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Analysis segregation and prediction of gene action controlling soybean tolerance to aluminum toxicity

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Abstract

This experiment consists of two stage i.e: (1) Study inheritance root re-growth in nutrient culture. The objective of this research was to study soybean inheritance tolerance to aluminum stress and gene action at seedling stage and acid soil. This research used 120 seeds of F_2 population generated from crossing between Argomulyo (Al-sensitive) with Tanggamus (Al-tolerant). Seeds were grown in nutrient culture for six days (two days without Al, two days with Al concentration 1.5 mM and pH 4.0 then two days more without Al) to see root length under condition stress and recovery. The result showed root length had high and medium heritability at condition stress and recovery, that means root length is easily be inherited because root length was larger influenced by genetic compared to the environment factors. The root re-growth on F_2 population at Argomulyo were 83 plants and Tanggamus were 33 plants. (2) Study inheritance of agronomy characters in the acid soil. Studied inheritance tolerance to Al stress at acid soil showed that number of productive branches, seed weight by plant and 100 seeds weight had moderate heritability so the characters were used as character selection for next generation.

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Introduction

Soybean is an alternative source of cheap protein nutrition for human and livestock in the developing countries. According to FAO (2013), average production soybean world from 1999 until 2012 is about 177 million tons per year. Soybean production in Indonesia in 2012 only reached 851.647 tons, the volume of soybean Indonesia reached 6 million tons so that Indonesia must import the rest of 85% (Statistic Center, 2013). Limitations the acreage planted is one of the low production of national soybean planted so the expansion area are needed to do.

Dry soil is the land that the potential for the expansion of soybean acreage planted. The extent of dry soil in indonesia reach 148 million hectares and is expected to 102.8 million hectares in acid (Soil Research, 2006). Acid soil characterized by fertility and low soil pH (pH <5.5) so that the solubility of Al be high. Al solubility is high may result in toxicity to plants. Besides, also caused an important nutrients deficiency, such as magnesium, calcium and phosphor (Kochian *et al.*, 2004). Toxicity Al can disturb growth and development of plant (Caniato *et al.*, 2007).

Several species of plants having different mechanism to minimize effects of poisoning Al. Mechanism plant to overcome stress Al can be classified into two mechanisms: 1. external mechanism e.g immobilisasi Al in cell walls, 2. internal mechanism, e.g anion organic acid secretion from roots (Singh *et al.*, 2011). Plant has mechanism of adaptation will be able to sustain growth, development and production in stress Al conditions. Plants which are able to maintain production in stress condition called tolerant.

Until now, Agriculture Ministry (2012) have produced 74 varieties, some of them are tolerant of acid soil as Sibayak, Ratai, Nanti and Tanggamus. Generally varieties tolerant acid soil has produced having small size seeds. Adie and Krisnawati (2007) made to grouping soybean seeds based on seed size, known that varieties Sibayak, Ratai, Nanti and Tanggamus includes group small seed (< 10 g/100 biji). This time consumers prefer to soybeans great seed. Therefore, conducted development of soybean varieties great seeds and tolerant acid soil. Genetic diversity of soybean great seeds and aluminum tolerant is still relatively low so need to conduct crossing between tolerant acid soil variety (Tanggamus) (Agriculture Ministry, 2012) and sensitive acid soil but great seeds variety (≥ 14 g/100 seeds) was Argomulyo (Agriculture Ministry, 2012) to obtain lines tolerant acid soil and great seeds.

Information about inheritance pattern is required to determine the methods and proper selection of characters. The election method and character selection so determines success or efficiency of selection (Wirnas *et al.*, 2006). Selection can be done within the controlled or in natural environment. In research has done study inheritance of the environmental controlled (nutrient culture) and acid soil. Studies in nutrient culture show that plant only affected by stress Al, while in acid soil influence besides stress Al difficult avoidable (Tester *et al.*, 2005)

One of the characters that have been used to observe nature of Al-tolerance in populations of segregation is character RRG (root re-growth). Character RRG has been used on a wheat plant (Silva *et al* 2010), Triticale and rye (*Secale cereale* L.) (Miftahudin *et al.*, 2004), barley (Zhao *et al.*, 2003 and rice (Roslim *et al.*, 2010). Plant roots tolerant Al will be slightly or no way damaged when got stress Al than roots plant sensitive Al (Yang *et al.*, 2000;Delhaize *et al.*, 2004; Liao *et al.*, 2006), so plant roots tolerant Al will have root growth ability higher return than plant roots sensitive Al. studied of tolerance stress Al in the fields has been carried out on many plants such as barley (Furukawa *et al.*, 2007) and sorghum (Caniato *et al.*, 2007). The objective of this research is to study inheritance soybean root ability to repair damage to roots (root re-growth) after receiving stress Al and tolerance soybeans towards stress Al in acid soil by using population of segregation.

