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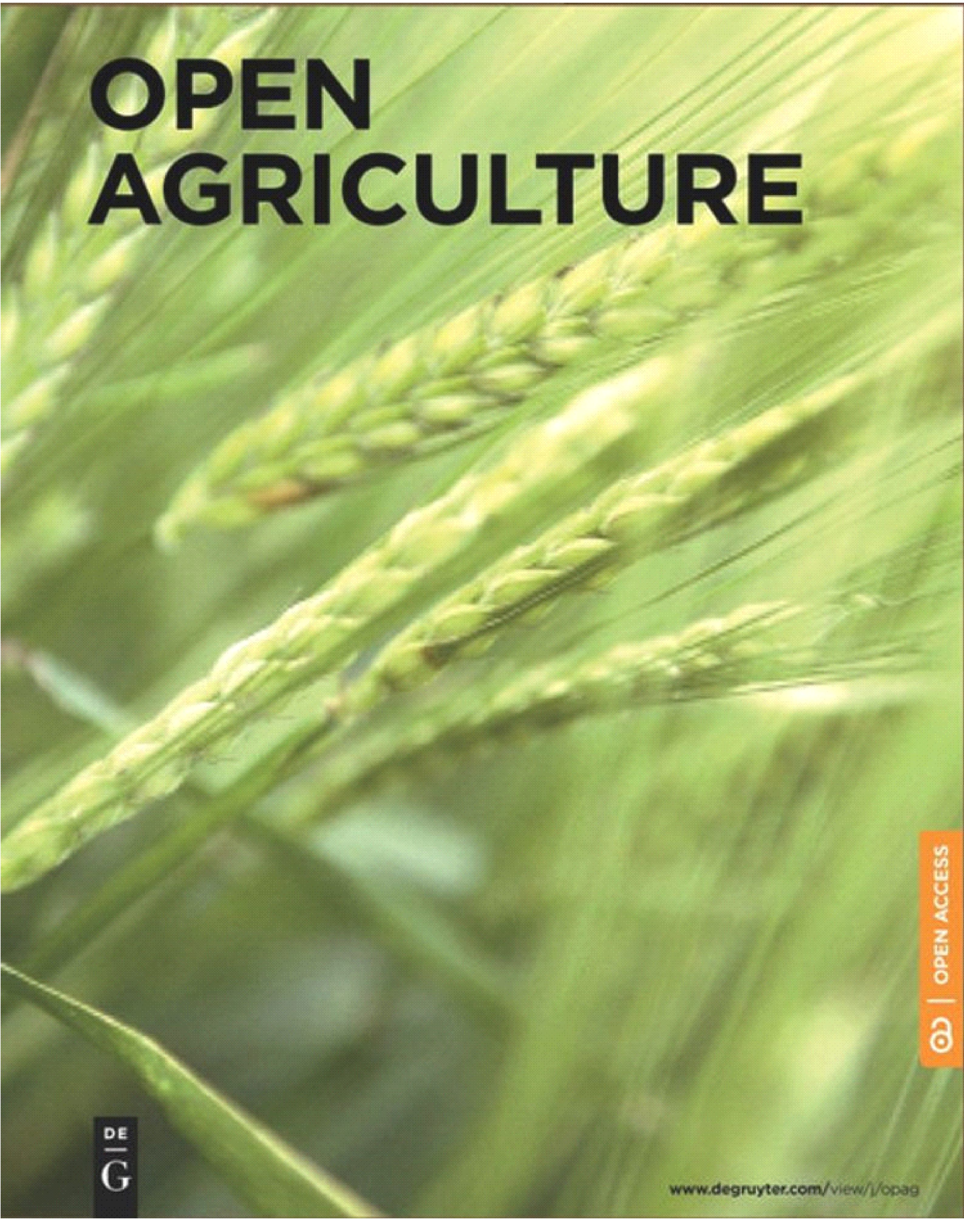

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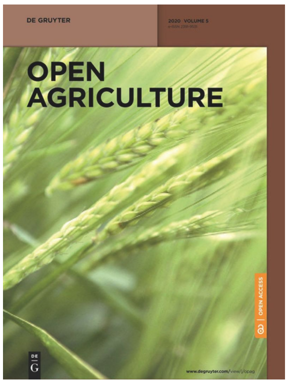

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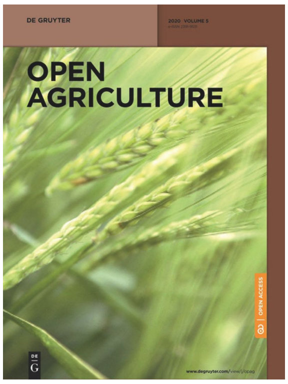

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Regular Articles

Open Access | January 2, 2023

The impact of COVID-19 pandemic on business risks and potato commercial model

Pujiharto Pujiharto, Sri Wahyuni

Article number: 20220158

Abstract

This study was aimed (1) to analyze the productivity, cost, and income of potato farming; (2) to analyze the risk of potato farming; and (3) to analyze the potato trade system at the level before and during COVID-19 pandemic. This study used a descriptive-quantitative research type. It was conducted in Banjarnegara Regency, Jawa Tengah Province, Indonesia. The data were collected through surveys, observations, and Focus Group Discussions. The unit of analysis is the farmers who plant potatoes. Data analysis was done descriptively. The results showed that there is no difference between the two marketing channels before and during pandemic. There are two channels of the trading system, namely farmer–collector–traders–wholesaler–exporter partners and farmer–collector–traders–wholesalers–retailers. However, the trading model maximizes the Agribusiness Sub Terminal (AST) as a potato trading agent that can provide direct price information, attract traders, and facilitate transactions and trading contacts. The trading model allows potato trading agents to provide direct price information, attract traders, and facilitate transactions and trading contacts. The implication of this study is to anticipate productivity risk and potato farming income risk through the AST function. This study contributes to the condition of farming before and during COVID-19 pandemic by comparing differences in productivity, costs, income, productivity risk, and income risk as well as the potato grading model.

Open Access | January 4, 2023

Effects of potato (*Solanum tuberosum* L.)–*Mucuna pruriens* intercropping pattern on the agronomic performances of potato and the soil physicochemical properties of the western highlands of Cameroon

Franck Junior Ngandjui Tchapga, Asafor Henry Chotangui, Maryline Temgoua Fouegag, Tankou Christopher Mubeteneh

Article number: 20220142

Abstract

A field experiment was conducted at the teaching and research farm of the Faculty of Agronomy and Agricultural Sciences of the University of Dschang to investigate the effects of potato– Mucuna intercropping pattern on the agronomic performances of potatoes and the soil physicochemical properties in western highlands of Cameroon. The experiment design was a randomized complete block with three replications. The treatments included a pure potato stand (T1), pure Mucuna stand (T2), 1:1 (T3), 1:2 (T4), and 2:1 (T5) potato– Mucuna intercropping patterns. The results revealed that potato– Mucuna intercropping patterns had no significant effect ($P > 0.05$) on potato growth variables, soil physical properties, and the relative crowding coefficient. The highest potato yield (24,913 kg ha^{-1}) and potato equivalent yield (81,513 kg ha^{-1}) were obtained from the 1:1 intercropping pattern. The highest total LER (2.17) and the lowest (1.38) were obtained with 1:1 and 1:2 intercropping patterns, respectively. Area time equivalent ratio values were greater than 1 in 1:1 (1.46) and 2:1 (1.29) intercropping patterns. Mucuna proved to be the most aggressive and competitive species according to Ap and competitive ratio values except for the 1:2 intercropping pattern with K indicating a yield advantage in all intercropping patterns. 1:1 and 2:1 intercropping patterns gave the best C/N (13.94) and cation exchange capacity (36.12 $\text{meq } 100\text{ g}^{-1}$), respectively. Late blight incidence was highest (16.88%) on potato sole crop stand and lowest (8.05%) on 1:2

intercropping pattern. Therefore, based on the findings of this experiment, 1:1 or 1:2 intercropping pattern could be recommended in potato– Mucuna intercropping system.

Open Access | January 7, 2023

Machine learning-based prediction of total phenolic and flavonoid in horticultural products

Kusumiyati Kusumiyati, Yonathan Asikin

Article number: 20220163

Abstract

The purpose of this study was to predict the total phenolic content (TPC) and total flavonoid content (TFC) in several horticultural commodities using near-infrared spectroscopy (NIRS) combined with machine learning. Although models are typically developed for a single product, expanding the coverage of the model can improve efficiency. In this study, 700 samples were used, including varieties of shallot, cayenne pepper, and red chili. The results showed that the TPC model developed yielded R 2 cal, root mean squares error in the calibration set, R 2 pred, root mean squares error in prediction set, and ratio of performance to deviation values of 0.79, 123.33, 0.78, 124.20, and 2.13, respectively. Meanwhile, the TFC model produced values of 0.71, 44.52, 0.72, 42.10, and 1.87, respectively. The wavelengths 912, 939, and 942 nm are closely related to phenolic compounds and flavonoids. The accuracy of the model in this study produced satisfactory results. Therefore, the application of NIRS and machine learning to horticultural products has a high potential of replacing conventional laboratory analysis TPC and TFC.

Open Access | January 7, 2023

Revamping agricultural sector and its implications on output and employment generation: Evidence from Nigeria

Abiola John Asaleye, Henry Inegbedion, Adedoyin Isola Lawal, Oluwayemisi Kadijat Adeleke, Uche Abamba Osakede, Elizabeth Bolatito Ogunwole

Article number: 20220140

Abstract

The Nigerian government has implemented a comprehensive spectrum of policies and programmes to diversify the economy and encourage broad-based growth through investment in the agricultural sector. However, the steady increase in the poverty and unemployment rate has raised controversial issues among scholars. In light of this, the study investigates the impact of selected macroeconomic variables on Nigeria’s agricultural performance using two models for output and employment. The Error Correction Model (ECM) approach was used to establish the short and long-run behaviours. In the first model, output in the agricultural sector was used as the independent variable, while in the second model, employment in the agricultural sector was used as the independent variable. The study's findings showed that output positively relates to credit to the agricultural sector and exchange rate. However, it was depicted that output and employment in the agricultural sector in both the short-run and the long-run are not statistically significant. The implication drawn from the study is that credit granted to the agricultural sector can foster aggregate output in the sector, which will promote long-term employment. The study suggests considerable investment in the agricultural sector and the need to strengthen institutions for proper management of resources to ensure effective evaluation of funds disbursed for improving the agricultural sector, among others.

Open Access | January 23, 2023

Does product certification matter? A review of mechanism to influence customer loyalty in the poultry feed industry

Kesturi Pandanwangi, Ahmad Romadhoni Surya Putra, Fransiskus Trisakti Haryadi, Andriyani Astuti, Suci Paramitasari Syahlani

Article number: 20220160

Abstract

Feed certification is released by authorized third parties as external cues indicating that products have met standard quality. However, farmers do not always take certification as the main consideration in product selection because of insufficient knowledge or they are skeptical about certification. This research aims to analyze the effect of feed certification, company image, opinion leader, perceived product quality, customer trust, and satisfaction to layer farmers' customer loyalty. Respondents were selected by using purposive sampling with the criteria that respondents were layer farmers with experience for at least 1 year and customers of concentrate or ready-made feed. Data were collected by using questionnaire and analyzed with the partial least square. Results show that feed certification influenced perceived product quality with $\beta = 0.127$ and $p \leq 0.1$; then, company image and opinion leader influenced perceived product quality with, $\beta = 0.690$ and $\beta = 0.157$ at $p \leq 0.05$. Perceived product quality affected customer trust ($\beta = 0.699$, $p \leq 0.01$) and customer satisfaction ($\beta = 0.689$, $p \leq 0.05$). Then, customer trust and customer satisfaction positively influenced customer loyalty with $\beta = 0.507$, and $\beta = 0.414$ at $p \leq 0.01$. Research findings indicated that feed certification was considered by layer farmers in feed purchasing behavior. However, company image was played as the most important factor among opinion leader and feed certification. These results implied that besides maintaining company image and the role of opinion leaders, feed mills and authorized institutions still urge to promote the importance of certification as product quality indicator.

Open Access | January 27, 2023

Farmer regeneration and knowledge co-creation in the sustainability of coconut agribusiness in Gorontalo, Indonesia

Wawan K. Tolinggi, Darmawan Salman, Rahmadanih, Hari Iswoyo

Article number: 20220162

Abstract

Farmer regeneration in agribusiness sustainability originates from the innovation of knowledge co-creation among farmer generations and interaction between stakeholders within and outside local contexts. The present work aims at exploring knowledge co-creation in the context of different orientations between young and old farmers. It also seeks to characterize the orientation of the two farmer groups from the aspect of agriculture, processing, and marketing of coconut through knowledge co-creation interaction to further their agricultural activities. All data in this grounded theory research came from in-depth interviews; the data were further examined using an open, axial, and selective coding method. The transcription of the field note was analyzed using an ATLAS.ti version 9, a program for analyzing qualitative data. The sample of the study was 13 of young farmers (25 to 45 years old) and 17 of old farmers (45 to 65 years old). The results revealed that the old farmers focused on revitalizing coconut trees for long-term purposes. The knowledge co-creation process among this farmer group (with other stakeholders) put an emphasis on copra and cooking oil production. Young farmers, however, focused on coconut tree integration with annual plants for short-term purposes, especially on the virgin coconut oil and innovative products from foreign technology adaptation. In conclusion, coconut business sustainability is the byproduct of knowledge co-creation and engagement between old and young farmers. This condition results in the survivability of coconut farmers. The novelty of this study lies in the classification of the orientation of the two coconut farmer groups in terms of agricultural, processing, and marketing aspects, which results in knowledge co-creation and its relation to the sustainability of coconut agriculture.

Open Access | February 1, 2023

Lablab purpureus: Analysis of landraces cultivation and distribution, farming systems, and some climatic trends in production areas in Tanzania

Julius S. Missanga, Pavithravani B. Venkataramana, Patrick A. Ndakidemi

Article number: 20220156

Abstract

Lablab is a multifunctional crop that is underutilized in Africa. This study was performed to assess Lablab landraces cultivation and distribution, farming systems, and some climatic trends in Lablab production areas in Tanzania. A socio-economic survey was engaged to locate the main production areas using Global Positioning System, while participatory research tools were used to assess farming systems, practices, and challenges perceived in Lablab production. Some weather data were collected to establish climatic trends in Lablab production areas. The study revealed a wide cultivation and distribution of Lablab landraces in five agro-ecological zones with some variations. These variations were influenced by market demand for Lablab in Kenya and its role in subsistence farming. Lablab was mainly produced for conservation agriculture and enhanced soil fertility (27.9%), marketing (22.1%), livestock feeding (21.5%), food during drought conditions (15.4%), traditional purposes (7.4%), regular consumption (3.8%), and other minor uses (1.8%) varied significantly across the zones ($\chi 2 = 37.639$, $p = 0.038$). The farming systems included intercropping (59.0%), mono-cropping (31.0%), home based gardening (5.0%), crop rotation (3.0%), and relaying cropping (2.0%) with no significant difference across the zones ($\chi 2 = 15.049$, $p = 0.314$). A wide range of farmers' practices were noted in Lablab production zone-wise. Unavailability of improved varieties and poor market channels were the farmers' key challenges in Lablab production. It was further noticed that Lablab was mainly produced in areas with dry conditions.

Finally, it was suggested that effort should be enhanced to improve genetic resource conservation, value addition, and market channels to other countries while developing improved varieties in terms of high yielding and drought tolerance.

Open Access | February 10, 2023

The effects of carrot (*Daucus carota* L.) waste juice on the performances of native chicken in North Sulawesi, Indonesia

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Article number: 20220173

Abstract

The abundance of agricultural products often causes environmental problems. The utilization of agricultural waste from carrots can reduce both the feed cost and environmental pollution and become a source of vitamin A for the health of the native chicken. The study aims to analyze carrot (Daucus carota L.) waste juice on native chicken performance. It was conducted from April to July 2019 at Pandu experimental field in North Minahasa Regency. The practical method used was a completely randomized design with four replications. The experimental livestock used in the study was 80-day-old chickens of native chicken. The concentration of carrot juice during the study was as follows: 100% drinking water without carrot juice (W0), 80% water drinking + 20% carrot juice (W1), 60% drinking water + 40% carrot juice (W2), and 20% drinking water + 80% carrot juice (W3). Observed variables included feed intake, body weight gain, feed conversion ratio (FCR), and mortality rate. The results showed that carrot waste juice significantly impacted the body weight gain, feed conversion rate, and 0% mortality rate during the 8 weeks. The concentration of 20% drinking water + 80% carrot juice (W3) with the feed intake ratio of 1.608 g, body weight gain value of 775.63 ± 301 g, and the FCR of 2.1 ± 0.06. However, the consumption ratio did not differ among treatments. The addition of carrot waste juice, as much as 80%, in the drinking water of native chickens showed an increase in body weight compared to other treatments. In conclusion, the current study showed that treatment of carrot waste juice has a significant effect on body weight in 8 weeks of maintenance. Meanwhile, the feed intake ratio of carrot waste juice treatment has no real effect. There was no dead chicken (0%) in the present study. The carrot waste juice can be used in chicken drinks 40–80% by paying attention to the balance of energy content and feed proteins used to grow chickens.

Open Access | February 17, 2023

Properties of potassium dihydrogen phosphate and its effects on plants and soil

Kristina Jančaitienė, Rasa Šlinkšienė, Renata Žvirdauskienė
Article number: 20220167

Abstract

One of the challenges of the modern world is to improve human nutrition and to safely increase the yield of agricultural production using existing agricultural land. It is clear that sufficient agricultural efficiency cannot be achieved without fertilizers, but fertilizers must cause minimal damage to the soil. Microorganisms, such as spore-forming bacteria, actinomycetes, fungi, algae, and protozoa play an important role in the soil and keep soil healthy. One of the soil substances involved in reactions that take place in plants is cellulose. This study investigated the effect of potassium dihydrogen phosphate (PDP), synthesized (via conversion between potassium chloride and ammonium dihydrophosphate) and granulated with the addition of microcrystalline cellulose (MC), on plants (winter wheat Toras, Lithuania) and soil microorganisms. The data of plants fertilized with pure KH 2 PO 4 , ones fertilized with PDP granulated with MC, and grown without fertilizers were compared in this study. Scanning electron microscopy and differential scanning calorimetry analysis were used to characterize the obtained product. One-way analysis of variance was used to evaluate the differences of the mean values between groups. In all cases, the significance level was $p \leq 0.05$. The effect of pure KH 2 PO 4 on plant indicators was found to be lower than that of granular PDP with MC. The length of the leaves was 29.63 and 31.20 cm, green mass was 0.471 and 0.763 g, ash mass was 0.015 and 0.019 g, respectively. In addition, granular PDP with MC did not adversely affect the soil microorganisms because the number of any species of bacteria (Spore b., mineral nitrogen assimilating bacteria, cellulose degrading bacteria) did not decrease and a slight increase in the number of Actinomycetes (from 8.5 × 10 5 to 2.9 × 10 6 KSV/g) and molds (from 3.0 × 10 4 to 1.4 × 10 5 KSV/g) was observed. The granular PDP with MC that we developed and used have better physical properties, higher agrochemical efficiency and cause less harm to soil microorganisms compared to pure PDP.

Open Access | February 20, 2023

Factors influencing the role and performance of independent agricultural extension workers in supporting agricultural extension

Kurnia Suci Indraningsih, A Ashari, S Syahyuti, Iwan Setiajie Anugrah, Sri Suharyono, S Saptana, Arief Iswariyadi, Adang Agustian, Tri Bastuti Purwantini, Mewa Ariani, Maesti Mardiharini
Article number: 20220164

Abstract

Extension activities play a significant role in the success of agricultural development programs. Farmers still need agricultural extension workers (EWs) in the form of assistance, technical guidance, and management intensively and continuously. With the limited number of government EWs, the role of independent agricultural extension (IAE) workers has become crucial. In Indonesia, IAE worker has been recognized since 2006, although it has not been effective. This article aims to: (1) identify conditions and characteristics of IAE and (2) analyze the influencing factors on the role of IAE officers in supporting agricultural extension. Data collection was carried out with a structured questionnaire using Google Forms involving 161 respondents. The analysis method uses inferential statistics, namely the structural equation modeling. The results showed that the factors that directly affect the role of IAE workers are work motivation and quantity or workload. The number of IAE workers directly influences their performance. A favorable working environment is required to achieve the ideal role of IAE workers. In addition, improvement of work management, horizontal and vertical relations, and regulations posit IAE workers as an essential part of agricultural extension activities. It is necessary to have a regional regulation that legalizes the allocation of regional budgets as regular incentives to facilitate the activities of agricultural EWs.

Open Access | February 23, 2023

The fate of probiotic species applied in intensive grow-out ponds in rearing water and intestinal tracts of white shrimp, *Litopenaeus vannamei*

Muhamad Amin, Yoga Pramujisunu, Mirni Lamid, Yudi Cahyoko, Olumide A. Odeyemi, Muhamad Ali, Awik P. D. Nurhayati

Article number: 20220152

Abstract

Introduction Probiotics have been commonly practiced in commercial shrimp farms to increase pond production. However, these possibilities were based on the results of in vitro studies or laboratory in vivo trials. While studies on probiotic applications in commercial-scale farms are still rarely investigated, this study addresses the fate of probiotic species in ponds and the intestinal tract of white shrimps reared in an intensive aquaculture system. Material and methods Four commercial probiotic species (Lactobacillus plantarum , Lactobacillus fermentum , Bacillus subtilis , and Pseudomonas putida) were applied to the commercial shrimp ponds (@800 m 2 area of high-density polyethene ponds) in the morning at a dose of 5 ppm once every 2 days in the first month, and once a week from second month onward. Then, the presence of the probiotic species was traced by collecting the rearing water and shrimp's intestines on day 47 of culture to monitor their composition and abundance using high-throughput

sequencing. Results None of the commercial probiotic species could be detected from both rearing water and shrimp intestinal tracts. These results suggest that the probiotic species had low viability and adaptability in the rearing pond as well as the shrimp intestines when applied on commercial-scale farms. These facts may explain the high variation in the yield among shrimp ponds in spite of having similar treatments. Conclusion Probiotic strains had low viability and adaptability in commercial farms. Thus, methods and strategies in probiotic application to commercial-scale shrimp farms should be evaluated and further developed to increase probiotic efficacy.

