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Expression of heterosis, heterobeltiosis, and gene action in quantitative characters of soybean (*Glycine max*)

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Abstract. *Krisnawati A, Adie MM. 2022. Expression of heterosis, heterobeltiosis, and gene action in quantitative characters on soybean (*Glycine max*). Biodiversitas 23: 1745-1751.* Most soybean (*Glycine max* (L.) Merrill) varieties have been created by crossing two or more parental genotypes. The study aimed to quantify the value of heterosis, heterobeltiosis, the degree of dominance as well as the gene action of the agronomic characters of F_1 plants derived from the four soybean cross combinations. All the parents and crosses were evaluated in the screen house of the Indonesian Legume and Tuber Crops Research Institute (Malang, East Java, Indonesia) during 2021. The estimation for mid-parent heterosis (hMP), high-parent heterosis or heterobeltiosis (hHP), degree of dominance, and gene action was done for seven quantitative characters (plant height, number of branches, number of nodes, number of filled pods, number of empty pods, weight of 10 seeds, and seed yield). The performance of the quantitative characters differs among cross combinations. The estimated value of heterosis mid-parent (hMP) for F_1 crosses from four parental combinations ranged from -61.20 to 27.57, heterobeltiosis (hHP) ranged from -71.17 to 9.84, and the degree of dominance ranged from -6.45 to 19.40. The crosses of Derap 1 × Gepak Kuning and Dering 1 × Gepak Kuning showed a positive hMP and hHP for seed yield character. Thus, these hybrids could be used to develop high-yielding varieties with desirable traits in soybean. Seed yield character in the cross of Derap 1 × Gepak Kuning exhibited the overdominance type of gene action, meanwhile, the Dering 1 × Gepak Kuning was incomplete dominance.

Keywords: Agronomy character, degree of dominance, F_1 generation, heterosis, seed yield

INTRODUCTION

Plant varieties play an important role in the structure of soybean cultivation and in determining productivity per unit area. Parental selection is crucial for establishing genetically diverse breeding populations for a characteristic under selection in soybean and other crop breeding (Friedrichs et al. 2016). Most soybean varieties are created by crossing two or more parents, and a few are created through mutation, introduction, or selection processes of local soybean varieties. Hybridization between parents with different genetic backgrounds will result in offspring with the genetic content of both parents.

The relationship between heredity and the ancestors has been a fascinating study over the last few decades, highlighting the phenomenon of heterosis (Fujimoto et al. 2018). Heterosis is considered one of the most important genetic contributions to agriculture, affecting agricultural seed yield significantly (Pandini et al. 2002). The knowledge of heterosis can assist breeders in selecting the best hybrid combinations that will serve as the basis for the selection of superior genotypes (Ahmad 2015). It can also be useful in obtaining pure lines if there is a significant contribution of the additive x additive epistatic interaction (Pimentel 1991). Furthermore, knowing its magnitude can aid the breeder in selecting a selection method and identifying the dominant gene effect in the evaluated crosses (Pandini et al. 2002).

In theory, heterosis is defined as an increase in F_1 vigor over the mean of parents as well as an increase in vigor over the superior parent (Hayes et al. 1955). Heterosis comes in three different types: mid parent (heterosis), standard variety (check parent), and better parent (heterobeltiosis). Offspring from crosses with superior characteristics to their parents are classified as having hybrid vigor or positive heterosis (Ghazy and Fouad 2021). Rialch et al. (2019) used the mean performance, heterosis, and combining ability values to determine the best soybean parents and crosses for quality traits on soybean. According to Yamgar et al. (2021), the soybean parent used for each cross combination determined the estimated value of mid-parent heterosis, better parent heterosis, and specific combing ability, and it was also reported in that study that the effect of dominant genes was maximum in F_1. A study by Krisnawati and Adie (2018) on five cross combinations performed reciprocally on soybeans showed that the hybrid of Rajabasa × G100H demonstrated consistently high heterosis and heterobeltiosis for the characters of the number of branches/plant, number of pods/plant, number of seed/plant, and seed yield/plant.

