance components and fractionating the total variation of a given trait, especially for unbalanced data. Therefore, in practice, the REML/BLUP method can provide a more accurate and unbiased prediction of the genetic parameters of the evaluated genotypes without prior knowledge of the variance components (Carvalho et al. 2020). The REML/BLUP method was first used to estimate genetic parameters in livestock breeding (Carvalho et al. 2020). Estimators such as the restricted maximum likelihood method have rarely been used to estimate variance components, heritability, and genetic correlation, especially in plant breeding in Iran.

In this context, the objectives of this study were to estimate genetic parameters, predict genotypic and phenotypic effects, estimate correlation coefficients among oil yield-related traits and determine the relationships between yield and its components by examining direct and indirect effects and sequential path coefficient analysis using the REML/BLUP method in 26 spring oilseed rape genotypes.

MATERIAL AND METHODS

Field description

This study was conducted in the experimental field of Moghan Agricultural Research Station, Parsabad, Iran (N39°39' E 47°68' N, altitude = 78 m) during the two cropping seasons 2018-2019 and 2019-2020. According to IRIMO data (Iran Meteorological Organization), this location has a semi-humid and mild-warm climate (251 mm mean annual precipitation over the last 30 years, mainly in autumn and early spring). The minimum and maximum precipitations are 72.9 and 523 mm per year, respectively, and the average annual maximum and minimum temperatures in the region are 35°C and 8°C. The average annual relative humidity is 71%. Meteorological data on the location during the experimental years are shown in Table 1.

The soil texture of the experimental field was sandy-loam, and the soil type was Cambisol, according to the World Reference Base for Soil Resources (WRB) – FAO (1998). The physicochemical properties of soils in the experimental field are shown in Table 2.

Table 1

Meteorological data during the experimental years

Date	2018-2019					2019-2020				
	min. (C°)	Max. (C°)	avr (C°)	prc (mm)	re (%)	min. (C°)	max. (C°)	avr (C°)	prc (mm)	re (%)
October	13.9	24.3	19.1	1.3	72.9	13.6	24.6	19.1	10.5	74.5
November	8.2	16.9	12.5	26.7	79.3	6.3	17.9	12.1	3.4	73.7
December	4.7	11.5	8.1	27.9	85.0	3.1	11.0	7.0	27.4	81.6
January	0.3	10.4	5.3	5.3	78.5	2.3	10.0	6.1	15.5	82.3
February	2.5	10.5	6.5	32.9	82.8	0.0	12.6	6.3	18.6	64.3
March	3.4	14.4	8.9	19.1	73.6	5.0	15.4	10.2	19.5	77.3
April	6.8	16.2	11.5	47.1	80.7	5.7	16.4	11.1	22.3	77.3
May	11.9	26.1	18.8	21.1	69.6	11.3	22.9	17.1	42.9	72.8
June	17.1	33.2	24.9	7.8	56.2	16.7	33.4	25.0	10.3	57.2

min. – minimum monthly temperature, max. – maximum monthly temperature, avr – average monthly temperature, prc – precipitation, re – average relative humidity

Table 2

Physiochemical properties of soils in the experimental field

Soil depth (cm)	Salinity (Ds m ⁻¹)	pH	Organic carbon (%)	N (%)	Available P (ppm)	Available K (ppm)	Zn (ppm)	Fe (ppm)
0-30	0.702	7.72	2.760	0.2	1.85	469	7.14	3.94
30-60	0.736	7.75	0.781	0.7	1.09	267	10.46	4.27

Plant material and experimental design

The plant material in this study consisted of 26 genotypes, including five hybrids and 21 open-pollinated promising lines and commercial cultivars described in Table 3.

Eighteen open-pollinated inbred lines (No. 1-18) belong to the spring canola breeding program in Iran. This study was conducted in a randomized complete block design with three replicates over two crop years.