Open Access | February 23, 2023

Yield stability and agronomic performances of provitamin A maize (*Zea mays* L.) genotypes in South-East of DR Congo

Hugues Ilunga Tabu, Jean Pierre Kabongo Tshiabukole, Amand Mbuya Kankolongo, Antoine Kanyenga Lubobo, Luciens Nyembo Kimuni

Article number: 20220177

Abstract

Genotype assessment across various environments is a basic condition for developing stable and superior genotypes for sustainable maize production in the South-East of the DR Congo. Therefore, this research's objectives were to identify the performance of newly developed provitamin A maize genotypes in various environments, and to recommend high-performing and stable genotypes for broader adaptation. Eight provitamin A maize genotypes, including one commercial variety, were planted at three sites during two consecutive cropping seasons (2020/2021 and 2021/2022) forming six environments. All genotypes in six environments were planted in a randomized complete block design containing three replications. Two stability analysis approaches, GGE biplot and Eberhart and Russell method are widely used to identify high yielding and stable genotypes. The combined analysis of variance revealed that G and E as well as their interaction (GEI) have significantly affected the emergence rate, cob's insertion height, days to anthesis and silking, cob length, cob grain weight and grain yield. Average grain yield varied from 8.30 t/ha for PVAH-7L to 9.41 t/ha for PVAH-1L. The Eberhart and Russell method and the CV identified PVAH-1L, PVAH-4L, PVAH-7L and PVAH-6L as the most stable genotypes, but could not reliably identify the high yielding genotypes. On the other hand, the GGE biplot reliably and graphically showed the stable and high-yielding genotypes (PVAH-1L > PVAH-6L) as well as the low-yielding genotypes (PVAH-7 > PVAH-4L). In additional, the GGE biplot showed that L'shi21 was the best test environment for selecting high performing and stable provitamin A maize genotype. The results of this study indicate that PVAH-1L and PVAH-6L are the stable, high-yielding provitamin A maize genotypes in the South-East of the Democratic Republic of the Congo and should be disseminated in this region.

Open Access | February 24, 2023

Diallel analysis of length and shape of rice using Hayman and Griffing method

Agus Riyanto, Ponendi Hidayat, Y. Suprayogi, Totok Agung Dwi Haryanto

Article number: 20220169

Abstract

Length and shape of rice are important physical qualities that determine public acceptance of a variety and determine the price. Improvement of length and shape of rice requires information on the genetic parameters of these traits. Diallel analysis is one of the methods usually used to estimate the genetic parameters of a trait. The purpose of this study was to estimate the genetic parameters of length and shape of rice using full diallel analysis. The plant material used was a full diallel cross-population of six rice genotypes, namely, Basmati Pakistan, Basmati Delta 9, Inpago Unsoed 1, Inpari 31, Koshihikari, and

Tarabas. Thirty-six genotypes consisting of parents, F 1 and F 1reciprocal , were planted using a randomized block design with three replications. The data of rice grain length and length:width ratio were used for diallel analysis using the Hayman and Griffing method-1. The results showed additive and non-additive gene action influencing the length and shape of rice. The effect of the additive gene action was greater than the non-additive gene action, while both broad-sense heritability and narrow-sense heritability were high, revealed that the selection of these traits at the early generation using the pedigree selection method may be considered. Length and shape of rice were not affected by the female parent cytoplasm so that F 2 and F 2reciprocal populations may be combined into one population the next generation.

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Traditional agri-food products and sustainability – A fruitful relationship for the development of rural areas in Portugal

Maria Lúcia Pato, Ana Sofia Duque

Article number: 20220157

Abstract

The protection of agri-food regional products is taking on growing importance in a market dominated by global companies and brands, often with no personality. Thirty years ago, the European Union (EU) agricultural product quality policy introduced the protection of geographical indications (GIs) for agricultural products and foodstuffs, with the aim of highlighting the quality of products resulting from a specific origin, therefore helping their communication and positioning in the market. This is important in countries with a considerable percentage of rural regions, as is the case of Portugal. Bearing this in mind, the purpose of this study is to see what are the drivers of the spatial distribution of traditional products (protected geographical indications, protected designations of origin, and traditional speciality guaranteed) in Portugal. For this purpose, the distribution of traditional products by regions and categories in Portugal will be presented. Also, Portugal's position will be analysed and compared to the other EU countries, regarding the number of traditional products. Results show that Portugal is the country with the fourth biggest number of traditional certified products in EU territory. In the national territory, the Northern Region of Portugal has the biggest percentage of protected products, followed by Alentejo and the Centre Region of Portugal. Also, in Portugal, looking at the type of products, from a list of ten different categories of GIs, the ranking is dominated by (1) fresh meat, (2) meat products (cooked, salted, or smoked), and (3) cheese

and milk-based products. If we consider that many of the aforementioned products are produced in less favoured regions, these results constitute an opportunity for their sustainable development. This benefits not only the producers, but also consumers who increasingly seek “authentic” and more natural products.

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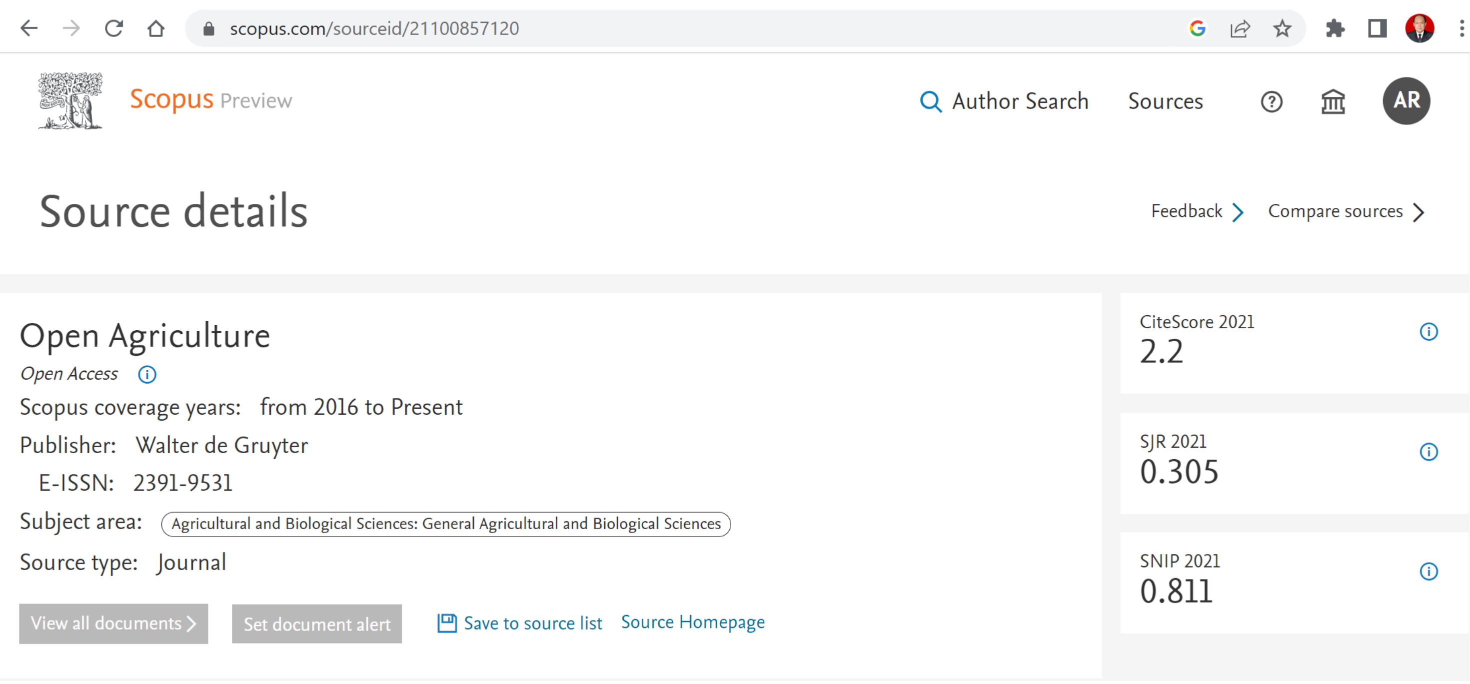

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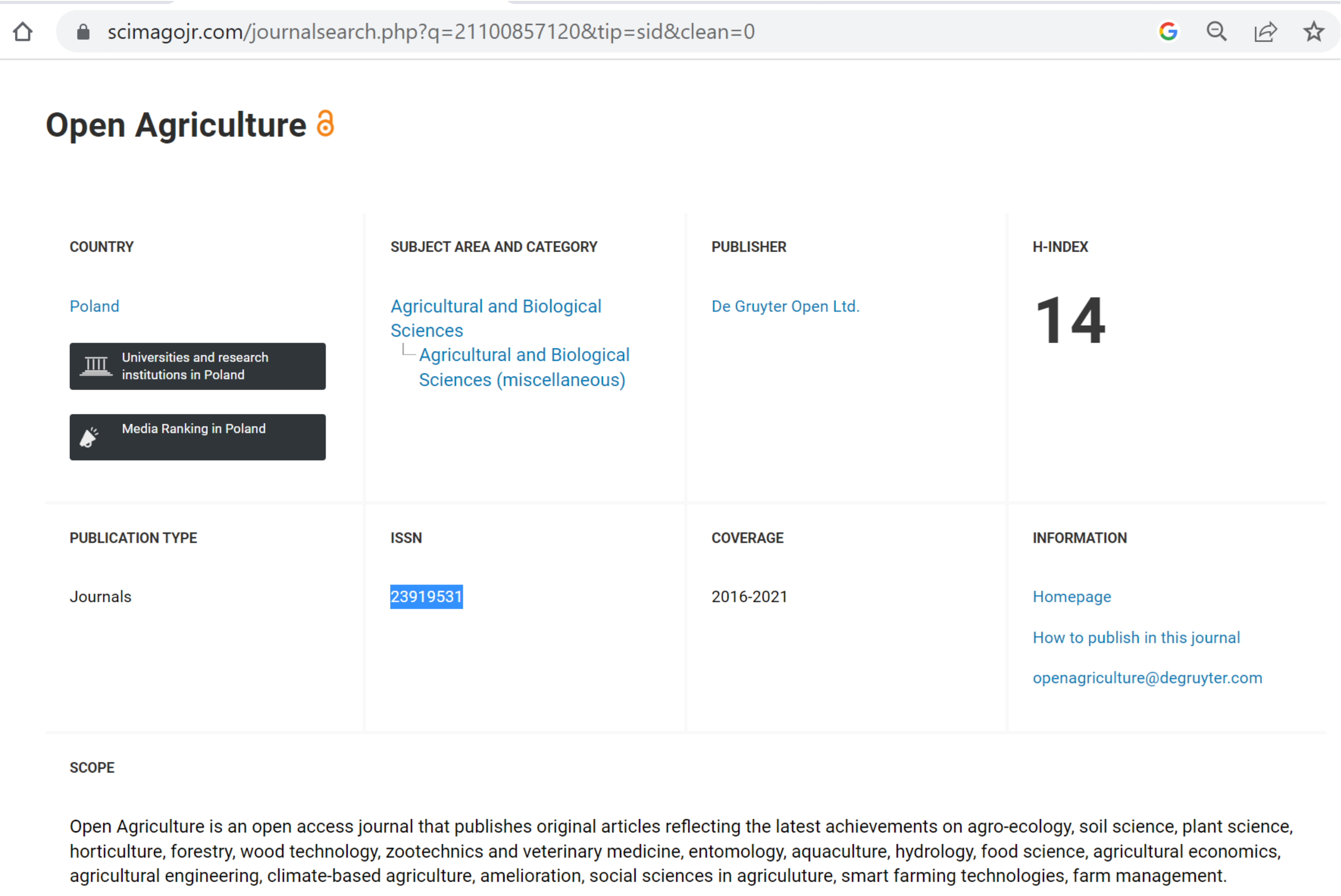

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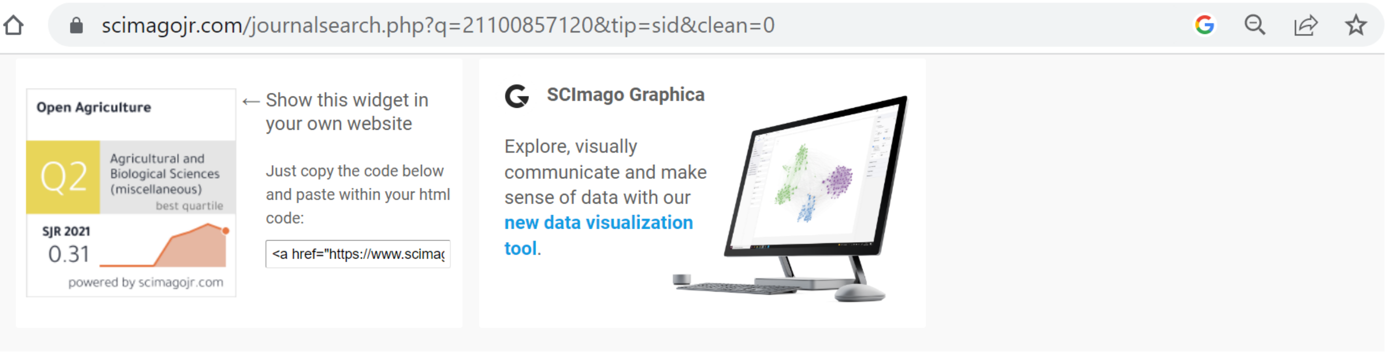

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Research Article

Agus Riyanto, Ponendi Hidayat, Y. Suprayogi, Totok Agung Dwi Haryanto*

Diallel analysis of length and shape of rice using Hayman and Griffing method

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Abstract: Length and shape of rice are important physical qualities that determine public acceptance of a variety and determine the price. Improvement of length and shape of rice requires information on the genetic parameters of these traits. Diallel analysis is one of the methods usually used to estimate the genetic parameters of a trait. The purpose of this study was to estimate the genetic parameters of length and shape of rice using full diallel analysis. The plant material used was a full diallel cross-population of six rice genotypes, namely, Basmati Pakistan, Basmati Delta 9, Inpago Unsoed 1, Inpari 31, Koshihikari, and Tarabas. Thirty-six genotypes consisting of parents, F_1 and $F_{1\text{reciprocal}}$, were planted using a randomized block design with three replications. The data of rice grain length and length:width ratio were used for diallel analysis using the Hayman and Griffing method-1. The results showed additive and non-additive gene action influencing the length and shape of rice. The effect of the additive gene action was greater than the non-additive gene action, while both broad-sense heritability and narrow-sense heritability were high, revealed that the selection of these traits at the early generation using the pedigree selection method may be considered. Length and shape of rice were not affected by the female parent cytoplasm so that F_2 and $F_{2\text{reciprocal}}$ populations may be combined into one population the next generation.

Keywords: diallel analysis, rice length, rice shape

1 Introduction

Rice (*Oryza sativa* L.) is one of the major food crops in the world. Nearly 50% of the world population consumes rice as the staple food; therefore, it has an important role in global food security [1,2]. Indonesia is the world's third largest rice producer, and it is also one of the world's main rice consumers [3]. More than 80% of Indonesian people consume rice as a staple food, and it contributes 62.1% of the energy intake [4]. It is the main source of income of approximately 18 million household farmers [5]. It also has strategic value from economic, environmental, social, and political aspects [6,7]. Therefore, rice self-sufficiency in Indonesia is required to fulfill the needs.

The government's program for rice self-sufficiency has four main targets, that is, to increase the national production, to stabilize the domestic prices and reserve stocks, and to minimize imports [8]. Improving yield potential of rice varieties through plant breeding plays an important role to increase the national production. High yielding rice varieties contributed to 56% of the national rice production [6]. Thus, rice breeding in Indonesia aims to develop high yielding varieties that are in accordance with ecosystem conditions, social, cultural, and community interests [9].

Yield still is the main target of rice development; however, rice grain quality is now getting more attention due to increasing awareness of its importance [10]. Rice grain quality determines the market price, consumer acceptability of a variety, and consumer acceptability of a variety and becomes the second goal of rice plant breeding after yield [11,12]. High yielding varieties with high rice grain quality are easy for farmers to adopt [13].

Grain quality consists of rice length, rice shape, rice translucency, and rice chalkiness. Rice quality directly affects consumer acceptance. Consumers determine the rice quality first from grain quality, that is, rice appearance, length and shape of rice, which is followed by cooking quality and taste [14,15]. Hence, length and shape of rice determine the level of rice market demands and

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price [16]. Therefore, breeding rice varieties that encompass desirable length and shape of rice became a major concern for rice breeders in Indonesia.

A rice breeding program begins with increasing genetic diversity by crossing rice genotypes with wide genetic differences, followed by the traits selection of interest. The effectiveness of plant breeding programs increases in conjunction with scientific research that expands knowledge of plant genetic information [17]. An effective and efficient breeding program is determined by the genetic information that controls the inheritance of traits under study [18,19]. Sometimes selection in segregation populations results in low-quality progenies to fulfill breeding objectives [20]. Hence, it is necessary to know genetic information of traits before determining a breeding and selection method [21]. Diallel analysis is one of the manners to obtain genetic information for grain quality traits in rice such as length and shape of grain.

Diallel analysis is a mating design, which involves mating a set of parents in all possible combinations, to produce a set of F_1 progeny [22,23]. This method is useful to obtain genetic information that controls the inheritance of traits under study in early generation [24,25]. It is also the quickest method for understanding the genetic control of the inheritance of quantitative traits [26].

Diallel analysis can be carried out using Hayman and Griffing methods. Hayman's method can be used to study gene action, genetic components, and heritability [27], whereas Griffing's method [28] is used to estimate general combining ability (GCA), specific combining ability (SCA), and reciprocal effects. Also, it can be used to calculate additive and non-additive effects. Hayman and Griffing methods are often used together for interpretation of complementary data [21]. Hayman and Griffing methods have been used (either one or both) to obtain genetic information of plant traits. It has been widely used to study genetic parameters of length and shape of rice [29–41]. The results of the study show various conclusions. Furthermore, this research is rarely performed in Indonesia [42]. The present research was conducted to study genetic components of F_1 population from a cross of six parents with various lengths and shapes of rice. The purpose of this study was to estimate the genetic parameters of length and shape of rice using the full diallel analysis.

2 Materials and methods

2.1 Location of the experiment

A field experiment was conducted at the experimental farm of Agriculture Faculty, Jenderal Soedirman University, Purwokerto, Central Java, Indonesia. This location is at coordinates 7°24′28.7″LS and 109°15′13.3″N, and it is at an altitude of 112 m above the sea level. The experiment was carried out from June 2019 to December 2019.

2.2 Plant material

Six rice genotypes, i.e., Basmati Delta 9, Basmati Pakistan, Inpari 31, Inpago Unsoed 1, Koshihikari, and Tarabas rice, were used as the parents in this study. These parents have different origins and have various length and shape of rice (Table 1). The research material used consisted of 36 rice genotypes, which were developed from full diallel crosses among six parents. It consists of 6 parents, $15F_{1,}$ and $15F_{1\text{reciprocal}}$.

2.3 Experimental design

The experimental design was a randomized complete block design with three replications. Seeds of 36 genotypes were sown in a seed box for 2 weeks, followed by transplanting to 35 cm × 40 cm polybags containing 8 kg of inceptisol soil. Each polybag consisted of one plant per genotype. Recommendations for rice cultivation and plant protection were adopted. Fertilizer applications of 0.4 g N/polybag and 1.0 g N-P-K/polybag was applied twice i.e., 10 days and 20 days after transplanting.

2.4 Data collection and analysis

At maturity, panicles were harvested from parents and all generations individually. Panicles were subjected as samples of length and shape of rice. The shape of rice is determined by rice length-to-width ratio [43]. Therefore, the observed trait in this study is rice length, width, and

Table 1: Six rice genotypes used for diallel mating design

No.	Genotype	Length and shape of rice	Origin
1	Basmati Delta 9	Extra-long, slender	India
2	Basmati Pakistan	Extra-long, slender	Pakistan
3	Inpari 31	Long, medium	Indonesia
4	Inpago Unsoed 1	Medium, medium	Indonesia
5	Koshihikari	Short, round	Japan
6	Tarabas	Short, round	Indonesia

length-to-width ratio measured with help of digital caliper. Data collected were used for diallel analysis to estimate the genetic parameters of length and shape of rice. Diallel analysis was perfomed according to Hayman and Griffing method-1 [44] and the results were calculated using the software Microsoft® Excel.

1. Analysis of variance for F_1 in full diallel crosses

   Analysis of variance for F_1 in full diallel crosses for length and shape of rice followed the statistical model

$$Y_{ijkl} = m + T_{ij} + b_k + (bT)_{ijk} + e_{ijkl}, \qquad (1)$$

where m is the general mean, T_{ij} is the effect of $i \times j$th genotype, b_k is the effect of kth block, $(bT)_{ijk}$ is the interaction effect, and e_{ijkl} is the error effect.

2. Genetic components of variation

Genetic components of variation were calculated using the following formulas:

$$\text{Regression coefficient of } b\ (W_r, V_r) = \frac{\mathrm{Cov}(W_r, V_r)}{\mathrm{Var}(V_r)}, \qquad (2)$$

where W_r is the covariance between parents and their offspring, V_r is the variance of each array, $\mathrm{Cov}(W_r,V_r)$ is the covariance of (W_r,V_r), and $\mathrm{Var}(V_r)$ is the variance of V_r.

$$\text{Additive genetic variance } (D) = V_{0L0} - E, \qquad (3)$$

where V_{0L0} is the variance of parents and E is the environmental variance.

