

Gene action studies through diallel analysis in *Brassica rapa* for quality traits

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Abstract: Pakistan needs to increase domestic production of edible oil, because the country is deficient in the production of such oil and has to import large quantities every year. *Brassica rapa* (cool season crop) may be a good choice for edible oil production in Pakistan, being yellow seeded and of short duration, but its major problem is erucic acid. This study used the Hayman and Jinks model to estimate genetic expression (i.e. gene action) on quality-related traits (oil percentage, glucosinolate, protein percentage, erucic acid, linolenic acid, oleic acid and moisture percentage) using four lines (UAF-11, Toria, BSA and TP-124-1) and their hybrids in a diallel fashion. All traits other than oil percentage and linolenic acid were found to be controlled by dominant gene action. Absence of non-allelic interaction (epistasis) was observed for all traits. Number of frequency of dominant genes was more frequent towards better parents, and recessive genes were greater than dominant genes in all traits, except in the case of linolenic acid. The best parents were TP-124-1 and UAF-11, which had the maximum dominant and maximum recessive genes, respectively, for the best traits (i.e. protein percentage, erucic acid, linolenic acid and oleic acid); they can be used as parents in future hybrid breeding and other future breeding programs.

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Introduction

In Pakistan, domestic production of edible oil is much lower than demand. The country's total oilseed requirement is 2 million tons, but local oilseed production is about 26% of this, at 0.606 million tons, of which rapeseed contributes 0.066 million tons (about 11.60%). Thus, in 2013-14, Pakistan spent 241.936 billion rupees (US\$ 2.50 billion) on the importation of edible oil. Industrial usage (cosmetics, paints and other products) of all available oil resources was 10% (Govt. of Pakistan, 2013-14). Clearly, immediate attention is needed to remedy this situation. In Pakistan, rapeseed and mustard (*Brassica* oilseed) crops are the second largest producer of vegetable oil after cottonseed. In 2013, these Brassicas covered 0.183 million hectares, in comparison to 8.693 million hectares of wheat and 2.311 million hectares of rice. The contribution of other oilseed crops (i.e. sunflower and soybean) to local production of edible oil was very low (Govt. of Pakistan, 2013-14). The most important oilseed crop, both globally and in Pakistan, is *Brassica rapa* (syn *campestris*, Order Brassicales and family Brassicaceae). It has an oil content of 35-46% (Kumar *et al.* 2011) and a maturity period of 100-140 days (Mumtaz *et al.*, 2014), and appears to be a good choice for bridging the gap between production and consumption of edible oil. The main

problems in the current varieties of *B.rapa* are the low quality of the oil (i.e. a high percentage of erucic acid), low yield, susceptibility to aphid attack and white rust of crucifer, shattering at maturity and a lodging problem due to rain and winds. Thus, development of varieties with a seed yield of economic value and a high percentage of high-quality oil is needed. Quality traits in oil are important for human and animal health, as discussed below. The polyunsaturated fatty acid linolenic acid is beneficial for human health because it lowers cholesterol level by increasing high density lipoprotein (HDL) and reduces the risk of cardiovascular disease (Grundy, 1987). Glucosinolate is a causative agent of goiter disease, in which the thyroid gland is enlarged (Tripathi and Mishra, 2007). However, it also has many beneficial effects; for example, it has anticancerous effects (Johnson, 2002) and protects against oxidative stress by eliminating reactive oxygen species (London *et al.*, 2000). Erucic acid constitutes about 30-60% of total fatty acids of *Brassica*. It is poorly absorbed, digested and metabolized than other fatty acids. It inhibits the overall rate of oxidation of fatty acids by mitochondria (Anonymous, 2003). The polyunsaturated oleic (omega 9) fatty acids reduce blood pressure, help in weight loss by increasing fat burning, protect cells from free radical damage and

prevent ulcerative colitis. Oleic acid is less susceptible to oxidation damage than omega-6 and omega-3, and it protects the cell membrane from free radicals and other oxidative stresses (Lim *et al.*, 2013).