Table 3

Description of the spring oilseed rape genotypes used in the trial

No.	Genotype name	Type	Origin
1	SRL-96-6	Open-pollinated	Iran
2	SRL-96-7	Open-pollinated	Iran
3	SRL-96-8	Open-pollinated	Iran
4	SRL-96-10	Open-pollinated	Iran
5	SRL-96-11	Open-pollinated	Iran
6	SRL-96-12	Open-pollinated	Iran
7	SRL-96-13	Open-pollinated	Iran
8	SRL-96-15	Open-pollinated	Iran
9	SRL-96-16	Open-pollinated	Iran
10	SRL-96-17	Open-pollinated	Iran
11	SRL-96-18	Open-pollinated	Iran
12	SRL-96-19	Open-pollinated	Iran
13	SRL-96-20	Open-pollinated	Iran
14	SRL-96-21	Open-pollinated	Iran
15	SRL-96-22	Open-pollinated	Iran
16	SRL-96-23	Open-pollinated	Iran
17	SRL-96-24	Open-pollinated	Iran
18	SRL-96-25	Open-pollinated	Iran
19	RGS003	Open-pollinated	Germany
20	Dalgan	Open-pollinated	Iran
21	Early one	Open-pollinated	US
22	D-800Z	Hybrid	China
23	Number 8	Hybrid	China
24	Wong-8	Hybrid	China
25	Number 18	Hybrid	China
26	Hyola 4815	Hybrid	Australia

Experimental procedure

Six 5 m long rows with 30 cm spacing were used in each experimental plot. Thus, the plant density was 60 plants per plot. Fertilizers were applied based on the results of the soil analysis. At the time of planting, an application of 150 kg ha⁻¹ of phosphorus in the form of triple superphosphate was carried out. Additionally, 200 kg ha⁻¹ of nitrogen was applied as ammonium nitrate with half of the nitrogen being applied at the planting time and the remaining half during the stem elongation stage. No evidence of disease was observed throughout the growing period, and weed management was conducted using chemical methods. Before planting, the herbicide trifluralin was applied to the field at a rate of 2 liters per hectare. Planting was done in the third decade of October of each crop year. The herbicide Gallant Super was applied at a rate of 0.8 l ha⁻¹ before the rosette stage. Irrigation was applied as needed by the crop.

Data collection

During the growing season, characteristics such as days to flower initiation (FI), days to flower completion (FC), flowering period (FP), days to maturity (MA), plant height (PH), first pod height (FPH), main stem length (MSL), number of lateral branches per plant (BN), number of pods per plant (PN), number of seeds per pod (SNP), stem diameter (SD), pod diameter (PD), 1000-seed weight (SW), seed yield (SY) and chlorophyll content (SPAD) were recorded. A hand-held SPAD-502 meter was used to measure leaf chlorophyll concentrations in a quick, accurate, and non-destructive manner (Markwell et al. 1995). At the final harvest, two lateral lines were removed as marginal strips. In order to ascertain the proportion of seed oil, a sample of 5 g of seed was extracted from each plot and subjected to analysis using NMR (Nuclear Magnetic Resonance) technology. The NMR analysis was performed using a German Broker Brand minispec mq20 Model in accordance with the guidelines outlined in International Standard ISO-5511 (1992). In order to achieve the intended objective, the device was subjected to daily calibration using a reference sample, followed by calibration of the product using pre-prepared standard samples. Subsequently, a minimum of 3 g of rapeseed was accurately weighed and transferred to the designated cell of the device. The specimen-containing cell was situated in a designated location, and the oil quantity was monitored for a duration of less than 1 minute. The quantity of rapeseed designated for the device marker is a minimum of 3 g of rapeseed, and for this particular experiment, it was chosen as 5 g. Oil yield (OY) was estimated by multiplying the oil content by the yield of the seeds used in the experiment.

Statistical analysis

Before analysis of variance, outliers were detected, and the normality of the data distribution was checked using the Grubb's test and the

Shapiro-Wilk test. Then, the assumption of homogeneity of variance was checked with the Bartlette's test.

The statistical model used for the analysis of variance is as follows:

$$Y_{ijk} = \mu + \text{Envi} + \text{Repj}(\text{Envi}) + \text{Genk} + \text{Envi} \times \text{Genk} + \epsilon_{ijk}$$

Where: Y_{ijk} – the trait of interest, μ – the mean effect, $\text{Repj}(\text{Envi})$ – the effect of the j th replicate within the i th environment, Genk – the effect of the k th genotype, ϵ_{ijk} – the error associated with the i th environment, j th replicate within the i th environment and k th genotype, which is considered to be normally and independently distributed, with a mean of zero and a variance of homoscedastic. All effects are treated as random in the calculation of BLUPs and broad-sense heritability.