In other leguminous plants, the heterosis phenomenon is also used to improve progeny via crossbreeding. The maximum positive standard heterosis and negative standard heterosis in peanuts are related to the parental genetic diversity, which is different for each agronomic trait (Waghmode et al. 2017). A study on cowpea by Verma et al. (2020) reported that eight hybrids had significant negative heterosis for days to 50% flowering and five hybrids had significant positive heterobeltiosis and produced more flowers per cluster. In dry beans, the seed yield character was controlled by a non-additive dominant gene, heritability was found to be low, and the heterosis and heterobeltiosis values of the F_1 generations were positive (Tamüksek and Ceyhan 2020). Meanwhile, Tampha et al. (2018) were successful in identifying crosses in the field pea, specifically KPMR 939 × Makhyatmubi, which demonstrated high heterosis over the better and standard parent for seed yield per plant and harvest index.

The majority of soybean varietal improvement programs aim to increase grain yields. Positive heterosis is generally preferred for traits like yield, whereas negative heterosis is preferred for traits like early maturity (Ghazy and Fouad 2021). The soybean cross USP 04-17.027 × USP 231-2224-12 was found to have a high specific combining ability on seed yield character (Rocha et al. 2018). In another study in soybean, a high potency ratio was reported in a cross between Rajabasa and G100H, indicating that the role of the additive/epistasis gene was less prominent than the role of the over-dominant gene (Krisnawati and Adie 2018). Understanding the various gene actions for each character is critical for a varietal development program to succeed. The study aimed to quantify the value of heterosis, heterobeltiosis, the degree of dominance as well as the gene action of the agronomic characters derived from the four soybean cross combinations.

MATERIALS AND METHODS

Plant material and study location

The materials for the study were comprised as F_1 plants derived from four cross combinations, namely Gepak Kuning × Wilis (87 F_1 plants), Gema × Gepak Kuning (79 F_1 plants), Derap 1 × Gepak Kuning (55 F_1 plants), and Dering 1 × Gepak Kuning (82 F_1 plants). In addition, all of the parents used in each cross combination were also planted. The cross was carried out in 2020 at the Indonesian Legume and Tubers Crop Research Institute (ILETRI) in Malang, Indonesia. F_1 seeds were planted at ILETRI from April to August 2020 to produce F_1 plants.

Experimental materials

Each cross seed, along with its parents, was sown in a plastic pot (Φ=18 cm) containing a mixture of soil and organic fertilizer (1:1). The fertilizer dose of NPK was 2.0 g/pot which was applied at the time of showing. Plant maintenance, which includes weeding, watering, was carried out optimally. Pests and diseases were effectively controlled. All quantitative characters were observed after the plant reached maturity, and some were observed after the seeds had been processed. Plant height (cm), number of branches, number of nodes, number of filled pods, number of empty pods, the weight of 10 seeds (g), and seed yield (g) were all quantified for each plant, including the parents used.

Data analysis

Each cross combination with the parent was subjected to descriptive statistics (mean, minimal value, maximum value, and standard deviation). The performance of seven quantitative characters was visualized using histogram. The mean of F_1 hybrids was used to estimate mid-parent heterosis and high parents heterosis (heterobeltiosis) following the formula by Ghazy and Fouad (2021):

$$\text{Mid-parent Heterosis (\%)} = \frac{\bar{F}_1 - MPV}{MPV}\ x\ 100$$

$$\text{High-parent Heterosis (\%)} = \frac{\bar{F}_1 - BPV}{BPV}\ x\ 100$$

The estimation for various gene effects using the relative of potency ratio (P) to determine the degree of dominance and its direction is as follows (Petr dan Frey 1966):

$$\text{Potence Ratio (P)} = \frac{F_1 - MPV}{BPV - MPV}$$

Where:

$\bar{F}_1$ = mean value of F_1 hybrids

MPV = mid-parent value (the average performance of the two parents)

BPV =$\bar{F}_1$ better parent value (the highest performance of the parents)

Based on the value of the potence ratio, the degree of dominance is classified as follows (Petr and Frey 1966; Ibrahim et al. 2021):

$P = 0$, there is no dominance (additive)
$P = \pm 1$ = complete dominance
$-1 > P > +1$ = partial dominance
$P > \pm 1$ = overdominance

The positive and negative signs indicate the direction of the dominance of either parent.