The genetic basis of the traits described above were studied in this research because they have a direct link with human health. Yellow-seeded varieties potentially have more oil (Kumar *et al.* 2011). Hence, breeding of high-yielding, yellow-seeded varieties with a short life cycle and quality traits would be beneficial. Little is known of the genetics of *B. rapa*; also, there is much confusion about the genetics. For example, for oil percentage, dominant gene action was observed by some authors (Abbas *et al.*, 2014; Ali *et al.*, 2014a; Pankaj *et al.*, 2008; Ahmed, 2010; Ali *et al.*, 2013) and additive gene action by other authors (Zada *et al.*, 2013; Iqbal *et al.*, 2014). Similarly, for glucosinolate, dominant gene action and maternal effects were observed in some studies (Iqbal *et al.*, 2003; Alemayehu and Heiko, 2005; Farooq *et al.*, 2011; Iqbal *et al.*, 2014) and additive gene action in a study by Zada *et al.*, 2014. For protein percentage, dominant gene action was observed by some authors (Ali *et al.*, 2011; Ali *et al.*, 2012; Ali *et al.*, 2014a,b; Alemayehu and Heiko, 2005; Nasim and Farhatullah, 2013; Iqbal *et al.*, 2014) and additive gene action by Zada *et al.*, 2013. For erucic acid, dominant gene action was observed in some studies (Chen and Heneen, 1989; Iqbal *et al.*, 2003; Alemayehu and Heiko, 2005; Iqbal *et al.*, 2014) and maternal effect in a study by Davik and Heneen (2009). For lenolenic acid, only dominant gene action was observed (Chen and Heneen, 1989; Iqbal *et al.*, 2003; Iqbal *et al.*, 2014). For oleic acid, dominant gene action was observed in two studies (Iqbal *et al.*, 2003; Iqbal *et al.*, 2014) and additive gene action in a study by Zada *et al.* (2013). Detailed research is needed to remove these ambiguities. The present study involved gathering and developing information on the statistical significance and genetic expression (i.e. gene action studies) of different quality-related traits of *B. rapa* that should be helpful for researchers seeking to improve its oil quality. Also, this improvement may help to convince farmers to increase the area and production of this crop.

Materials and methods

The present research was conducted at the research farm of the Department of Plant Breeding and Genetics, University of Agriculture, Faisalabad during 2013–2014. Four accessions of *B. rapa* – namely, UAF-11, BSA, Toria and TP-124–1 – were sown and crossed in diallel fashion in all possible combinations, including self and reciprocal crosses. All the agronomic practices recommended for *B. rapa* (i.e. three times hoeing, insecticide spray for control

of aphids, fertilizer application and irrigation at the proper time) were followed throughout the growing season. Precautionary measures (covering the flowers with butter paper bags and sterilization of emasculated material) were taken to avoid contamination of the genetic material at the time of crossing.

Statistical design: Twelve hybrids, along with their parents, were sown during November 2013 in the field and harvested in February 2014. The weather was slightly warm in November 2013 and February 2014, and cool in December 2013 and January 2014. A randomized complete block design was used.

Sample preparation: The crop was harvested manually in February, and seeds from each plant were collected in a single bag. For each sample, six bags from each entry for each trait were prepared as follows: 4–5 g of seeds taken randomly for each sample from all plants were collected in a polythene bag and sent to the Nuclear Institute for Food and Agriculture (NIFA), Peshawar, Pakistan for analysis of quality traits.

Traits studied: Data were collected on the quality traits (oil percentage, glucosinolate, protein percentage, erucic acid, lenolenic acid, oleic acid and moisture percentage), determined according to the procedure outlined below. The samples were scanned on a monochromator (NIR Systems, model 6500) equipped with a sample autochanger. The standard ring cup, which requires a seed volume of about 5 g, was used. For each sample, the reflectance spectrum ($\log 1/R$) from 400 to 2500 nm was recorded at 2-nm intervals. Calibration and validation procedures were carried out with ISI software, version 1a.1 (Infrasoft International) as described by Anonymous (1998).

Statistical analysis: Statistical analysis was done following Steel *et al.* (1997).

Diallel analysis: Diallel analysis was done following Hayman, (1954) and Jinks (1954).

The traits glucosinolate, protein percentage, oil percentage, erucic acid, lenolenic acid, oleic acid and moisture percentage were determined by NIR, as described above.

Methods of genetic analysis

Adequacy of the genetic model to the data set was determined using a scaling test, known as regression coefficient (b) analysis. According to Hayman (1954), regression coefficient (b) must deviate significantly from zero, but not from unity if all the assumptions under the model are fulfilled. To carry out the genetic analysis, the data for each trait were presented in the form of a diallel table, taking the mean of direct and reciprocal crosses. From the diallel table, variance (V_r) of each array and covariance (W_r) of parents with the non-recurrent parental means were calculated. The formulae are given below.

Variance of these means with non-recurrent parents

$$V_r = \{\sum X^2 - (\sum X)^2/n\}/n-1$$

where,

V_r = variance of genotypic means

N = number of genotypes

X = mean value of genotypes.

