RESEARCH ARTICLE

SABRAO Journal
of Breeding and Genetics
52 (4) 506-522, 2020

WHEAT TRANSGRESSIVE SEGREGANTS AND THEIR ADAPTATION IN THE TROPICAL REGION

N.E. PUTRI[1], S.H. SUTJAHJO[2], TRIKOESOEMANINGTYAS[2],
A. NUR[3], W.B. SUWARNO[2] and Y. WAHYU[2*]

1

[1] Graduate School, Plant Breeding and Biotechnology Study Program, IPB University, Jl. Raya Darmaga, Bogor, West Java, Indonesia
[2] Department of Agronomy and Horticulture, Faculty of Agriculture, IPB University, Jl. Meranti, Babakan, Darmaga, Bogor, West Java, Indonesia
[3] Gorontalo Assessment Institute for Agricultural Technology, Jl. Mohamad Van Gobel No. 270, Bone Bolango, Gorontalo, Indonesia
*Corresponding author email: yudiwanti@apps.ipb.ac.id
Email addresses of coauthors: nurwanita2015@gmail.com, surjonoagh@apps.ipb.ac.id, trikadytia@gmail.com, iceriamin76@gmail.com, willy@apps.ipb.ac.id

SUMMARY

Efforts are needed to develop wheat cultivars that are adapted to tropical agroecology in Indonesia. This study is aimed to identify transgressive segregants of six F_2 populations and to determine its relationship to the degree of adaptation in Indonesia. The study was conducted from April to December of 2017 at the experimental field of the Indonesian Ornamental Crops Research Institute, Cipanas, Cianjur, West Java, Indonesia. The evaluation of the six F_2 populations (Guri1/Selayar, Guri2/Selayar, Guri3/Selayar, HP1744/Selayar, Jarissa/Selayar, and Vee/Selayar) and seven parental lines (Guri 1, Guri 2, Guri 3, HP1744, Jarissa, Vee, and Selayar) was performed using an augmented, randomized complete block design with three replications for parental lines. The experiment consisted of two sets (except F_2 Guri1/Selayar and Guri3/Selayar populations), and each set contained three blocks with each block contained 13 plots (7 lines and 6 F_2 populations). Observations were made based on the seed weight per plant in all F_2 individuals and 10 sample plants per replication of the parental lines. Results showed that F_2 populations of HP1744/Selayar, Jarissa/Selayar, and Vee/Selayar had higher CGV values compared to other populations. The highest transgressive index was found in HP1744/Selayar and the lowest in Guri2/Selayar populations. All the populations have transgressive segregation of more than 50% of the total population for both directions. The number of individual classified as adapted and highly adapted in each of F2 population were as follows: 8 and 3 individuals on Guri1/Selayar, 3 and 2 individuals on Guri2/Selayar, 11 and 6 individuals on Guri3/Selayar, 7 and 3 individuals on HP1744/Selayar, 16 and 8 individuals on Jarissa/Selayar, and 4 and 3 individuals on Vee/Selayar. Those individuals that belong to the adapted and highly adapted group were the transgressive segregants. This showed that transgressive segregation selection increased the adaptability of selected genotypes in wheat.

Keywords: Adaptation group, seed weight per plant, transgressive index

Key findings: The transgressive index can be used to estimate transgressive segregation in F_2 population. Transgressive segregation selection will increase the adaptability of selected wheat genotypes.

Manuscript received: June 27, 2020; Decision on manuscript: October 10, 2020; Accepted: November 5, 2020.

Communicating Editor: Dr. Naqib Ullah Khan

INTRODUCTION

Wheat is one of the most consumed cereals in the world, including Indonesia. It is widely used in the food and feed industry in Indonesia so the demand for wheat tends to increase each year and is fulfilled through imports. Wheat imports in 2016, 2017, and 2018 respectively were 10.5 million tons, 11.4 million tons, and 10.09 million tons with a value of 2.4 million USD, 2.6 million USD, and 2.5 million USD, respectively (BPS, 2019). Efforts to partly meet increasing demand is carried out by planting wheat in Indonesia. Wheat cultivars that have been released are Selayar, Nias, Dewata, Timor, Guri 1, Guri 2, Guri 3, Guri 4, Guri 5, Guri 6 Unand, and Guri 6 Agritan which are all from introduction. These varieties are still used as breeding lines in the origin countries. Sumarno and Mejaya (2016) stated that the average wheat production varied from 0.97 t/ha to 8 t/ha in wheat producing countries. Erythrina and Zaini (2016) explained that wheat production in Indonesia were 2.9-4.8 t/ha in high land and 1 - 2.5 t/ha in medium land.

To be able to cope up with the production, wheat originating from subtropical regions must be able to adapt in tropical agroecology which has higher temperature and humidity. Indonesia has an average temperature of 27 °C with rainfall ranging from 800 to 2800 mm per year (Marpaung, 2010; Purwantara, 2015). The adaptability of wheat can be improved by developing tropical wheat cultivars through hybridization. Hybridization is a technique that develops new genotypes by combining the characteristics of the parental lines. Hybridization in self-pollinating crops such as wheat will produce the highest segregation in the F_2 generation. Segregation of alleles in the F_2 generation may results in segregants with phenotypic values exceeding the two parents. This phenomenon is known as transgressive segregation. Rieseberg *et al*. (2003) and Kagawa and Takimoto (2019) reported that transgressive segregation resulted in individuals with a higher level of adaptation than their parents.

This transgressive segregants can be identified from the F_2 generation, as individuals with phenotypes that are superior to their parents. The phenomenon of transgressive segregation is not only found in wheat but also in other plants including lentils (Chahota *et al*., 2007), barley (Kuczyńska *et al*., 2007), pigeonpea (Ajay *et al*., 2014), mung beans (Jambormias *et al*., 2015), tomatoes (Rodríguez *et al*., 2005), peanuts (Shreya*et al*., 2017), and cotton (Anusha *et al*., 2019). DeVicente and Tanksley (1993) stated that transgressive segregation in interspecific tomato crossing is caused by over-dominance. Yadav *et al*. (1998) reported that crosses that have a high SCA effect have the potential to produce transgressive segregation in wheat. Mao *et al*. (2011) reported that transgressive segregants of rice plants can occur due to the action of epistasis and complementary genes. Koide *et al*. (2019) reported that in rice plants, transgressive segregation for flowering age was obtained from the crossing of parents with a small different flowering age with a high additive variance.

The number of transgressive segregants of a segregating population can be estimated from the distance of the phenotypes of both parents (Kuczyńska *et al*., 2007). Stelkens and Seehausen (2009) reported that there is a real positive correlation between genetic distance and transgressive frequency. In this study, we compared the estimation of the number of transgressive segregants based on the transgressive index with the results of the identification of transgressive segregants in the six F_2 populations.