RESULTS AND DISCUSSION

The performance of the quantitative characters

Soybean genetic improvement using four cross combinations revealed variability in hybrid performance (Table 1, Figure 1). A cross between Gepak Kuning and Wilis produced two characters with higher averages than the two parental genotypes, namely the number of branches and the number of nodes. Three characters (number of filling pods, number of empty pods, and seed weight) have lower averages than the two parents, whereas plant height and seed yield have averaged between the two parental genotypes. According to He and Li (2020), the availability of genetic diversity is essential for breeding success, and a large range of variations allows breeders to select varieties with consistently better crop performance.

F_1 plants from a cross of Gema × Gepak Kuning had a higher average number of branches than the parents, but it showed a lower number of empty pods. The plant height, number of branches, number of nodes, number of filled pods, and number of empty pods of the cross of Derap 1 × Gepak Kuning were lower than the two parents, while the number of branches was higher than the parents. The average plant height, number of branches, and number of empty pods of the cross of Dering 1 × Gepak Kuning were lower than the two parents, whereas the other characters are between two parents. A study by Kataliko et al. (2018) found the parental genotypes were generally taller compared to their F_1 progenies, meanwhile Gavioli et al. (2006) found progenies to be taller than parents.

The high mean performance recorded by some crosses than all parental genotypes may be as a result of recombination of additive alleles or interaction between two alleles of two different genes due to a wide variation between genotypes of their parents (Marame et al. 2009; Umar et al. 2017). Furthermore, genetic diversity and phenotypic variability resulted from differential gene expression (Friedrichs et al. 2016). Due to the fact that soybean is a paleopolyploid with two polyploidy events (Schlueter et al. 2004), as a result, 75% of the genes have multiple copies, with the majority displaying differential expression (Roulin et al. 2013).

Table 1. Descriptive statistics of quantitative characters of F_1 plants derived from four soybean cross combinations

Cross combination	**DS**	**Quantitative character**						
		PHG	**NOB**	**NON**	**NFP**	**NEP**	**SWG**	**YLD**
Gepak Kuning × Wilis (n = 87 F_1)	Mean	59.70	4.86	20.91	41.18	1.39	10.96	1.11
	Min	29.00	3.00	10.00	14.00	0.00	4.10	0.77
	Max	89.00	8.00	39.00	84.00	7.00	49.77	1.54
	Std	12.39	1.20	6.22	13.16	1.50	5.40	0.18
Gema × Gepak Kuning (n = 79 F_1)	Mean	51.63	4.24	17.09	35.01	0.52	9.12	1.00
	Min	30.00	1.00	7.00	14.00	0.00	3.74	0.61
	Max	81.00	8.00	35.00	70.00	3.00	16.80	1.70
	Std	10.59	1.37	5.14	11.16	0.93	2.54	0.18
Derap 1 × Gepak Kuning (n = 55 F_1)	Mean	46.25	4.16	15.35	34.64	1.00	10.88	1.19
	Min	26.00	0.00	6.00	16.00	0.00	4.67	0.52
	Max	69.00	8.00	31.00	56.00	5.00	18.79	1.63
	Std	9.73	1.40	4.94	10.34	1.31	3.29	0.22
Dering 1 × Gepak Kuning (n = 82 F_1)	Mean	48.16	4.44	17.09	49.30	1.39	11.53	1.00
	Min	27.00	2.00	6.00	12.00	0.00	2.85	0.63
	Max	74.00	7.00	37.00	130.00	10.00	26.68	1.34
	Std	11.29	1.16	5.67	22.30	2.22	4.59	0.15
Parental:								
Gepak Kuning	Mean	53.80	3.20	18.80	49.20	2.20	12.63	0.62
	Min	48.00	2.00	17.00	46.00	1.00	11.74	0.29
	Max	59.00	4.00	21.00	54.00	4.00	14.17	0.74
	Std	3.97	0.75	1.60	2.93	0.98	0.88	0.17
Wilis	Mean	61.40	3.20	20.60	48.20	1.80	14.60	1.36
	Min	59.00	3.00	18.00	45.00	0.00	13.97	1.22
	Max	66.00	4.00	23.00	51.00	4.00	15.40	1.61
	Std	2.58	0.40	1.85	2.04	1.33	0.54	0.14
Gema	Mean	45.20	3.00	15.20	34.20	1.60	8.07	1.12
	Min	42.00	2.00	13.00	29.00	0.00	7.13	1.01
	Max	48.00	4.00	19.00	40.00	4.00	9.40	1.26
	Std	2.14	0.63	2.14	3.87	1.50	0.94	0.08
Derap 1	Mean	52.00	2.80	17.00	35.80	2.00	10.04	1.45
	Min	48.00	2.00	14.00	29.00	1.00	7.11	1.41
	Max	57.00	3.00	20.00	42.00	4.00	14.01	1.51
	Std	3.29	0.40	2.19	4.31	1.10	2.87	0.04
Dering 1	Mean	54.60	3.60	22.20	50.60	2.00	11.01	1.04
	Min	52.00	3.00	19.00	40.00	0.00	8.36	0.87
	Max	57.00	4.00	26.00	61.00	4.00	13.68	1.20
	Std	1.74	0.49	2.32	6.71	1.41	1.85	0.11