Estimation of genotypic and phenotypic coefficients of variation:

$$GCV = \frac{\sqrt{\sigma_g^2}}{\bar{x}} \times 100,$$

$$PCV = \frac{\sqrt{\sigma_p^2}}{\bar{x}} \times 100,$$

where:

σ_p^2 – phenotypic variance

σ_g^2 – genotypic variance

\bar{x} – grand mean of a trait

The genotype mean was used to determine broad-sense heritability (h^2), which is represented as a percentage of the ratio of genotypic variation (g) to phenotypic variance (p):

$$h^2 = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_{ge}^2/n\text{Envs} + \sigma_e^2/(n\text{Envs} \times n\text{reps})},$$

where: – the variance component of the genotype by environment interaction and is the number of environments in the analysis and – the number of replicates.

Phenotypic correlations between traits are simple Pearson correlations between different pairs of traits.

The technique was used to determine genetic advance (GA) and genetic advance as a percentage of the mean (GAM), assuming selection of the top 5% of genotypes:

$$GA = \frac{K \times \sqrt{\sigma_p^2} \times \sigma_g^2}{\sigma_p^2},$$

where:

GA – expected genetic advance

K – standardized differential selection at 5% selection intensity ($K = 2.063$)

$$GAM(\%) = \frac{GA}{\bar{x}} \times 100.$$

Several experimental units were missed during the study. Therefore, genetic characteristics, heritability, and genetic advance in oilseed rape genotypes were estimated using the restricted maximum likelihood (REML)/Best Unbiased Linear Prediction (BLUP) method. META-R software (Alvarado et al. 2020) used in this research calculates BLUPs for all traits when genotypes are considered with random effects; the BLUP for each genotype is the grand mean added to the estimated random effect from each genotype. The coefficients of correlation between various pairs of attributes were calculated. The predictor variables were then organized into first- and second-order paths based on their contributions to the overall variance of total weight and minimal collinearity using sequential stepwise multiple regressions. The sequential correlation diagram and heatmap were plotted using AMOS and JMP, respectively.

RESULTS AND DISCUSSION

Combined analysis of variance and phenotype variation

For all characteristics investigated, there was a highly significant difference between oilseed rape genotypes ($p < 0.05$). These findings implied that there was a great presence of variance among the tested oilseed rape genotypes, and they showed the suitable selection for crop improvement (Table 4). Similarly, Chaghakaboodi et al. (2012) reported significant differences among 16 oilseed rape genotypes for seed yield and related traits. These results are also in agreement with those of Ali et al. (2002). Ahmad et al. (2013) also reported highly significant differences in oil yield and related attributes among the rapeseed genotypes they tested. Except for FI, PH, FPH, MSL, BN, SD, PN, PT and SNP, the other traits were influenced by genotype by environment interaction in the combined analysis (Table 4).

Estimation of variance components and coefficients of variations

Estimates of phenotypic, genotypic, genotype by environment and environmental variances as well as Phenotypic Coefficients of Variation (PCV) and Genotypic Coefficients of Variation (GCV) are given in Table 5. The GCV ranged from 1.42 for FI to 12.99 for OY. Similarly, PCV ranged from 0.99 for MA to 16.74 for PN. In this study, the PCV values were higher than those of GCV, indicating that the environment played an important role in expressing these traits. These results are in agreement with those of Ali et al. (2002), Aytacı et al. (2008), Marjanović-Jeromela et al. (2011), Chaghakaboodi et al. (2012), Ahmad et al. (2013), Halder et al. (2014), Sikarwar et al. (2017), Laghari et al. (2020) and Aftab et al. (2020).