Materials and methods

Research consisted of two experiments: 1. study the inheritance root re-growth in nutrient culture in stress Al conditions, 2. inheritance of agronomic characters in acid soil. Experiment 1 was carried out in green house University Farm IPB Cikabayan, Bogor in March 2013 and experiment 2 was carried out on the land farmers in Jasinga from May until August 2012.

Study inheritance root re-growth in nutrient culture

The genetic material is 120 F_2 generation of population segregation results crossing Argomulyo x Tanggamus (Agriculture Ministry 2012; Adie and Krisnawati 2007) and both of parents each are 20 plants. The planting medium used is a solution of Ohki (1987) with a complete nutrient composition below 1.5 mM $Ca(NO_3)_2.4H_20$; 1.0 mM NH_4NO_3; 1.0 mM KCl; 0.4 mM $MgSO_4.7H_20$; 1.0 mM KH_2PO_4, 0.50 ppm $MnSO_4.H_2O$; 0.02 ppm $CUSO_4.5H_2$; 0.05 ppm $ZnSO_4.7H_20$; 0.50 ppm H_3BO_3; 0.01 ppm $NH_6Mo_70_{24}.4H_20$; 0.068 mM $Fe(C_6H_70_7)$, pH 4.0 and Al 1.50 mM

Soybean seed is germinated in advance on the media chaff sterile moist fuel. After seedling has two pieces of leaves trifoliat with length roots is uniform. Stem sprouts wrapped with soft foam and inserted into hole made in the stryofoam and put in a pot containing nutrient solution as much as 2 quarts/pot. Nutrient solution supplemented with Al compounds as much as 1.50 mM, given 2 days after plants transplanted into pot already contains solution. the pH is governed at pH 4.0±0.1 with addition NaOH 1M or 1M HCl. Nutrient solution given aeration using aerator to prevent Al and other nutrient settles. Water is lost due to transpiration was replaced by adding aquades everyday (see limit measure 2 liters pot). Observations made on roots length after experiencing stress, ability to root re-growth as well as wet and dry weights roots at the time of harvest. Root re-growth is difference in roots length at the time of the restoration with roots length after Al treatment. Root length is measured when plant has given stress Al for 48 hours. Then plant was transferred to nutrient solution (Ohki 1978) without treatment Al. Observation root length carried out again after plants grown for 48 hours (recovery) in solution without Al and plants left to harvest. Harvesting is done on the sixth day when plants reach four-leaf trifoliat growth phase. Plant was harvested and dried in oven at temperature 60°C for 2 x 24 hours then weighted.

Analysis data was conducted by counting the middle value each character observed and continued with prediction action genes through analysis skewness and kurtosis of scattered value of phenotype in the population F_2 (Roy 2000) and genetic parameters was analyzed by:

$$\text{Variance (V)} = \sum_{i=1}^{n} \frac{(x_i-\mu)^2}{n-1}$$

Variace phenotype (V_P) = V_{F2}

Variace environment (V_E) = $(V_{P1} + V_{P2} + V_{F1})/3$

Variance genotype (V_G) = V_{F2} - V_E

Heritability board sense (h^2_{bs}) = (V_G/V_{F2}) X 100%

Number of gene prediction based on analysis of the F2 population segregated according to Singh and Chaudhary (1979) using Chi-square Mendel method.

$$\chi^2 = [\ \Sigma \frac{(f_o - f_e)}{f_e}]$$

Where : χ^2: Value chi-square

f_e : Frequency expectation

f_o: Frequency observation

Study inheritance of agronomic characters in the acid soil

Plant material used for experiments on the acid soil consists of 20 plants F_1 and 600 plants F_2 of crossing Argomulyo (Al-sensitive) with Tanggamus (Al-tolerant) and both parents each are 20 plants. Planting on ultisol soil with pH 4.3 and Al dd 1.76 me/100 g soil. Seeds were planted with spacing of plants 30 cm x 15 cm by one seed by hole. Seeds are given 3 g Karbofura on every hole for planting to address pest attack. Plant was given basic fertilizer with dosage of 50 kg/ha of Urea, 100 kg/ha SP36 (TSP) and 100 kg/ha KCl (Soil Research, 2006; Agriculture Ministry, 2012). Observations were made characters number of trifoliate leaves, plant height, number of branches, number of book, number of pithy pods, number of vacuum pods, weight of 100 seeds and weight of seeds/plant.