Dominance variance

$$H_1 = V_{0L0} - 4W_{0L01} + 4V_{1L1} - (3n - 2)E/n, \qquad (4)$$

where V_{0L0} is the variance of parents, W_{0L01} is the covariance between the parents and the arrays, V_{1L1} is the mean variance of the arrays, n is the number of parents, and E is the environmental variance.

Proportions of positive or negative genes in the parent

$$H_2 = 4V_{1L1} - 4V_{0L1} - 2E, \qquad (5)$$

where V_{1L1} is the mean variance of the arrays, V_{0L1} is the variance of the mean of arrays, and E is the environmental variance.

Mean covariance of additive and dominance

$$F = 2V_{0L0} - 4W_{0L0} - 2(n - 2)E/n, \qquad (6)$$

where V_{0L0} is the variance of parents, W_{0L01} is the covariance between the parents and the arrays, n is the number of parents, and E is the environmental variance.

Dominance effect

$$h^2 = 4(M_{L1} - M_{L0})^2 - 4(n - 1)E/n^2, \qquad (7)$$

where $(M_{L1} - M_{L0})^2$ is the difference between the mean of the parents and the mean of their n^2 progeny, n is the number of parents, and E is the environmental variance.

Environmental variance

$$E = 1/r(\text{Error SS} + \text{Rep. SS})/[((r-1) + (c - 1)) \times (r - 1)], \qquad (8)$$

where Error SS is the sum square of error, Rep. SS is the sum square of replication, r is the number of replications, and c is the number of errors.

$$\text{Average degree of dominance} = (H_1/D)^{1/2}, \qquad (9)$$

where H_1 is the dominance variance and D is the additive genetic variance.

The proportion of genes with positive and negative effects in the parent $= H_2/4H_1$, (10)

where H_1 is the dominance variance and H_2 is the proportion of positive or negative genes in the parent.

The ratio dominant and recessive gene in the parent $= [(4DH_1)^{1/2} + F]/(4DH_1)^{1/2} - F$, (11)

where D is the additive genetic variance, H_1 is the dominance variance, and F is the mean covariance of additive and dominance.

$$\text{Number of gene groups} = h^2/H_2, \qquad (12)$$

where h^2 is the dominance effect and H_2 is the proportion of positive or negative genes in the parent.

The coefficient correlation between

$$(W_r + V_r) \text{ and } Y_r(r) = \frac{\mathrm{Cov}\ (W_r + V_r),\ Y_r}{\sqrt{\mathrm{Var}\ (W_r + Y_r) \cdot \mathrm{Var}(Y_r)}}, \qquad (13)$$

where $(W_r + V_r)$ is the parental order of dominance, Y_r is the parental measurement, $\mathrm{Cov}(W_r + V_r)$ is the covariance of $(W_r + V_r)$, $\mathrm{Var}(W_r + V_r)$ is the variance of $(W_r + V_r)$, and $\mathrm{Var}(Y_r)$ is the variance of Y_r.

Broad-sense heritability

$$h^2_{\mathrm{bs}} = (1/2D + 1/2H_1 - 1/4H_2 - 1/2F)/ \\ (1/2D + 1/2H_1 - 1/4H_2 - 1/2F + E), \qquad (14)$$

where D is the additive genetic variance, H_1 is the dominance variance, H_2 is the proportion of positive or negative genes in the parent, F is the mean covariance of additive and dominance, and E is the environmental variance.

Narrow-sense heritability

$$h^2_{\mathrm{ns}} = (1/2D + 1/2H_1 - 1/2H_2 - 1/2F)/ \\ (1/2D + 1/2H_1 - 1/2H_2 - 1/2F + E), \qquad (15)$$

where D is the additive genetic variance, H_1 is the dominance variance, H_2 is the proportion of positive or negative genes in the parent, F is the mean covariance of additive and dominance, and E is the environmental variance.

2.5 Combining ability analysis

The statistical model for the analysis variance of combining ability that was used was as follows:

$$Y_{ij} = m + g_i + g_j + S_{ij} + r_{ij} + \frac{1}{bc}\sum\sum e_{ijkl}, \tag{16}$$

where Y_{ij} is the mean of $i \times j$th genotype, m is the general mean, g_i is the general combing ability (gca) effect of ith parent, g_j is the general combing ability (gca) effect of jth parent, S_{ij} is the interaction, i.e., SCA effect, r_{ij} is the reciprocal effect, and $\frac{1}{bc}\sum\sum e_{ijkl}$ is the mean error effect.

$$\text{GCA variance } (g_i) = \frac{1}{2n}\sum(Y_{i.} + Y_{.j}) - \frac{1}{n^2}Y^2, \tag{17}$$

where $Y_{i.}$ is the total mean value of ith genotype cross, $Y_{.j}$ is the total mean value of jth genotype selfing, n is the number of parents, and Y is the grand total.

$$\begin{aligned}\text{SCA variance } (s_{ij}) = {} & \frac{1}{2}(Y_{ij} + Y_{ij}) - \frac{1}{2n}(Y_{i.} + Y_{.i} + Y_{j.} \\ & + Y_{.j}) + \frac{1}{n^2}Y,\end{aligned} \tag{18}$$

where Y_{ij} is the mean of $i \times j$th genotype, Y_{ji} is the mean of $j \times i$th genotype, $Y_{i.}$ is the total of mean value of ith genotype cross, $Y_{.i}$ is the total of mean value of ith genotype selfing, $Y_{j.}$ is the total of mean value of jth genotype cross, $Y_{.j}$ is the total of mean value of jth genotype selfing, n is the number of parents, and Y is the grand total.

$$\text{Reciprocal variance } (r_{ij}) = \frac{1}{2} = (Y_{ij} - Y_{ji}), \tag{19}$$

where Y_{ij} is the mean of $i \times j$th genotype and Y_{ji} is the mean of $j \times i$th genotype.

3 Results and discussion

3.1 Analysis of variance for genotypes

Analysis of variance showed significant difference among genotypes for length and shape of rice grain (Table 2). Similar findings were also reported by Bano and Singh [39] and Hijam et al. [37]. Significantly different in the analysis of variance among genotypes is a requirement for estimating genetic parameters using diallel analysis [44]. Thus, significant differences among the genotypes for length and shape of rice indicate that they are suitable for further genetic studies.

Table 2: Analysis of variance for F_1 in a full diallel cross for length and shape of rice

Source of variation	Degrees of freedom	Mean square	
		Rice length (mm)	Rice shape
Block	2	0.06	0.01
Genotype	35	3.16*	1.51*
Error	70	0.04	0.02

*Significantly different at the level of 5%.

3.2 Genetic components of variation

3.2.1 Gene interaction

The values of regression coefficient of $b(W_r, V_r)$ for length and shape of rice (1.20 and 1.15, respectively) were not significantly different from one (Table 3). Similar results reported by Bano and Singh [39] for kernel length before cooking (rice length) and kernel length/breadth ratio before cooking (rice length). The value of regression of coefficient of $b(W_r, V_r)$ may be used to determine the gene

Table 3: Estimates of genetic components of variation for length and shape of rice

Genetic components	Rice length (mm)	Rice shape
$b(W_r, V_r)$	1.20ns	1.15ns
D	2.72*	1.36*
H_1	0.26*	0.19*
H_2	0.25*	0.17*
F	0.44*	0.33*
h^2	−0.01ns	0.04ns
E	0.01ns	0.01ns
$(H_1/D)^{1/2}$	0.31	0.38
$H_2/4H_1$	0.23	0.22
Kd/Kr	1.71	1.95
h^2/H_2	−0.03	0.22
$r[(W_r + V_r),Y_r]$	0.69	0.89
h^2_{bs}	0.99	0.99
h^2_{ns}	0.94	0.91
Ratio of h^2_{ns}:h^2_{bs}	0.95	0.92

*Significantly different at the level of 5%, ns = not significantly different.

interaction of a trait. Based on t test, a significantly different value of $b(W_r, V_r)$ from one indicates gene interaction, while a non-significantly different value of $b(W_r, V_r)$ from one reflected no gene interaction [44]. It means that there is no interaction between genes controlling length and shape of rice in this study.

3.2.2 Additive (D) and dominance (H_1) variance

Additive (D) and dominance (H_1) variance were significantly different for length and shape of rice (Table 3). Significantly different values of the components D and H_1 indicated the importance of both additive and non-additive gene action in the expression of traits [45], so that length and shape of rice are influenced by both additive and non-additive types of gene action. Similar findings were also observed by Kato [29], Fu et al. [31], Daradjat and Rumanti [42], Kumar et al. [32,33], Rafii et al. [30], and Senthil Kumar and Mudhalvan [38] for length and size of rice.

The results showed the value of additive variance (D) for length and shape of rice is 2.72 and 1.36, respectively, and the value of dominance variance (H_1) for length and shape of rice is 0.26 and 0.19, respectively (Table 3). These showed that the influence of additive variance is greater than dominance variance ($D > H_1$) for length and shape of rice. Higher magnitude of additive variance (D) indicated the greater role of additive gene action, while dominance variance indicated the greater importance of non-additive gene action *vice versa* [40,45]. The value of the additive variance, which is greater than the dominance variance, indicates the increasing importance of additive gene action [32,33]. This means that in this study, length and shape of rice are more influenced by additive gene action than non-additive gene action. These results are in accordance with the findings of Kato [29] and Thattil and Perera [46] for length and size of rice. However, Daradjat and Rumanti [42] and Senthil Kumar and Mudhalvan [38] reported that the non-additive gene action dominated over additive gene action for length and size of rice.

3.2.3 Gene distribution in the parents

Gene distribution in the parents can be determined by H_2 values. The results showed that the H_2 values for length and shape of rice were significantly different (Table 3). This indicates that the genes determining the inheritance of length and shape of rice are not evenly distributed among the parents. Genes controlling length and shape of rice that are not evenly distributed in parents have also been reported [38].

Proportion of positive genes to negative genes is indicated by the value of H_1 component against H_2 component. The value of H_1 is greater than the H_2 indicating the number of positive genes would be higher than negative genes. On contrary, the value of the H_1 is smaller than H_2 reflecting that the number of positive genes would be fewer than the negative genes [21,47]. Table 3 shows that the value of H_1 is 0.26 and 0.19, respectively, and the value of H_2 is 0.27 and 0.17, respectively, for length and shape of rice. It shows that the value of H_1 is greater than H_2 for length and shape of rice, meaning that positive genes are more involved in determining length and shape of rice than negative genes. The results were in agreement with those of Raju et al. [40].

Proportion of positive genes to negative genes in all parents also can be seen from ratio of $H_2/4H_1$. Values lower than 0.25 indicate that positive and negative genes are not present in unequal proportions in the parents [45,48]. The results showed the value of $H_2/4H_1$ for length and shape of rice is 0.23 and 0.22, respectively (Table 3). They were lower than 0.25, reflecting the unequal distribution of positive and negative genes in the parents. Similar findings were reported by previous studies [38–40].

3.2.4 Dominance level

The influence of dominance can be seen from the value of mean degree of dominance as estimated by $(H_1/D)^{1/2}$. A value $(H_1/D)^{1/2}$ more than 1 indicates over dominance, while a value $(H_1/D)^{1/2}$ between 0 and 1 indicates partial dominance (Hayman, 1954). Table 3 shows the value $(H_1/D)^{1/2}$ of length and shape of rice is less than 1 (0.31 and 0.38, respectively), which indicated the existence of partial dominance in these traits. Rice length controlled by a partial dominance gene was also reported by Kato [29].

3.2.5 Dominance effect

Dominance effect is indicated by the h^2 value. Table 3 shows that h^2 values were not significantly different for length and shape of rice. This indicated no difference in average deviation of F_1 from most parents [47].

3.2.6 Environmental variance

Table 3 shows that environmental variance exhibited no significant influence on length and shape of rice. This

reflected no influence of environmental factor on the expression of the traits studied [45]. Therefore, it is known that the expression of length and shape of rice is more influenced by genetic than environment effects.

3.2.7 Proportion of dominant gene to recessive gene

Proportion of dominant genes to recessive genes is shown by F component and Kd/Kr ratio. The positive value of F component reflects a greater number of dominant genes than recessive genes in the parent [47,49]. A ratio of Kd/Kr greater than one indicates more dominant genes in the parent; conversely, the ratio of Kd/Kr smaller than one indicated more recessive genes in the parent [44]. The results showed a positive value of F component, and a ratio of Kd/Kr of the length and shape of rice is greater than one (1.71 and 1.95, respectively) (Table 3), which indicated more dominant genes in the parent for length and shape of rice. The same finding was reported by Raju et al. [40].

3.2.8 Number of gene groups

Component of h^2/H_2 gives an indication of the number of gene groups that control a trait. The h_2/H_2 values of length and shape of rice are −0.03 and 0.22, respectively, lower than one. The ratio smaller than one indicated the involvement of single gene or one group of genes, which are responsible for their genetic control [45]. As a result, length and shape of rice are controlled by at least a single group of genes.

3.2.9 Direction and order of dominance

The positive value of the correlation between ($W_r + V_r$) and Y_r and close to unity indicates that dominant alleles have predominantly negative effects, i.e., acting in the direction of lower yields [50]. A positive value is obtained in the correlation ($W_r + V_r$) and Y_r for length and shape of rice (Table 3). That is, in length and shape of rice, the dominant genes cause the rice to be short and round.

The direction and order of dominance can be seen in the value ($W_r + V_r$) component. Based on the value ($W_r + V_r$) in Table 4, the dominance order of length and shape of rice was Inpago Unsoed 1, Koshihikari, Tarabas, Basmati Delta 9, and Basmati Pakistan. This is reinforced by the graph of the relationship between the covariance (W_r) and variance (V_r) in Figures 1 and 2.

Table 4: Value ($W_r + V_r$) of length and shape of rice

Genotypes	Rice length	Rice shape
Basmati Delta 9	2.32	1.30
Basmati Pakistan	2.46	1.43
Inpari 31	1.99	0.93
Inpago Unsoed 1	1.00	0.37
Koshihikari	1.75	0.69
Tarabas	1.87	0.73

Distribution of parental array points along the regression line reflected genetic diversity of a trait [51]. The array point was scattered along the regression line for length and shape of rice, indicating genetic diversity for these traits. The position of the parents on the graph of the relationship between the covariance (W_r) and variance (V_r) reflects the order of dominance. The position of parent which is closer to zero point indicating it is the most dominant genes [47,50]. Inpago Unsoed 1 is the closest to zero, reflecting that this parent has the mostly dominant genes for length and shape of rice. Mostly, Basmati Pakistan contains a recessive gene for length and shape of rice since it is the farthest from zero. Basmati, which has extra-long and slender rice, contains the most recessive gene, and this means that the gene controlling long and slender rice is recessive to the short and round rice gene. This result is in agreement with the findings of Kato [29], Murai and Kinoshita [41], and Ali et al. [52].

The straight line intercepted the vertical axis (W_r) above the origin for length and shape of rice (Figures 1 and 2). The straight line that intercepted the vertical axis (W_r) above the origin indicated partial dominance of the genes controlling a trait [21,50,51]. This reveals that length and shape of rice were controlled by a partial dominant gene as described previously. Partial dominance results in the appearance of each trait having a tendency to approach the mid-parent value and not having overdominance, which exceeds the best parent [53]. This is reflected in the h^2 value of length and shape of rice, which is not significantly different, so that there is no difference between the F_1 average and the parents' average.

3.2.10 Heritability

Broad sense heritability (h^2_{bs}) estimates for length and shape of rice are similar to 0.99. Narrow sense heritability (h^2_{ns}) estimates for these traits are 0.94 and 0.91,

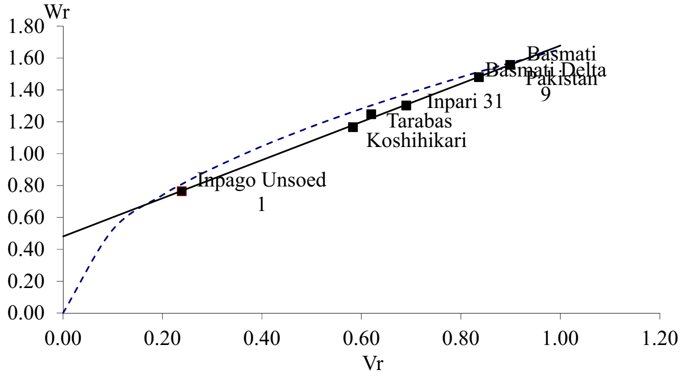

Figure 1: Covariance (W_r) and variance (V_r) graph of rice length.

respectively (Table 3). Values of heritability more than 0.5 are categorized as high (Stansfield, 1991); thus, broad-sense heritability (h^2_{bs}) for length and shape of rice is categorized as high heritability. Similar findings were reported by previous studies [54].

The estimated value of broad-sense heritability indicates the relative contribution of genetic factors to the variation of the observed trait [55]. A high broad-sense heritability value indicates that traits are more influenced by genetic than environmental factors [56]. In this study, broad-sense heritability estimate of length and shape of rice is high, indicating the influence of genetic was greater than environmental factors. Low influence of environmental factors was also reflected in the non-significant environmental variance observed in Table 3.

Narrow sense heritability estimates indicate the role of additive gene action in a trait. Estimates of narrow-sense heritability indicate more additive gene action than non-additive gene action [4,57–59]. In this study, the narrow sense heritability estimate of length and shape of rice was high, meaning that additive gene action played a more important role than non-additive gene action.

Ratio of narrow-sense heritability and broad-sense heritability reflects the role of additive and non-additive gene action in a trait. The ratio value closer to one indicates the total genetic variance of a trait is caused by additive gene action [60]. Table 3 shows that the ratio of narrow-sense heritability and broad-sense heritability is 0.95 for rice length and 0.92 for rice shape, respectively. This indicates that additive gene action determines size and shape of rice more than non-additive gene action as previously described. Traits that have high additive variance and heritability in the F_1 population may be selected using individual selection. Individual selection may be applied to traits that have additive variance and high heritability in the F_1 population [21] so that the selection of length and shape of rice may be carried out using individual selection such as pedigree. This finding was in agreement with that of Raju et al. [40].

3.3 Combining ability estimation of length and shape of rice

Gene action and cytoplasm influence of the female parent for a trait can be predicted through combining ability. Variances of GCA, SCA, and reciprocals were obtained from diallel analysis of Griffing method-1. Variances of

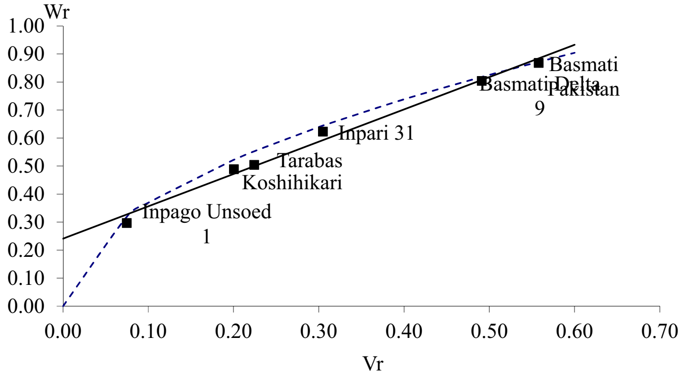

Figure 2: Covariance (W_r) and variance (V_r) graph of rice shape.

Table 5: Analysis of variance of combining ability and GCA:SCA ratio of length and shape of rice

Source of variance	Degree of freedom	Mean square	
		Rice length	Rice shape
GCA	5	6.909*	3.154*
SCA	15	0.138*	0.092*
Reciprocal	15	0.020^{ns}	0.006^{ns}
Error	70	0.015	0.007
GCA:SCA ratio		50.060	34.280

*Significantly different at the level of 5%, ns = not significantly different.

GCA and SCA are associated with non-additive and additive gene actions, respectively [61–63]. Reciprocal variance is useful for knowing the effect of female parent cytoplasm of a trait [64].

GCA is endorsed to additive gene action, and SCA is mainly attributed to non-additive gene action [59,65]. This study shows significant effects of GCA and SCA on length and shape of rice (Table 5). The significant GCA and SCA indicated the importance of both additive and non-additive gene actions in the expression of these traits. This finding was in agreement with that of Singh et al. and Soni et al. [66,67].

The magnitude of the effect of additive gene action and non-additive gene action on a trait can be determined from GCA:SCA ratio [68]. A high GCA:SCA ratio indicates that additive gene action plays a more important role in the expression of a trait than non-additive gene action [69]. Ratio of GCA:SCA greater than one indicates that additive gene action has more influence on the expression of a trait, and conversely, a GCA:SCA ratio less than one reflected that non-additive gene action has more influence on the expression of a trait [70]. In this study, ratio of GCA:SCA of length and shape of rice is greater than one (50.060 and 32.280, respectively) (Table 5), indicating that additive gene action is more influential than non-additive gene action on the expression of these traits. These results agree with the estimation of gene action using the Hayman method as described previously. Additive gene action in length and shape of grain has been previously reported [66,67]. Therefore, the selection of length and shape of grain will be effective using pedigree method [71].

Non-significant reciprocal effects were observed for both length and shape of rice (Table 5). This indicated that there was no influence of the female parent cytoplasm on the inheritance of these traits [64,72] so that the size and shape of the rice are not affected by the female parent cytoplasm.

4 Conclusion

The influence of additive and non-additive gene actions on length and shape of rice was confirmed. The effect of the additive gene action was greater than the non-additive gene action, while both broad-sense heritability and narrow-sense heritability were high. This revealed that the selection of these traits at the early generation using the pedigree selection method may be considered. Length and shape of rice were not affected by the female parent cytoplasm so that F_2 and $F_{2\text{reciprocal}}$ populations might be combined into one population in the next selection generation.