Combined analysis of variance for oil yield and related traits in 26 spring oilseed rape genotypes

S.o.V	Y	R(Y)	G	GE	E
df	1	4	25	25	100
FI	3286.26**	65.14**	45.44**	19.22	17.62
FC	4807.41**	17.58	72.92**	27.93**	7.23
FP	144.23**	53.85**	74.57**	34.78**	12.17
MA	194.08**	12.76*	27.96**	13.64**	4.02
PH	127239.75**	279.40*	533.85**	143.07	101.93
FPH	111524.34**	303.29*	324.87**	114.34	93.05
MSL	827.08*	94.6	360.32**	230.3	155.84
BN	33.94**	9.40**	4.32**	1.45	1.17
SD	515.86**	17.19**	3.71*	2.47	2.08
PN	734321.85**	21520.26**	10881.94**	4651.08	3245.29
PL	0.48	0.74*	2.57**	0.54*	0.29
PT	0.53	0.52	0.76**	0.3	0.22
SNP	7.54	12.65	43.88**	14.83	11.88
SW	6.82**	0.17	1.49**	0.31*	0.17
SY	19056837.03**	124821.86	1143552.92**	494933.55**	205580.25
OY	3338594.9197**	20030.1286	285498.0152**	94961.6571**	35832.1196
SPAD	59.4467	27.1121	29.2868**	40.043**	9.2999

FI – days to flower initiation, FC – days to flower completion, FP – flowering period, MA – days to maturity, PH – plant height, FPH – first pod height, MSL – main stem length, BN – number of lateral branches per plant, PN – number of pods per plant, SNP – number of seeds per pod, SD – stem diameter, PT – pod thickness, SW – 1000-seed weight, SY – seed yield, OY – oil yield, SPAD – chlorophyll content

The environment generally has a significant impact on quantitative traits. Deshmukh et al. (1986) found that PCV and GCV levels greater than 20% are regarded as high, values less than 10% are considered low, and values between 10% and 20% are considered medium. Accordingly, OY, SW, PN and BN had medium GCV, whereas the other traits had lower values for GCV. The PCV for OY, SY, SW, PL, PN, and BN was moderate, whereas the PCV for the other characteristics was low. Selection may be effective based on traits with high and medium PCV and GCV, and their phenotypic manifestation would be a good sign of genetic potential (Teklu et al. 2014).

Heritability and genetic advance

Table 5 shows a heritability estimate for the characteristics under investigation. Heritability is a reliable predictor of the transfer of parental traits to offspring. Heritability values are useful in projecting the predicted prog-

Table 5
Heritability, variance components and other genetic parameters of the 26 spring oilseed rape genotypes

Traits	H ²	V _G	V _{G×Y}	V _E	V _P	Grand mean	CV (%)	Min.	Max.	GCV	PCV	GA	GAM (%)
FI	57.71	4.37*	0.53	41.28**	7.57	146.79	2.86	134.00	164.00	1.42	1.87	3.28	2.23
FC	61.7	7.50*	6.90**	61.14**	12.15	192.68	1.40	178.00	207.00	1.42	1.81	4.44	2.30
FP	53.36	6.63*	7.54**	0.87	12.43	45.88	7.60	33.00	60.00	5.61	7.68	3.88	8.46
MA	51.22	2.39	3.20**	2.20	4.66	217.78	0.92	211.00	224.00	0.71	0.99	2.28	1.05
PH	73.2	65.13**	13.71	1627.15**	88.98	145.03	6.96	87.67	200.40	5.56	6.50	14.24	9.82
FPH	64.81	35.09*	7.09	1425.63**	54.14	89.54	10.77	41.00	152.00	6.62	8.22	9.84	10.99
MSL	36.09	21.67	25.60	7.65	60.05	103.52	11.97	67.00	153.00	4.50	7.49	5.77	5.57
BN	66.34	0.48**	0.09	0.31	0.72	5.71	18.97	2.33	10.00	12.10	14.86	1.16	20.34
SD	33.42	0.21	0.13	6.39*	0.62	11.05	13.06	5.38	16.81	4.11	7.11	0.54	4.90
PN	57.26	1038.47*	468.60	9120.47**	1813.66	254.39	22.39	66.00	478.00	12.67	16.74	50.31	19.77
PL	78.99	0.34**	0.08*	0.000	0.43	5.97	9.04	3.70	8.70	9.77	10.97	1.07	17.88
PT	60.6	0.08*	0.03	0.000	0.13	4.95	9.43	3.40	6.59	5.61	7.20	0.45	9.00
SNP	66.19	4.89**	0.88	0.000	7.31	27.15	12.71	16.20	38.80	8.14	9.96	3.69	13.60
SW	79.09	0.20**	0.05*	0.08**	0.25	3.92	10.42	2.29	6.18	11.32	12.73	0.81	20.77
SY	56.72	108103.22*	97486.47**	237973.04**	190892.15	3310.46	13.59	1330.00	5831.00	9.93	13.19	510.84	15.43
OY	66.74	31756.06**	19912.43**	41585.09**	47583.00	1372.07	13.68	566.58	2607.04	12.99	15.90	300.33	21.89
SPAD	8.81	0.60	9.57**	0.44	6.87	45.54	6.54	35.30	57.50	1.71	5.75	0.48	1.05