Selection of adapted individuals to an agroecology can be done in a population of the F_2 generation. In wheat, the adaptability of F_2 generations in tropical agroecology can be seen from its ability to produce seeds. High grain weight per plant indicates that the segregant is adaptive to tropical agro-ecological conditions. Altuhaish *et al*. (2014) reported that wheat adapted in the tropical environment was able to produce grain weights per plant of 5.26 to 16.18 g. Tropical wheat assembly through hybridization has not been widely reported in Indonesia. Natawijaya (2012) has carried out several crosses of introduced wheat and produced several F2 populations. Furthermore, Wardani *et al.* (2015) conducted a pedigree selection of the F2 population of Selayar and Rabe crosses to form the F3 family. The results showed that the seed weight per plant had high heritability so that it could increase the average seed weight per plant in the F3 population. The use of transgressive segregation on mung beans in Indonesia has been reported by Jambormias *et al.* (2015). However, there are no reports on the use of transgressive segregation selection in producing new wheat varieties. Therefore, this study is important to identify the transgressive segregants in the F_2 generation and to evaluate the relationship between the transgressive segregants and its adaptability in the tropical environments.

MATERIALS AND METHODS

This study was conducted from April to December of 2017 at the experimental field of the Indonesian Ornamental Crops Research Institute, Cipanas Cianjur Regency, West Java Province, Indonesia (at a 1100 m above sea level). The soil type was Andosol. The minimum, maximum, and average temperatures during the study were 14.5 °C, 27.8 °C, and 22 °C. (BMKG, 2018). The evaluation of the six F_2 populations (Guri1/Selayar, Guri2/Selayar, Guri3/Selayar, HP1744/Selayar, Jarissa/Selayar, and Vee/Selayar) and seven parental lines (Guri 1, Guri 2, Guri 3, HP1744, Jarissa, Vee, and Selayar) was conducted using an augmented, randomized complete block design with three replications for the parental lines. The number of living plants for each F2 population was below 100. Thus, the second planted lines was done without F2 Guri1/Selayar and Guri2/Selayar because they had no seed anymore. Therefore, the experiment consisted of two sets, except for F_2 of Guri1/Selayar and Guri2/Selayar populations, and the difference between the two sets lied in planting time, i.e., the second set was planted 21 days after planting the first set. Each set contained 3 blocks with each block contained 13 plots, each measuring 5 x 1 m. The plot of parental lines and the six F_2 populations were randomly assigned to each block. Plant spacing was 30 cm x 20 cm so that each plot contains 75 plants. Each F_2 population had 450 individual plants in the two sets if they germinated and lived until harvest. Each plant in the F_2 population plot was observed, while in the parent plot only 10 sample plants were observed. Observations were made on the character of grain weight per plant.

Other materials used were manure, inorganic fertilizer (Urea, SP36, KCl), and Furadan 3G. Fertilizer was applied twice, the first application was at the age of 10 DAP (days after planting) with a dose of 150 kg/ha urea, 200 kg/ha SP36, and 100 kg/ha KCl. The second fertilizer was applied at 30 DAP by giving 150 kg/ha Urea. Plant maintenance was carried out in the form of fertilizing, watering, and controlling pests and diseases. Application of pesticides was based on symptoms in the field. Harvesting was done when the plants were at 80% yellow and the seeds were hard.

Data Analysis

The combined data analysis was performed on both sets of experiments. Observational data were adjusted according to Petersen (1994) and followed by data analysis using least squared means (LS means).

1. Mean of seed weight per plant

$$(\bar{x}) = \frac{\Sigma X_i}{n} \ ,$$

X= observed data,
n=individual number

2. Coefficient of genetic variance

$$(\mathrm{CGV}) = \frac{\sqrt{\sigma_g^2}}{\bar{X}} \times 100\% \ .$$

(Singh and Chaudhary, 1985).

$$\sigma_p^2 = \sigma_{F_2}^2 \ ,$$

$$\sigma_e^2 = \frac{\sigma_{P_1}^2 + \sigma_{P_2}^2}{2} \ ,$$

$$\sigma_g^2 = \sigma_p^2 - \sigma_e^2 \ ,$$

where σ_p^2 = phenotypic variance, σ_e^2 = environment variance, σ_g^2 = genetic variance, $\sigma_{P_1}^2$ = parent 1 variance, and $\sigma_{P_2}^2$ = parent 2 variance (Allard, 1999).

3. Transgressive index (Koide *et al*., 2019)

$$\text{TI} = \frac{F_{2\max\square} - F_{2min}}{P_1 - P_2},$$

where TI = transgressive index, F_2 max = the highest grain weight per plant in the F_2 population, F_2 min = the lowest grain weight per plant in the F_2 population, $P_1 - P_2$ = difference between the two parental lines.

4. Adaptation grouping

Evaluation and adaptation was carried out by grouping individuals in each population based on grain weight per plant. The grouping was made following Walpole (1982) and Sastrosoemarjo *et al*. (2005) as follows (Table 1).

$$\Delta P = \frac{b - a}{n},$$

where ΔP = difference among group for variable grain weight per plant, b = highest grain weight, a = lowest grain weight, and n = number of adaptation groups.

5. Classifications of transgressive segregants

According to Rieseberg *et al*. (2003), the transgressive segregants are individuals with phenotype values higher than the best parent and those with phenotype values smaller than the lowest parent. Regarding adaptability determination, individuals classified as transgressive segregants were only those with phenotype value greater than the best parent, or positive transgressive segregants, while the rest were classified as non-transgressive ones. The classification was done for each F_2 population.

RESULTS AND DISCUSSION

The grain weight per plant is an important character in cereal crops such as wheat. This character reflects the ability of plants to accumulate photosynthates during their growth and development phases. Therefore, this character becomes a target trait in wheat breeding programs. Grain weights per plant of the parental lines are presented in Table 2.

The level of variability in a segregating population depends on the difference between the parental lines on the trait of interest. Table 2 showed that all the parental lines of the F_2 population have the same grain weight, except for parental lines of the F_2 Jarissa/Selayar populations. The parental lines Guri1, Guri2, Guri3, and Selayar are national cultivars with a mean yield of 5.8, 5.6, 3.5, and 2.95 t/ha, respectively (MOA 2003, 2013). The parental lines HP1744, Jarissa, and Vee were introduced genotypes, HP1744 and Vee came from CIMMYT collections, while Jarissa was from Slovakia.