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Cover Letter

May 30, 2022

Dear De Gruyter Poland Ltd,

We wish to resubmit an original research article entitled “Diallel Analysis of Rice Length and Shape using Hayman and Griffing Method” for consideration by Open Agriculture.

We confirm that this work is original and has not been published elsewhere, nor is it currently under consideration for publication elsewhere.

In this paper, we report breeding for rice length and shape in Indonesia. This is significant because rice is the staple food of the Indonesian people, but the breeding for rice length and shape has not been carried out.

We believe that this manuscript is appropriate for publication by Open Agriculture because it plant science

Indonesia is one of the largest rice producing and consuming countries in the world. Until now, it still imports long and slender rice. Long and slender rice breeding has not been carried out in this country. The purpose of this study was to estimate the genetic parameters of rice length and shape using full diallel analysis. This use for the basis of breeding long and slender rice in Indonesia. This study uses parent, one of which is long and slender rice originating from India and Pakistan which have a different environment from Indonesia. Furthermore, this genetic study was carried out in a different environment from the origin of long and slender rice and involved parent from Indonesia. So, the results of this genetic study become a novelty.

We have no conflicts of interest to disclose.

Thank you for your consideration of this manuscript.

Sincerely,

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DIALLEL ANALYSIS OF RICE LENGTH AND SHAPE USING HAYMAN AND GRIFFING METHOD

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DIALLEL ANALYSIS OF RICE LENGTH AND SHAPE USING HAYMAN AND GRIFFING METHOD

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Abstract

Rice size and shape are important physical qualities that determine public acceptance of a variety and determine the price. Improvement of rice size and shape requires information on the genetic parameters of these traits. Diallel analysis is one of the methods usually used to estimate the genetic parameters of a trait. The purpose of this study was to estimate the genetic parameters of rice length and shape using full diallel analysis. The plant material used was a full diallel cross population of six rice genotypes, namely Basmati Pakistan, Basmati Delta 9, Inpago Unsoed 1, Inpari 31, Koshihikari and Tarabas. Thirty-six genotypes consisting of parents, F_1 and $F_{1\ \text{reciprocal}}$ were planted using a randomized block design with three replications. The data of rice grain length and length:width ratio was used for diallel analysis using the Hayman and Griffing method-1. The results showed additive and non-additive genes action influencing the rice length and shape. The effect of the additive gene action is greater than the non-additive gene action and the heritability value, both broad sense and narrow sense heritability is high, revealed the selection of these traits at the early generation using the pedigree selection method may be considered. Rice length and shape were not affected by the female parent cytoplasm so that F_2 and $F_{2\text{reciprocal}}$ populations may be combined into one population the next generation.

Keywords: diallel analysis, rice lenght, rice shape.

1. Introduction

Rice (*Oryza sativa* L.) is one of the major food crops in the world. Nearly 50% of the world population consumes rice as the staple food therefore it has an important role in global food security (1,2). Indonesia, is the world's third largest rice producer and it is also one of the world's main rice consumers (3). More than 80% of Indonesian people consumes rice as a staple food, and it contributes 62.1% of the energy intake (4). It is the main source of income of approximately 18 million household farmers (5). It is also have strategic value from economic, environmental, social and political aspects (6,7). Therefore, rice self-sufficiency in Indonesia is required to fulfil the needs.

The government's program for rice self-sufficiency has four main targets i.e. to increase the national production, to stabilize the domestic prices and reserve stocks, and to minimize the import (8). Improving yield potential of rice varieties through plant breeding has been an important component of increase the national production. High yielding rice varieties contributed to 56% of the national rice production (6). Thus, rice breeding in Indonesia is aimed intended for development high yielding varieties that are in accordance with ecosystem conditions, social, cultural, and community interests (9).

Yield still the main target of rice development, however rice grain quality is now getting more attention due to increasing awareness of its importance (10). Rice grain quality determines the price level of rice in the market, consumer acceptance of a variety and becomes the second goal of rice plant breeding after high yielding (11,12). High yielding varieties with high rice grain quality are easy for farmers to adopted (13).

Grain quality is one of the rice qualities and it consists of the rice length, rice shape, rice translucency and rice chalkiness. Rice quality directly affects consumer acceptance. Consumers determine the rice quality first from grain quality i.e. rice appearance, rice length and shape, after that consumer determine cooking quality and taste (14,15). Hence, rice length and shape determine the level of rice market demands and price (16). Therefore, breeding rice varieties that encompass desirable rice length and shape become one of major concern for rice breeders in Indonesia.

Rice breeding program begins with increasing genetic diversity may be increased by crossing between rice genotypes with wide genetic difference, followed by selection of the interest. The effectiveness of plant breeding programs increases in conjunction with scientific research that expands knowledge of plant genetic information (17). Effective and efficient breeding program determined by the genetic information that controls the inheritance of traits under study (18,19). Sometime selection after crossing in segregation population result in low quality progenies to fulfill breeding objectives (20). Hence, it's necessary to know genetic information of traits before determining breeding and selection method (21). Diallel analysis Is one of the manners to obtain genetic information for grain quality traits in rice such as grain length and shape.

Diallel analysis is mating designs which involves mating a set of parents in all possible combinations, to produce a set of F_1 progeny (22,23). This method is useful to obtain genetic information that controls the inheritance of traits under study in early generation (24,25). It’s also as the quickest method for understanding the genetic control of quantitative traits inheritance (26).

Diallel analysis can be carried out using Hayman and Griffing method. Hayman's method can be used to study of genes action, genetic components and heritability (27). Whereas, utilized Griffing method (28) is to estimated general combining ability, specific combining ability and reciprocal effect. It’s also can be used to calculate additive and non-additive effects. Hayman and Griffing method are often used together for complementary data interpretation (21). Hayman and Griffing method have been used (either one or both) for obtain genetic information of plant traits. It has been widely used for study genetic parameters of length and shape in rice (29–41). The results of the study show various conclusions. Furthermore, this research is rarely done in Indonesia (42). The present research was conducted to genetic study of F_1 population from a cross of six parents with various rice length and shape. The purpose of this study was to estimate the genetic parameters of rice length and shape using full diallel analysis.

2. Materials and Methods

2.1. Location of the experiment

A field experiment was conducted at experimental farm of Agriculture Faculty, Jenderal Soedirman University, Purwokerto, Central Java, Indonesia. This location is at coordinates 7°24'28.7"LS and 109°15'13.3"N and it’s at an altitude of 112 meters above sea level. The experiment was carried out from June 2019 to December 2019.

2.2. Plant material

Six rice genotypes i.e., Basmati Delta 9, Basmati Pakistan, Inpari 31, Inpago Unsoed 1, Koshihikari and Tarabas rice used as the parent in this study. These parents have different origins and have various grain size and shape (Table 1). The research material used was thirty-six rice genotypes from full diallel crosses among six parents. It consists of 6 parents 15 F_1 and 15$F_{1reciprocal}$.

Table 1. Six rice genotypes used for diallel mating design

No.	Genotype	Rice length and shape	Origin
1	Basmati Delta 9	Extra-long, slender	India
2	Basmati Pakistan	Extra-long, slender	Pakistan
3	Inpari 31	Long, medium	Indonesia
4	Inpago Unsoed 1	Medium, medium	Indonesia
5	Koshihikari	Short, round	Japan
6	Tarabas	Short, round	Indonesia

2.3. Experimental design

The experiment designed in a randomized complete block design (RCBD) with 3 replications. Seeds of 36 genotype were sown in a seed box for 2 weeks, followed with transplanted to 35 cm x 40 cm polybag containing 8 kg of inceptisol soil. Each polybag consists of 1 plant. Recommendations for rice cultivation and plant protection was adopted. Fertilizer applications were 0,4 g N/ polybag dan 1.0 g N-P-K/polybag was applied. Fertilizer is applied twice i.e., 10 day and 20 days after transplanting.

2.4. Data collection and analysis

At maturity, panicles were harvested from parents and all generations individually. Panicles were subjected as samples of rice length and shape. Rice shape is determined by grain length to width ratio. (43). Therefore, the observed trait in this study is rice length, width and length to width ratio. Digital caliper was used to measure the grain length and width. Data collected was used for diallel analysis to estimation of genetic parameters of rice length and shape. Diallel analysis performed using Hayman and Griffing method-1 (44) as follows.

1. *Analysis of variance for F_1 in full-diallel crosses*

Analysis of variance for F_1 in full-diallel crosses for rice length and shape follow as the statistical model $Y_{ijkl} = m + T_{ij} + b_k + (bT)_{ijk} + e_{ijkl}$

2. *Genetic components of variation estimated*

Genetic components of variation calculated by formula follow as.

Regression coefficient of b(Wr, Vr) = $\frac{\mathrm{Cov(Wr,Vr)}}{\mathrm{Var(Vr)}}$

Additive genetic variance (D) = V0L0 – E

Dominance variance (H_1) = $V_{0L0} - 4W_{0L1} + 4V_{1L1} - (3n-2)E/n$

Proportions of positive or negative genes in the parent (H_2) = $4V_{1L1} – 4V_{0L1} – 2E$

Mean covariance of additive and dominance (F) = $2V_{0L0} – 4W_{0L0} – 2(n\text{-}2)E/n$

Dominance effect (h^2) = $4(M_{L1} – M_{L0})^2 – 4(n\text{-}1)E/n^2$

Environmental variance (E) = 1/r (Error SS + Rep. SS] / [(r – 1) + (c – 1) (r – 1)]

Average degree of dominance = $(H_1/D)^{1/2}$

The proportion of genes with positive and negative effect in the parent = $H_2/4H_1$

The ratio dominant and recessive gen in the parent = $[(4DH_1)^{1/2} + F]/(4DH_1)^{1/2}–F$

Number of gene groups = h^2/H_2

The coefficient correlation between (Wr+Vr) and Yr (r) = $\frac{\text{Cov ((Wr+Vr),Yr}}{\sqrt{\text{Var (Wr+Yr).Var(Yr)}}}$

Broad sense heritability (h^2_{bs}) = $({}^1/{}_2D+{}^1/{}_2H_1–{}^1/{}_4H_2–{}^1/2F)/({}^1/{}_2D+{}^1/{}_2H_1–{}^1/{}_4H_2–{}^1/{}_2F+E)$

Narrow sense heritability (h^2_{ns}) = $({}^1/{}_2D+{}^1/{}_2H_1–{}^1/{}_2H_2–{}^1/2F)/({}^1/{}_2D+{}^1/{}_2H_1–{}^1/{}_2H_2–{}^1/{}_2F+E)$

3. Combining ability analysis

The statistical model for analysis variance of combining ability follows as.

$Y_{ij} = m + g_i + g_j + S_{ij} + r_{ij} + \frac{1}{bc}\sum\sum e_{ijkl}$

General combining ability (GCA) variance (g_i) = $\frac{1}{2n}\sum\left(Y_{i.} + Y_{.j}\right) - \frac{1}{n^2}Y^2..$

Specific combining ability (SCA) variance (s_{ij}) = $\frac{1}{2}\left(Y_{ij} + Y_{ij}\right) - \frac{1}{2n}\left(Y_{i.} + Y_{.i} + Y_{j.} + Y_{.j}\right) + \frac{1}{n^2}Y..$

Reciprocal variance (r_{ij}) = $\frac{1}{2} = \left(Y_{ij} - Y_{ji}\right)$

3. Result and discussion

3.1. Analysis of variance for genotypes

Analysis of variance showed significantly different among genotypes for rice grain length and shape (Table 2). Similar findings were also reported by Bano and Singh (31) and Hijam et al. (40). Significantly different analysis of variance among genotypes is a requirement for estimating genetic parameters using diallel analysis (44). Thus, significance differences among the genotypes for rice length and shape indicate that they are suitable for further genetic studies.

Table 2. Analysis of variance for F_1 in a full-diallel cross for rice length and shape

Source of variation	Degree of freedom	Mean square	
		Rice length (mm)	Rice shape
Block	2	0,06	0,01
Genotype	35	3,16 *	1,51 *
Error	70	0,04	0,02

* = significantly different at the level of 5%.

3.2. Genetic Components of Variation

3.2.1. Gene interaction

The values of regression coefficient of b (Wr, Vr) for rice length and shape were not significantly different from one (Table 3). Similar result reported by Bano and Singh (31). The value of regression of coefficient of b (Wr, Vr) may be used to determine the gene interaction of a trait. Based on t test, significantly different value of b (Wr, Vr) from one indicates gene interaction, and not significantly different value of b (Wr, Vr) from one reflected no gene interaction (44). It means there is no interaction between genes in controlling of rice length and shape in this study.

Table 3. Estimates of genetic components of variation for rice length and shape

Genetic components	Rice length (mm)	Rice shape
b (Wr, Vr)	1,20 ns	1,15 ns
D	2,72 *	1,36 *
H_1	0,26 *	0,19 *
H_2	0,25 *	0,17 *
F	0,44 *	0,33 *
h^2	-0,01 ns	0,04 ns
E	0,01 ns	0,01 ns
$(H_1/D)^{1/2}$	0,31	0,38
$H_2/4H_1$	0,23	0,22
Kd/Kr	1,71	1,95
h^2/H_2	-0,03	0,22
r [(Wr+Vr),Yr]	0,69	0,89
h^2_{bs}	0,99	0,99
h^2_{ns}	0,94	0,91
Ratio of h^2_{ns}: h^2_{bs}	0,95	0,92

* = significantly different at the level of 5%, ns = not significantly different.

3.2.2. Additive (D) and dominance (H1) variance

Additive (D) and dominance (H_1) variance were significantly different for rice length and shape (Table 3). Significant different values of the components D and H_1 indicated the importance of both additive and non-additive gene action in the expression of traits (45). So that, rice length and shape are influenced by both additive and non-additive types of gene action. The similar findings were also observed by Kato (29), Fu et al (34), Daradjat & Rumanti (42) Kumar et al (35,36), Rafii et al (30) and Senthil Kumar & Mudhalvan (41)

The influence of additive variance is greater than dominance variance ($D>H_1$) for rice length and shape (Table 3). Higher magnitude of additive variance (D) indicated the greater role of additive gene action while *vice versa* dominance variance indicated the greater importance of non-additive gene action (32,45). The value of the additive variance which is greater than the dominance variance indicates the increasing importance of additive gene action (35,36). This means that in this study, rice grain and shape are more influenced by additive gene action more than non-additive gene action. These results are in accordance with the findings of Kato (29) and Thattil and Perera (46). However, Daradjat & Rumanti (42) and Senthil Kumar & Mudhalvan (41) reported different results that there is an indication that the non-additive gene action more predominant than additive gene action.

3.2.3. Gene distribution in the parent

Gene distribution in the parents can be determine by H_2 values. The results showed that the H_2 values for rice length and shape were significantly different (Table 3.) This indicates that the genes determining the inheritance of rice length and shape are not evenly distributed among the parents. Genes controlling rice length and shape that are not evenly distributed in parents have also been reported (41).

Proportion of positive genes to negative genes is indicated by value of H_1 component against H_2 component. The value of H_1 is greater than the H_2 indicating more positive genes than negative genes, *vice versa* the value of the H_1 is smaller than H_2 reflecting the positive gene less than the negative gene (21,47). Table 3 shows the value of H_1 greater than H_2 for the rice length and shape, meaning that positive genes are more involved in determining the rice length and shape than negative genes. The result were agreement with that Raju et al. (32).

Proportion of positive genes to negative genes in all parents also can be seen from ratio of $H_2/4H_1$. Values lower than 0.25 indicate positive and negative genes are not present unequal proportions in the parents (45,48). The results showed the value of $H_2/4H_1$ for rice length and shape is 0.23 and 0.22 respectively (Table 3). it was lower than 0.25, reflecting the unequal distribution of positive and negative genes in the parents. Similar findings were reported by previous studies (31,32,41).

3.2.4. Dominance level

The influence of dominance can be seen from the value of mean degree of dominance as estimated by $(H_1/D)^{1/2}$. A value $(H_1/D)^{1/2}$ more than 1 indicates over dominance, while a value $(H_1/D)^{1/2}$ between 0 and 1 indicates partial dominance (Hayman, 1954). Table 3. shows the value $(H_1/D)^{1/2}$ of the rice length and shape is less than 1, indicated existence of partial dominance in these traits. Rice length controlled by a partial dominance gene was also reported by Kato (29).

3.2.5. Dominance effect

Dominance effect indicating by h^2 value. Table 3. shows that h^2 values were not significantly different for rice length and shape. This is indicating no difference average deviation of F_1 from most parent (47).

3.2.6. Environmental variance

Table 3 showed environmental variance exhibited no significantly for rice length and shape. This is reflected no influence of environmental factor for the expression of the traits studied (45). Therefore, it is known that expression of rice length and shape more influence by genetic than those of environment.

3.2.7. Proportion of dominant gene to recessive gene

Proportion of dominant genes to recessive genes is shown by F component and Kd/Kr ratio. The positive value of F component reflects a greater number of dominant genes than recessive genes in the parent (47,49). The ratio of Kd/Kr greater than one indicating more dominant genes in the parent, conversely, the ratio of Kd/Kr smaller than one indicates more recessive genes in the parent (44). The results showed a positive value of F component and a ratio of Kd/Kr greater than one (Table 3.), indicated more dominant genes in the parent for rice length and shape. The same finding was reported by Raju et al. (32).

3.2.8. Number of gene groups

Component of h^2/H_2 indicating number of gene groups that control a trait. The h_2/H_2 values of rice length and shape are -0.03 and 0.22, respectively, lower than one. The ratio smaller than one indicated the involvement of single gene or one group of genes which are responsible for their genetically control (45). It means rice length and shape are controlled by at least single group of genes.

3.2.9. Direction and order of dominance

The positive value of the correlation between (Wr + Vr) and Y r and close to unity, indicates that dominant alleles have predominantly negative effects, i.e., act in the direction of lower yields (50). A positive value is obtained in the correlation (Wr+Vr) and Yr for rice length and shape (Table 3). That is, in rice length and shape, the dominant genes cause the rice to be short and round.

The direction and order of dominance can be seen in the value (Wr+Vr) component. Based on the value (Wr+Vr) in Table 4 it can be seen that the dominance order of rice grain length and shape was Inpago Unsoed 1, Koshihikari, Tarabas, Basmati Delta 9 and Basmati Pakistan. This is reinforced by the graph of the relationship between the covariance (Wr) and variance (Vr) in Figure 1 and 2.

Distribution of parental array points along the regression line reflected genetic diversity of a trait (51). The array point was scattered along the regression line for rice length and shape, indicating genetic diversity for these traits. The position of the parents on the graph of the relationship between the covariance (Wr) and variance (Vr) reflects the order of dominance. The position of parent which is closer to zero indicating it contains most dominant genes, vice versa farther away a parent position to zero reflecting it contains more recessive genes (47,50). Inpago Unsoed 1 is the closest to zero, reflecting that this parent has the mostly dominant genes for rice length and shape. Basmati Pakistan contain most a recessive gene for the rice length and shape since it is the farthest from zero. Basmati which has extra-long and slender rice contains the most recessive gene, this means that the gene controlling long and slender rice is recessive to the short and round rice gene. This result agreement with finding of Kato (29), Murai & Kinoshita (33) and Ali et al. (52).

Tabel 4. The value (Wr+Vr) of rice length and shape

Genotypes	Rice length	Rice shape
Basmati Delta 9	2,32	1,30
Basmati Pakistan	2,46	1,43
Inpari 31	1,99	0,93
Inpago Unsoed 1	1,00	0,37
Koshihikari	1,75	0,69
Tarabas	1,87	0,73

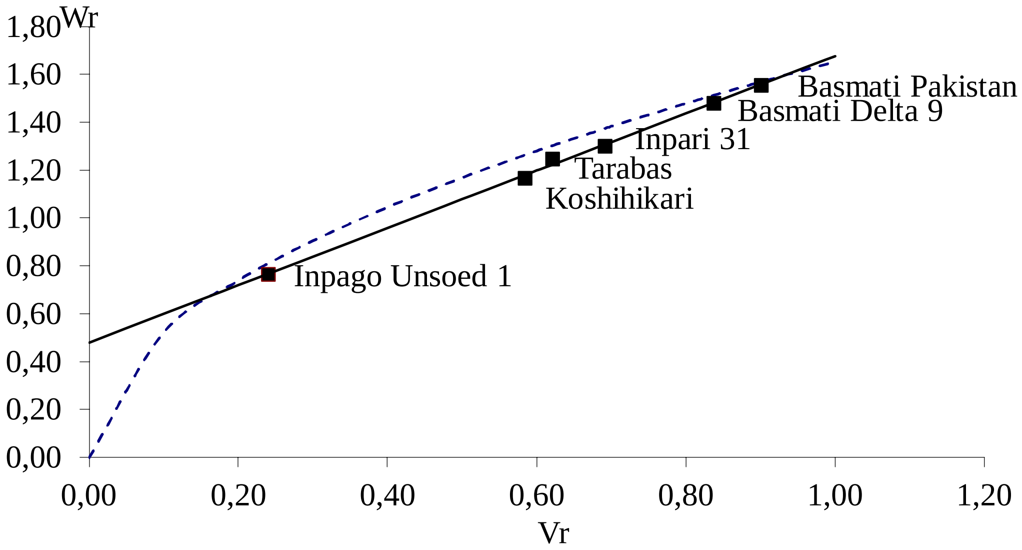

Figure 1. Covariance (Wr) and variance (Vr) graph of rice length.