Note: DS: descriptive statistic, Min: minimal value, Max: maximum value, Std: standard deviation, PHG: plant height (cm), NOB: number of branches, NOD: number of nodes, NFP: number of filled pods, NEP: number of empty pods, SWG: 10 seeds weight (g), YLD: seed yield/plant (g)

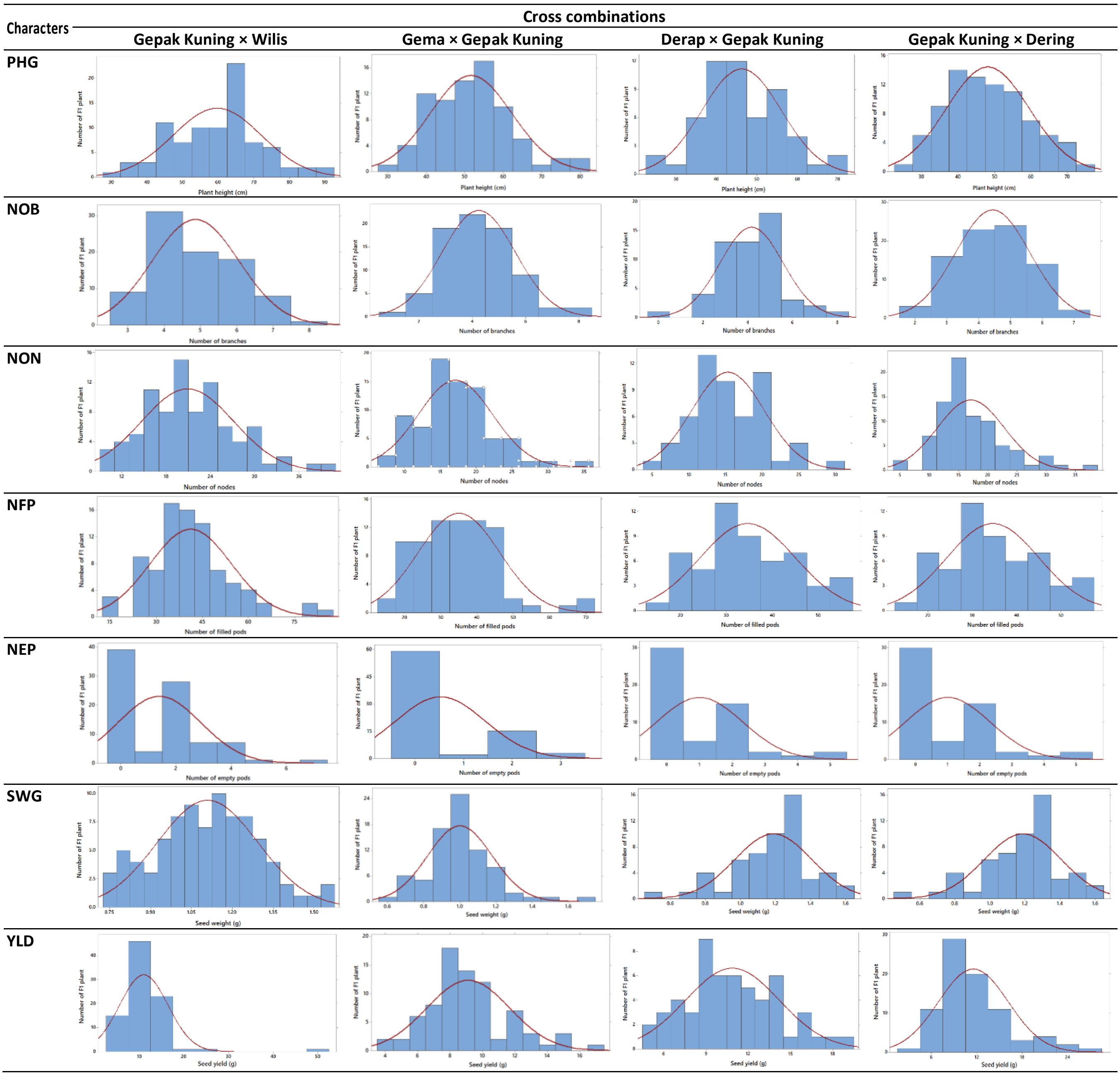

Figure 1. The performance of quantitative characters of F_1plant from four cross combinations. Note: PHG: plant height, NOB: number of branches, NON: number of nodes, NFP: number of filled pods, NEP: number of empty pods, SWG: 10 seeds weight, YLD: seed yield

Estimation for heterosis and heterobeltiosis

The estimation for mid-parent heterosis (hMP) and high-parent heterosis or heterobeltiosis (hHP) revealed a variation in value among quantitative characters, as well as cross-combination. Heterosis reflects F_1plants' superiority over the mean parents, whereas heterobeltiosis represents the F_1plants' superiority over better parent value.

In this study, hMP and hHP for seed yield of four cross combinations ranged from -13.05% to 6.61% and -24.88% to 4.73%, respectively. The seed yield characters in the crosses of Gepak Kuning × Wilis and Gema × Gepak Kuning showed negative hMP and hHP values, on the other hand, the crosses of Derap 1 × Gepak Kuning and Dering 1 × Gepak Kuning have positive values. A high seed yield is a desirable attribute in soybean crops. Therefore, significant positive heterosis was considered desirable for this character. Thus, the opportunity to achieve a high yield increase are possible through the crosses of Derap 1 × Gepak Kuning, and Dering 1 × Gepak Kuning. The highest hMP and hHP values for yield were exhibited by the hybrid of the Dering 1 × Gepak Kuning. The high heterosis value of this generation suggested that these hybrid generations could be a significant source of greater seed yield per plant. Pandini et