FI – days to flower initiation, FC – days to flower completion, FP – flowering period, MA – days to maturity, PH – plant height, FPH – first pod height, MSL – main stem length, BN – number of lateral branches per plant, PN – number of pods per plant, SNP – number of seeds per pod, SD – stem diameter, PT – pod thickness, SW – 1000-seed weight, SY – seed yield, OY – oil yield, SPAD – chlorophyll content

ress made throughout the selection process. Plant breeders select genotypes from distinct genetic populations using heritability estimates. Therefore, high heritability helps in the effective selection of a particular character. Heritability ranged from 8.81% for SPAD to 79.09% for SW. Heritability rates of more than 80% are considered extremely high; values between 60 and 79% are considered moderately high; values between 40 and 59% are considered medium; and values less than 40 percent are considered low. Accordingly, the heritability estimate was moderately high for FC, PH, FPH, BN, PL, PT, SNP, SW, and OY; medium for FI, FP, MA, PN, and SY; and low for MSL, SD, and SPAD. A high heritability indicates that selection will be effective. Heritability has long been used in plant breeding programs to evaluate the heritable share of variance in a phenotypic characteristic within a population. It is regarded as the most important notion in selective breeding (Aftab et al. 2020). Johnson et al. (1955) found that heritability and genetic advance together predict selection effects better than heritability alone. High heritability and genetic advance for OY were observed in this research (Table 5). Similar results in oilseed rape have previously been reported by Aytaç et al. (2008), which validates our findings. They also stated that high heritability and genetic advance allow mass selection in oilseed rape breeding. Additive genes are expected to influence characteristics with high heritability and genetic advance, stressing the importance of phenotypic selection in plant breeding.

Johnson et al. (1955) characterized genetic advance as a percentage of the mean (GAM); values ranging from 20% and above are considered high, 10-20% are considered moderate, and values ranging from 0-10% are considered low. Based on this classification, the range for GAM was from 1.05% for PH and SPAD to 21.89% for OY. High GAM was observed for BN (20.34%), SW (20.77%), medium for FPH (10.99%), PN (19.77%), PL (17.88%), SNP (13.60%), SY (15.43%), and low for FI (2.23%), FC (2.30%), FP (8.46%), MA (1.05%), PH (9.82%), MSL (5.57%), SD (4.90%), PT (9.00%), and SPAD (1.05%) (Table 5). High GAM was also reported for SY in Aytaç et al. (2008) and Bayat et al. (2008). Moderately high heritability in a broad sense with a high genetic advance in percent of the mean was found in SW, BN and OY indicating the possible presence of additive genes. Zebarjadi et al. (2011) also showed a high genetic advance as a result of additive gene activity in OY (2011).

Moderately high heritability (73.2 and 60.6%) and low genetic advance (9.82 and 9.00%) were found in PH and PT, respectively. Environmental factors were more influential in the expression of PH and PT than genotypic variation. Similarly, the heritability of PH was found by Aytaç et al. (2008) and Naznin (2013) to be relatively high with low genetic advance. In this study, medium heritability (56.72%) and medium genetic advance (15.43%) were observed for SY (Table 5). These values were 36 and 14.82% in Rameeh (2016), 32.49 and 14.85% in Kahrizi and Alaahvarand (2012), 29.27 and

14.61% in Halder et al. (2014), 84 and 31.46% in Bayat et al. (2008), 87 and 22.29% in Aytac et al. (2008), 48.8 and 23.71% in Ali et al. (2002).