Jarissa was known as Is-Jarissa in its original country. In this study, Jarissa had a flowering time of 117 DAP and a longer maturity days of 168 DAP compared to other parents. Similar results were reported by Altuhaish *et al*. (2014) that Jarissa has the longest flowering time and maturity days among other genotypes. Zubaidi *et al*. (2018) stated that plants that are late in entering the generative phase have low yields. In this study, Jarissa began flowering at the end of August 2017 and harvested in mid-November 2017.

Table 1. Grouping of genotypes through evaluation and adaptation (Walpole, 1982; Sastrosoemarjo *et al*., 2005).

Score	Adaptation group	Class grouping
1	Not adapted	$x < \Delta P + a$
2	Less adapted	$\Delta P + a \leq x < (\Delta P + a) + \Delta P$
3	Moderately adapted	$(\Delta P + a) + \Delta P \leq x < (\Delta P + a) + 2\,\Delta P$
4	Adapted	$(\Delta P + a) + 2\,\Delta P \leq x < (\Delta P + a) + 3\,\Delta P$
5	Highly adapted	$x \geq (\Delta P + a) + 3\,\Delta P$

ΔP = difference among group for variable grain weight per plant, a = lowest grain weight, x = observed value

Table 2. Grain weight per plant of parental lines of six F_2 wheat populations.

F_2 populations	P_1 (g)	P_2 (g)	*P*-value
Guri1/Selayar	23.44	22.78	0.88
Guri2/Selayar[a]	28.45	13.40	0.28
Guri3/Selayar[a]	23.17	13.40	0.05
HP1744/Selayar	23.15	22.78	0.92
Jarissa/Selayar	03.74	22.78	0.03*
Vee/Selayar	20.90	22.78	0.70

The grain weight data shown was corrected according to Petersen (1994); a = only in one set P_1 = female parent; P_2 = male parent; * = significantly different between P_1 and P_2 based on α 0.05 paired t-test.

BMKG (2018) reported that rainfall in August and November was 83 (low category) and 624 mm (very high category). The maximum temperature in August was 27.2 °C. This showed that Jarissa was exposed to high temperatures at the beginning of flowering and high rainfall at the time of grain filling until maturity. Rain causes lower light intensity needed for the photosynthesis process, resulting in lower photosynthate accumulated in the grain and they become small grain. Therefore, Jarissa in this study had low grain weight per plant (3.74 g). This genotype entered the generative phase when other genotypes have entered the harvest phase. Jarissa faced high temperatures at the beginning of flowering and high intensity rain during grain filling and harvesting (BMKG 2018). These factors caused the grain weight per plant to be very low. On the other hand, it reported that Jarissa planted in several locations in West Sumatra Province with elevation of >900 m above sea level produced seed weight per plant up to 23.1 g (Chaniago *et al*., 2014). The F_2 populations of HP1744/Selayar, Vee/Selayar, and Jarissa/Selayar had a wide distribution of flowering time and maturity days than others.

Hybridization of self-pollinating plants resulted in segregation and recombination starting from the F_2 generation. This segregation can be seen from the wide distribution of grain weight per plant from individuals in each cross combination. The F_2 populations of HP/Selayar, Jarissa/Selayar, and Vee/Selayar have wide grain weight intervals than the others (Table 3). The CGV values of these populations were relatively high (>60%). Besides those populations, Guri1/Selayar had also high CGV

Table 3. Grain weight per plant and coefficient of genetic variance (CGV) of six F_2 wheat populations.

F_2 Populations	N	Range (g)	Mean (g)	CGV (%)
Guri1/Selayar	97	−11.27−63.54	15.11 ± 14.06	73.70
Guri2/Selayar	81	−1.25−57.31	13.12 ± 12.60	0.00
Guri3/Selayar	56	1.06−62.42	27.00 ± 16.50	47.61
HP1744/Selayar	170	−13.09−99.78	20.84 ± 22.16	92.42
Jarissa/Selayar	160	−12.69−92.09	26.52 ± 21.50	75.09
Vee/Selayar	218	−12.89−171.01	23.10 ± 30.65	126.71

The grain weight data shown were corrected according to Petersen (1994); N = total living plants.