Covariance of these means with non-recurrent parents

$$W_r = \{\sum XY - (\sum X) \Sigma(Y/n)\}/n - 1$$

where,

W_r = covariance

$\sum X$ = sum of mean value of variable X

$\sum Y$ = sum of mean value of variable Y

n = number of genotypes

$\sum XY$ = sum of products of variance of variable X and Y .

Regression coefficient

Regression coefficient was calculated using the formula:

$$b = \text{Cov}(W_r V_r) / \text{Var}(V_r)$$

Standard error

Standard error (SE) of regression line slope was estimated using the formula:

$$SE = \text{Var}(\text{Cov}) - b\{\text{cov}(\text{Var}, W_r)\} / \text{Var}(\text{Var}) \times (n - 2)$$

The statistical significance of regression coefficient (b) was tested using the 't' test against $n-2$ degree of freedom at 5% and 1% probability levels. The information on gene action was obtained by plotting the covariance (W_r) of each array against its variance (V_r). The slope and position of the regression line were fitted to the array points. If the line is a unit slope ($b = 1$) and passes through the origin, complete dominance is indicated. The movement of the line upwards or downwards denotes decreasing and increasing dominance, respectively. If the line intercepts the W_r axis below the origin, it shows over dominance, whereas if the line is almost tangential to the parabola, it shows an additive type of gene action. The position of the array of points on the regression line indicates the distribution of the dominant and the recessive genes within the common parent of the array. These statistics were used to estimate four genetic components of variation: D (additive effect of gene), H_1 and H_2 (dominance effects of genes) and F , which provides an estimate of the relative frequency of dominant to recessive alleles in the parental lines and the variation in the dominance over the loci. Hence, F is positive whenever the dominant alleles are more frequent than the recessive alleles, irrespective of whether or not the alleles have increasing or decreasing effects. In the additive-dominance model, reciprocal F_1 families have identical expectations and are generally averaged before computing these

statistics; thus, they have the environmental component, E (Hayman and Jinks, 1977).

Soft wares: Statistix 8.1 was used to determine statistical significance, and Microsoft Excel and AN-DIA version 1.0 were used for calculation of Hayman and Jinks diallel parameters.

Results

The mean values of all plant traits were measured and statistically analyzed according to Steel *et al.* (1997). The combined ANOVA (Table 1) showed that all the traits (oil percentage, glucosinolate, protein percentage, erucic acid, lenolenic acid, oleic acid and moisture percentage) differed significantly for their mean squares ($\alpha=0.01$). Replication in all traits showed non-significant differences for its mean squares ($\alpha=0.05$), which indicated that it has no effect in controlling the experimental error. CV% indicated that data were reliable in all traits except oleic acid, in which data were partially reliable (Table 1). Combined ANOVA showed high variability, which meant that the Hayman (1954) and Jinks (1954) simple additive model could be used to analyze the data. The adequacy of this model was determined through a scaling test; that is, joint regression analysis and regression coefficient (b) of every trait (Table 2). The parameters in Table 3 were calculated as described in the Materials and methods section.

Hayman and Jinks diallel

The significant difference within the array ($W_r - V_r$) for oil percentage, glucosinolate and erucic acid indicated the absence of epistasis; also, the non-significant differences within the array ($W_r - V_r$) for protein percentage, lenolenic acid and oleic acid indicated the presence of dominant gene action. These results showed that the additive dominance model was appropriate for both tests. The significant difference between arrays ($W_r + V_r$) and within the array ($W_r - V_r$) for oil percentage, glucosinolate and erucic acid showed inter-allelic interaction in the inheritance of these characters. This means that the additive dominance model was appropriate for these characteristics. In contrast, the significant differences between arrays and the non-significant difference within the array for protein percentage, lenolenic acid, oleic acid and moisture percentage showed that the additive dominance model was partially suitable for these characteristics. Regression coefficient (b) should deviate from zero as well as from unity, according to Hayman (1954). The results of the scaling tests indicated that the regression coefficient (b) was deviating from zero for oil percentage ($1.02 + 0.05$), glucosinolate ($0.82 + 0.12$), protein percentage ($0.97 + 0.03$), erucic acid ($0.99 + 0.07$), lenolenic acid ($0.94 +$

0.06) and oleic acid (0.97 + 0.06). These findings showed that these data were fit for genetic analysis. Genetic analysis information was estimated through W_r/V_r graphical presentation, as suggested by Hayman (1954) and Jink (1954), from slope and position of regression line (see Graphs 1–7).

