RESEARCH ARTICLE

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ESTIMATION OF GENE ACTION THROUGH COMBINING ABILITY FOR MATURITY IN SOYBEAN

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SUMMARY

In a breeding program, information on the combining ability is needed for selection of both parents and crossing partners, as well as identification of offspring for developing high-yielding varieties. The parents used to create F_1 and its reciprocal F_1 consisted of soybean cultivars: Nanti, Dempo, Dieng, Malabar, and Grobogan. This research was conducted in July 2009 at the Jambegede Experiment Farm, Kepanjen, Malang Regency, East Java Province. The statistical method used for genetic analysis followed the Griffing's model I. The components of variance for general combining ability (σ^2_{GCA}) and specific combining ability (σ^2_{SCA}) were estimated by equating the mean squares to their expectations and solving the equations for the parameters involved. Analysis of variance showed significant differences between parental genotypes and crosses for days to maturity, indicating that there was genetic variation in the population. Analysis of variance of the combining ability revealed that mean squares due to GCA, SCA, and reciprocal combining ability (RCA) were significant for maturity. A set of parents used had a higher proportion of the GCA effects than that of the SCA, indicating that additive type of gene action affected the inheritance of maturity. Furthermore, the GCA and SCA values were highly significant for the maturity character components studied, suggesting that additive and non-additive genetic variances are important in the inheritance of maturity. A combination of two parents of a single cross could be predicted on the basis of GCA and SCA. Grobogan and Malabar as the parents and crossing partners could be used to improve early maturity and high yielding varieties.

Key words: Combining ability, gene action, maturity, soybean

Key findings: One of the main objectives of soybean breeding in Indonesia is to produce an early maturing soybean variety with high productivity. Days to maturity was found to be controlled by additive gene action. Among the materials used, Grobogan and Malabar varieties were considered to be the best general combiners for improvement of early maturity, and its use in breeding programs would produce progenies with early maturity.

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INTRODUCTION

Improvement of the soybean maturity is one of the plant breeding programs to produce an early maturing soybean variety with high productivity. The initial information needed is parents that have the potential to produce early maturing offspring. The success of a plant breeding program is mostly determined by the selection of desired parents (Farshadfar *et al*., 2013) and the combining ability of the mother that is used as a parent in crossing. Combining ability is defined as the ability to transfer the desired properties of appropriated lines entered into hybrid combinations to hybrid offspring (Hayes and Immer, 1942), whereas the general combining ability (GCA) outlined as the average performance of a line in a hybrid combination, and specific combining ability (SCA) as the better or poorer performance than expected of a given hybrid combination (Sprague and Tatum, 1942).

Knowledge of the estimated GCA and SCA as well as gene action is needed at the initial stage of the effort to improve a plant character (Durai and Subbalakshmi, 2010) in order to identify which combination of parents will produce the desirable offspring (Allard, 1989; Tan, 2010; Machikowa *et al.,* 2011). Moreover, the information about the desirable parental combinations is important, because it can represent a high degree of heterotic response (Pingali, 1997). Additive and non-additive genetic effects due to variance of GCA and SCA arise from dominance and epistatic deviations (Akbar *et al.,* 2008). Variance for GCA is the additive portion, while SCA is the non-additive portion of total variance (Malik *et al*., 2004).

Diallel crossing analysis is an excellent tool in providing the breeder with the nature and amount of genetic parameter, and the general and specific combining ability of parents and their hybrids, respectively. Through diallel crossing, it is possible to choose a parent and provide information on the GCA of the parent and the SCA of the crossing combination, which helps the breeder to increase/improve and select the segregant population. Specific combining ability and general combining ability also provide information about the type of gene action controlling a trait. There are two main approaches for diallel analysis, namely Griffing's approach and Hayman's approach (Nassar, 2013). Genetic analysis formulated by Griffing (1956) provides a workable approach, to evaluate newly developed cultivars for their parental usefulness and to assess the gene-action involved in various attributes, so as to design an efficient breeding plan, for further genetic upgrading of the existing material (Ajmal *et al*., 2004). In order that the implementation of the selection of the desired character can be passed down to the hybrid offspring, the inbred parent must possess the ability to bequeath/hand down a character in the assembly of a new variety (Fehr, 1987).