al. (2002) found the most expressive values of positive heterosis were obtained for seed yield among other agronomic traits in soybean. A study by Ya-li et al. (2018) in soybean obtained the positive mid-parent yield heterosis combinations accounted for 55%, heterobeltiosis combinations accounted for 30%, and more than 20% of mid-parent and over-high parent heterosis accounted for 15%. Positive heterosis in seed yield of soybean also obtained in other studies (Samant et al. 2014; Krisnawati and Adie 2018; Waly and Ibrahim 2021), suggest that for some combinations, considerable yield gains are achievable. In other plants, such as sesame, Nehra et al. (2021) obtained the heterosis ranged between -25.6% to 49.53% for seed yield per plant. According to Pandini et al. (2002), the expressive levels of heterosis discovered for seed yield may justify the use of recurrent selection and the future use of commercial hybrids in soybeans.

In terms of yield, medium-tall or tall soybean plants with a good number of pods per plant are preferred. For plant height character, hMP ranged from -10.56% to 5.82% and hHP ranged from -11.80% to 0.38%. The F_1 plants from the cross of Derap 1 × Gepak Kuning and Dering 1 × Gepak Kuning had negative hMP and hHP values, while Gema × Gepak Kuning had positive hMP and hHP, and Gepak Kuning × Wilis had a positive hMP value but a negative hHP value. A study by Sen (2020) found all crosses in soybean had highly significant positive heterosis effects relative to mid- parent, which ranged from 3.69 to 36.01. In another study, a varying value of heterosis for plant height was also obtained, with hMP ranging from -6% to +6% and hHP ranging from -7% to +4% (Perez et al. 2009). In a more recent study (Yamgar et al. 2021), the highest hMP and hHP in desirable direction for plant height was reported in F_1 of JS335 × SDP 18 (25.08% and 21.21%, respectively).