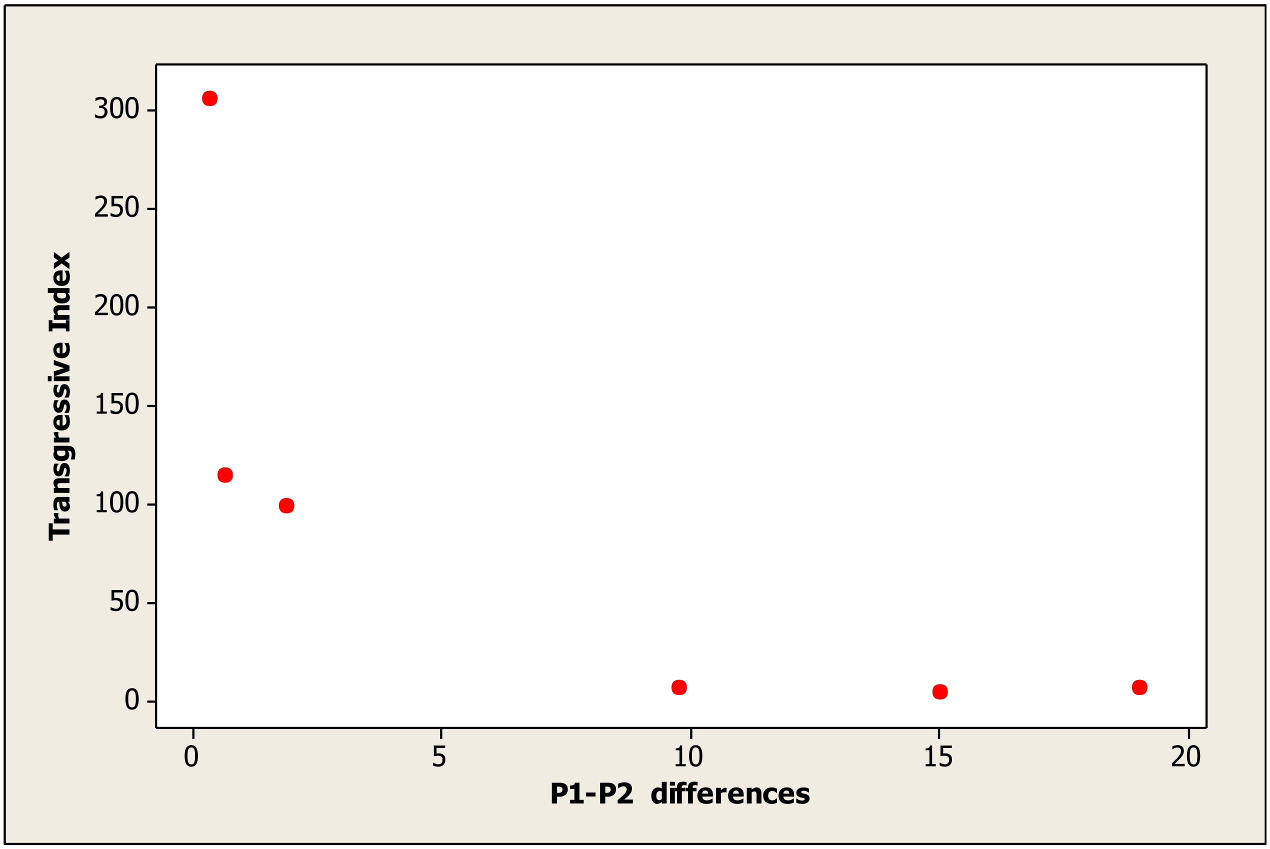

Figure 1. Relationship of P1 – P2 differences and transgressive index in the six F2 wheat populations.

values. Selection can be made in these populations to improve the grain weight per plant. The CGV showed the amount of genetic variability that occurs in a population. The parental lines HP1744, Jarissa, and Vee were introduced wheat lines that have different genetic backgrounds so that the crossing involving these parental lines can increase the variability of the segregating populations. The adaptation of HP1744, Jarissa, and Vee in Indonesia was thought to increase variations in several loci so hybridization with Selayar produces segregation with a higher level of variability. In contrast, the F_2 population of Guri1/Selayar, Guri2/Selayar, Guri3/Selayar had a narrow distribution of grain weight per plant compared to other populations (Table 3). The genetic variability of these populations ranged from 0.00% to 73.70%.

The wide distribution of grain weight per plant in the F_2 population resulted in segregants that have extreme phenotypic values compared to both parents. This phenomenon is known as transgressive segregation (Chang *et al*., 1973; Rieseberg *et al*., 2003). Anusha *et al.* (2019) stated that hybridization causes the accumulation of genes in the same direction giving rise to a phenotype that exceeds its parents.

The approach that can be used to estimate transgressive segregation in F_2 population is the transgressive index. The transgressive index is estimated as the proportion of the difference in grain weight per plant in the F_2 population to the difference between the two parents. The transgressive index for the six F_2 populations ranges from 3.89 to 305.05 (Table 4). The F_2 population of HP1744/Selayar had the highest transgressive index. This was due to the small difference in grain weight per plant of the two parental lines (0.37) and the wide distribution of the F_2 individuals (112.87). The grain weight distribution of F_2 genotypes was also supported by the high CGV value (Table 3). The smaller the value of the difference in the parents, the greater the transgressive index (Figure 1). Koide *et al*. (2019) stated that the greater the value of the transgressive index, the greater the chance of getting transgressive segregation in the F_2 population.

Transgressive segregants are a collection of individuals that come from two directions, those with phenotype values higher than the best parent and those with phenotype values smaller than the lowest parent. The F_2 populations of HP1744/Selayar, Vee/Selayar, and Guri1/Selayar have the most transgressive segregants compared to the other three populations. The first two populations were crossses of national wheat cultivars (Selayar) with introduced wheat lines. However, the introduced parents have the same seed weight per plant as Selayar according to Table 2. Rieseberg *et al*. (1999) predicted that the more similar phenotype of parents, the greater the likelihood of transgressive segregation will be observed in F_2. Transgressive segregation analysis on F_2 helps determine potential populations to be selected at the start of a generation and reduces population size in later generations (Bharathi and Reddy, 2019).

The transgressive indexes in the F_2 population of HP1744/Selayar, Guri1/Selayar, and Vee/Selayar were higher compared to others (Table 4). In line with this, these three populations had a high proportion of transgressive segregants, i.e., 98.24%, 97.94%, and 97.71%, respectively (Table 5). The F_2 population of Guri3/Selayar, Jarissa/Selayar, and Guri2/Selayar had a lower transgressive index (Table 4), as well as a lower proportion of transgressive segregants, i.e., 71.43%, 56.88%, and 76.54% (Table 5). Based on these data, the more transgressive index, the more transgressive segregant (Figure 2).