Many researchers used the diallel technique to study the plant genetics. The results of research on (days to) maturity have been reported by Estakhr and Heidari (2012) affirming the role of additive and non-additive gene action in the maturity character of maize. Furthermore, a study in sunflower also revealed that days to maturity depict the preponderance of non-additive type gene action (Tan, 2010). A 6 × 6 diallel experiment on F_1 generation of Brown mustard was performed by Iqbal *et al*. (2003) to study the genetic control of some important agronomic and quality characters. Highly significant differences among parents and their hybrids in F_1 generation were revealed by analysis of variance, for all the characters except for days to maturity. The genetic analysis indicated that days to flowering and erucic acid were under the control of additive gene action. A genetic analysis in soybean was carried out by Agrawal *et al*. (2005) using 5 x 5 diallel set of soybean crosses along with the parents. The analysis of six plants and four yield attributing characters revealed that most of plant characters might be governed by additive gene effects, whereas the non-additive and complex of additive and non-additive gene effects played an important role in the expression of yield attributing characters. Similarly, Shiv *et al*. (2011) also using 5 × 5 diallel set of soybean crosses along with the parents for estimation of combining ability. The analysis revealed that the parents and crosses differ significantly for general combining ability and specific combining ability effects. The GCA and SCA components suggested predominance of additive gene effects for days to 50% flowering, days to maturity and plant height and non-additive gene effects for all the traits.

The choice of appropriate parents, especially in terms of the desired character should be performed significantly in order to obtain the right parents. The objective of this study was to estimate the gene action of parents and the crossing partners through the estimated value of the combining ability on the maturity character of soybean.

MATERIALS AND METHODS

The research was carried out from July 2009 to September 2009 at Jambegede Experimental Farm in Malang Regency, East Java. The genetic materials used were derived from F_1 cross of 5 parental strains (Nanti, Dempo, Dieng, Malabar, and Grobogan) which crossed in a diallel fashion (Griffing, 1956).

Soybeans were planted with a planting space/distance of 40 cm x 15 cm, 1 plant/hill so that each row of 2.5 m contained 15 plants. Fertilizer was applied seven days after planting by arrangement between rows, in a dose of 50 kg/ha of Urea, 100 kg/ha of SP-36, and 75 kg/ha KC1. The experimental design used was a randomized complete block design. Plant maintenance was done intensively through irrigation, weeding, monitoring, and control of pests and diseases. Harvesting was done to all individual plants according to their (days to) maturity (days after planting) at the time when 90% of the pods were ripe (R_8), which was marked by the colour of the pods that turned brown and their days to maturity. Data analysis of maturity followed Griffing's model, Method 1 in Singh and Chaudary (1979). The components of variance for general (σ^2_{GCA}) and specific (σ^2_{SCA}) combining abilities were estimated by equating the mean squares to their expectations and solving the equations for the parameters involved.

RESULTS AND DISCUSSION

Early maturity is a desirable trait from soybean breeding perspective in Indonesia. An early maturing soybean will relatively exhibit drought stress through escape mechanism (Heatherly and Elmore, 2004; Rose *et al*., 1992; Kyei-Boahen and Zhang, 2006) and also escape from pest and disease attack. Knowledge on combining ability is essential for selection of suitable parents for hybridization and identification of promising hybrids in breeding program. Therefore, information in general/specific combining ability effects for soybean maturing day is important in conducting a successful breeding program to develop a new early maturing soybean variety.

In this study, analysis of variance showed a significant difference between parents and crossing on the means of the maturity of parent and F_1 (Table 1). This indicated that there was genetic variation in the population. Gavioli's research (2008) affirmed that the genetic variation in a population on the maturity character of soybean was caused by an additive gene action. An additive gene action indicates genes that control characters are jointly and mutually reinforcing so that the value of the resultant character will exist between the two parents. The character that is dominated by the additive gene action, the selection is applied with a simple method at the beginning of the generation (Farshadfar *et al.,* 2013), by adopting the method of selecting the period or offspring or family tree/pedigree (Durai and Subbalakshmi, 2010).