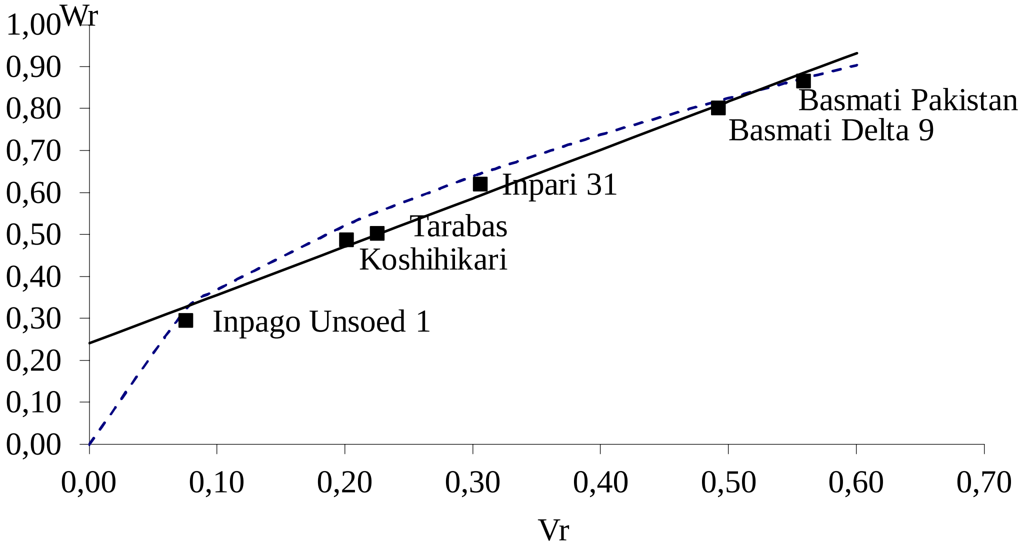

Figure 2. Covariance (Wr) and variance (Vr) graph of rice shape.

The straight line intercepted the vertical axis (Wr) above the origin for rice length and shape (Figure 1 and 2). The straight line intercepted the vertical axis (Wr) above the origin indicated the indicating partial dominance of the genes controlling a trait (21,50,51). This reveals that the rice length and shape was controlled by a partial dominant gene as described previously. Partial dominance results in the appearance of each trait having a tendency to approach the mid parent value and not being having over dominant which exceeds the best parent (53). This is reflected in the h^2 value of rice length and shape which is not significantly different so that there is no difference between the F_1 average and the parents' average.

3.2.10. Heritability

Broad sense heritability (h^2_{bs}) estimates for rice length and shape are similar, 0,99. Narrow sense heritability (h^2_{ns}) estimates for these traits is 0.94 and 0.91, respectively (Table 3.). Heritability values more than 0.5 are categorized as high (Stansfield, 1991), thus broad sense heritability (h^2_{bs}) for rice length and shape categorized as high heritability. Similar findings were reported by previous studies (54)

The estimated value of broad sense heritability indicating the relative contribution of genetic factors to variation of observed trait (55). high broad sense heritability value indicates that traits are more influenced by genetic than environmental factors (56). In this study, broad sense heritability estimate of rice length and shape is high, indicating the influence of genetic was greater than environmental factors. Low influence of environmental factors also indicated by not significantly different of environmental variance (E) as described previously (Table 3.).

Narrow sense heritability estimates indicate the role of additive gene action on a trait. High estimated of narrow sense heritability indicates more additive gene action than non-additive gene action (4,57–59). In this study, the narrow sense heritability estimate of rice length and shape was high, meaning that additive gene action played a more important role than non-additive gene action.

Ratio of narrow sense heritability and broad sense heritability reflecting the role of additive and non-additive gene action for a trait. The ratio value closer to one indicates the total genetic variance of a trait is caused by additive gene action (60). Table 3 shows ratio of narrow sense heritability and broad sense heritability ratios are 0.95 for rice length and 0.92 for rice shape respectively. This indicating that additive gene action determines the rice size and shape more than non-additive gene action as previously described. Traits that have high additive variance and heritability in the F_1 population may be selected using individual selection. Individual selection may be applied to traits that have additive variance and high heritability in the F_1 population (21) so that selection of rice length and shape may be carried out using individual selection such as pedigree. This finding agreement with Raju et al. (32).

3.3. Combining ability estimation of rice length and shape

Gene action and influence of cytoplasm female parent for a trait can be predicted through combining ability. Variance of general combining ability (GCA), specific combining ability (SCA), and reciprocal were obtained from diallel analysis of Griffing approach method-1. GCA and SCA variance, which is associated with non-additive and additive gene action, respectively (61–63). Reciprocal variance is useful for knowing the effect of female parent cytoplasm of a trait (64).

General combining ability (GCA) is endorsed to additive gene action and specific combining ability (SCA) usually attributable for non-additive gene action (59,65). This study shows mean square of GCA and SCA of rice length and shape is significantly different (Table 4). The significant GCA and SCA indicated the importance of both additive and non-additive gene actions in the expression of these characters traits. This finding agreement with V. Singh et al. and Soni et al. (66,67).

Table 4. Analysis of variance of combining ability and GCA:SCA ratio of rice length and shape

Source of variance	Degree of freedom	Mean square Rice length		Mean square Rice shape	
General combining ability (GCA)	5	6,909	*	3,154	*
Specific combining ability (SCA)	15	0,138	*	0,092	*
Reciprocal	15	0,020	ns	0,006	ns
Error	70	0,015		0,007	
GCA:SCA ratio		50,06		34,28	

* = significantly different at the level of 5%, ns = not significantly different

The magnitude of the effect of additive gene action and non-additive gene action on a trait can be determined from GCA:SCA ratio (68). A high GCA:SCA ratio indicates that additive gene action plays a more important role in the expression of a trait than non-additive gene action (69). Ratio of GCA:SCA greater than one indicates that additive gene action has more influence on the expression of a trait and conversely, a GCA:SCA ratio less than one reflected that non-additive gene action has more influence on the expression of a trait (70). In this study, ratio of GCA:SCA of rice length and shape is greater than one (Table 4), indicating additive gene action is more influential than non-additive gene action on the expression of these traits. These results are in agreement with the estimation of gene action using the Hayman method as described previously. Grain length and shape more influence by additive gen action already reported reported (66,67). Therefore, the selection for grain length and shape will be effective using pedigree method (71).

Reciprocal mean square of rice length and shape has no significant difference (Table 4). Reciprocal variance was not significantly different, indicating that there was no influence of the female parent cytoplasm of the inheritance of a trait (64,72). So that, the size and shape of the rice are not affected by the female parent cytoplasm.

4. CONCLUSION

Additive and non-additive genes action influencing the rice length and shape are confirmed. The effect of the additive gene action is greater than the non-additive gene action and the heritability value, both broad sense and narrow sense heritability is high, revealed that the selection of these traits at the early generation using the pedigree selection method may be considered. Rice length and shape were characters that not affected by the female parent cytoplasm so that F_2 and $F_{2reciprocal}$ populations might be combined into one population in the next selection generation.

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6. DAFTAR PUSTAKA

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DIALLEL ANALYSIS OF RICE LENGTH AND SHAPE USING HAYMAN AND GRIFFING METHOD

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Abstract

Rice length and shape are important physical qualities that determine public acceptance of a variety and determine the price. Improvement of rice length and shape requires information on the genetic parameters of these traits. Diallel analysis is one of the methods usually used to estimate the genetic parameters of a trait. The purpose of this study was to estimate the genetic parameters of rice length and shape using full diallel analysis. The plant material used was a full diallel cross population of six rice genotypes, namely Basmati Pakistan, Basmati Delta 9, Inpago Unsoed 1, Inpari 31, Koshihikari and Tarabas. Thirty-six genotypes consisting of parents, F_1 and $F_{1\ \mathrm{reciprocal}}$ were planted using a randomized block design with three replications. The data of rice grain length and length:width ratio was used for diallel analysis using the Hayman and Griffing method-1. The results showed additive and non-additive genes action influencing the rice length and shape. The effect of the additive gene action is greater than the non-additive gene action and the heritability value, both broad sense and narrow sense heritability is high, revealed the selection of these traits at the early generation using the pedigree selection method may be considered. Rice length and shape were not affected by the female parent cytoplasm so that F_2 and $F_{2\mathrm{reciprocal}}$ populations may be combined into one population the next generation.

Keywords: diallel analysis, rice length, rice shape.

1. Introduction

Rice (*Oryza sativa* L.) is one of the major food crops in the world. Nearly 50% of the world population consumes rice as the staple food therefore it has an important role in global

food security (1,2). Indonesia, is the world's third largest rice producer and it is also one of the world's main rice consumers (3). More than 80% of Indonesian people consumes rice as a staple food, and it contributes 62.1% of the energy intake (4). It is the main source of income of approximately 18 million household farmers (5). It is also have strategic value from economic, environmental, social and political aspects (6,7). Therefore, rice self-sufficiency in Indonesia is required to fulfil the needs.

The government's program for rice self-sufficiency has four main targets i.e. to increase the national production, to stabilize the domestic prices and reserve stocks, and to minimize the import (8). Improving yield potential of rice varieties through plant breeding has been an important component of increase the national production. High yielding rice varieties contributed to 56% of the national rice production (6). Thus, rice breeding in Indonesia is aimed intended for development high yielding varieties that are in accordance with ecosystem conditions, social, cultural, and community interests (9).

Yield still the main target of rice development, however rice grain quality is now getting more attention due to increasing awareness of its importance (10). Rice grain quality determines the price level of rice in the market, consumer acceptance of a variety and becomes the second goal of rice plant breeding after high yielding (11,12). High yielding varieties with high rice grain quality are easy for farmers to adopted (13).

Grain quality is one of the rice qualities and it consists of the rice length, rice shape, rice translucency and rice chalkiness. Rice quality directly affects consumer acceptance. Consumers determine the rice quality first from grain quality i.e. rice appearance, rice length and shape, after that consumer determine cooking quality and taste (14,15). Hence, rice length and shape determine the level of rice market demands and price (16). Therefore, breeding rice varieties that encompass desirable rice length and shape become one of major concern for rice breeders in Indonesia.

Rice breeding program begins with increasing genetic diversity may be increased by crossing between rice genotypes with wide genetic difference, followed by selection of the interest. The effectiveness of plant breeding programs increases in conjunction with scientific research that expands knowledge of plant genetic information (17). Effective and efficient breeding program determined by the genetic information that controls the inheritance of traits under study (18,19). Sometime selection after crossing in segregation population result in low quality progenies to fulfill breeding objectives (20). Hence, it's necessary to know genetic information of traits before determining breeding and selection method (21). Diallel analysis Is one of the manners to obtain genetic information for grain quality traits in rice such as grain length and shape.

Diallel analysis is mating designs which involves mating a set of parents in all possible combinations, to produce a set of F_1 progeny (22,23). This method is useful to obtain genetic information that controls the inheritance of traits under study in early generation (24,25). It's also as the quickest method for understanding the genetic control of quantitative traits inheritance (26).

Diallel analysis can be carried out using Hayman and Griffing method. Hayman's method can be used to study of genes action, genetic components and heritability (27). Whereas, utilized Griffing method (28) is to estimated general combining ability, specific combining ability and reciprocal effect. It's also can be used to calculate additive and non-additive effects. Hayman and Griffing method are often used together for complementary data interpretation (21). Hayman and Griffing method have been used (either one or both) for obtain genetic information of plant traits. It has been widely used for study genetic parameters of length and shape in rice (29–41). The results of the study show various conclusions. Furthermore, this research is rarely done in Indonesia (42). The present research was conducted to genetic study of F_1 population from a cross of six parents with various rice length and shape. The purpose of this study was to estimate the genetic parameters of rice length and shape using full diallel analysis.

2. Materials and Methods

2.1. Location of the experiment

A field experiment was conducted at experimental farm of Agriculture Faculty, Jenderal Soedirman University, Purwokerto, Central Java, Indonesia. This location is at coordinates

7°24'28.7"LS and 109°15'13.3"N and it's at an altitude of 112 meters above sea level. The experiment was carried out from June 2019 to December 2019.

2.2. Plant material

Six rice genotypes i.e., Basmati Delta 9, Basmati Pakistan, Inpari 31, Inpago Unsoed 1, Koshihikari and Tarabas rice used as the parent in this study. These parents have different origins and have various grain size and shape (Table 1). The research material used was thirty-six rice genotypes from full diallel crosses among six parents. It consists of 6 parents 15 F_1 and 15 $F_{1reciprocal}$.

Table 1. Six rice genotypes used for diallel mating design

No.	Genotype	Rice length and shape	Origin
1	Basmati Delta 9	Extra-long, slender	India
2	Basmati Pakistan	Extra-long, slender	Pakistan
3	Inpari 31	Long, medium	Indonesia
4	Inpago Unsoed 1	Medium, medium	Indonesia
5	Koshihikari	Short, round	Japan
6	Tarabas	Short, round	Indonesia

2.3. Experimental design

The experiment designed in a randomized complete block design (RCBD) with 3 replications. Seeds of 36 genotype were sown in a seed box for 2 weeks, followed with transplanted to 35 cm x 40 cm polybag containing 8 kg of inceptisol soil. Each polybag consists of 1 plant. Recommendations for rice cultivation and plant protection was adopted. Fertilizer applications were 0,4 g N/ polybag dan 1.0 g N-P-K/polybag was applied. Fertilizer is applied twice i.e., 10 day and 20 days after transplanting.

2.4. Data collection and analysis

At maturity, panicles were harvested from parents and all generations individually. Panicles were subjected as samples of rice length and shape. Rice shape is determined by grain length to width ratio. (43). Therefore, the observed trait in this study is rice length, width and length to width ratio. Digital caliper was used to measure the grain length and width. Data collected was used for diallel analysis to estimation of genetic parameters of rice length and shape. Diallel analysis performed using Hayman and Griffing method-1 (44) as follows.

1. Analysis of variance for F_1 in full-diallel crosses

Analysis of variance for F_1 in full-diallel crosses for rice length and shape follow as the statistical model $Y_{ijkl} = m + T_{ij} + b_k + (bT)_{ijk} + e_{ijkl}$ (1)

2. Genetic components of variation estimated

Genetic components of variation calculated by formula follow as.

Regression coefficient of b(Wr, Vr) = $\frac{\mathrm{Cov(Wr,Vr)}}{\mathrm{Var(Vr)}}$ (2)

Additive genetic variance (D) = V0L0 – E (3)

Dominance variance (H_1) = $V_{0L0} - 4W_{0L1} + 4V_{1L1} - (3n-2)E/n$ (4)

Proportions of positive or negative genes in the parent (H_2) = $4V_{1L1} - 4V_{0L1} - 2E$ (5)

Mean covariance of additive and dominance (F) = $2V_{0L0} - 4W_{0L0} - 2(n-2)E/n$ (6)

Dominance effect (h^2) = $4(M_{L1} - M_{L0})^2 - 4(n-1)E/n^2$ (7)

Environmental variance (E) = 1/r (Error SS + Rep. SS] / [(r – 1) + (c – 1) (r – 1)] (8)

Average degree of dominance = $(H_1/D)^{1/2}$ (9)

The proportion of genes with positive and negative effect in the parent = $H_2/4H_1$ (10)

The ratio dominant and recessive gene in the parent = $[(4DH_1)^{1/2} + F]/(4DH_1)^{1/2}$–F (11)

Number of gene groups = h^2/H_2 (13)

The coefficient correlation between (Wr+Vr) and Yr (r) = $\frac{\mathrm{Cov\ ((Wr+Vr),Yr}}{\sqrt{\mathrm{Var\ (Wr+Yr).Var(Yr)}}}$ (15)

Broad sense heritability (h^2_{bs}) =

$(^1/_2D+^1/_2H_1-^1/_4H_2-^1/2F)/(^1/_2D+^1/_2H_1-^1/_4H_2-^1/_2F+E)$ (16)

Narrow sense heritability (h^2_{ns}) =

$(^1/_2D+^1/_2H_1-^1/_2H_2-^1/2F)/(^1/_2D+^1/_2H_1-^1/_2H_2-^1/_2F+E)$ (17)

3. Combining ability analysis

The statistical model for analysis variance of combining ability follows as.

$Y_{ij} = m + g_i + g_j + S_{ij} + r_{ij} + \frac{1}{bc}\sum\sum e_{ijkl}$ (18)

General combining ability (GCA) variance (g_i) = $\frac{1}{2n}\sum\left(Y_{i.} + Y_{.j}\right) - \frac{1}{n^2}Y^2..$ (19)

Specific combining ability (SCA) variance (s_{ij}) =

$\frac{1}{2}\left(Y_{ij} + Y_{ij}\right) - \frac{1}{2n}\left(Y_{i.} + Y_{.i} + Y_{j.} + Y_{.j}\right) + \frac{1}{n^2}Y..$ (20)

Reciprocal variance (r_{ij}) = $\frac{1}{2} = \left(Y_{ij} - Y_{ji}\right)$ (21)

3. Result and discussion

3.1. Analysis of variance for genotypes

Analysis of variance showed significantly different among genotypes for rice grain length and shape (Table 2). Similar findings were also reported by Bano and Singh (31) and Hijam et al. (40). Significantly different analysis of variance among genotypes is a requirement for estimating genetic parameters using diallel analysis (44). Thus, significance differences among the genotypes for rice length and shape indicate that they are suitable for further genetic studies.

Table 2. Analysis of variance for F_1 in a full-diallel cross for rice length and shape

Source of variation	Degree of freedom	Mean square	
		Rice length (mm)	Rice shape
Block	2	0,06	0,01
Genotype	35	3,16 *	1,51 *
Error	70	0,04	0,02

* = significantly different at the level of 5%.

3.2. Genetic Components of Variation

3.2.1. Gene interaction

The values of regression coefficient of b (Wr, Vr) for rice length and shape were not significantly different from one (Table 3). Similar result reported by Bano and Singh (31). The value of regression of coefficient of b (Wr, Vr) may be used to determine the gene interaction of a trait. Based on t test, significantly different value of b (Wr, Vr) from one indicates gene interaction, and not significantly different value of b (Wr, Vr) from one reflected no gene interaction (44). It means there is no interaction between genes in controlling of rice length and shape in this study.

3.2.2. Additive (D) and dominance (H1) variance

Additive (D) and dominance (H_1) variance were significantly different for rice length and shape (Table 3). Significant different values of the components D and H_1 indicated the importance of both additive and non-additive gene action in the expression of traits (45). So that, rice length and shape are influenced by both additive and non-additive types of gene action. The similar findings were also observed by Kato (29), Fu et al (34), Daradjat & Rumanti (42) Kumar et al (35,36), Rafii et al (30) and Senthil Kumar & Mudhalvan (41)

The influence of additive variance is greater than dominance variance ($D>H_1$) for rice length and shape (Table 3). Higher magnitude of additive variance (D) indicated the greater role of additive gene action while *vice versa* dominance variance indicated the greater importance of non-additive gene action (32,45). The value of the additive variance which is greater than the dominance variance indicates the increasing importance of additive gene action (35,36). This means that in this study, rice grain and shape are more influenced by additive gene action more than non-additive gene action. These results are in accordance with the findings of Kato (29) and Thattil and Perera (46). However, Daradjat & Rumanti (42) and Senthil Kumar & Mudhalvan (41) reported different results that there is an indication that the non-additive gene action more predominant than additive gene action.

Table 3. Estimates of genetic components of variation for rice length and shape

Genetic components	Rice length (mm)	Rice shape
b (Wr, Vr)	1,20 ns	1,15 ns
D	2,72 *	1,36 *
H_1	0,26 *	0,19 *
H_2	0,25 *	0,17 *
F	0,44 *	0,33 *
h^2	-0,01 ns	0,04 ns
E	0,01 ns	0,01 ns
$(H_1/D)^{1/2}$	0,31	0,38
$H_2/4H_1$	0,23	0,22
Kd/Kr	1,71	1,95
h^2/H_2	-0,03	0,22
r [(Wr+Vr),Yr]	0,69	0,89
h^2_{bs}	0,99	0,99
h^2_{ns}	0,94	0,91
Ratio of h^2_{ns}: h^2_{bs}	0,95	0,92

* = significantly different at the level of 5%, ns = not significantly different.

3.2.3. Gene distribution in the parent

Gene distribution in the parents can be determine by H_2 values. The results showed that the H_2 values for rice length and shape were significantly different (Table 3.) This indicates that the genes determining the inheritance of rice length and shape are not evenly distributed among the parents. Genes controlling rice length and shape that are not evenly distributed in parents have also been reported (41).

Proportion of positive genes to negative genes is indicated by value of H_1 component against H_2 component. The value of H_1 is greater than the H_2 indicating more positive genes than negative genes, *vice versa* the value of the H_1 is smaller than H_2 reflecting the positive gene less than the negative gene (21,47). Table 3 shows the value of H_1 greater than H_2 for the rice length and shape, meaning that positive genes are more involved in determining the rice length and shape than negative genes. The result were agreement with that Raju et al. (32).

Proportion of positive genes to negative genes in all parents also can be seen from ratio of $H_2/4H_1$. Values lower than 0.25 indicate positive and negative genes are not present unequal proportions in the parents (45,48). The results showed the value of $H_2/4H_1$ for rice length and shape is 0.23 and 0.22 respectively (Table 3). it was lower than 0.25, reflecting the unequal distribution of positive and negative genes in the parents. Similar findings were reported by previous studies (31,32,41).

3.2.4. Dominance level

The influence of dominance can be seen from the value of mean degree of dominance as estimated by $(H_1/D)^{1/2}$. A value $(H_1/D)^{1/2}$ more than 1 indicates over dominance, while a value $(H_1/D)^{1/2}$ between 0 and 1 indicates partial dominance (Hayman, 1954). Table 3. shows the value $(H_1/D)^{1/2}$ of the rice length and shape is less than 1, indicated existence of partial dominance in these traits. Rice length controlled by a partial dominance gene was also reported by Kato (29).

3.2.5. Dominance effect

Dominance effect indicating by h^2 value. Table 3. shows that h^2 values were not significantly different for rice length and shape. This is indicating no difference average deviation of F_1 from most parent (47).

3.2.6. Environmental variance

Table 3 showed environmental variance exhibited no significantly for rice length and shape. This is reflected no influence of environmental factor for the expression of the traits studied (45). Therefore, it is known that expression of rice length and shape more influence by genetic than those of environment.