Analysis data was conducted by counting the middle value each character observed, genetic parameters and continued with prediction action genes through analysis skewness and kurtosis of scattered value of phenotype in the population F_2 (Roy 2000). According to Roy (2000) if:

- Skewness = 0 ; gene action additive
- Skewness < 0 ; gene action additive with duplicate epistatic
- Skewness > 0 ; gene action additive with complementer epistatic
- Kurtosis negative ; grafic distribution platykurtic and controlled many genes
- Kurtosis positive ; grafic distribution leptokurtic and controlled little genes

Skewness and Kurtosis were analyzed by equation:

$$Skewness = \frac{\sum_{i=1}^{N}(Yi-\bar{Y})^{3}}{(N-1)s^{3}}$$

$$Kurtosis = \frac{\sum_{i=1}^{N}(Yi-\bar{Y})^{4}}{(N-1)s^{4}}$$

Where: Y_i = genotype value to-$_i$

S = standrad deviation

N = number data

Results and discusscion

Study inheritance root re-growth in nutrient culture

The results showed that parent Argomulyo had mean all observed characters are inferior compared to Tanggamus, whereas population F_2 generated from crossing between Argomulyo (Al-sensitive) with Tanggamus (Al-tolerant) had had mean all observed characters between the both parents. This indicates that Argomulyo is sensitive variety on aluminum stress conditions (Table 1).

Table 1. Middle value character roots parents Argomulyo, Tanggamus and F_2 on stress aluminum in root re-growth.

Character	Argomulyo	Tanggamus	P-Value	F_2
Root length under stress (cm)	9.15 ± 1.33	20.30 ± 1.68	0.00*	16.30 ± 2.29
Root length after recovery (cm)	9.73 ± 0.38	21.30 ± 0.40	0.00*	18.12 ± 2.74
Root re-growth (cm)	0.63 ± 0.71	1.03 ± 0.99	0.00*	0.80 ± 0.77
Wet weight root (g)	0.11 ± 0.08	0.10 ± 0.04	0.88^{ns}	0.08 ± 0.06
Dry weight root (g)	0.02 ± 0.01	0.02 ± 0.01	0.94^{ns}	0.02 ± 0.01

Note: * = significant on 5% test-t and ns = no significant on 5% test-t.

The results of root re-growth showed that Tanggamus had roots length were longer and significant compared to Argomulyo on condition were aluminum stress and recovery. According to Arsyad *et al.* (2007) and Agriculture Ministry (2012) Tanggamus constituting a variety of being recommended for cultivation on soil acid and commonly variety argomulyo planted in wet rice field after paddy.

Table 2 showed the soybean seedling stadia skewness population F_2 generated from crossing between Argomulyo (Al-sensitive) with Tanggamus (Al-tolerant) for root length character condition stress, recovery and the RRG is not equal to 0, while the character wet and dry weight roots skewness greater than 0. It can be presumed on the character root length condition stress, recovery and RRG also controlled by additive gene action as well as by the interaction of alleles from different loci (epistasis) (Bnejdi *et al.*, 2010).

The root length character on condition stress, recovery and RRG skewness < 0.5 and negative. This showed that root length character has approaching normal distribution and controlled by additive gene action and influence the action of duplicate epistasis genes. According to Bnejdi *et al.* (2011) the action of a gene that controls a character in early generation difficult separated from duplicate epistasis. Duplicate epistasis is interaction between gene additive x additive, interactions between loci may increase soybean tolerance under conditions stress Al.

Table 2. Values of skewness, action genes and kurtosis population F_2 crossing of Argomulyo and Tanggamus on stress aluminum in root re-growth.