For the number of branches, the highest positive hMP and hHP were shown by crosses of Gepak Kuning × Wilis (27.51% and 9.84%, respectively). The cross of Dering 1 × Gepak Kuning also had positive hMP and hHP (10.61% and 0.29%, respectively). Meanwhile, the crosses of Gema × Gepak Kuning dan Derap 1 × Gepak Kuning had positive hMP but negative hHP. Another study found the highest positive hMP in F1 was 32.20% (Yamgar et al. 2021). The high value of heterosis indicates that hybridization would be effective in generating improved varieties. On the character of the number of nodes, the cross of Gepak Kuning × Wilis exhibited the highest positive hMP and hHP (9.45% and 1.50%, respectively). The crosses of Derap 1 × Gepak Kuning, and Dering 1 × Gepak Kuning showed negative hMP and hHP; meanwhile, Gema ×Gepak Kuning had a positive hMP and a negative hHP.

In the number of filled pods per plant, negative hMP and hHP were found, except for Dering 1 × Gepak Kuning which showed a positive hMP. A study by Sen (2020) obtained a highly significant positive heterotic effect in several crosses of soybean ranging from 3.09 to 37.74 and 2.59 to 18.13 relative to the mid and better-parent respectively. Another study reported that eleven crosses in F_1 and five crosses in F2 had significant positive hHP for the number of pods/plant (Waly and Ibrahim 2021). Furthermore, the number of empty pods had negative hMP and hHP with a range from -3.25% to -61.20% and -22.73% to -71.17%, respectively. Similarly, the seed weight per plant showed negative hMP and hHP with a range from -5.62% to -8.77% and -6.85% to -18.34%, respectively. The cross combinations with negative hMP and hHP on the quantitative characters (number of empty pods, number of filled pods, 10 seeds weight) showed that the three characters have a lower average value than those of their parental genotypes.

In general, estimates of hMP and hHP were variable among characters and parents' combinations, suggesting that heterotic effects are significantly affected by the genetic variability of parental genotypes (Ibrahim et al. 2021; Ismail et al. 2020; Jeeva et al. 2020). Burton and Brownie (2006) proposed that gene complementation, linked dominant alleles inherited as a unit, a greater number of dominant alleles in the F_1 than in the parents, and multiple dosage-dependent regulatory loci and/or overdominance as possible genetic bases for heterosis in soybean.

Table 2. Heterosis (hMP) and heterobeltiosis (hHP) of quantitative characters derived from four soybean cross combinations

Cross combination	Hete-rosis (%)	Quantitative character						
		PHG	**NOB**	**NON**	**NFP**	**NEP**	**SWG**	**YLD**
Gepak Kuning x Wilis	hMP	5.82	27.51	9.45	-6.65	-3.25	-8.77	-13.05
	hHP	-2.77	9.84	1.50	-14.56	-22.73	-18.34	-24.88
Gema x Gepak Kuning	hMP	6.86	14.20	4.18	-5.67	-61.20	-8.76	-2.47
	hHP	0.38	-4.20	-2.94	-12.54	-71.17	-6.85	-14.18
Derap 1 x Gepak Kuning	hMP	-10.56	15.24	-11.32	-8.65	-34.96	-5.92	5.33
	hHP	-11.05	-5.93	-12.84	-13.48	-50.00	-18.19	2.42
Dering 1 x Gepak Kuning	hMP	-9.17	10.61	-14.16	8.80	-9.58	-5.62	6.61
	hHP	-11.80	0.29	-23.04	-2.56	-30.49	-7.17	4.73

Note: hMP: heterosis mid parent, hHP: heterobeltiosis, PHG: plant height (cm), NOB: number of branches, NOD: number of nodes, NFP: number of filled pods, NEP: number of empty pods, SWG: 10 seeds weight (g), YLD: seed yield/plant (g)

Table 3. The degree of dominance of quantitative characters derived from four soybean cross combinations