3.2.7. Proportion of dominant gene to recessive gene

Proportion of dominant genes to recessive genes is shown by F component and Kd/Kr ratio. The positive value of F component reflects a greater number of dominant genes than recessive genes in the parent (47,49). The ratio of Kd/Kr greater than one indicating more dominant genes in the parent, conversely, the ratio of Kd/Kr smaller than one indicates more recessive genes in the parent (44). The results showed a positive value of F component and a ratio of Kd/Kr greater than one (Table 3.), indicated more dominant genes in the parent for rice length and shape. The same finding was reported by Raju et al. (32).

3.2.8. Number of gene groups

Component of h^2/H_2 indicating number of gene groups that control a trait. The h_2/H_2 values of rice length and shape are -0.03 and 0.22, respectively, lower than one. The ratio smaller than one indicated the involvement of single gene or one group of genes which are responsible for their genetically control (45). It means rice length and shape are controlled by at least single group of genes.

3.2.9. Direction and order of dominance

The positive value of the correlation between (Wr + Vr) and Y r and close to unity, indicates that dominant alleles have predominantly negative effects, i.e., act in the direction of lower yields (50). A positive value is obtained in the correlation (Wr+Vr) and Yr for rice length and shape (Table 3). That is, in rice length and shape, the dominant genes cause the rice to be short and round.

The direction and order of dominance can be seen in the value (Wr+Vr) component. Based on the value (Wr+Vr) in Table 4 it can be seen that the dominance order of rice grain length and shape was Inpago Unsoed 1, Koshihikari, Tarabas, Basmati Delta 9 and Basmati Pakistan. This is reinforced by the graph of the relationship between the covariance (Wr) and variance (Vr) in Figure 1 and 2.

Distribution of parental array points along the regression line reflected genetic diversity of a trait (51). The array point was scattered along the regression line for rice length and shape, indicating genetic diversity for these traits. The position of the parents on the graph of the relationship between the covariance (Wr) and variance (Vr) reflects the order of dominance. The position of parent which is closer to zero indicating it contains most dominant genes, vice versa farther away a parent position to zero reflecting it contains more recessive genes (47,50). Inpago Unsoed 1 is the closest to zero, reflecting that this parent has the mostly dominant genes for rice length and shape. Basmati Pakistan contain most a recessive gene for the rice length and shape since it is the farthest from zero. Basmati which has extra-long and slender rice contains the most recessive gene, this means that the gene controlling long and slender rice is recessive to the short and round rice gene. This result agreement with finding of Kato (29), Murai & Kinoshita (33) and Ali et al. (52).

Tabel 4. The value (Wr+Vr) of rice length and shape

Genotypes	Rice length	Rice shape
Basmati Delta 9	2,32	1,30
Basmati Pakistan	2,46	1,43
Inpari 31	1,99	0,93
Inpago Unsoed 1	1,00	0,37
Koshihikari	1,75	0,69
Tarabas	1,87	0,73

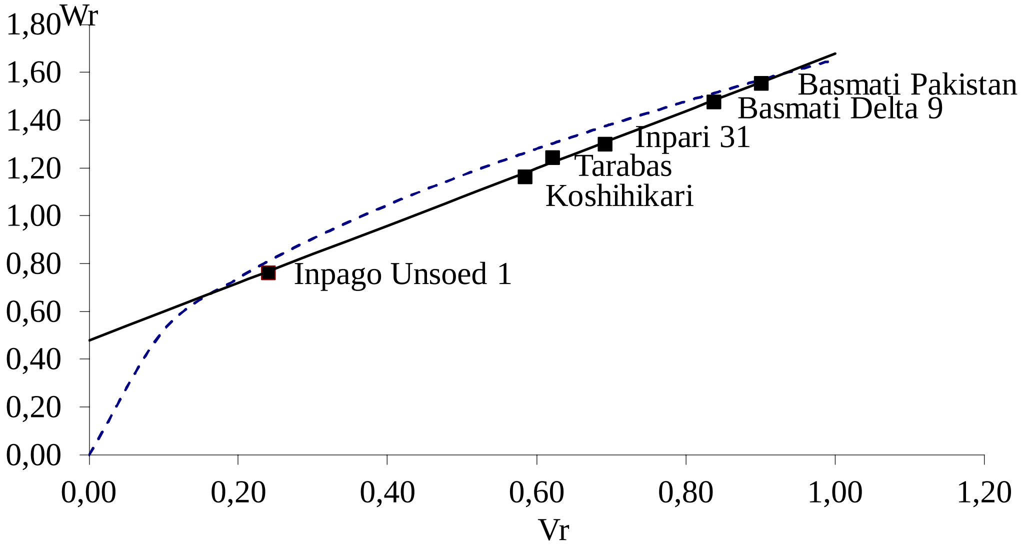

Figure 1. Covariance (Wr) and variance (Vr) graph of rice length.

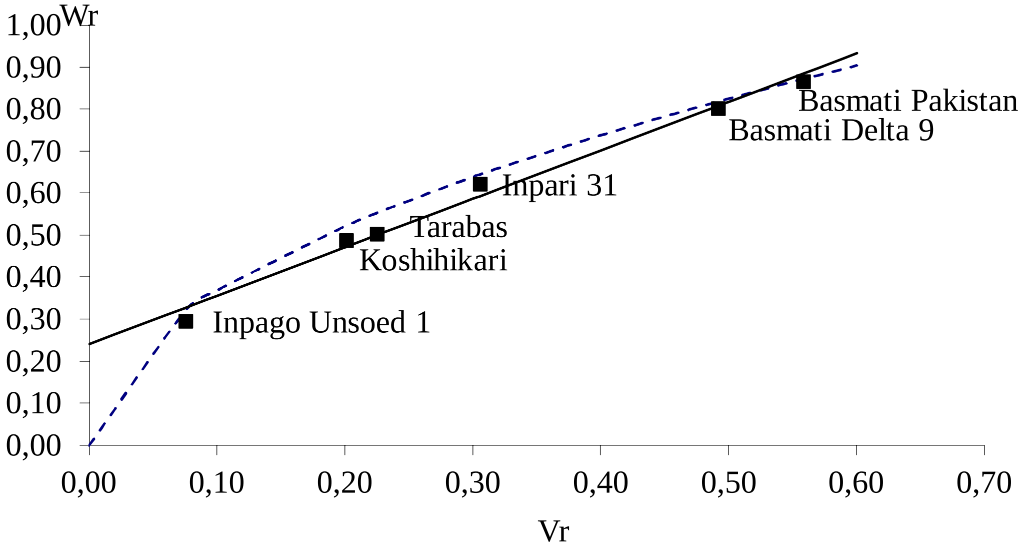

Figure 2. Covariance (Wr) and variance (Vr) graph of rice shape.

The straight line intercepted the vertical axis (Wr) above the origin for rice length and shape (Figure 1 and 2). The straight line intercepted the vertical axis (Wr) above the origin indicated the indicating partial dominance of the genes controlling a trait (21,50,51). This reveals that the rice length and shape was controlled by a partial dominant gene as described previously. Partial dominance results in the appearance of each trait having a tendency to approach the mid parent value and not being having over dominant which exceeds the best parent (53). This is reflected in the h^2 value of rice length and shape which is not significantly different so that there is no difference between the F_1 average and the parents' average.

3.2.10. Heritability

Broad sense heritability (h^2_{bs}) estimates for rice length and shape are similar, 0,99. Narrow sense heritability (h^2_{ns}) estimates for these traits is 0.94 and 0.91, respectively (Table 3.). Heritability values more than 0.5 are categorized as high (Stansfield, 1991), thus broad sense heritability (h^2_{bs}) for rice length and shape categorized as high heritability. Similar findings were reported by previous studies (54)

The estimated value of broad sense heritability indicating the relative contribution of genetic factors to variation of observed trait (55). high broad sense heritability value indicates that traits are more influenced by genetic than environmental factors (56). In this study, broad sense heritability estimate of rice length and shape is high, indicating the influence of genetic was greater than environmental factors. Low influence of environmental factors also indicated by not significantly different of environmental variance (E) as described previously (Table 3.).

Narrow sense heritability estimates indicate the role of additive gene action on a trait. High estimated of narrow sense heritability indicates more additive gene action than non-additive gene action (4,57–59). In this study, the narrow sense heritability estimate of rice length and shape was high, meaning that additive gene action played a more important role than non-additive gene action.

Ratio of narrow sense heritability and broad sense heritability reflecting the role of additive and non-additive gene action for a trait. The ratio value closer to one indicates the total genetic variance of a trait is caused by additive gene action (60). Table 3 shows ratio of narrow sense heritability and broad sense heritability ratios are 0.95 for rice length and 0.92 for rice shape respectively. This indicating that additive gene action determines the rice size and shape more than non-additive gene action as previously described. Traits that have high additive variance and heritability in the F_1 population may be selected using individual selection. Individual selection may be applied to traits that have additive variance and high heritability in the F_1 population (21) so that selection of rice length and shape may be carried out using individual selection such as pedigree. This finding agreement with Raju et al. (32).

3.3. Combining ability estimation of rice length and shape

Gene action and influence of cytoplasm female parent for a trait can be predicted through combining ability. Variance of general combining ability (GCA), specific combining ability (SCA), and reciprocal were obtained from diallel analysis of Griffing approach method-1. GCA and SCA variance, which is associated with non-additive and additive gene action, respectively (61–63). Reciprocal variance is useful for knowing the effect of female parent cytoplasm of a trait (64).

General combining ability (GCA) is endorsed to additive gene action and specific combining ability (SCA) usually attributable for non-additive gene action (59,65). This study shows mean square of GCA and SCA of rice length and shape is significantly different (Table 4). The significant GCA and SCA indicated the importance of both additive and non-additive gene actions in the expression of these characters traits. This finding agreement with V. Singh et al. and Soni et al. (66,67).

Table 4. Analysis of variance of combining ability and GCA:SCA ratio of rice length and shape

Source of variance	Degree of freedom	Mean square	
		Rice length	Rice shape
General combining ability (GCA)	5	6,909 *	3,154 *
Specific combining ability (SCA)	15	0,138 *	0,092 *
Reciprocal	15	0,020 ns	0,006 ns
Error	70	0,015	0,007
GCA:SCA ratio		50,06	34,28

* = significantly different at the level of 5%, ns = not significantly different

The magnitude of the effect of additive gene action and non-additive gene action on a trait can be determined from GCA:SCA ratio (68). A high GCA:SCA ratio indicates that additive gene action plays a more important role in the expression of a trait than non-additive gene action (69). Ratio of GCA:SCA greater than one indicates that additive gene action has more influence on the expression of a trait and conversely, a GCA:SCA ratio less than one

reflected that non-additive gene action has more influence on the expression of a trait (70). In this study, ratio of GCA:SCA of rice length and shape is greater than one (Table 4), indicating additive gene action is more influential than non-additive gene action on the expression of these traits. These results are in agreement with the estimation of gene action using the Hayman method as described previously. Grain length and shape more influence by additive gen action already reported (66,67). Therefore, the selection for grain length and shape will be effective using pedigree method (71).

Reciprocal mean square of rice length and shape has no significant difference (Table 4). Reciprocal variance was not significantly different, indicating that there was no influence of the female parent cytoplasm of the inheritance of a trait (64,72). So that, the size and shape of the rice are not affected by the female parent cytoplasm.

4. CONCLUSION

Additive and non-additive genes action influencing the rice length and shape are confirmed. The effect of the additive gene action is greater than the non-additive gene action and the heritability value, both broad sense and narrow sense heritability is high, revealed that the selection of these traits at the early generation using the pedigree selection method may be considered. Rice length and shape were characters that not affected by the female parent cytoplasm so that F_2 and $F_{2reciprocal}$ populations might be combined into one population in the next selection generation.

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Dear Dr. Agus Riyanto,

Reviewers have now commented on your paper. You will see that they are advising that you revise your manuscript. If you are prepared to undertake the work required, I would be happy to receive your revised paper.

For your guidance, reviewers' comments are appended below.

If you decide to revise the work, please submit a list of changes or a rebuttal against each point which is being raised when you submit the revised manuscript. Please, also make sure that all changes in the revised manuscript are highlighted and references are prepared according to our Instructions (https://www.degruyter.com/publication/journal_key/OPAG/downloadAsset/OPAG_Instructions%20for%20Authors.pdf).

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Yours sincerely,
Oskar Szczepaniak, MSc
Managing Editor
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Reviewers' comments:

Reviewer #1:
Comment 1- Please add all the grain length and shape data as supplemental data.

Comment 2- Line 51 Grammatical error- 'Yield is still..'

Comment 3- Line 57 replace 'qualities' with something else, repetition of word 'quality'.

Comment 4- Line 73 Typing mistake 'Diallel analysis is..'

Comment 5- Line 114 Grammatical error 'The experiment was designed…'

Comment 6- Line 117 Please clarify Each poly bag contained one plant per genotype or all the plants of one genotype?

Comment 7- Section 3.2 Please add each of the value of estimated of genetic components of variation in their respective sections. The author keeps referring table 3, providing those values in their section will be helpful for reading.

Reviewer #2:

The paper contains good research and sound conclusions were made on the results obtained, although the paper needs to be English edited. A number of sentences needs to be rephrased and typing errors needs to be corrected. These were too many to be typed here. Please consult the pdf document uploaded which indicated the required comments and suggestions for improvement.

Managing Editor: The raw data of rice length and shape needs to be added as supplementary data.

There is additional documentation related to this decision letter. To access the file(s), please click the link below. You may also login to the system and click the 'View Attachments' link in the Action column.
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DIALLEL ANALYSIS OF RICE LENGTH AND SHAPE USING HAYMAN AND GRIFFING METHOD

--Manuscript Draft--

Manuscript Number:	OPAG-D-22-00063R1
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Abstract:	Rice length and shape are important physical qualities that determine public acceptance of a variety and determine the price. Improvement of rice length and shape requires information on the genetic parameters of these traits. Diallel analysis is one of the methods usually used to estimate the genetic parameters of a trait. The purpose of this study was to estimate the genetic parameters of rice length and shape using full diallel analysis. The plant material used was a full diallel cross population of six rice genotypes, namely Basmati Pakistan, Basmati Delta 9, Inpago Unsoed 1, Inpari 31, Koshihikari and Tarabas. Thirty-six genotypes consisting of parents, F 1 and F1 reciprocal were planted using a randomized block design with three replications. The data of rice grain length and length:width ratio was used for diallel analysis using the Hayman and Griffing method-1. The results showed additive and non-additive genes action influencing the rice length and shape. The effect of the additive gene action is greater than the non-additive gene action and the heritability value, both broad sense and narrow sense heritability is high, revealed the selection of these traits at the early generation using the pedigree selection method may be considered. Rice length and shape were not affected by the female parent cytoplasm so that F 2 and F 2reciprocal populations may be combined into one population the next generation.
Opposed Reviewers:	
Response to Reviewers:	thank you for the review the article has been corrected according to the suggestions Thank you
Additional Information:	
Question	**Response**

DIALLEL ANALYSIS OF RICE LENGTH AND SHAPE USING HAYMAN AND GRIFFING METHOD

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Abstract

Rice length and shape are important physical qualities that determine public acceptance of a variety and determine the price. Improvement of rice length and shape requires information on the genetic parameters of these traits. Diallel analysis is one of the methods usually used to estimate the genetic parameters of a trait. The purpose of this study was to estimate the genetic parameters of rice length and shape using full diallel analysis. The plant material used was a full diallel cross population of six rice genotypes, namely Basmati Pakistan, Basmati Delta 9, Inpago Unsoed 1, Inpari 31, Koshihikari and Tarabas. Thirty-six genotypes consisting of parents, F_1 and $F_{1\ \mathrm{reciprocal}}$ were planted using a randomized block design with three replications. The data of rice grain length and length:width ratio was used for diallel analysis using the Hayman and Griffing method-1. The results showed additive and non-additive genes action influencing the rice length and shape. The effect of the additive gene action is greater than the non-additive gene action and the heritability value, both broad sense and narrow sense heritability is high, revealed the selection of these traits at the early generation using the pedigree selection method may be considered. Rice length and shape were not affected by the female parent cytoplasm so that F_2 and $F_{2\mathrm{reciprocal}}$ populations may be combined into one population the next generation.

Keywords: diallel analysis, rice length, rice shape.

1. Introduction

Rice (*Oryza sativa* L.) is one of the major food crops in the world. Nearly 50% of the world population consumes rice as the staple food therefore it has an important role in global

food security (1,2). Indonesia, is the world’s third largest rice producer and it is also one of the world’s main rice consumers (3). More than 80% of Indonesian people consumes rice as a staple food, and it contributes 62.1% of the energy intake (4). It is the main source of income of approximately 18 million household farmers (5). It is also has strategic value from economic, environmental, social and political aspects (6,7). Therefore, rice self-sufficiency in Indonesia is required to fulfil the needs.

The government's program for rice self-sufficiency has four main targets i.e. to increase the national production, to stabilize the domestic prices and reserve stocks, and to minimize imports (8). Improving yield potential of rice varieties through plant breeding plays an important role to increase national production to increase the national production. High yielding rice varieties contributed to 56% of the national rice production (6). Thus, rice breeding in Indonesia aims to develop high yielding varieties that are in accordance with ecosystem conditions, social, cultural, and community interests (9).

Yield still the main target of rice development, however rice grain quality is now getting more attention due to increasing awareness of its importance (10). Rice grain quality determines the market price, consumer acceptability of a variety and consumer acceptability of a variety and becomes the second goal of rice plant breeding after yield (11,12). High yielding varieties with high rice grain quality are easy for farmers to adopted (13).

Grain quality it consists of rice length, rice shape, rice translucency and rice chalkiness. Rice quality directly affects consumer acceptance. Consumers determine the rice quality first from grain quality i.e. rice appearance, rice length and shape, which is followed by cooking quality and taste (14,15). Hence, rice length and shape determine the level of rice market demands and price (16). Therefore, breeding rice varieties that encompass desirable rice length and shape became a major concern for rice breeders in Indonesia.

A rice breeding program begins with increasing genetic diversity by crossing rice genotypes with wide genetic differences, followed by selection of the interest. The effectiveness of plant breeding programs increases in conjunction with scientific research that expands knowledge of plant genetic information (17). An effective and efficient

breeding program is determined by the genetic information that controls the inheritance of traits under study (18,19). Sometimes selection in segregation populations result in low quality progenies to fulfill breeding objectives (20). Hence, it's necessary to know genetic information of traits before determining a breeding and selection method (21). Diallel analysis is one of the manners to obtain genetic information for grain quality traits in rice such as grain length and shape.

Diallel analysis is a mating designs which involves mating a set of parents in all possible combinations, to produce a set of F_1 progeny (22,23). This method is useful to obtain genetic information that controls the inheritance of traits under study in early generation (24,25). It's also as the quickest method for understanding the genetic control of quantitative traits inheritance (26).

Diallel analysis can be carried out using Hayman and Griffing methods. Hayman's method can be used to study of genes action, genetic components and heritability (27). Whereas, Griffing's method (28) is to used estimated general combining ability, specific combining ability and reciprocal effects. It's also can be used to calculate additive and non-additive effects. Hayman and Griffing methods are often used together for complementary data interpretation (21). Hayman and Griffing methods have been used (either one or both) to obtain genetic information of plant traits. It has been widely used to study genetic parameters of length and shape in rice (29,30,39–41,31–38). The results of the study show various conclusions. Furthermore, this research is rarely done in Indonesia (42). The present research was conducted to study genetic components of F_1 population from a cross of six parents with various rice length and shape. The purpose of this study was to estimate the genetic parameters of rice length and shape using full diallel analysis.

2. Materials and Methods

2.1. Location of the experiment

A field experiment was conducted at the experimental farm of Agriculture Faculty, Jenderal Soedirman University, Purwokerto, Central Java, Indonesia. This location is at

coordinates 7°24'28.7"LS and 109°15'13.3"N and it's at an altitude of 112 meters above sea level. The experiment was carried out from June 2019 to December 2019.

2.2. Plant material

Six rice genotypes i.e., Basmati Delta 9, Basmati Pakistan, Inpari 31, Inpago Unsoed 1, Koshihikari and Tarabas rice were used as the parents in this study. These parents have different origins and have various grain size and shape (Table 1). The research material used consisted of 36 rice genotypes which were develop from full diallel crosses among six parents. It consists of six parents, 15 F_1 and 15 $F_{1reciprocal}$.

Table 1. Six rice genotypes used for diallel mating design

No.	Genotype	Rice length and shape	Origin
1	Basmati Delta 9	Extra-long, slender	India
2	Basmati Pakistan	Extra-long, slender	Pakistan
3	Inpari 31	Long, medium	Indonesia
4	Inpago Unsoed 1	Medium, medium	Indonesia
5	Koshihikari	Short, round	Japan
6	Tarabas	Short, round	Indonesia

2.3. Experimental design

The experimental design was a randomized complete block design (RCBD) with three replications. Seeds of 36 genotype were sown in a seed box for two weeks, followed with transplanting to 35 cm x 40 cm polybags containing eight kg of inceptisol soil. Each polybag consisted of one plant per genotype. Recommendations for rice cultivation and plant protection was adopted. Fertilizer applications were 0,4 g N/ polybag and 1.0 g N-P-K/polybag was applied. Fertilizer was applied twice i.e., 10 days and 20 days after transplanting.

2.4. Data collection and analysis

At maturity, panicles were harvested from parents and all generations individually. Panicles were subjected as samples of rice length and shape. Rice shape is determined by grain length to width ratio. (43). Therefore, the observed trait in this study is rice length, width and length to width ratio. Digital caliper was used to measure the grain length and

width. Data collected was used for diallel analysis to estimate the genetic parameters of rice length and shape. Diallel analysis was performed using Hayman and Griffing method-1 (44).

1. Analysis of variance for F_1 in full-diallel crosses

Analysis of variance for F_1 in full-diallel crosses for rice length and shape followed as the statistical model $Y_{ijkl} = m + T_{ij} + b_k + (bT)_{ijk} + e_{ijkl}$ (1)

Where m is the general mean, T_{ij} is the effect of *i* x *j*th genotype, b_k is the effect of *k*th block, $(bT)_{ijk}$ is the interaction effect and e_{ijkl} is the error effect.