According to analysis of variance, highly significant difference was recorded, and then the data was subjected to combining ability analysis. General/specific combining ability can be estimated through various methods, and the most common of which is diallel analysis. The diallel analysis as presented by Griffing (1956) has been widely used for studying genetic variation and useful for identifying crosses to produce superior segregants. The GCA refers to the average performance of particular inbred parents in a series of hybrid combinations, whereas SCA refers to the performance of a combination of specific inbred in a particular cross (Sprague and Tatum, 1942). The results of analysis of variance on GCA, SCA, and the reciprocal of maturity character showed the significant difference (Table 2). A significance GCA means that there is a difference in the ability to form pairs on the maturity character between the parents, which can be used as an indicator for the choice of parents to be used in a breeding program (Farshadfar *et al*., 2013). The significance of both GCA and SCA for days to maturity as this study was also reported in previous studies (Harer and Deshmukh, 1993; Rahangdale and Raut, 2002).

In this study, the GCA mean square was higher than the SCA mean square. According to Nasim *et al*. (2014), a trait which exhibited higher magnitude of GCA compared to SCA reveals prevalence of additive type of gene action. A greater magnitude of the mean squares for GCA in relation

Table 1. Analysis of variance for maturity character.

Source of variation	d.f.	Sum of squares	Mean squares	F calculated values	Probability
Replications	2	6.26	3.13	1.61	0.21
Crossing	24	982.05	40.92	20.99**	<0.01
Error	48	93.56	1.95		

** = Significant at $P \leq 0.01$

Table 2. Diallel analysis of variance for the Griffing Method 1.

Source of variation	d.f.	Sum of square	Mean square	F calc	Probability
General combining ability	4	698.99	174.75	87.53**	<0.01
Specific combining ability	10	210.81	21.08	10.56**	<0.01
Reciprocals	10	72.25	7.23	3.62**	<0.01
Error	48	99.82	1.96		

** = Significant at $P \leq 0.01$

to the mean square for SCA indicates the efficiency for genetic progress in the advanced segregating generations, due to the larger additive effect of the genes in the populations (Gravina *et al.,* 2004). Previous studies also found that GCA mean square was larger than SCA mean square for days to maturity (Gavioli, 2008; Durai and Subbalakshmi, 2010).

Significant mean squares (Table 2) indicated that the two types of genetic effects (additive and non-additive) were operative in days to maturity expression, respectively. Furthermore, the GCA and SCA values were highly significant for the maturity character components studied, suggesting that additive and non-additive genetic variances are important in the inheritance of maturity.

The pre-dominance of additive gene action and highly significant genotypic mean square for days to maturity indicated that selection might be suitable in early segregating generations either following mass selection or progeny selection or hybridization and selection with pedigree breeding. Furthermore, the ratio of the mean square, 2GCA / (2GCA + SCA) was 0.94, indicated that there was an effect of additive genes (Cho and Scott, 2006) and of the additive × additive (Mebrahtu and Devine, 2008) which had an important role in the inheritance of maturity character.

The negative combining ability effects in days to maturity are desirable. Estimates of general combining ability for days to maturity were shown in Table 3. Significant and negative GCA effects were detected for two varieties Grobogan (-2.45) and Malabar (-2.47), respectively. On the other hand, the parent Nanti had the highest positive GCA (2.92) followed by Dempo (1.58), and Dieng (0.42). This implies that Grobogan and Malabar were the best general

Table 3. Estimates of general combining ability (GCA) for maturity character.

Parental genotypes	GCA effects
Nanti	2.92
Dempo	1.58
Dieng	0.42
Grobogan	-2.45
Malabar	-2.47

Table 4. Estimates of specific combining ability (SCA) for maturity character.

Parental gentoypes	Dempo	Dieng	Grobogan	Malabar
Nanti	0.69	-1.94	-2.35	-1.83
Dempo		1.19	-0.29	-0.79
Dieng			0.84	1.41
Grobogan				-0.53

combiners for improvement of early maturity, and its use in breeding programs would produce progenies with early maturity. Nanti was the worst general combiner because of its highly positive GCA value. The estimated value of the GCA of Malabar and Grobogan varieties was marked negative, meaning that the offspring of the pairs had an earlier maturity than those of Nanti, Dempo, and Dieng varieties. Although, the estimated value of GCA was fairly similar between the parents, the soybean of Grobogan and Malabar varieties had a better GCA and both had early maturity. The early maturity related to negative GCA effects of days to maturity. The high and negative value of GCA was desirable in this research because the offspring of the parental pair that had those GCA value will likely produce offspring with early maturity. The results of this study were similar with those previously obtained by Nassar (2013). A highly significant GCA effects were also found in another crop by Shehzad *et al.* (2015), and revealed an additive genetic effects for days to maturity in rapeseed genotypes. The parents that showed the appropriate and significant effect of GCA were useful in breeding through conventional crossing (Kakar *et al*., 1999).