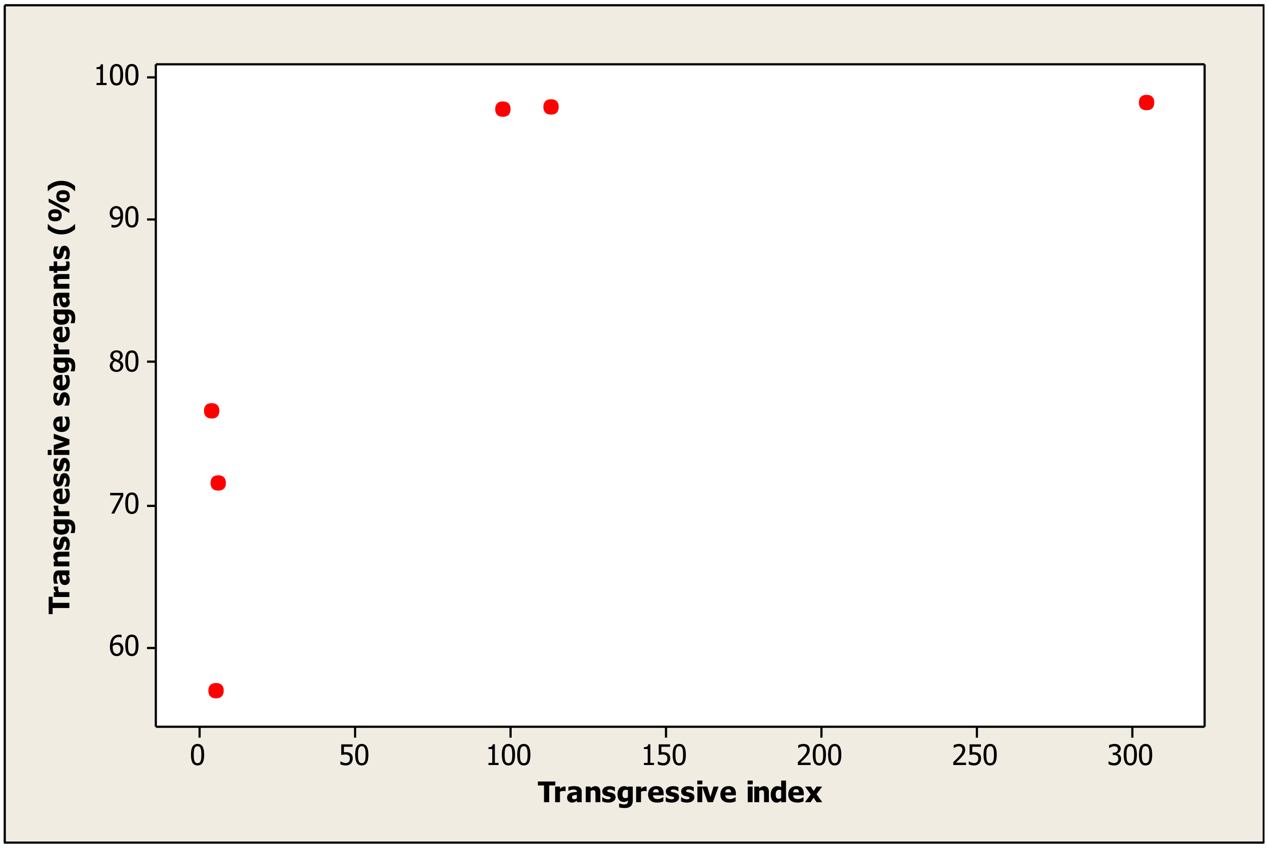

Figure 2. Relationship of transgressive index and total transgressive segregant (%) in six F_2 wheat populations.

Table 4. Transgressive index of grain weight per plant in six F_2 wheat populations.

F_2 populations	F_2 max − F_2 min (g)	Parental difference (g)	Transgressive index
Guri1/Selayar	74.81	0.66	113.35
Guri2/Selayar	58.56	15.05	3.89
Guri3/Selayar	61.36	9.77	6.28
HP1744/Selayar	112.87	0.37	305.05
Jarissa/Selayar	104.78	19.04	5.50
Vee/Selayar	183.90	1.88	97.82

The grain weight data shown were corrected according to Petersen (1994).

Table 5. Transgressive segregants of grain weight per plant in six F_2 wheat populations.

F_2 Populations	N	Grain weight of parents		Number of transgressive segregants			
		Low parent (LP)	High parent (HP)	Less than LP	Greater than HP	Total (%)	Greater than HP (%)
Guri1/Selayar	97	22.78	23.44	74	21	95 (97.94)	21.65
Guri2/Selayar	81	13.40	28.45	51	11	62 (76.54)	13.58
Guri3/Selayar	56	13.40	23.17	13	27	40 (71.43)	48.21
HP1744/Selayar	170	22.78	23.15	91	76	167 (98.24)	44.71
Jarissa/Selayar	160	03.74	22.78	13	78	91 (56.88)	48.75
Vee/Selayar	218	20.90	22.78	113	100	213 (97.71)	45.87

The grain weight data shown were corrected according to Petersen (1994), N = no. of plants.

The populations of Guri3/Selayar and Jarissa/Selayar were not in line with the theory of Koide *et al*. (2019), which mentioned that these two populations should have more transgressive segregants. The low number of transgressive segregants in the Guri3/Selayar population was likely caused by the small number of living segregants that cannot yet represent the true of its potential transgressive segregation. The F_2 Jarissa/Selayar population tended to have long maturity days like its parent, Jarissa. They faced heat stress at the flowering stage and high rainfall at the grain filling periods. These conditions were not optimum for pollination. Besides, the photosynthetic processes for assimilate accumulation to the grain were disturbed. Therefore, only a small number of segregants had grain weight per plant exceeding their best parent, Selayar. The F_2 Jarissa/Selayar population has less number of transgressive segregants than other populations. The phenotypic values of its parental lines on grain weight per plant were significantly different. It means that there was a large difference between Jarissa and Selayar. This condition was thought causing the total percentage of transgressive segregants (56.88%) were not as much as other populations whose parental lines have a smaller difference in their phenotypic values.

The percentage of transgressive segregants higher than the high parent (positive direction) was more than 40% in four F_2 populations, namely, Guri3/Selayar, HP1744/Selayar, Jarissa/Selayar, and Vee/Selayar (Table 5). This was due to the small phenotypic difference between the parental lines which caused more segregants with a phenotypic value higher than the best parents. They were *putative transgressive segregants.* However, the heterozygote could not be distinguished from the homozygote segregants. For practical breeding, planting all of the 40% transgressive segregants in the next generation may not be efficient because it needs high cost and place for maintaining, so selection on the F_2 putative transgressive segregants should be done but not strict.

The phenotypic value in F_2 generation can be overexpressed by its gene action, like epistasis. Amin

(2013) found three types of epistatic gene actions that controlled some agronomic characters of wheat, i.e., additive × additive, additive × dominance, and dominance × dominance. Characters controlled by epistasis could show a decreasing value in the next generation. Jambormias (2014) who worked with mungbean reported that the families with the best performance that have been uniform in the previous generation, behaved poorly in the next generation because of the emergence of epistatic recessive homozygotes. This was the reason why the selection on the F_2 putative transgressive segregants population should be not strict, i.e. 20%–30%. These putative-transgressive segregants need to be verified in the next F2.3 generation by plant-to-row plantings. Some of them may not have a higher mean than their best parent in F2.3 family generation and the rest may still consistently higher. It will be expected that the transgressive segregants, which were consistently have higher mean with low variability, are homozygous. These homozygous transgressive segregants will support the acceleration of breeding improved wheat cultivars.

Transgressive segregation generated from a biparental cross is influenced by several factors, including the phenotypic dissimilarity among the parental lines used. Rieseberg *et al*. (1999) predicted that the frequency of transgression will be positively correlated with genetic divergence of the parental lines. On the other hand, Fabrizius *et al.* (1998) reported that no correlation were observed between genetic distance and numbers of transgressive segregants in wheat intraspesific crosses. The F_2 populations of Guri2/Selayar and HP1744/Selayar have parents which were not significantly different in grain weight per plant (Table 2). Koide *et al*. (2019) stated that transgressive segregation is not directly influenced by the genetic differences of the parents but more of the similarity of the phenotype.

The probability of the occurrence of transgressive segregation cannot be separated from the role of gene action controlling the trait. Genetic studies related to transgressive segregation have also been carried out. Xu *et al*. (1998) reported that complementary gene action is responsible for the occurrence of transgressive segregation in intraspecific crosses. Others reported that the additive gene action and the small differences between the two parents increase the chances of getting a transgressive segregation (Kuczyńska *et al*., 2007; Chahota *et al*., 2007). In addition to the over-dominant and epistatic gene actions as causes of transgressive segregation, the main cause of transgressive segregation is the action of complementary genes (Rieseberg *et al*., 1999; Koide *et al*., 2019).