Phenological traits (FI, FC, FP and MA) had moderately to moderately high heritability with low genetic advance (Table 5). These characteristics may have a non-additive (dominant or epistatic) gene effect. This finding was consistent with those of Bayat et al. (2008) and Rameeh (2016). Rameeh (2016) also found that a trait with high heritability did not necessarily result in a high genetic advance. The results of Kahrizi and Alaahvarand (2012) for phenological traits were high heritability with medium genetic advance.

Relationship among characters

Figure 1 shows the phenotypic relationships between SY and OY with other traits. OY (0.940**), SPAD value (0.646**), and SD (0.544**) had a positive and significant correlation with SY, whereas BN (-0.540**) had a negative and significant correlation with SY (Figure 1). A negative correla-

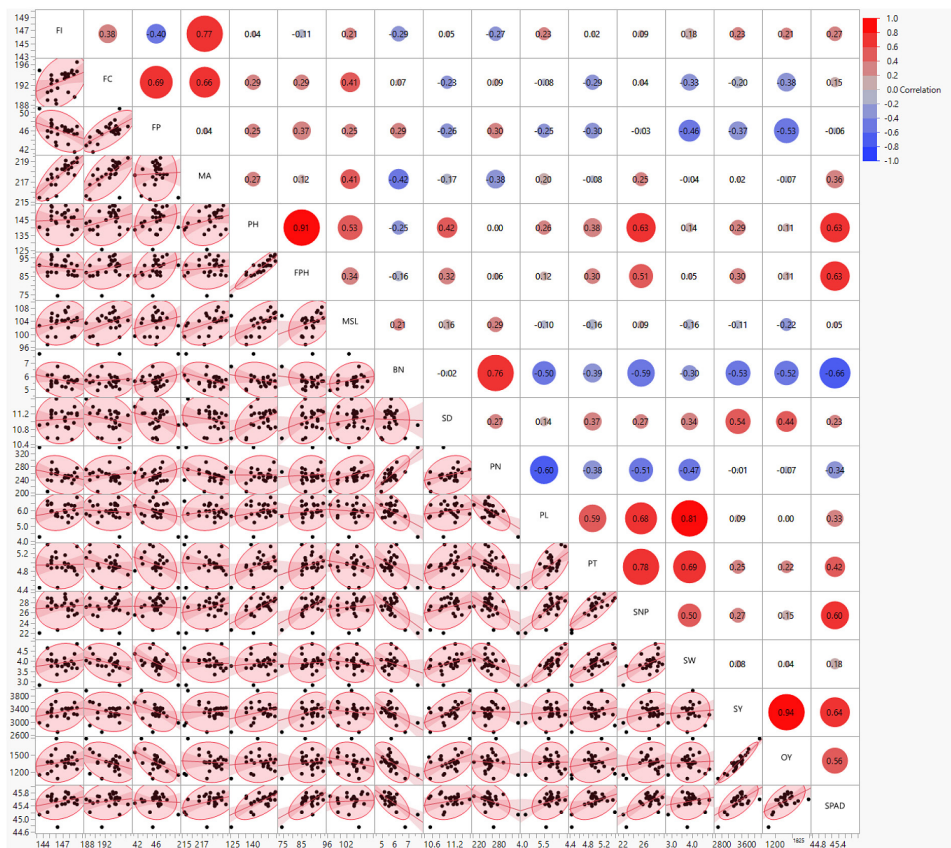


Fig 1. Phenotypic correlations of oil yield and related traits in the 26 spring oilseed rape genotypes

tion of BN with OY was found in Tunçturk and Ciftci (2007) and Sharafi et al. (2018) studies, which was similar to the current results. On the contrary, BN had a positive and significant correlation with SY in Ali et al. (2002), Baradaran et al. (2007), Tunçturk and Ciftci (2007), Bayat et al. (2008), Halder et al. (2014), Tiwari et al. (2017) and Laghari et al. (2020), whereas it was positive and non-significant in Rabiee et al. (2012), Nasim et al. (2013), Sandhu et al. (2017) and Biabani et al. (2021) studies.