Oil percentage

The distribution of genotypic values in Graph 1 shows that UAF-11 is farthest from the origin whereas TP-124–1 is nearest to the origin, and toria and BSA are in the middle. The components of variation in relation to the oil percentage are given in Table 3. The value of D (149.09) was greater than H_1 (62.721) and H_2 (131.779); the value of $\frac{1}{4}H_2/H_1$ (0.005) was less than 0.25 and the value of $(H_1/D)^{1/2}$ (1.345) was greater than 1. Direction of dominance h^2 (45.072) was positive. The value of $[(4DH_1)^{1/2}+F]/[(4DH_1)^{1/2}-F]$ (0.423) was greater than that of F (-162.62). The value of narrow sense heritability was 0.992 (i.e. 99.2%).

Glucosinolate

The distribution of genotypic values in Graph 2 shows that TP-124–1 is farthest from the origin, whereas toria is near to the origin, and UAF-11 and BSA are in the middle. The components of variation in relation to glucosinolate are given in Table 3. The value for H_1 (1842.06) was greater than D (796.21), although the value of D (796.21) was greater than H_2 (378.44); the value of $\frac{1}{4}H_2/H_1$ (0.051) was less than 0.25 and the value of $(H_1/D)^{1/2}$ (1.52) was greater than 1. The direction of dominance h^2 (213.74) was positive. The value of $[(4DH_1)^{1/2}+F]/[(4DH_1)^{1/2}-F]$ (0.604) was greater than that of F (-598.21). The value of narrow sense heritability was 0.937 (i.e. 93.7%).

Protein percentage

The distribution of genotypic values in Graph 3 shows that TP-124–1 is farthest from the origin, whereas toria and UAF-11 are near to the origin, and BSA is in the middle. The components of variation in relation to the protein percentage are given in Table 3. The value of H_1 (87.21) was greater than D (45.75) although value of D (45.75) was greater than H_2 (-0.88); the value of $\frac{1}{4}H_2/H_1$ (-0.003) was less than 0.25 and the value of $(H_1/D)^{1/2}$ (1.381) was greater than 1. Direction of dominance h^2 (19.75) was positive. The value of $[(4DH_1)^{1/2}+F]/[(4DH_1)^{1/2}-F]$ (0.356) was greater than that of F (-59.96). The value of narrow sense heritability was 0.992 (i.e. 99.2%).

Erucic acid

The distribution of genotypic values in Graph 4 shows that UAF-11, BSA and toria are farthest from

the origin at almost same positions, while TP-124–1 is near to origin. The components of variation in relation to the erucic acid are given in Table 3. The value of H_1 (493.36) was greater than D (302.69) although value of D (302.69) was greater than H_2 (29.59); the value of $\frac{1}{4}H_2/H_1$ (0.015) was less than 0.25 and the value of $(H_1/D)^{1/2}$ (1.277) was greater than 1. Direction of dominance h^2 (230.72) was positive. The value of $[(4DH_1)^{1/2}+F]/[(4DH_1)^{1/2}-F]$ (0.431) was greater than F (-306.99). The value of narrow sense heritability was 0.985 (i.e. 98.5%).

Lenolenic acids

The distribution of genotypic values in Graph 5 shows that BSA is farthest from the origin, whereas UAF-11 and toria are near to origin, and TP-124–1 is in the middle. The components of variation relative magnitude for lenolenic acid are given in Table 3. The value for H_1 (10.30) and H_2 (13.99) was greater than D (1.05); the value of $\frac{1}{4}H_2/H_1$ (-0.015) was less than 0.25 and the value of $(H_1/D)^{1/2}$ (1.370) was greater than 1. Direction of dominance h^2 (3.01) was positive. The value of $[(4DH_1)^{1/2}+F]/[(4DH_1)^{1/2}-F]$ (0.330) was greater than F (-10.30). The value of narrow sense heritability was 0.951 (i.e. 95.1%).

Oleic acid

The distribution of genotypic values in Graph 6 shows that TP-124–1 is farthest from the origin, whereas UAF-11 is near to the origin, and toria and BSA are in the middle. The components of variation relative magnitude for oleic acid are given in Table 3. The value for H_1 (269.47) was greater than D (149.09) although value of D (149.09) was greater than H_2 (6.05); the value of $\frac{1}{4}H_2/H_1$ (0.006) was less than 0.25 and the value of $(H_1/D)^{1/2}$ (1.344) was greater than 1. Direction of dominance h^2 (3.01) was positive. The value of $[(4DH_1)^{1/2}+F]/[(4DH_1)^{1/2}-F]$ (0.330) was greater than F (-10.30). The value of narrow sense heritability was 0.951 (i.e. 95.1%).