The development of wheat in Indonesia is an effort to adapt wheat in the tropics. One of the limiting factors is high temperature. High temperature stress affects physiology, biochemistry, growth, and development and in the end resulted in lower yield (Akter and Islam, 2017). Recent studies showed that for every 1 °C increase in temperature will reduce wheat yield up to 4.1%–6.4% (Asseng *et al*., 2015, Liu *et al*., 2016). High temperature interferes with translocation from the source to sink and also reduce pollen viability (Altuhaish *et al*., 2014). High temperature stress after the anthesis phase can suppress grain set and grain size (Nuttall *et al*., 2017). Adaptive plants in tropical environments are shown by their ability to produce high grain yield.

Table 6 shows the number of individual plants in the adaptation group of each F_2 population. Each group had a mean value of grain weight per plant. The LSD (least significant difference) test was applied to compare the mean value of each group to both their parents. The result showed that there were groups with significantly higher or lower mean than their parents. The groups with statistically higher mean than their high parent must consist of several or all segregants with a high value of grain weight per plant because they could increase the mean values of the group. Adapted and highly adapted groups in all F_2 populations have mean values better than the high parent. The number of adapted and highly adapted individuals was different among groups. These explained that we could identify individual segregants in these groups with higher grain weight per plant than their parents.

The focus of this study was to evaluate each F_2 population into adaptation groups. For the next discussions, the term 'transgressive segregation' will refer to explain the ‘positive’ transgressive segregation (greater than the highest parent). Adaptation groups of the F_2 population aimed to obtain preliminary information about segregants that can be selected and develop in the tropical wheat breeding program.

Table 6. Individual adaptation grouping in six F_2 wheat populations based on grain weight per plant.

Adaptation groups	F_2 Guri1/Selayar		F_2 Guri2/Selayar		F_2 Guri3/Selayar	
	N	Mean	n	Mean	n	Mean
Not adapted	14	−1.97b	42	04.10b	13	07.06b
Less adapted	54	10.16b	23	14.96	16	18.90
Moderately adapted	18	25.42	11	28.89	10	31.25a
Adapted	8	38.89a	3	39.23a	11	42.28a
Highly adapted	3	58.52a	2	55.71a	6	56.73a
Parental lines						
P_1		**23.44**		**28.45**		**23.17**
P_2		22.78		13.40		13.40

	F_2 HP1744/Selayar		F_2 Jarissa / Selayar		F_2Vee/Selayar	
	N	Mean	n	Mean	n	Mean
Not adapted	59	−2.70b	26	01.16b	123	03.27b
Less adapted	57	21.37	76	17.64	78	37.67a
Moderately adapted	44	40.42a	34	38.39a	10	77.12a
Adapted	7	60.87a	16	56.23a	4	116.97a
Highly adapted	3	93.13a	8	83.38a	3	152.09a
Parental lines						
P_1		**23.15**		03.74		20.90
P_2		22.78		**22.78**		**22.78**

The mean grain weight data shown were corrected according to Petersen (1994); parental with bold attribute was the higher parent; n = number of individual plants; a, b = significantly higher or lower than the high parent, respectively, based on the LSD test at α 0.05.

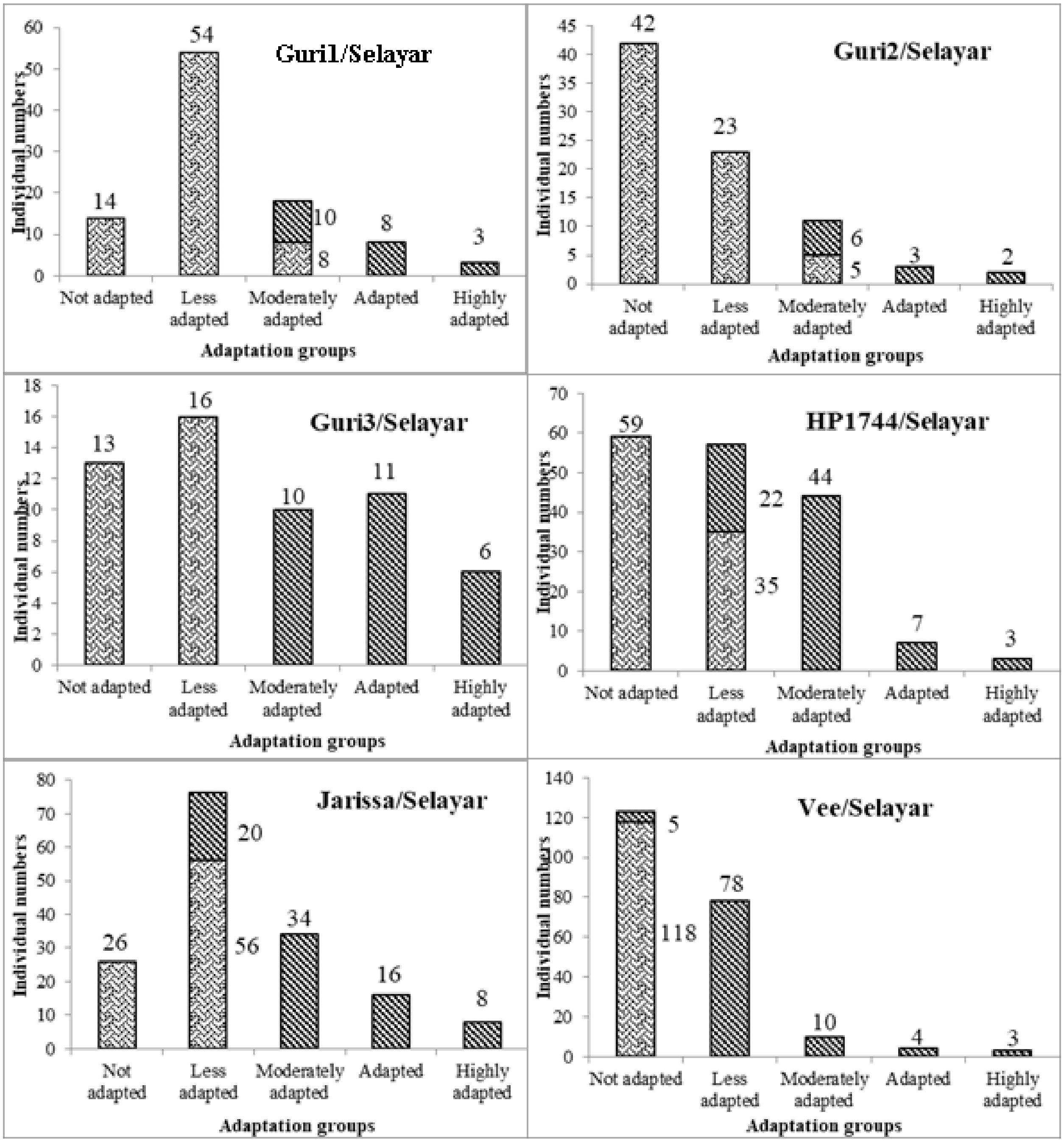

Figure 3. Distribution of transgressive segregants in adaptation groups of six F_2 wheat populations. ■ positive transgressive segregants (segregants which are greater than the highest parent), ▨ others (all segregants which are lower than the highest parent).