BN also had positive and significant phenotypic correlations with PN (0.759**), whereas it had negative and significant correlations with MA (-0.428*), SPAD (-0.653**), SNP (-0.583**), PL (-0.489*), and PT (-0.389*). These results demonstrated that selection should be performed through lower BN for higher OY and SY. SW had positive and significant phenotypic correlations with PL (0.808**), PT (0.693**) and SNP (0.496**), while having negative and significant correlations with PN (-0.468*) and FP (-0.463*). SW was found to have a non-significant and positive correlation with SNP in Tunçturk and Ciftci (2007) and Biabani et al. (2021), whereas it was found to have a significant and positive correlation with SNP in Özer et al. (1999) and Ivanovska et al. (2007). PL had positive and significant phenotypic correlations with PT (0.591**) and SNP (0.677**). Similar results were found in Özer et al. (1999), Ivanovska et al. (2007) and Biabani et al. (2021). PH had positive and significant phenotypic correlations with SPAD value (0.631**), SNP (0.626**), SD (0.425*), MSL (0.532**) and FPH (0.906**), while having non-significant and positive correlations with SY and OY. A non-significant and positive correlation of SY with PH was also reported by Özer et al. (1999), Ali et al. (2002), Tunçturk and Ciftci (2007), Ivanovska et al. (2007) and Laghari et al. (2020).

Conventional and sequential path analysis

Conventional path analysis was used for the data to establish the relative significance of the traits. Path analysis separates the correlation coefficient's components into direct and indirect effects. Table 6 shows the results of the direct impacts of component traits on oilseed rape oil yield, where oil-related traits were treated as first-order variables and oil yield as the response variable. Several traits, especially those with significant direct effects on OY, like SY, SW, SNP, PN, FPH, PH, MA, and FI, exhibited substantial collinearity (Table 6). It was discovered that matrices with traits having VIFs greater than 10 and TOLs less than 0.1 exhibited extreme multicollinearity (Mansfield, Helms 1982).

Sequential path analysis simplifies the interrelationship between traits and their impact on OY compared to conventional path analysis. The results indicated that the VIF values of the first model were much higher than those of the second model. Variable collinearity was decreased using stepwise regression analysis, and by reducing effect mixing, each variable's actual participation rate was precisely calculated along distinct paths. SY, FP, and

Table 6

Direct effects of first-order predictor variables on oil yield and measures of collinearity in model 1 (conventional path analysis)

Predictor variables	Direct effect	Tolerance	VIF
FI	0.137	0.084	11.934
FC	-0.200	0.254	3.932
MA	-0.137	0.054	18.372
PH	0.095	0.032	30.983
FPH	-0.170	0.047	21.414
MSL	0.023	0.196	5.091
BN	0.009	0.044	22.858
SD	0.008	0.211	4.731
PN	-0.162	0.089	11.214
PL	-0.018	0.115	8.716
PT	0.129	0.117	8.521
SNP	-0.196	0.087	11.541
SW	-0.204	0.091	11.031
SPAD	0.171	0.182	5.495
SY	0.827	0.064	15.598

SW showed the most significant direct effects on OY (0.933, -0.321 and -0.182, respectively) – Table 7. The interesting point here was that despite the negative direct effect of SW on OY, its indirect effect through SY and FP was positive (Table 7).

According to Sabaghnia et al. (2010), SW is the most intriguing attribute to employ as an indirect yield selection method in oilseed rape. This trait's heritability is often high and its ease of determination exceeds that of yield, making it an important yield component. Leilah and Al-Khateeb (2005) and Ivanovska et al. (2007) found that there is a strong, positive, and statistically significant association between SW and SY. In addition, Tuncturk and Ciftci (2007) and Marjanović-Jeromela et al. (2008) revealed a moderate, positive and statistically significant association between SW and SY. Contrarily, Lee et al. (1977), Lefort-Buson and Dattee (1985), Engqvist and Becker (1993) and Basalma (2008) showed no significant association between these two characteristics that were in accordance with this study.

According to the stepwise regression of second-order variables over the first-order variables, SPAD value, SD, and PH showed the most significant direct effects on SY (0.788, -0.543, and -0.434, respectively) – Table 7. Similar to the OY, despite the negative direct effect of PH on SY, its indirect effect through SPAD value and SD was positive (Table 6). SPAD value and SD also had a positive and direct effect on SY, while their indirect effects on SY through PH were negative.