Cross combination	Degree of dominance and the gene action for the quantitative characters						
	PHG	**NOB**	**NON**	**NFP**	**NEP**	**SWG**	**YLD**
Gepak Kuning × Wilis	0.66 ID	-0.02 ID	1.21 OD	-0.72 ID	-0.13 ID	-0.75 ID	-0.83 ID
Gema × Gepak Kuning	1.06 OD	0.74 ID	0.57 ID	-0.72 ID	-1.77 OD	4.28 OD	-0.18 ID
Derap 1 × Gepak Kuning	19.40 OD	0.68 ID	-6.45 OD	-1.55 OD	-1.16 OD	-0.39 ID	1.87 OD
Dering 1 × Gepak Kuning	1.58 OD	0.41 ID	2.30 OD	5.28 OD	0.46 ID	0.02 ID	0.19 ID

Note: PHG: plant height (cm), NOB: number of branches, NOD: number of nodes, NFP: number of filled pods, NEP: number of empty pods, SWG: 10 seeds weight (g), YLD: seed yield/plant (g), ID: incomplete dominance, OD: overdominance

The degree of dominance

The degree of dominance (P) of the seven quantitative characters of the four cross combinations ranges from -6.45 to 19.40 (Table 3). In the cross of Gepak Kuning × Wilis, six characters (plant height, number of branches, number of filled pods, number of empty pods, 10 seeds weight, and seed yield) indicated the presence of the incomplete dominance type of gene action in the inheritance of these traits. Meanwhile, overdominance was exhibited by all the hybrids towards a higher number of nodes. As a result, the selection of this character must be postponed until the F3 or F4 generation. This delay allows for the loss of non-additive genetic variances due to inbreeding, allowing the additive genetic variances to be evaluated more clearly (Said 2014). When considering the magnitude of the degree of dominance, the F_1 plant from the cross of Gepak Kuning × Wilis had a slightly lower average yield than its parents, as well as the performance of other quantitative characters, except for the number of nodes, which was greater than the two parents.

Overdominance gene action was observed in the cross of Gema × Gepak Kuning for the characters of plant height, the number of empty pods, and 10 seeds weight. Furthermore, incomplete dominance was observed in the characters of the number of branches, number of nodes, number of filled pods, and seed yield. In the cross of Derap 1 × Gepak Kuning, the potency ratio indicated the presence of overdominance for almost all the characters, except the number of branches and 10 seeds weight which exhibited the incomplete dominance gene action. Similar findings for the overdominance gene action for the seed yield in soybean were also reported by Sen (2020). Other studies reported the preponderance of additive gene action controlling seed yield and its related traits in soybean (Adsul et al. 2016; Otusanya et al. 2021), suggesting that selection for grain yield in soybeans may be more effective in the F2 and later generations (Kataliko et al. 2018). In other crops, non-additive gene effects were reported to be low for seed yield based on a study of F_1 plants from several fresh bean crops, although heterosis and heterobeltiosis values were positive (Kepildek and Ceyhan 2018).

Furthermore, the cross of Dering 1 × Gepak Kuning exhibited the incomplete dominance type of gene action for the four characters, namely number of branches, number of empty pods, 10 seeds weight, and seed yield. Meanwhile, overdominance was exhibited by all the heterotic hybrids towards higher plant height, the number of nodes, and the number of filled pods. A study by Pandini et al. (2002) in yield and yield components in soybean, found additive and dominance gene effects played a role in the genetic control of these traits. Another study found the significance of additive gene action for the days to 50% flowering, days to maturity, the number of pods/plant, and 100-seed weight in soybean (Umar et al. 2017). Both additive and dominant effects were reported to have a significant influence in determining plant height (Gavioli et al. 2006; Wanderi 2012), meanwhile Kataliko et al. (2018) found both additive and non-additive gene action controlled the inheritance of the trait.

In conclusion, a cross between parents is used to improve genetic potential, particularly potential seed yield. The estimated value of hMP for F_1 crosses from four parental combinations ranged from -61.20 to 27.57, heterobeltiosis ranged from -71.17 to 9.84, and the degree of dominance ranged from -6.45 to 19.40. The crosses of Derap 1 × Gepak Kuning and Dering 1 × Gepak Kuning showed positive hMP and hHP values for their seed yield. As a result, these hybrids could be used to develop high-yielding varieties with desirable traits in soybean. Seed yield character in the cross of Derap 1 × Gepak Kuning exhibited the overdominance type of gene action, meanwhile, the Dering 1 × Gepak Kuning was incomplete dominance.

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