Moisture percentage

The distribution of genotypic values in Graph 7 shows that toria is farthest from the origin, whereas TP-124–1 is near to the origin, and UAF-11 and BSA are in the middle. The components of variation relative magnitude for moisture percentage are given in Table 3. The value for H_1 (3.21) was greater than D (2.32) although value of D (2.32) was greater than H_2 (-1.95; the value of $\frac{1}{4}H_2/H_1$ (-0.15) was less than 0.25 and the value of $(H_1/D)^{1/2}$ (1.18) was greater than 1. Direction of dominance h^2 (0.80) was positive. The value of $[(4DH_1)^{1/2}+F]/[(4DH_1)^{1/2}-F]$ (0.08) was greater than F (-4.66). The value of narrow sense heritability was 0.91 (i.e. 91%).

Table 1. Combined ANOVA and CV% for different traits in *Brassica rapa*

| Traits | Replication (DF=1) | Genotype (DF=15) | Error (DF=15) | CV %age |
|---------------------|--------------------|------------------|---------------|---------|
| Oil percentage | 32.00 | 22.05** | 0.0006 | 19 |
| Glucosinolate | 24.15 | 698.57** | 0.07 | 4 |
| Protein percentage | 32 | 3.09** | 0.0007 | 2 |
| Erucic acid | 26.28 | 108.84** | 0.08 | 2 |
| Lenolenic acid | 33.42 | 2.55** | 0.01 | 3 |
| Oleic acid | 33.42 | 22.69** | 0.45 | 35 |
| Moisture percentage | 4.86 | 1.18** | 0.02 | 1 |

** = Highly significant at 1% F value, * = Significant at 5% F value, ns = Non-Significant

Table 2. Scaling test (Joint regression analysis) of different plant traits of *Brassica rapa*

| Traits | B | b=0 | b=1 | Wr+Vr | Wr-Vr |
|---------------------|-------------|--------|---------------------|-----------|---------------------|
| Oil percentage | 1.02 + 0.05 | 21.56* | -0.42 ^{NS} | 391.44** | 6.55* |
| Glucosinolate | 0.82 + 0.12 | 7.09* | 1.54 ^{NS} | 1494.42** | -124.80** |
| Protein percentage | 0.97 + 0.03 | 36.10* | 1.08 ^{NS} | 96.50** | -1.21 ^{NS} |
| Erucic acid | 0.99 + 0.07 | 13.29* | 0.19 ^{NS} | 561.68** | 38.37** |
| Lenolenic acid | 0.94 + 0.06 | 15.37* | 1.04 ^{NS} | 16.80** | -0.39 ^{NS} |
| Oleic acid | 0.97+ 0.06 | 15.75* | 0.55 ^{NS} | 290.08** | -1.55 ^{NS} |
| Moisture percentage | 0.97 ± 0.07 | 12.98* | 0.41 ^{NS} | 6.48** | 0.01 ^{NS} |

(t at n-2 df ($\alpha = 5\%$) = 4.303, Highly significant, * = Significant, ns = Non-Significant