Character	Skewness	Gene Action	Kurtosis	Description
Root length after stress	-0.28	additive + epistasis duplicate	-0.79	Controlled many gene
Root length after recovery	-0.27	additive + epistasis duplicate	-0.71	Controlled many gene
Root Re-growth	-0.27	additive + epistasis duplicate	-0.71	Controlled many gene
Wet weight root	1.30	additive + epistasis complementer	2.77	Controlled many gene
Dry weight root	0.76	additive + epistasis complementer	0.98	Controlled many gene

Variance, heritability and CVG value root length characters stadia soybean seedling population F_2 generated from crossing between Argomulyo (Al-sensitive) with Tanggamus (Al-tolerant) shown on table 3. On the conditions stress and recovery root length character had heritability and KKG was high, while for the character RRG was moderate.

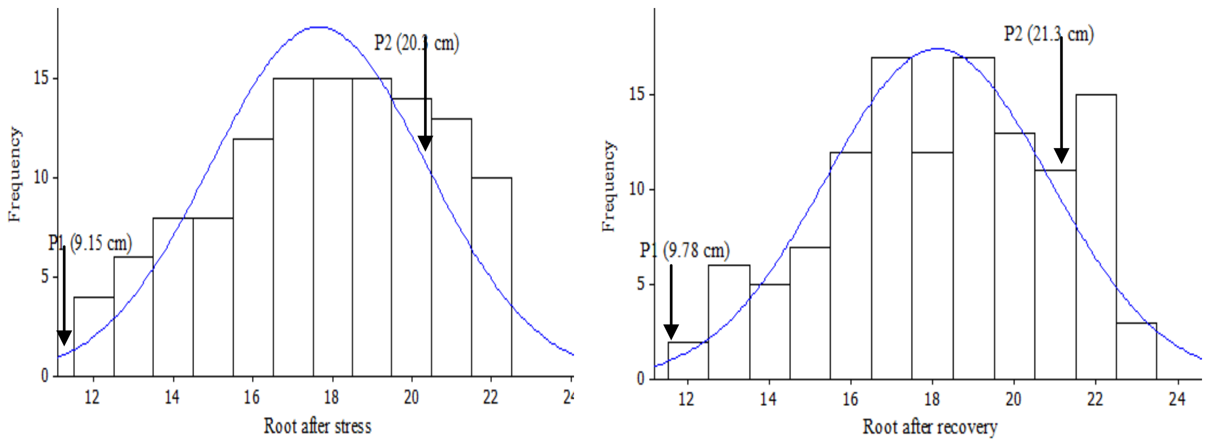
Table 3. Value prediction and heritability components broader sense population F_2 on stress aluminum on root re-growth.

Character	σ^2p	σ^2e	σ^2g	CVG	h^2bs	Criteria*
Root length after stress	5.25	2.30	2.95	47.74	56.24	high
Root length after recovery	7.52	3.04	4.48	21.77	59.60	high
Root re-growth	0.744	0.741	0.003	6.12	35.37	moderat
Wet weight root	0.36	0.03	0.34	62.52	92.72	high
Dry weight root	0.0009	0.0004	0.0005	8.55	54.39	high

Note: CVG= Coeffisien Varian Genetic.

Root length character under condition stress, recovery and RRG had abnormally distribution, happen because of involvement in controlling the genes non additive diversity in the population F_2 or because of large and environmental influences controlled by the action of genes additive duplicate epistasis on all observed characters.

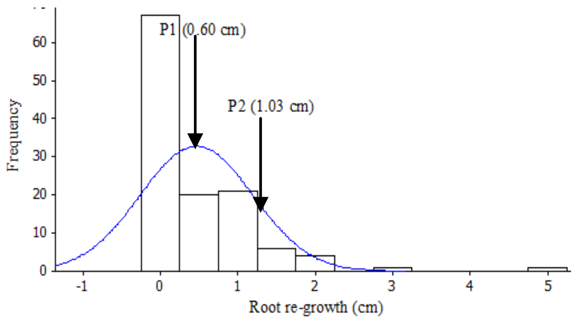
Analysis of distribution pattern on root length condition stress, recovery and RRG on Fig. 1 and 2. The root length character condition stress, recovery and RRG have distribution patterns are continuous, indicating that those characters are controlled by many genes. Root length Characters character condition stress, recovery and RRG F_2 population generated from crossing between Argomulyo (Al-sensitive) with Tanggamus (Al-tolerant) did not have a normal distribution is indicated by skewness is not equal to 0 (running to left or right).



Note : P1= Argomulyo; P2= Tanggamus

Fig. 1. Graphic root length distribution population F_2 condition after stress and recovery.