The effect of GCA and SCA can have a positive or negative value. The negative GCA effect of Grobogan and Malabar showed that the maturity character of F_1 offspring that involved the parent concerned had an earlier maturity than the means of all crossings. According to Ramalho *et al.,* (1993), GCA values are important to the breeders who work with autogamous plants due to the existing additive genetic variance. Another study concerning the role of GCA effects in field beans was conducted by Oliveira Júnior *et al.* (1999), and concluded that the GCA effect play an important role as the predictor in the performance of segregating field beans of F_3 populations. This is based on the principle that the phenotypic value of F_1 is strongly determined by the heterotic effects conditioned by the dominance deviations, which are not transferred to posterior generations (Gravina *et al*., 2004).

The estimates of specific combining ability for days to maturity were presented in Table 4. Significant negative SCA effects of days to maturity were desirable, and found in 6 out of 10 crosses. A significant negative SCA for maturity date was also obtained in three crosses in soybean (Nasssar, 2013), and other crops, for example in Indian mustard (Gupta *et al.,* 2011; Vaghela *et al.,* 2011), and rapeseed (Amiri-Oghan *et al.,* 2009). In this study, the cross combination Nanti × Grobogan had the most negative SCA value (-2.35), followed by Nanti × Dieng (-1.94), Nanti × Malabar (-1.83), Dempo × Malabar (-0.79), Grobogan × Malabar (-0.53), and Dempo × Grobogan (-0.29). The rest of the parents were poor combiners for early maturity. The effect of SCA from the crossing of two different parents had a negative and higher effect than the value of their GCA, which means that the F_1 offspring had an earlier maturity as compared with the level of the expected maturity obtained from the means of GCA of the two parents. The lowest negative value of SCA effect was found in the crosses of Nanti × Grobogan with the value of -2.35. The days to maturity characters of soybean crossing of Nanti × Grobogan and were possibly determined by more than two genes (polygenic) (Gatut_Wahyu *et al*., 2014). There was no crossing partners between soybean with early maturity and soybean with early maturity that had an earlier maturity than their parents, which was evident from the lower value of SCA (Table 4). According to Simmonds (1979), a parent with high mean values may not always be inherited its superior trait into their progenies. Another study by Gatut_Wahyu *et al*. (2014) found that the F_1 population derived from the cross combination Grobogan and Malabar had days to maturity the same as the parents. Both of Grobogan and Malabar have early days to maturity, i.e. 76 days and 70 days, respectively (ILETRI, 2012). Grobogan is a popular variety in Indonesia, released in 2008, and known as an early maturing variety, and also due to its large seed size and high yield. The utilization of Grobogan as a parent in soybean crossing have been performed in the development of whitefly-tolerant soybean (Sulistyo, 2015), which is expected to obtain whitefly-tolerant varieties with early maturity, large seed size, and high yield.

The character under the effect of SCA is influenced by a non-additive gene or a dominant gene action and/or an epistatic gene action (Falconer and Mackay, 1989). Crossing parents with an SCA effect are appropriate for hybrid development (Kakar *et al*., 1999) and illustrates the additive gene action (Ahmad *et al*., 2013), therefore, selection should be delayed to later generations (Singh *et al*., 1992). However, Grobogan and Malabar varieties have a high negative estimated value of GCA and SCA so that the parent and its crossing combiners could be used in the improvement of soybean with early maturity and with large seed size. The choice of parent and crossing combiner will be useful for further designing of a breeding program.

CONCLUSIONS

The parental set used had a greater proportion of GCA than SCA, which shows that the type of additive gene action affects the inheritance of maturity character. The combination of single crossing of two parents can be predicted from the GCA and SCA. Grobogan and Malabar are the parents that could be optimally used for the improvement of high-yielding and early maturing varieties.

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