Table 3. Components of variation in oil percentage of *Brassica rapa*

| Component | Oil percentage Parameters ± S.E. | Glucosinolate Parameters ± S.E. | Protein percentage Parameters ± S.E. | Erucic acid Parameters ± S.E. | Lenolenic acid Parameters ± S.E. | Oleic acid Parameters ± S.E. | Moisture percentage Parameters ± S.E. |
|---|----------------------------------|---------------------------------|--------------------------------------|-------------------------------|----------------------------------|------------------------------|---------------------------------------|
| D | 149.09 ± 35.61 | 796.21 ± 280.18 | 45.75 ± 5.95 | 302.69 ± 74.17 | 1.05 ± 0.08 | 149.09 ± 74.00 | 2.32 ± 0.17 |
| F | -162.62 ± 36.57 | -598.21 ± 242.86 | -59.96 ± 6.81 | -306.99 ± 74.70 | 7.46 ± 1.17 | -162.62 ± 77.29 | -4.66 ± 0.25 |
| H ₁ | 62.721 ± 45.48 | 1842.06 ± 426.16 | 87.21 ± 8.21 | 493.36 ± 94.69 | -10.30 ± 1.37 | 269.47 ± 99.49 | 3.21 ± 0.35 |
| H ₂ | 131.779 ± 6.03 | 378.44 ± 193.16 | -0.88 ± 0.82 | 29.59 ± 23.19 | 13.99 ± 0.33 | 6.05 ± 1.91 | -1.95 ± 0.29 |
| h ² | 45.072 ± 29.51 | 213.74 ± 145.17 | 19.75 ± 3.91 | 230.72 ± 64.76 | -0.83 ± 0.36 | 62.19 ± 17.79 | 0.80 ± 0.23 |
| (H ₁ /D) ^{1/2} | 1.345 | 1.521 | 1.381 | 1.521 | 1.370 | 1.344 | 1.18 |
| 1/4H ₂ /H ₁ | 0.005 | 0.051 | -0.003 | 0.051 | -0.015 | 0.006 | -0.15 |
| h ² /H ₂ | 10.28 | 0.56 | -22.529 | 0.56 | -3.643 | 10.277 | -0.41 |
| [(4DH ₁) ^{1/2} +F]/[(4DH ₁) ^{1/2} -F] | 0.423 | 0.604 | 0.356 | 0.604 | 0.330 | 0.423 | 0.08 |
| h ² ns | 0.992 | 0.937 | 0.992 | 0.937 | 0.951 | 0.992 | 0.91 |

D= Additive Gene effect, H₁ and H₂= Dominance effects of genes, F= Frequency of dominant alleles, h²= Direction of dominance and h²ns = Narrow sense heritability, S.E. = Standard Error

Discussion

In all graphs, the covariance for all traits covariance was above the origin, and the deviation of the estimated regression line was non-significant from the unit slope. This finding indicated that allelic interaction was present in all traits. Based on the graphs, for oil percentage, UAF-11 has the greatest number of recessive genes, TP-124-1 has the greatest number of dominant genes, and toria and BSA have an intermediate number of dominant and recessive genes. For glucosinolate, TP-124-1 has the greatest number of recessive genes, toria has the greatest number of dominant genes, and UAF-11 and BSA have an intermediate number of dominant and recessive genes. For protein percentage, TP-124-1 has the greatest number of recessive genes, toria and UAF-11 have the greatest number of dominant genes for protein percentage, and BSA has an intermediate number of dominant and recessive genes. For erucic acid, UAF-11, BSA and toria have the greatest number of

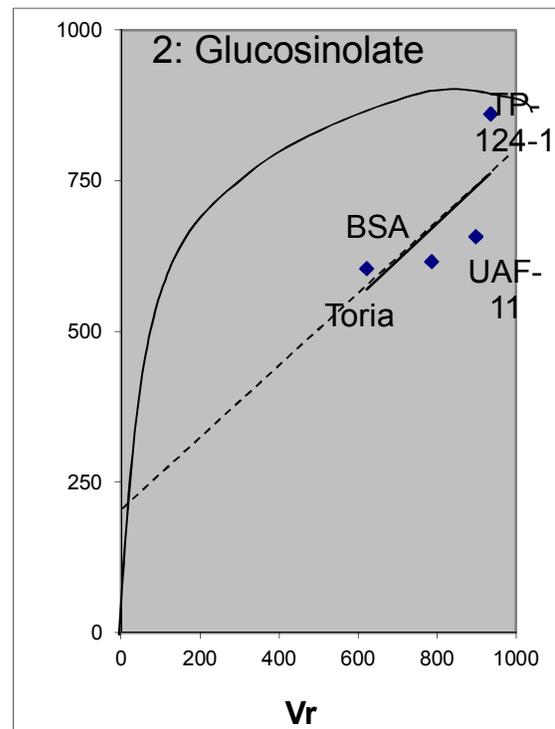
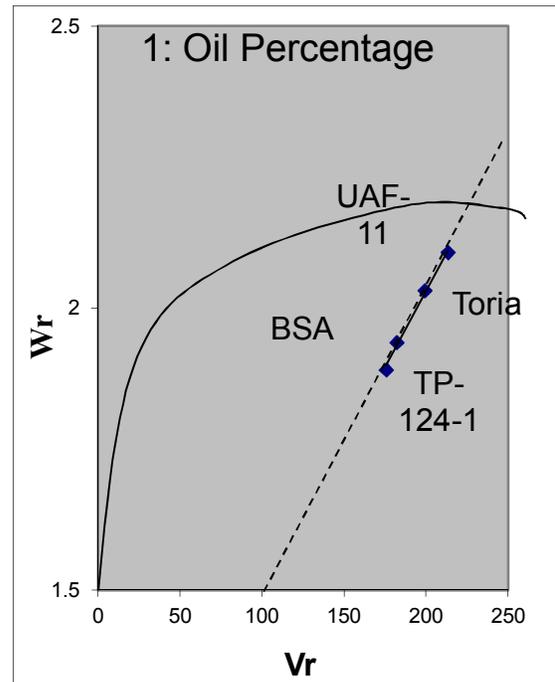
recessive genes while TP-124-1 has the greatest number of dominant genes. For lenolenic acid, BSA has the greatest number of recessive genes, UAF-11 and toria have the greatest number of dominant genes, and TP-124-1 has an intermediate number of dominant and recessive genes. For oleic acid, TP-124-1 has the greatest number of recessive genes, UAF-11 has the greatest number of dominant genes for oleic acid and toria, and BSA has an intermediate number of dominant and recessive genes. For moisture, toria has the greatest number of recessive genes, TP-124-1 has the greatest number of dominant genes, and UAF-11 and BSA have an intermediate number of dominant and recessive genes. As in component of variation, a value of D that is higher than H₁ and H₂ indicates a dominant type of gene action, a value of D that is less than H₂ indicates some type of additive genetic control, and a value of D that is less than both H₁ and H₂ indicates complete additive genetic control. A value of 1/4H₂/H₁ (0.003) of less than 0.25 indicates a