The results RRG character observations in the population F_2 soybeans showed that spread the value of comparative pattern approaching the RRG Mendel 3: 1 (Fig. 2). The F_2 phenotype ratio of population prediction using the Chi-square test according to Singh and Chaudhary (1979).



Note : P1= Argomulyo; P2= Tanggamus

Fig. 2. Graphic RRG distribution population F_2 on stadia seedling.

According Roslim *et al* (2010) in rice RRG is polygenic and can be used as parameter of Al tolerance then effectively can be applied to determine trait each individual's plants Al tolerant on segregating population F_2.

The observations showed that the dominant character of the RRG is 3: 1 ratio. This is indicated by the value of X^2hitung in the population of F_2 = 0.4 smaller than X^2table = 3.84 (db= 1, α= 5%) (Table 4). Based on such comparisons, the character RRG controlled by one dominant gene because according to the Mendelian ratios of 3: 1. Comparison of the 3: 1 refers to that ¾ part of the population sensitive F2 (87 genotype) like Argomulyo and 1/4 part (33 genotype) are tolerant as Tanggamus.

Table 4. Chi-square value root re-growth on F_2 population.

Genotype	Phenotype	Observation (O)	Expectation (E)	(O – E)²/E
F_2	sensitive	87	90	0.1
	tolerant	33	30	0.3
				Chi-square = 0.4

Soybean RRG character had genetic ratio 3:1, that was same with Murti *et al.*, 2004 said that a character with the genetic ratio of 3: 1 indicates that the character is controlled by one locus in two allele/locus and going on interactions between alleles at the same locus (intra locus).

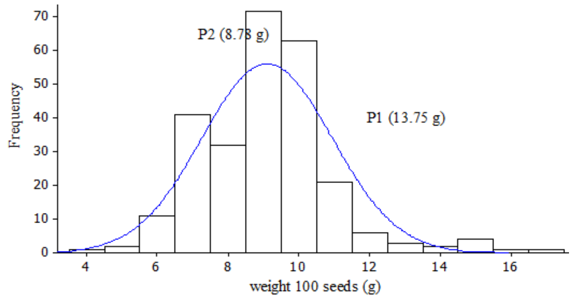
Study inheritance of agronomic characters in the acid soil

According to Table 5, the results showed that Al tolerant soybean on soil acid obtained information that the mean all observed characters between both parents were insignificant, only 100 seeds weight were significant, while F_2 population generated from crossing between Argomulyo (Al-sensitive) with Tanggamus (Al-tolerant) had mean plant height, number of pithy pods and 100 seeds weight was between the both parent (Fig. 3). F_2 populations had mean that exceeds of both parents for number of branch and seed weights plant^{-1} character.

Table 5. Middle value character roots parents Argomulyo (P_1), Tanggamus (P_2) and F_2 on stress aluminum in acid soil.

Character	Argomulyo	Tanggamus	P-Value	F_2
Plant height (cm)	21.99 ± 4.37	21.18 ± 2.81	0.49^{tn}	15.70 ± 4.08
Number of branch	0.67 ± 1.65	0.40 ± 0.99	0.53^{tn}	1.00 ± 0.87
number of leaves (sheet)	8.10 ± 1.92	7.90 ± 1.15	0.76^{tn}	5.00 ± 2.11
Number of book	10.05 ± 2.28	9.60 ± 2.30	0.54^{tn}	8.00 ± 2.28
Number of pithy pods	8.90 ± 4.36	7.75 ± 3.04	0.34^{tn}	8.00 ± 3.26
Number of vacuum pods	0.35 ± 0.49	0.05 ± 0.22	0.02^{*}	0.50 ± 0.32
Weight of seed by plant (g)	1.12 ± 0.64	1.16 ± 0.71	0.82^{tn}	1.38 ± 0.66
Weight of 100 seeds (g)	13.75 ± 2.13	8.78 ± 0.86	0.00^{*}	9.10 ± 1.85

Note: * = significant on 5% test-t and ns = no significant on 5% test-t.



Note : P1= Argomulyo; P2= Tanggamus

Fig. 3. Graphic weight 100 seeds distribution population F_2 on acid soil.