Figure 3 shows the distribution of the positive transgressive segregants of each F_2 population adaptation group. Crossing Selayar with introduced parent genotypes (HP1744, Jarissa, and Vee) resulted in a high number of positive transgressive segregants than others.

We predicted that introduced genotypes have new allele combinations to Selayar (a national variety) due to their segregants were more able to survive in the tropical environment. All individual segregants in the adaptive and highly adaptive groups were positive transgressive segregants with different numbers among the populations.

The different distributions of the transgressive segregation among the adaptation groups in these three F_2 populations were thought to be caused by the variation of alleles controlling adaptation contributed by the parents involved. Rieseberg *et al*. (2003) stated that individuals having only positive alleles or negative alleles from both parents will have an extreme appearance. This indicated that highly adaptive individuals inherited alleles with a direct positive influence from their parents. Therefore, it can be explained that transgressive segregation plays a role in plant adaptation. Rieseberg *et al*. (2003) stated that transgressive segregation was a fast and large mechanism in evolution because hybridization produces a combination of genes and alleles that have been tested through selection.

Adapted and highly adapted individual wheat plants were promising to be developed in Indonesia. Figure 3 shows that all individuals classified as adapted or highly adapted were transgressive segregants. These results supported the studies made by Rieseberg *et al*. (2003) and Kagawa and Takimoto (2019) that transgressive segregation selection resulted in individuals with a higher level of adaptation. There were 8 and 3 individuals of Guri1/Selayar classified as adaptive and highly adaptive. In other F_2 populations, the number of adaptive and highly adaptive individual plants were as follows: 3 and 2 individuals on Guri2/Selayar, 11 and 6 individuals on Guri3/Selayar, 7 and 3 individuals on HP1744/Selayar, 16 and 8 individuals on Jarissa/Selayar, and 4 and 3 individuals on Vee/Selayar. These individuals should be plant-to-row spaced planted in F2.3 generation to examine which of them will be transgressive segregant lines, i.e. have greater grain weight per plant than their highest parent and have low variance which shows that no, or minimum, segregation because they have homozygote for all, or almost all, loci.

CONCLUSION

The F_2 populations of HP1744/Selayar, Jarissa/Selayar, and Vee/Selayar have a high value of coefficient genetic of variance (CGV) compared to other populations. Populations that have the highest to lowest transgressive index successively were the F_2 population of HP1744/Selayar, Guri1/Selayar, Vee/Selayar, Guri3/Selayar, Jarissa/Selayar, and Guri2/Selayar. All populations have transgressive segregants of more than 50% of the total individuals in each population. The number of individuals classified as adapted and highly adapted in each of F_2 population were as follows: 8 and 3 individuals on Guri1/Selayar, 3 and 2 individuals on Guri2/Selayar, 11 and 6 individuals on Guri3/Selayar, 7 and 3 individuals on HP1744/Selayar, 16 and 8 individuals on Jarissa/Selayar, and 4 and 3 individuals on Vee/Selayar. All individuals that were classified into adapted and highly adapted groups were transgressive segregants which means that transgressive segregation selection will increase the adaptability of selected wheat genotypes. Segregants classified into adaptive and highly adaptive could be continued to F2.3 generation to verify whether these segregants still have a high grain weight per plant with low variability.

ACKNOWLEDGEMENTS

This research was funded by the Ministry of Research, Technology, and Higher Education of the Republic of Indonesia, through the 2018 IPB University Higher Education Basic Research (PDUPT-IPB) scheme with Contract Number: 1801/IT3.11/PN/2018 on behalf of Yudiwanti Wahyu.

REFERENCES

Ajay B, Byregowda M, H PB, Gn VK, Reena M (2014). Variability and transgressive segregation for yield and yield contributing traits in pigeonpea crosses. *Electr. J. Plant Breed.* 5(4):786–791.

Akter N, Islam M (2017). Heat stress effects and management in wheat. A review. *Agron. Sustain. Dev.* 37(5):37-53.

Allard RW (1999). *Principles of Plant Breeding.* 2 nd edition. John Wiley & Sons, Inc. New York.

Altuhasish AAK, Miftahudin, Trikoesoemaningtyas, Yahya S (2014). Field adaptation of some introduced wheat (*Triticum aestivum* L.) genotypes in two altitudes of tropical agro-ecosystem environment of Indonesia. *HAYATI J. Biosci*. 21(1):31–38.

Amin, IA (2013). Genetic behaviour of some agronomic traits in two durum wheat crosses under heat stress. *Alex. J. Agric. Res.* 58(1):53-66.

Anusha G, Rasal PN, Patil MR, Lavanya B, Menora BN, Shankaraiah K (2019). Studies on transgressive segregation in F2 generation in Deshi Cotton (*Gossypium arboreum* L.). *Int. J. Pure Appl. Biosci.* 7(1):172–176.

Bharathi Y, Reddy KH (2019). Variability, heritability and transgressive segregation on yield and its components in F2 progenies of sesame (*Sesamum indicum* L.). *Electr. J. Plant Breed.* 10(1):312–317.

[BMKG] Badan Meteorologi, Klimatologi, dan Geofisika (2018). Rainfall and Temperature Periode 2016-2018 in Bogor. Bogor Climatology Station, Bogor, Indonesia.

[BPS] Badan Pusat Statistik (2019). Impor Biji Gandum dan Meslin Menurut Negara Asal utama, tahun 2010-2017. BPS, Jakarta. https://www.bps.go.id/statictable/2019/02/14/2016/ impor-biji-gandum-dan-meslin-menurut-negara-asal-utama-2010-2019.html

Chahota RK, Kishore N, Dhiman KC, Sharma TR, Sharma SK (2007). Predicting transgressive segregants in early generation using single seed descent method-derived micro-macrosperma genepool of lentil (*Lens culinaris* Medikus). *Euphytica.* 156(3):305–310.

Chang T-T, Li C-C, Oscar T (1973). Genotypic correlation, hetorosis, inbreeding depression and transgressif segregation of agronomic traits in a diallel cross of rice (*Oryza sativa* L.) cultivar. *Bot. Bull. Acad. Sin.* 14:89–93.