Table 7

Direct effects, tolerance, and variance inflation factor (VIF) values for the predictor variables in model 2 (sequencing path analysis)

Response variable	Predictor variables	Adjusted R ²	Tolerance	VIF	Direct effect	Indirect effect via		
						SY	FP	SW
OY	SY	0.935	0.850	1.177	0.933**	-	0.120	-0.015
	FP		0.673	1.487	-0.321**	-0.349	-	0.084
	SW		0.777	1.287	-0.182*	0.078	0.149	-
						SPAD	SD	PH
SY	SPAD	0.622	0.599	1.668	0.788**	-	0.129	-0.274
	SD		0.817	1.224	0.543**	0.180	-	-0.184
	PH		0.518	1.930	-0.434*	0.497	0.231	-
						PL	PT	SNP
SW	PL	0.797	0.532	1.880	0.795**	-	0.385	-0.372
	PT		0.383	2.609	0.652**	0.470	-	-0.429
	SNP		0.320	3.128	-0.550**	0.538	0.509	-
						PH	FP	PN
SD	PH	0.419	0.932	1.074	0.556**	-	-0.132	0.001
	FP		0.850	1.176	-0.528**	0.139	-	0.125
	PN		0.908	1.102	0.423*	0.002	-0.156	-

PL, PT and SNP had the most significant direct effects on SW (0.795, 0.652, and -0.550, respectively) – Table 7. Like SY and OY, despite the negative direct effect of SNP on SW, its indirect effect through PL and PT was positive (Table 7). PL and PT also had an indirect positive effect on SW, while the indirect effects of these traits via SNP were negative (Table 7).

There was a high correlation coefficient between morpho-physiological traits in this study, which meant that it was hard to determine the exact contribution of each component to total seed and oil production in spring oil seed rape genotypes because of mixed or muddled effects. Path analysis is used to understand the magnitude and direction of direct and indirect contributions of component characteristics to yield since correlation coefficients do not convey the entire picture when the causative factors are interconnected and interdependent.

Studies on various plants have shown that sequencing path analysis is more effective than conventional path analysis (Kozak, Azevedo 2014, Mohammadi et al. 2014, Olivoto et al. 2017, Mahmoud et al. 2020, Göre et al. 2023). Diepenbrock (2000) reported that, for breeding purposes in oil-seed rape, the correlation between PL and SNP is very important; the pod's length can be measured objectively, suggesting it might be used as a trait for indirect selection. PH, FP and PN had the most significant direct effects on SD (0.556, -0.528 and 0.423, respectively). FP had an indirect positive effect

on SD via PH, while the indirect effects of PH and PN via FP were negative (Table 7).

CONCLUSION

The efficiency of crop breeding programs is largely driven by the availability of genetic diversity and the inheritance of desirable traits. The analysis of genetic variation enables the breeder to determine the best method and selection criteria to apply for improving the desired traits. Among the examined genotypes, various levels of variability, heritability, and genetic advance as a percentage of the mean were observed. This study found greater PCV values than GCV, showing that the environment influenced these traits. Broad-sense heritability ranged from low (8.81% for SPAD) to moderately high (79.09% for SW). The heritability estimate was moderately high for FC, PH, FPH, BN, PL, PT, SNP, SW, and OY; medium for FI, FP, MA, PN, and SY; and low for MSL, SD, and SPAD. High heritability and genetic advance for OY were also observed in this research. SW, BN, and OY had moderately high heritability in the broad sense with high GAM, demonstrating the existence of additive genes that regulate these characteristics and, thus, selection will be effective in crop improvement. Conventional path analysis showed that several traits, especially those with significant direct effects on OY exhibited substantial collinearity. Sequential path analysis revealed that SY, FP, and SW showed the most significant direct effects on OY. The highest indirect effects on OY were FP via SY, on SY was PH via SPAD, on SW was SNP via PL, and on SD was PN via FP. It can be concluded that SW and PL with high broad-sense heritability and GAM are good traits for indirect selection in the breeding program for spring oilseed rape genotypes.

Author contribution

The author confirms that the text, figures, and tables are original and that they have not been published before.

Ethical approval

Ethics committee approval is not required.

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