The result of acid soil showed that all observed characters (except 100 seeds weight) Tanggamus no significant with Argomulyo because Tanggamus is tolerant varieties acid soil which are wet while in jasinga is dry and acid soil by pH 4.3 (very low) and Al dd content 1.76 me/100 g soil (Soil research 2006) and climate condition is very dry at beginning planting which resulted in growth vegetative plant is not maximum.

Ability grow roots longer is thought to determine the level tolerant Tanggamus against Al stress because the tolerant plant for soil acid which growth its roots undisturbed under aluminum stress condition (Silva *et al.*, 2012; Maron *et al.*, 2008).

Table 6 showed value skewness and kurtosis all observed characters not equal to 0 and positive so that may be suspected on all observed characters except additive gene there is also interaction alleles of different locus (epistasis).

Table 6. Values of skewness, action genes and kurtosis population F_2 crossing of Argomulyo and Tanggamus on stress aluminum in acid soil.

Character	Skewness	Action Gene	Kurtosis	Description
Plant height	0.21	additive + epistasis complementer	0.03	Controlled many gene
Number of branch	1.23	additive + epistasis complementer	1.67	Controlled many gene
Number of leaves	0.33	additive + epistasis complementer	0.24	Controlled many gene
Number of book	1.17	additive + epistasis complementer	3.50	Controlled many gene
Number of pithy pods	2.37	additive + epistasis complementer	9.22	Controlled many gene
Number of vacuum pods	5.69	additive + epistasis complementer	34.62	Controlled many gene
Weight of seed by plant	2.10	additive + epistasis complementer	6.58	Controlled many gene
Weight of 100 seeds	0.88	additive + epistasis complementer	2.69	Controlled many gene

F_2 population had mean all observed characters were between both parent and did not have normal distribution shown by skewness was not equal to 0 (running to left or right). According to Roy (2000) and Jayaramachandran *et al.* (2010) plants quantitative character spread running to left or right, indicates the presence of environment influences, interaction genotype and environment, gene linked and epistasis.

All observed characters in soil acid had skewness and kurtosis > 0 and positive. Skewness and kurtosis value means that all observed characters in F_2 population in acid soil was assumptioned to be controlled by additive gene action with polygenic and there is influence of complementer epistasis. Based on assumption genes action can be explained that phenotype value of potential segregants were better than best parent due to epistasis and additive genetic values were not for influence of overdominan. Pantalone *et al* (1996) said that data was polygenic had normal and continue distribution curve.

Based on Table 7, research results tolerance soybean Al in acid soil obtained information that all characters observed had heritability broad sense ranges from low (plant height , number leaves, number books, vacuum pods and pithy pods) and moderate (number productive branches, seed weight plant^{-1} and 100 seeds weight). This means that the observed characters are more controlled genetic factors (gene diversity, dominant and additive epistasis) compared to environmental factors as genetic diversity and the environment implies the appearance of phenotypic plants expressed on each character and heritable (Karasu *et al*., 2009; Bnejdi and Gazzah 2010).

Table 7. Value prediction and heritability components broader sense population F_2 on stress aluminum on acid soil.

Character	$\sigma^2 p$	$\sigma^2 e$	$\sigma^2 g$	KKG	$h^2 bs$	Criteria*
Plant height	16.62	16.47	0.14	9.57	0.87	moderat
Number of branch	0.76	0.58	0.18	41.93	23.22	moderat
number of leaves	4.44	4.11	0.33	25.84	7.52	moderat
Number of book	5.13	4.85	0.28	18.86	5.55	moderat
Number of pithy pods	10.65	10.36	0.29	18.99	2.71	moderat
Number of vacuum pods	0.10	0.10	0.01	10.45	5.36	moderat
Weight of seed by plant	0.43	0.34	0.10	25.69	21.15	moderat
Weight of 100 seeds	3.41	2.64	0.77	31.01	22.47	moderat

Gene action epistatic additive will affect the heritability value, especially heritability broad sense because on heritability broad sense there are variance dominant, additive and epistasis genes. The presence of epistasis causes heritability broad sense value was low.

Conclusion

All observed characters are (except root re-growth) on nutrient culture had heritability broad sense was high and duplicate epistasis genes action happened on root length character under stress and recovery, while in acid soil character number productive branches, seed weight plant^{-1} and 100 seeds weight had heritability broad sense were moderate and gene action complementer epistasis occurs in all observed character. Character RRG can be used as a character for selection on stadia seedlings and based on RRG obtained 87 seeds like Argomulyo and 33 seeds like Tanggamus.

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