2. Genetic components of variation estimated

Genetic components of variation were calculated using the following formulas.

Regression coefficient of b(Wr, Vr) = $\frac{\text{Cov(Wr,Vr)}}{\text{Var(Vr)}}$ (2)

Where Wr is the covariance between parents and their off-sping, Vr is the variance of each array, Cov(Wr,Vr) is the covariance of (Wr,Vr) and Var(Vr) is the variance of Vr.

Additive genetic variance (D) = $V_{0L0} - E$ (3)

Where V_{0L0} is the variance of parents and E is the environmental variance

Dominance variance (H_1) = $V_{0L0} - 4W_{0L01} + 4V_{1L1} - (3n-2)E/n$ (4)

Where V_{0L0} is the variance of parents, W_{0L01} is the covariance between the parents and the arrays, V_{1L1} is the mean variance of the arrays, n is the number of parents and E is the environmental variance.

Proportions of positive or negative genes in the parent (H_2) = $4V_{1L1} - 4V_{0L1} - 2E$ (5)

Where V_{1L1} is the mean variance of the arrays, V_{0L1} is the variance of the mean of arrays and E is the environmental variance.

Mean covariance of additive and dominance (F) = $2V_{0L0} - 4W_{0L0} - 2(n-2)E/n$ (6)

Where V_{0L0} is the variance of parents, W_{0L01} is the covariance between the parents and the arrays, n is the number of parents and E is the environmental variance.

Dominance effect (h^2) = $4(M_{L1} – M_{L0})^2 – 4(n-1)E/n^2$ (7)

Where $(M_{L1} – M_{L0})^2$ is the difference between the mean of the parents and the mean og their n^2 progeny, n is the number of parents and E is the environmental variance.

Environmental variance (E) = $1/r$ (Error SS + Rep. SS) / $[((r – 1) + (c – 1)) x (r – 1)]$ (8)

Where Error SS is the sum square of error, Rep. SS is the sum square of replication, r is the number of replications, and c is the number of errors.

Average degree of dominance = $(H_1/D)^{1/2}$ (9)

Where H_1 is the dominance variance and D is the additive genetic variance.

The proportion of genes with positive and negative effect in the parent = $H_2/4H_1$ (10)

Where H_1 is the dominance variance and H_2 is the Proportions of positive or negative genes in the parent.

The ratio dominant and recessive gene in the parent = $[(4DH_1)^{1/2} + F]/(4DH_1)^{1/2}–F$ (11)

Where D is the additive genetic variance, H_1 is the dominance variance and F is the mean covariance of additive and dominance.

Number of gene groups = h^2/H_2 (13)

Where h^2 is the dominance effect and H_2 is the Proportions of positive or negative genes in the parent.

The coefficient correlation between (Wr+Vr) and Yr (r) = $\frac{\text{Cov (Wr+Vr),Yr}}{\sqrt{\text{Var (Wr+Yr).Var(Yr)}}}$ (15)

Where (Wr+Vr) is the parental order of dominance, Y_r is the parental measurement, Cov(Wr + Vr) is the covariance of (Wr + Vr), Var(Wr + Vr) is the variance of (Wr + Vr) and Var (Y_r) is the variance of Y_r

Broad sense heritability (h^2_{bs}) =

$(^1/_2D+^1/_2H_1–^1/_4H_2–^1/2F)/(^1/_2D+^1/_2H_1–^1/_4H_2–^1/_2F+E)$ (16)

Where D is the additive genetic variance, H_1 is the dominance variance, H_2 is the Proportions of positive or negative genes in the parent, F is the mean covariance of additive and dominance and E is the environmental variance.

Narrow sense heritability (h^2_{ns}) =

$$(^1/_2D+^1/_2H_1-^1/_2H_2-^1/2F)/(^1/_2D+^1/_2H_1-^1/_2H_2-^1/_2F+E) \qquad (17)$$

Where D is the additive genetic variance, H_1 is the dominance variance, H_2 is the Proportions of positive or negative genes in the parent, F is the mean covariance of additive and dominance and E is the environmental variance.

3. Combining ability analysis

The statistical model for analysis variance of combining ability that were used was:

$$Y_{ij} = m + g_i + g_j + S_{ij} + r_{ij} + \frac{1}{bc}\sum\sum e_{ijkl} \qquad (18)$$

Where Y_{ij} is the mean of *i* x *j*th genotype, m is the general mean, gi is the general combing ability (*gca*) effect of *i*th parent, g_j is the general combing ability (*gca*) effect of *j*th parent, S_{ij} is the interaction, *i.e.* specific combining ability effect, r_{ij} is the reciprocal effect, and $\frac{1}{bc}\sum\sum e_{ijkl}$ is the mean error effect.

General combining ability (GCA) variance (g_i) = $\frac{1}{2n}\sum(Y_{i.} + Y_{.j}) - \frac{1}{n^2}Y^2..$ (19)

Where $Y_{i.}$ is the total of mean value of *i*th genotype cross, $Y_{.j}$ is the total of mean value of *j*th genotype selfing, n is the number of parents and Y is the grand total.

Specific combining ability (SCA) variance (s_{ij}) =

$$\frac{1}{2}(Y_{ij} + Y_{ij}) - \frac{1}{2n}(Y_{i.} + Y_{.i} + Y_{j.} + Y_{.j}) + \frac{1}{n^2}Y.. \qquad (20)$$

Where Y_{ij} is the mean of *i* x *j*th genotype, Y_{ji} is the mean of *j* x *i*th genotype, $Y_{i.}$ is the total of mean value of *i*th genotype cross, $Y_{.i}$ is the total of mean value of *i*th genotype selfing, $Y_{j.}$ is the total of mean value of *j*th genotype cross, $Y_{.j}$ is the total of mean value of *j*th genotype selfing , n is the number of parents and Y is the grand total.

Reciprocal variance (r_{ij}) = $\frac{1}{2} = (Y_{ij} - Y_{ji})$ (21)

Where Y_{ij} is the mean of *i* x *j*th genotype and Y_{ji} is the mean of *j* x *i*th genotype.

3. Result and discussion

3.1. Analysis of variance for genotypes

Analysis of variance showed significantly different among genotypes for rice grain length and shape (Table 2). Similar findings were also reported by Bano and Singh (39) and Hijam et al. (37). Significantly different analysis of variance among genotypes is a requirement for estimating genetic parameters using diallel analysis (44). Thus, significance differences among the genotypes for rice length and shape indicate that they are suitable for further genetic studies.

Table 2. Analysis of variance for F_1 in a full-diallel cross for rice length and shape

Source of variation	Degrees of freedom	Mean square	
		Rice length (mm)	Rice shape
Block	2	0.06	0.01
Genotype	35	3.16 *	1.51 *
Error	70	0.04	0.02

* = significantly different at the level of 5%.

3.2. Genetic components of variation

3.2.1. Gene interaction

The values of regression coefficient of b (Wr, Vr) for rice length and shape (1.20 and 1.15, respectively) were not significantly different from one (Table 3). Similar result reported by Bano and Singh (39) for kernel length before cooking (rice length) and kernel length/breadth ratio before cooking (rice length). The value of regression of coefficient of b (Wr, Vr) may be used to determine the gene interaction of a trait. Based on t test, a significantly different value of b (Wr, Vr) from one indicates gene interaction, while a non-significantly different value of b (Wr, Vr) from one reflected no gene interaction (44). It means there is no interaction between genes controlling rice length and shape in this study.

3.2.2. Additive (D) and dominance (H1) variance

Additive (D) and dominance (H_1) variance were significantly different for rice length and shape (Table 3). Significant different values of the components D and H_1 indicated the importance of both additive and non-additive gene action in the expression of traits (45). So that, rice length and shape are influenced by both additive and non-additive types of gene action. Similar findings were also observed by Kato (29), Fu et al. (31), Daradjat & Rumanti (42) Kumar et al. (32,33), Rafii et al. (30) and Senthil Kumar & Mudhalvan (38) for rice length and size.

The results showed the value of additive variance (D) for rice length and shape is 2.72 and 1.36, respectively and the value of dominance variance (H_1) for rice length and shape is 0.26 and 0.19, respectively (Table 3). These showed that the influence of additive variance is greater than dominance variance ($D>H_1$) for rice length and shape. Higher magnitude of additive variance (D) indicated the greater role of additive gene action while *vice versa* dominance variance indicated the greater importance of non-additive gene action (40,45). The value of the additive variance which is greater than the dominance variance indicates the increasing importance of additive gene action (32,33). This means that in this study, rice length and shape are more influenced by additive gene action than non-additive gene action. These results are in accordance with the findings of Kato (29) and Thattil and Perera (46) for rice length and size. However, Daradjat & Rumanti (42) and Senthil Kumar & Mudhalvan (38) reported different results that there is an indication that the non-additive gene action was more predominant than additive gene action for rice length and size.

3.2.3. Gene distribution in the parent

Gene distribution in the parents can be were determined by H_2 values. The results showed that the H_2 values for rice length and shape were significantly different (Table 3.) This indicates that the genes determining the inheritance of rice length and shape are not evenly distributed among the parents. Genes controlling rice length and shape that are not evenly distributed in parents have also been reported (38).

Table 3. Estimates of genetic components of variation for rice length and shape

Genetic components	Rice length (mm)	Rice shape
b (Wr, Vr)	1.20 ^{ns}	1.15 ^{ns}
D	2.72 *	1.36 *
H_1	0.26 *	0.19 *
H_2	0.25 *	0.17 *
F	0.44 *	0.33 *
h^2	-0.01 ^{ns}	0.04 ^{ns}
E	0.01 ^{ns}	0.01 ^{ns}
$(H_1/D)^{1/2}$	0.31	0.38
$H_2/4H_1$	0.23	0.22
Kd/Kr	1.71	1.95
h^2/H_2	-0.03	0.22
r [(Wr+Vr),Yr]	0.69	0.89
h^2_{bs}	0.99	0.99
h^2_{ns}	0.94	0.91
Ratio of h^2_{ns}: h^2_{bs}	0.95	0.92

* = significantly different at the level of 5%, ns = not significantly different.

Proportion of positive genes to negative genes is indicated by value of H_1 component against H_2 component. The value of H_1 is greater than the H_2 indicating more positive genes than negative genes, *vice versa* the value of the H_1 is smaller than H_2 reflecting the positive are gene less than the negative genes (21,47). Table 3 showed the value of H_1 is 0.26 and 0.19, respectively and the value of H_2 is 0.27 and 0.17, respectively for rice length and shape. Its shows the value of H_1 is greater than H_2 for rice length and shape, meaning that positive genes are more involved in determining rice length and shape than negative genes. The results were agreement with that Raju et al. (40).

Proportion of positive genes to negative genes in all parents also can be seen from ratio of $H_2/4H_1$. Values lower than 0.25 indicate positive and negative genes are not present in unequal proportions in the parents (45,48). The results showed the value of $H_2/4H_1$ for rice length and shape is 0.23 and 0.22 respectively (Table 3). They were lower than 0.25, reflecting the unequal distribution of positive and negative genes in the parents. Similar findings were reported by previous studies (38–40).

3.2.4. Dominance level

The influence of dominance can be seen from the value of mean degree of dominance as estimated by $(H_1/D)^{1/2}$. A value $(H_1/D)^{1/2}$ more than 1 indicates over dominance, while a value $(H_1/D)^{1/2}$ between 0 and 1 indicates partial dominance (Hayman, 1954). Table 3 showed the value $(H_1/D)^{1/2}$ of the rice length and shape is less than 1 (0.31 and 0.38, respectively) indicated existence of partial dominance in these traits. Rice length controlled by a partial dominance gene was also reported by Kato (29).

3.2.5. Dominance effect

Dominance effect is indicated by the h^2 value. Table 3 showed that h^2 values were not significantly different for rice length and shape. This indicated no difference in average deviation of F_1 from most parents (47).

3.2.6. Environmental variance

Table 3 showed that environmental variance exhibited no significant influence on rice length and shape. This reflected no influence of environmental factor on the expression of the traits studied (45). Therefore, it is known that expression of rice length and shape are more influenced by genetic than environment effects.

3.2.7. Proportion of dominant gene to recessive gene

Proportion of dominant genes to recessive genes is shown by F component and Kd/Kr ratio. The positive value of F component reflects a greater number of dominant genes than recessive genes in the parent (47,49). A ratio of Kd/Kr greater than one indicating more dominant genes in the parent, conversely, the ratio of Kd/Kr smaller than one indicated more recessive genes in the parent (44). The results showed a positive value of F component and a ratio of Kd/Kr of the rice length and shape is greater than one (1.71 and 1.95, respectively) (Table 3.), which indicated more dominant genes in the parent for rice length and shape. The same finding was reported by Raju et al. (40).

3.2.8. Number of gene groups

Component of h^2/H_2 gives an indication of the number of gene groups that control a trait. The h_2/H_2 values of rice length and shape are -0.03 and 0.22, respectively, lower than one. The ratio smaller than one indicated the involvement of single gene or one group of genes which are responsible for their genetic control (45). As a result, rice length and shape are controlled by at least a single group of genes.

3.2.9. Direction and order of dominance

The positive value of the correlation between (Wr + Vr) and Yr and close to unity, indicates that dominant alleles have predominantly negative effects, i.e., act in the direction of lower yields (50). A positive value is obtained in the correlation (Wr+Vr) and Yr for rice length and shape (Table 3). That is, in rice length and shape, the dominant genes cause the rice to be short and round.

The direction and order of dominance can be seen in the value (Wr+Vr) component. Based on the value (Wr+Vr) in Table 4 the dominance order of rice grain length and shape was Inpago Unsoed 1, Koshihikari, Tarabas, Basmati Delta 9 and Basmati Pakistan. This is reinforced by the graph of the relationship between the covariance (Wr) and variance (Vr) in Figure 1 and 2.

Distribution of parental array points along the regression line reflected genetic diversity of a trait (51). The array point was scattered along the regression line for rice length and shape, indicating genetic diversity for these traits. The position of the parents on the graph of the relationship between the covariance (Wr) and variance (Vr) reflects the order of dominance. The position of parent which is closer to zero indicating it contains most dominant genes, vice versa farther away a parent position to zero reflecting it contains more recessive genes (47,50). Inpago Unsoed 1 is the closest to zero, reflecting that this parent has the mostly dominant genes for rice length and shape. Basmati Pakistan contain most a recessive gene for the rice length and shape since it is the farthest from zero. Basmati which has extra-long and slender rice contains the most recessive gene, this means that the gene controlling long and slender rice is recessive to the short and round rice gene. This result agreement with finding of Kato (29), Murai & Kinoshita (41) and Ali et al. (52).

Tabel 4. The value (Wr+Vr) of rice length and shape

Genotypes	Rice length	Rice shape
Basmati Delta 9	2,32	1,30
Basmati Pakistan	2,46	1,43
Inpari 31	1,99	0,93
Inpago Unsoed 1	1,00	0,37
Koshihikari	1,75	0,69
Tarabas	1,87	0,73

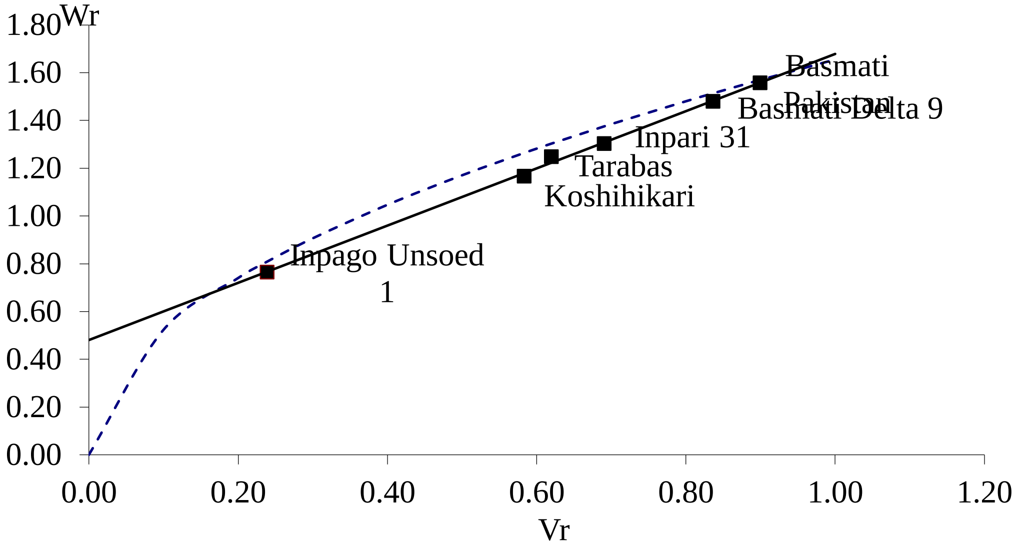

Figure 1. Covariance (Wr) and variance (Vr) graph of rice length.

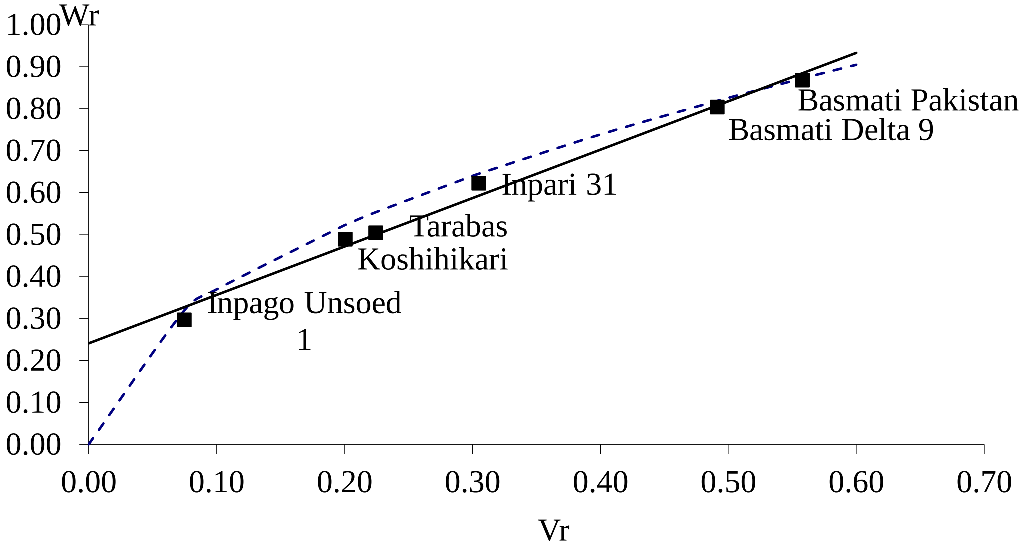

Figure 2. Covariance (Wr) and variance (Vr) graph of rice shape.

The straight line intercepted the vertical axis (Wr) above the origin for rice length and shape (Figure 1 and 2). The straight line intercepted the vertical axis (Wr) above the origin indicated the indicating partial dominance of the genes controlling a trait (21,50,51). This reveals that the rice length and shape was controlled by a partial dominant gene as described previously. Partial dominance results in the appearance of each trait having a tendency to approach the mid parent value and not having over dominance which exceeds the best parent (53). This is reflected in the h^2 value of rice length and shape which is not significantly different so that there is no difference between the F_1 average and the parents' average.

3.2.10. Heritability

Broad sense heritability (h^2_{bs}) estimates for rice length and shape are similar, 0,99. Narrow sense heritability (h^2_{ns}) estimates for these traits is 0.94 and 0.91, respectively (Table 3.). Heritability values more than 0.5 are categorized as high (Stansfield, 1991), thus broad sense heritability (h^2_{bs}) for rice length and shape categorized as high heritability. Similar findings were reported by previous studies (54)

The estimated value of broad sense heritability indicates the relative contribution of genetic factors to variation of the observed trait (55). A high broad sense heritability value indicates that traits are more influenced by genetic than environmental factors (56). In this study, broad sense heritability estimate of rice length and shape is high, indicating the influence of genetic was greater than environmental factors. Low influence of environmental factors were also reflected in the non-significant environmental variance observed in Table 3.

Narrow sense heritability estimates indicate the role of additive gene action on a trait. High estimated of narrow sense heritability indicates more additive gene action than non-additive gene action (4,57–59). In this study, the narrow sense heritability estimate of rice length and shape was high, meaning that additive gene action played a more important role than non-additive gene action.

Ratio of narrow sense heritability and broad sense heritability reflecting the role of additive and non-additive gene action for a trait. The ratio value closer to one indicates the total genetic variance of a trait is caused by additive gene action (60). Table 3 showed ratio of narrow sense heritability and broad sense heritability ratios are 0.95 for rice length and 0.92 for rice shape respectively. This indicating that additive gene action determines the rice size and shape more than non-additive gene action as previously described. Traits that have high additive variance and heritability in the F_1 population may be selected using individual selection. Individual selection may be applied to traits that have additive variance and high heritability in the F_1 population (21) so that selection of rice length and shape may be carried out using individual selection such as pedigree. This finding agreement with Raju et al. (40).

3.3. Combining ability estimation of rice length and shape

Gene action and cytoplasm influence of the female parent for a trait can be predicted through combining ability. Variances of general combining ability (GCA), specific combining ability (SCA), and reciprocals were obtained from diallel analysis of Griffing method-1. GCA and SCA variance are associated with non-additive and additive gene action, respectively (61–63). Reciprocal variance is useful for knowing the effect of female parent cytoplasm of a trait (64).

General combining ability (GCA) is endorsed to additive gene action and specific combining ability (SCA) is mainly attributed to non-additive gene action (59,65). This study showed significant GCA and SCA effects of rice length and shape (Table 4). The significant GCA and SCA indicated the importance of both additive and non-additive gene actions in the expression of these traits. This finding was in agreement with Singh et al. and Soni et al. (66,67).