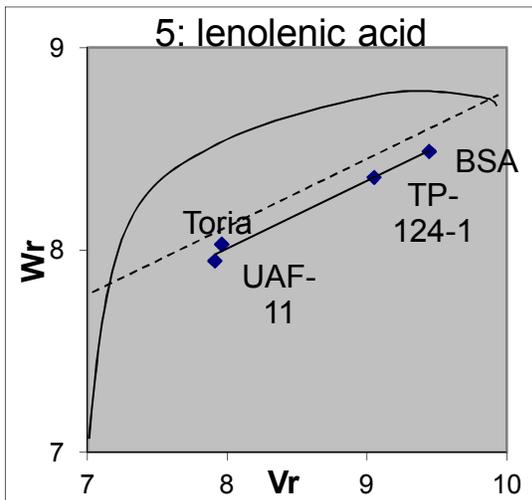
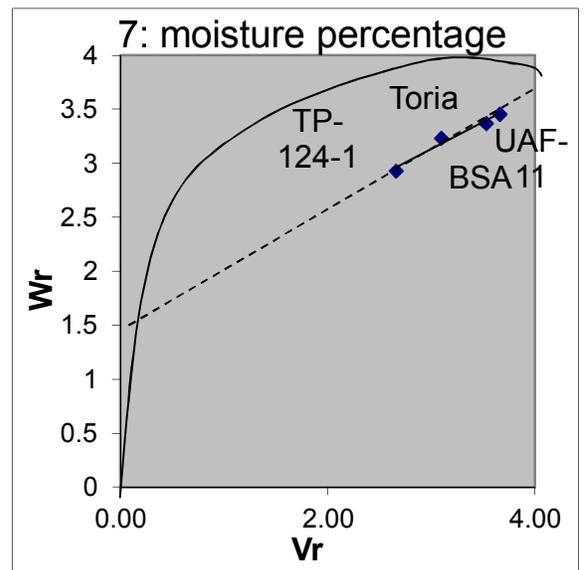
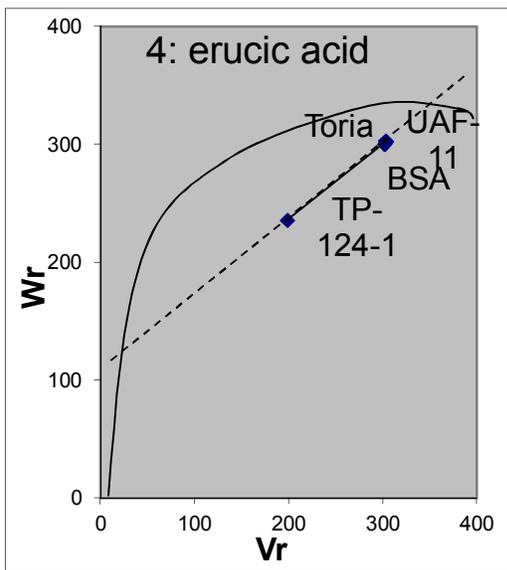
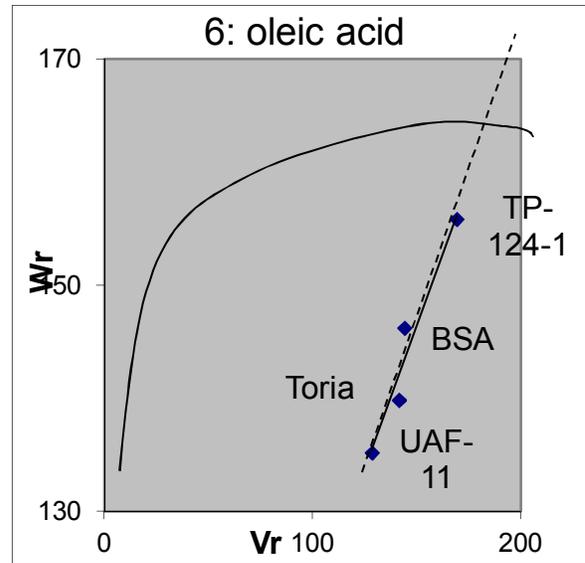
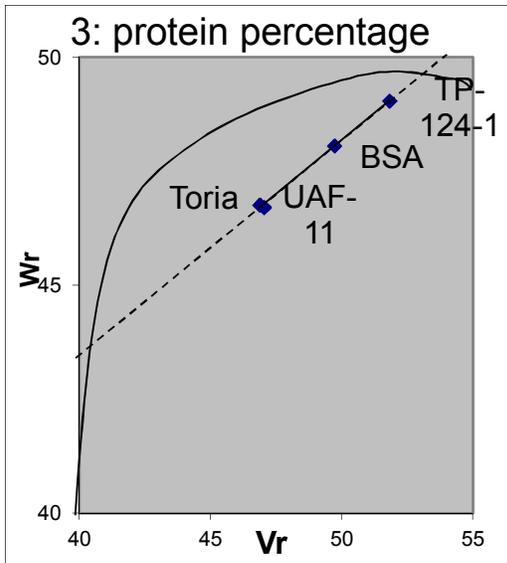
maternal effect. Average degree of dominance was observed from $(H_1/D)^{1/2}$. If that value is greater than 1, it indicates the presence of partial dominance in control of variation. Direction of dominance is indicated by h^2 ; if that value is positive, it shows frequency of dominant genes towards better parents, and if it is negative, it shows frequency of recessive genes towards better parents. If the value of $[(4DH_1)^{1/2}+F]/[(4DH_1)^{1/2}-F]$ is greater than the value of F , it indicates that the number of recessive genes exceeds the number of dominant genes, and vice versa (Hayman and Jinks, 1977). Our results suggested that oil percentage and lenolenic acid were controlled by additive gene action. In contrast, glucosinolate, protein percentage, erucic acid, oleic acid and moisture percentage were controlled by dominant gene action, with control of additive gene action present to some extent. For all traits, maternal effects were also present; direction of dominance was more frequent towards better parents, except in the case of lenolenic acid; and numbers of recessive genes were greater than number of dominant genes in the parents, again except in the case of lenolenic acid. The high value of narrow sense heritability showed that selection on the basis of all these traits could be helpful in future breeding programs. These findings support those of Chen and Heneen (1989), Iqbal *et al.* (2003), Alemayehu and Heiko (2005), Pankaj *et al.* (2008), Davik and Heneen (2009), Ahmed (2010), Ali *et al.*, (2010); Ali *et al.* (2013), Nasim and Farhatullah (2013); Ali *et al.*, (2014) and Iqbal *et al.* (2014), as described in the introduction.

Conclusion

Glucosinolate, protein percentage, erucic acid, oleic acid and moisture percentage were controlled by dominant gene action whereas lenolenic acid and oil percentage was controlled by additive gene action. Number of frequency of dominant genes were more frequent towards better parents except in the case of lenolenic acid. Recessive genes were more numerous than dominant genes for all traits other than lenolenic acid. A highly heritable trait was protein percentage, which had the highest narrow sense heritability. Non-allelic interaction (epistasis) was observed in all traits, and maternal effect was present in all traits. For selection of best parents in starting of a hybrid program, the best parents were TP-124-1 and UAF-11, as they had the greatest number of dominant and recessive genes, especially for oil percentage, protein percentage, erucic acid, oleic acid and moisture percentage respectively for best traits. Hence, they can be used as parents in future hybrid breeding and other future breeding programs.

Graphs: 1, 2, 3, 4, 5, 6 and 7





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