Chaniago I, Suliansyah I, Kasim M, Reflinaldon R (2014). Studies on wheat (*Triticum aestivum* L.) adaptability in the province of West Sumatera, Indonesia. *Int. J. Adv. Sci. Eng. Inf. Technol.* 4(5):358.

DeVicente M., Tanksley S (1993). QTL analysis of transgressive segregation in an interspecific tomato cross. *Genet*. 134(1):585–596.

Erythrina, Zaini Z (2016). Dinamika penelitian gandum di Indonesia. In: *Gandum: Peluang Pengembangan di Indonesia.* Praptana RH, Hermanto (eds). IAARD Press, Jakarta.

Jambormias E (2014). Analisis genetik dan segregasi transgresif berbasis informasi kekerabatan untuk potensi hasil dan panen serempak kacang hijau. Disertasi. Sekolah Pascasarjana Institut Pertanian Bogor, Bogor.

Jambormias E, Sutjahjo SH, Mattjik AA, Wahyu Y, Wirnas D, Siregar A, Patty JR, Laisina JK, Madubun EL, Ririhena RE (2015). Transgressive segregation analysis of multiple traits in mungbean (*Vigna radiata* L. Wilczek). *SABRAO J. Breed. Genet.* 47(2):201–213.

Kagawa K, Takimoto G (2019). Hybridization can promote adaptive radiation by means of transgressive segregation. *Ecol. Lett.* 21(2):264–274.

Koide Y, Uchiyama T, Ota Y, Sakaguchi S, Tezuka A, Nagano AJ, Ishiguro S, Takamure I, Kishima Y (2019). Genetic basis of transgressive segregation in rice heading phenotypes. *Genes, Genomes, Genet.* 9:1655–1662.

Kuczyńska A, Surma M, Adamski T (2007). Methods to predict transgressive segregation in barley and other self-pollinated crops. *J. Appl. Genet.* 48(4):321–328.

Liu B, Asseng S, Müller C, Ewert F, Elliott J, Lobell DB, Martre P, Ruane AC, Wallach D, Jones JW, *et al.* (2016). Similar estimates of temperature impacts on global wheat yield by three independent methods. *Nat. Clim. Chang.* 6(12):1130–1136.

Mao D, Liu T, Xu C, Li X, Xing Y (2011). Epistasis and complementary gene action adequately account for the genetic bases of transgressive segregation of kilo-grain weight in rice. *Euphytica.* 180(2):261–271.

Marpaung S. (2010). Pengaruh topografi terhadap curah hujan musiman dan tahunan di Provinsi Bali berdasarkan data observasi resolusi tinggi. *Pros. Semin. Penerbangan dan Antariksa*: 104–110.

[MOA] Ministry of Agriculture (2003). Description of Selayar Variety. Ministry of Agriculture's Decision of Selayar as superior wheat variety. Ministry of Agriculture, Jakarta.

[MOA] Ministry of Agriculture (2013). Description of Guri 1 and Guri 2 varieties. Ministry of Agriculture's Decision of Guri 1 and Guri 2 as superior wheat varieties. Ministry of Agriculture, Jakarta.

Nuttall JG, O'Leary GJ, Panozzo JF, Walker CK, Barlow KM, Fitzgerald GJ (2017). Models of grain quality in wheat - A Review. *Field Crop. Res.* 202:136–145.

Petersen RG (1994). *Agricultural Field Experiments: Design and Analysis*. Marcel Dekker, Inc. New York.

Purwantara S (2015). Studi temperatur udara terkini di wilayah di Jawa Tengah dan DIY. *Geomedia.* 13(1): 41–52.

Rieseberg LH, Archer MA, Wayne RK (1999). Short review: transgressive segregation, adaptation and speciation. *Heredity (Edinb).* 83:363–372.

Rieseberg LH, Widmer A, Arntz AM, Burke JM, Carr DE, Abbott RJ, Meagher TR (2003). The genetic architecture necessary for transgressive segregation is common in both natural and domesticated populations. *Philos. Trans. R. Soc. Biol. Sci.* 358(1434):1141–1147.

Rodríguez GR, Pratta GR, Zorzoli R, Picardi LA (2005). Transgressive segregation for fruit quality traits in a cross between exotic and mutant genotypes of lycopersicon. *New Zealand J. Crop Hort. Sci.* 33(4): 373–379.

Sastrosoemarjo S, Bamahry N, Trikoesoemaningtyas (2005). Evaluasi daya adaptasi galur-galur introduksi tanaman gandum pada daerah elevasi rendah. Di dalam: Efendi D, Surahman M, Hadad M, Suhartanto MR, Sujiprihati S, Subandriyo, Trikoesoemangtyas, editor. *Simposium PERIPI: Menuju Indonesia Berswasembada Varietas Unggul*; 2004 Agustus 5-7; Bogor, Indonesia. PERIPI, Bogor. hlm. pp. 1–9.

Sihaloho, AN (2015). Identifikasi aksi gen epistasis pada toleransi kedelai terhadap cekaman aluminium. *J. Agron. Indonesia* 43(1):30-35.

Singh RK, Chaudhary BD (1985). *Biometrical Methods in Quantitative Genetics Analysis*. Kalyani Publisher, New Delhi.

Shreya, Ainmisha, Vasanthi RP (2017). Transgressive segregation study in F_3 population of four groundnutcrosses. *Int. J. Curr. Microbiol. Appl. Sci.* 6(4): 2054–2059.

Stelkens R, Seehausen O (2009). Genetic distance between species predicts novel trait expression in their hybrids. *Evolution (N. Y).* 63(4):884–897.

Sumarno, Mejaya MJ (2016). Pertanaman dan produksi gandum di dunia. In: *Gandum: Peluang Pengembangan di Indonesia.* Praptana RH, Hermanto (eds). IAARD Press, Jakarta.

Walpole RE (1982). *Pengantar Statistika*. Ed ke-3. Diterjemahkan oleh Bambang Sumantri. Gramedia, Jakarta.

Wardani S, Wirnas D, Wahyu Y (2015). Seleksi segregan gandum (*Triticum aestivum* L .) pada dataran tinggi. *J. Agron. Indonesia.* 43(1):45–51.

Yadav B, Tyagi CS, Singh D (1998). Genetics of transgressive segregation for yield and yield components in wheat. *Ann. Appl. Biol.* 133(2):227–235.

Zubaidi A, Ma'shum M, Gill G, McDonald GK (2018). Wheat (*Triticum aestivum* L.) adaptation to Lombok island Indonesia. *AGRIVITA J. Agric. Sci.* 40(3):556–566.