The magnitude of the effect of additive gene action and non-additive gene action on a trait can be determined from GCA:SCA ratio (68). A high GCA:SCA ratio indicates that additive gene action plays a more important role in the expression of a trait than non-additive gene action (69). Ratio of GCA:SCA greater than one indicates that additive gene action has more influence on the expression of a trait and conversely, a GCA:SCA ratio less than one

reflected that non-additive gene action has more influence on the expression of a trait (70). In this study, ratio of GCA:SCA of rice length and shape is greater than one (50.060 and 32.280, respectively) (Table 4), indicating additive gene action is more influential than non-additive gene action on the expression of these traits. These results agree with the estimation of gene action using the Hayman method as described previously. Additive gene action in grain length and shape has been previously reported (66,67). Therefore, the selection for grain length and shape will be effective using pedigree method (71).

Table 4. Analysis of variance of combining ability and GCA:SCA ratio of rice length and shape

Source of variance	Degree of freedom	Mean square	
		Rice length	Rice shape
General combining ability (GCA)	5	6.909 *	3.154 *
Specific combining ability (SCA)	15	0.138 *	0.092 *
Reciprocal	15	0.020 ^{ns}	0.006 ^{ns}
Error	70	0.015	0.007
GCA:SCA ratio		50.060	34.280

* = significantly different at the level of 5%, ns = not significantly different

Non-significant reciprocal effects were observed for both rice length and shape (Table 4). This indicated that there was no influence of the female parent cytoplasm on the inheritance of these traits (64,72). So that, the size and shape of the rice are not affected by the female parent cytoplasm.

4. CONCLUSION

The influence of additive and non-additive gene action on rice length and shape were confirmed. The effect of the additive gene action was greater than the non-additive gene action while both broad sense and narrow sense heritability were high. This revealed that that the selection of these traits at the early generation using the pedigree selection method may be considered. Rice length and shape were not affected by the female parent cytoplasm so that F_2 and $F_{2reciprocal}$ populations might be combined into one population in the next selection generation.

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6. DAFTAR PUSTAKA

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Variable: rice length (mm)

Parent	Basmati Delta 9	Basmati Pakistan	Inpari 31	Inpago Unsoed 1	Koshihikari	Tarabas
Basmati Delta 9	8.68	8.94	7.77	7.17	6.99	7.56
Basmati Delta 9	9.24	8.96	8.92	7.02	7.20	6.93
Basmati Delta 9	8.91	8.91	8.02	7.22	7.18	7.24
Basmati Pakistan	8.93	8.71	7.75	6.95	6.96	6.97
Basmati Pakistan	8.77	8.83	7.75	7.16	6.80	6.90
Basmati Pakistan	8.82	8.87	7.67	7.23	6.85	6.93
Inpari 31	7.27	7.87	6.59	6.19	6.35	5.99
Inpari 31	7.85	7.81	6.75	6.21	6.80	5.95
Inpari 31	8.30	6.98	6.71	6.15	6.57	5.97
Inpago Unsoed 1	6.98	6.96	6.01	6.05	5.89	6.15
Inpago Unsoed 1	7.06	6.84	6.26	6.06	6.06	6.28
Inpago Unsoed 1	7.08	7.09	6.10	6.06	6.00	6.29
Koshihikari	7.00	6.52	6.58	6.62	5.49	5.30
Koshihikari	7.21	6.80	6.51	6.00	5.50	5.26
Koshihikari	6.88	6.82	6.56	6.06	5.12	5.16
Tarabas	6.44	7.03	5.69	6.16	5.12	5.23
Tarabas	6.90	6.72	6.04	6.03	5.23	5.18
Tarabas	7.01	6.99	5.87	6.04	5.22	5.25

Variable: rice shape (length:wide ratio)

Parent		Basmati Delta 9	Basmati Pakistan	Inpari 31	Inpago Unsoed 1	Koshihikari	Tarabas
Basmati Delta 9	A	4.07	4.32	3.32	2.95	2.79	2.95
Basmati Delta 9	A	4.34	4.22	4.21	2.93	2.86	2.81
Basmati Delta 9	A	4.21	4.27	3.51	2.99	2.86	2.88
Basmati Pakistan	B	4.36	4.46	3.54	2.92	2.91	2.83
Basmati Pakistan	B	4.23	4.46	3.54	3.05	2.83	2.87
Basmati Pakistan	B	4.25	4.52	3.48	2.89	2.85	2.85
Inpari 31	C	3.28	3.73	2.94	2.48	2.63	2.23
Inpari 31	C	3.42	3.62	2.99	2.50	2.71	2.24
Inpari 31	C	3.71	3.03	2.90	2.45	2.65	2.31
Inpago Unsoed 1	D	2.84	2.93	2.42	2.27	2.20	2.50
Inpago Unsoed 1	D	2.42	2.88	2.51	2.35	2.30	2.57
Inpago Unsoed 1	D	2.92	3.01	2.41	2.36	2.27	2.46
Koshihikari	E	2.49	2.64	2.63	2.44	1.97	1.77
Koshihikari	E	2.89	2.81	2.45	2.26	1.98	1.77
Koshihikari	E	2.74	2.85	2.54	2.26	1.68	1.75
Tarabas	F	2.61	2.84	2.20	2.50	1.92	1.79
Tarabas	F	2.86	2.70	2.22	2.42	1.78	1.78
Tarabas	F	2.98	2.83	2.23	2.40	1.75	1.80

Response to Reviewers

thank you for the review

the article has been corrected according to the suggestions

Thank you

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DIALLEL ANALYSIS OF RICE LENGTH AND SHAPE USING HAYMAN AND GRIFFING METHOD

--Manuscript Draft--

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DIALLEL ANALYSIS OF RICE LENGTH AND SHAPE USING HAYMAN AND GRIFFING METHOD

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Abstract

Rice length and shape are important physical qualities that determine public acceptance of a variety and determine the price. Improvement of rice length and shape requires information on the genetic parameters of these traits. Diallel analysis is one of the methods usually used to estimate the genetic parameters of a trait. The purpose of this study was to estimate the genetic parameters of rice length and shape using full diallel analysis. The plant material used was a full diallel cross population of six rice genotypes, namely Basmati Pakistan, Basmati Delta 9, Inpago Unsoed 1, Inpari 31, Koshihikari and Tarabas. Thirty-six genotypes consisting of parents, F_1 and $F_{1\ \mathrm{reciprocal}}$ were planted using a randomized block design with three replications. The data of rice grain length and length:width ratio was used for diallel analysis using the Hayman and Griffing method-1. The results showed additive and non-additive genes action influencing the rice length and shape. The effect of the additive gene action is greater than the non-additive gene action and the heritability value, both broad sense and narrow sense heritability is high, revealed the selection of these traits at the early generation using the pedigree selection method may be considered. Rice length and shape were not affected by the female parent cytoplasm so that F_2 and $F_{2\mathrm{reciprocal}}$ populations may be combined into one population the next generation.

Keywords: diallel analysis, rice length, rice shape.

1. Introduction

Rice (*Oryza sativa* L.) is one of the major food crops in the world. Nearly 50% of the world population consumes rice as the staple food therefore it has an important role in global

food security (1,2). Indonesia, is the world's third largest rice producer and it is also one of the world's main rice consumers (3). More than 80% of Indonesian people consumes rice as a staple food, and it contributes 62.1% of the energy intake (4). It is the main source of income of approximately 18 million household farmers (5). It is also have strategic value from economic, environmental, social and political aspects (6,7). Therefore, rice self-sufficiency in Indonesia is required to fulfil the needs.

The government's program for rice self-sufficiency has four main targets i.e. to increase the national production, to stabilize the domestic prices and reserve stocks, and to minimize ~~the~~ import (8). Improving yield potential of rice varieties through plant breeding ~~has been an important component~~ ~~of~~ increase the national production. High yielding rice varieties contributed to 56% of the national rice production (6). Thus, rice breeding in Indonesia ~~is aimed intended for development~~ high yielding varieties that are in accordance with ecosystem conditions, social, cultural, and community interests (9).

Yield still the main target of rice development, however rice grain quality is now getting more attention due to increasing awareness of its importance (10). Rice grain quality determines the ~~price level of rice in the market~~, consumer ~~acceptance~~ of a variety and becomes the second goal of rice plant breeding after ~~high~~ yield~~ing~~ (11,12). High yielding varieties with high rice grain quality are easy for farmers to adopted (13).

Grain quality ~~is one of the rice qualities and it~~ consists of ~~the~~ rice length, rice shape, rice translucency and rice chalkiness. Rice quality directly affects consumer acceptance. Consumers determine the rice quality first from grain quality i.e. rice appearance, rice length and shape, ~~after that consumer determine~~ cooking quality and taste (14,15). Hence, rice length and shape determine the level of rice market demands and price (16). Therefore, breeding rice varieties that encompass desirable rice length and shape ~~become one of~~ major concern for rice breeders in Indonesia.

Rice breeding program begins with increasing genetic diversity ~~may be increased~~ by crossing ~~between~~ rice genotypes with wide genetic difference, followed by selection of the interest. The effectiveness of plant breeding programs increases in conjunction with scientific research that expands knowledge of plant genetic information (17). Effective and efficient breeding program determined by the genetic information that controls the inheritance of traits under study (18,19). Sometime selection ~~after crossing~~ in segregation population result in low quality progenies to fulfill breeding objectives (20). Hence, it's necessary to know genetic information of traits before determining breeding and selection method (21). Diallel analysis Is one of the manners to obtain genetic information for grain quality traits in rice such as grain length and shape.

Diallel analysis is mating design~~s~~ which involves mating a set of parents in all possible combinations, to produce a set of F_1 progeny (22,23). This method is useful to obtain genetic information that controls the inheritance of traits under study in early generation (24,25). It's also as the quickest method for understanding the genetic control of quantitative trait~~s~~ inheritance (26).

Diallel analysis can be carried out using Hayman and Griffing method. Hayman's method can be used to study ~~of~~ gene~~s~~ action, genetic components and heritability (27). Whereas, ~~utilized~~ Griffing method (28) is to estimated general combining ability, specific combining ability and reciprocal effect. It's also can be used to calculate additive and non-additive effects. Hayman and Griffing method are often used together for complementary data interpretation (21). Hayman and Griffing method have been used (either one or both) ~~for~~ obtain genetic information of plant traits. It has been widely used ~~for~~ study genetic parameters of length and shape in rice (29–41). The results of the study show various conclusions. Furthermore, this research is rarely done in Indonesia (42). The present research was conducted to ~~genetic~~ study of F_1 population from a cross of six parents with various rice length and shape. The purpose of this study was to estimate the genetic parameters of rice length and shape using full diallel analysis.

2. Materials and Methods

2.1. Location of the experiment

A field experiment was conducted at experimental farm of Agriculture Faculty, Jenderal Soedirman University, Purwokerto, Central Java, Indonesia. This location is at coordinates

7°24'28.7"LS and 109°15'13.3"N and it’s at an altitude of 112 meters above sea level. The experiment was carried out from June 2019 to December 2019.

2.2. Plant material

Six rice genotypes i.e., Basmati Delta 9, Basmati Pakistan, Inpari 31, Inpago Unsoed 1, Koshihikari and Tarabas rice used as the parent in this study. These parents have different origins and have various grain size and shape (Table 1). The research material used ~~was~~ thirty-six rice genotypes from full diallel crosses among six parents. It consists of 6 parents 15 F_1 and 15 $F_{1reciprocal}$.

Table 1. Six rice genotypes used for diallel mating design

No.	Genotype	Rice length and shape	Origin
1	Basmati Delta 9	Extra-long, slender	India
2	Basmati Pakistan	Extra-long, slender	Pakistan
3	Inpari 31	Long, medium	Indonesia
4	Inpago Unsoed 1	Medium, medium	Indonesia
5	Koshihikari	Short, round	Japan
6	Tarabas	Short, round	Indonesia

2.3. Experimental design

The ~~experiment~~ design~~ed~~ ~~in~~ a randomized complete block design (RCBD) with 3 replications. Seeds of 36 genotype were sown in a seed box for 2 weeks, followed ~~with~~ transplanted to 35 cm x 40 cm ~~polybag~~ containing 8 kg of inceptisol soil. Each polybag ~~consists~~ of 1 plant. Recommendations for rice cultivation and plant protection was adopted. Fertilizer applications were 0,4 g N/ polybag dan 1.0 g N-P-K/polybag was applied. Fertilizer ~~is~~ applied twice i.e., 10 ~~day~~ and 20 days after transplanting.

2.4. Data collection and analysis

At maturity, panicles were harvested from parents and all generations individually. Panicles were subjected as samples of rice length and shape. Rice shape is determined by grain length to width ratio. (43). Therefore, the observed trait in this study is rice length, width and length to width ratio. Digital caliper was used to measure the grain length and width. Data collected was used for diallel analysis to ~~estimation of~~ genetic parameters of rice length and shape. Diallel analysis performed using Hayman and Griffing method-1 (44) ~~as follows~~.

1. Analysis of variance for F_1 in full-diallel crosses

Analysis of variance for F_1 in full-diallel crosses for rice length and shape ~~follow as~~ the statistical model $Y_{ijkl} = m + T_{ij} + b_k + (bT)_{ijk} + e_{ijkl}$ (1)

2. Genetic components of variation estimated

Genetic components of variation calculated ~~by~~ formula ~~follow as~~.

Regression coefficient of b(Wr, Vr) = $\frac{\mathrm{Cov(Wr,Vr)}}{\mathrm{Var(Vr)}}$ (2)

Additive genetic variance (D) = V0L0 – E (3)

Dominance variance (H_1) = $V_{0L0} - 4W_{0L1} + 4V_{1L1} - (3n-2)E/n$ (4)

Proportions of positive or negative genes in the parent (H_2) = $4V_{1L1} - 4V_{0L1} - 2E$ (5)

Mean covariance of additive and dominance (F) = $2V_{0L0} - 4W_{0L0} - 2(n-2)E/n$ (6)

Dominance effect (h^2) = $4(M_{L1} - M_{L0})^2 - 4(n-1)E/n^2$ (7)

Environmental variance (E) = 1/r (Error SS + Rep. SS] / [(r – 1) + (c – 1) (r – 1)] (8)

Average degree of dominance = $(H_1/D)^{1/2}$ (9)

The proportion of genes with positive and negative effect in the parent = $H_2/4H_1$ (10)

The ratio dominant and recessive gene in the parent = $[(4DH_1)^{1/2} + F]/(4DH_1)^{1/2}–F$ (11)

Number of gene groups = h^2/H_2 (13)

The coefficient correlation between (Wr+Vr) and Yr (r) = $\frac{\mathrm{Cov\ ((Wr+Vr),Yr}}{\sqrt{\mathrm{Var\ (Wr+Yr).Var(Yr)}}}$ (15)

Broad sense heritability (h^2_{bs}) =

$(^1/_2D+^1/_2H_1-^1/_4H_2-^1/2F)/(^1/_2D+^1/_2H_1-^1/_4H_2-^1/_2F+E)$ (16)

Narrow sense heritability (h^2_{ns}) =

$(^1/_2D+^1/_2H_1-^1/_2H_2-^1/2F)/(^1/_2D+^1/_2H_1-^1/_2H_2-^1/_2F+E)$ (17)

3. Combining ability analysis

The statistical model for analysis variance of combining ability ~~follows as~~.

$Y_{ij} = m + g_i + g_j + S_{ij} + r_{ij} + \frac{1}{bc}\sum\sum e_{ijkl}$ (18)

General combining ability (GCA) variance (g_i) = $\frac{1}{2n}\sum(Y_{i.} + Y_{.j}) - \frac{1}{n^2}Y^2..$ (19)

Specific combining ability (SCA) variance (s_{ij}) =

$\frac{1}{2}(Y_{ij} + Y_{ij}) - \frac{1}{2n}(Y_{i.} + Y_{.i} + Y_{j.} + Y_{.j}) + \frac{1}{n^2}Y..$ (20)

Reciprocal variance (r_{ij}) = $\frac{1}{2} = (Y_{ij} - Y_{ji})$ (21)

3. Result and discussion

3.1. Analysis of variance for genotypes

Analysis of variance showed significantly different among genotypes for rice grain length and shape (Table 2). Similar findings were also reported by Bano and Singh (31) and Hijam et al. (40). Significantly different analysis of variance among genotypes is a requirement for estimating genetic parameters using diallel analysis (44). Thus, significance differences among the genotypes for rice length and shape indicate that they are suitable for further genetic studies.

Table 2. Analysis of variance for F_1 in a full-diallel cross for rice length and shape

Source of variation	Degree of freedom	Mean square	
		Rice length (mm)	Rice shape
Block	2	0,06	0,01
Genotype	35	3,16 *	1,51 *
Error	70	0,04	0,02

* = significantly different at the level of 5%.

3.2. Genetic Components of Variation

3.2.1. Gene interaction

The values of regression coefficient of b (Wr, Vr) for rice length and shape were not significantly different from one (Table 3). Similar result reported by Bano and Singh (31). The value of regression of coefficient of b (Wr, Vr) may be used to determine the gene interaction of a trait. Based on t test, significantly different value of b (Wr, Vr) from one indicates gene interaction, ~~and not~~ significantly different value of b (Wr, Vr) from one reflected no gene interaction (44). It means there is no interaction between genes ~~in~~ controlling ~~of~~ rice length and shape in this study.

3.2.2. Additive (D) and dominance (H1) variance

Additive (D) and dominance (H_1) variance were significantly different for rice length and shape (Table 3). Significant different values of the components D and H_1 indicated the importance of both additive and non-additive gene action in the expression of traits (45). So that, rice length and shape are influenced by both additive and non-additive types of gene action. ~~The similar~~ findings were also observed by Kato (29), Fu et al (34), Daradjat & Rumanti (42) Kumar et al (35,36), Rafii et al (30) and Senthil Kumar & Mudhalvan (41)

The influence of additive variance is greater than dominance variance ($D>H_1$) for rice length and shape (Table 3). Higher magnitude of additive variance (D) indicated the greater role of additive gene action while *vice versa* dominance variance indicated the greater importance of non-additive gene action (32,45). The value of the additive variance which is greater than the dominance variance indicates the increasing importance of additive gene action (35,36). This means that in this study, rice ~~grain~~ and shape are more influenced by additive gene action ~~more~~ than non-additive gene action. These results are in accordance with the findings of Kato (29) and Thattil and Perera (46). However, Daradjat & Rumanti (42) and Senthil Kumar & Mudhalvan (41) reported different results that there is an indication that the non-additive gene action more predominant than additive gene action.

Table 3. Estimates of genetic components of variation for rice length and shape

Genetic components	Rice length (mm)	Rice shape
b (Wr, Vr)	1,20 ^{ns}	1,15 ^{ns}
D	2,72 *	1,36 *
H_1	0,26 *	0,19 *
H_2	0,25 *	0,17 *
F	0,44 *	0,33 *
h^2	-0,01 ^{ns}	0,04 ^{ns}
E	0,01 ^{ns}	0,01 ^{ns}
$(H_1/D)^{1/2}$	0,31	0,38
$H_2/4H_1$	0,23	0,22
Kd/Kr	1,71	1,95
h^2/H_2	-0,03	0,22
r [(Wr+Vr),Yr]	0,69	0,89
h^2_{bs}	0,99	0,99
h^2_{ns}	0,94	0,91
Ratio of h^2_{ns}: h^2_{bs}	0,95	0,92

* = significantly different at the level of 5%, ns = not significantly different.

3.2.3. Gene distribution in the parent

Gene distribution in the parents ~~can be~~ ~~determine~~ by H_2 values. The results showed that the H_2 values for rice length and shape were significantly different (Table 3.) This indicates that the genes determining the inheritance of rice length and shape are not evenly distributed among the parents. Genes controlling rice length and shape that are not evenly distributed in parents have also been reported (41).

Proportion of positive genes to negative genes is indicated by value of H_1 component against H_2 component. The value of H_1 is greater than the H_2 indicating more positive genes than negative genes, *vice versa* the value of the H_1 is smaller than H_2 reflecting the positive gene less than the negative ~~gene~~ (21,47). Table 3 shows the value of H_1 greater than H_2 for ~~the~~ rice length and shape, meaning that positive genes are more involved in determining ~~the~~ rice length and shape than negative genes. The ~~result~~ were agreement with that Raju et al. (32).

Proportion of positive genes to negative genes in all parents also can be seen from ratio of $H_2/4H_1$. Values lower than 0.25 indicate positive and negative genes are not present unequal proportions in the parents (45,48). The results showed the value of $H_2/4H_1$ for rice length and shape is 0.23 and 0.22 respectively (Table 3). ~~it was~~ lower than 0.25, reflecting the unequal distribution of positive and negative genes in the parents. Similar findings were reported by previous studies (31,32,41).

3.2.4. Dominance level

The influence of dominance can be seen from the value of mean degree of dominance as estimated by $(H_1/D)^{1/2}$. A value $(H_1/D)^{1/2}$ more than 1 indicates over dominance, while a value $(H_1/D)^{1/2}$ between 0 and 1 indicates partial dominance (Hayman, 1954). Table 3. shows the value $(H_1/D)^{1/2}$ of the rice length and shape is less than 1, indicated existence of partial dominance in these traits. Rice length controlled by a partial dominance gene was also reported by Kato (29).

3.2.5. Dominance effect

Dominance effect ~~indicating~~ by h^2 value. Table 3~~.~~ ~~shows~~ that h^2 values were not significantly different for rice length and shape. This ~~is~~ ~~indicating~~ no difference average deviation of F_1 from most ~~parent~~ (47).

3.2.6. Environmental variance

Table 3 showed environmental variance exhibited no significant~~ly~~ for rice length and shape. This ~~is~~ reflected no influence of environmental ~~factor for~~ the expression of the traits studied (45). Therefore, it is known that expression of rice length and shape more ~~influence~~ by genetic than ~~those of~~ environment.

3.2.7. Proportion of dominant gene to recessive gene

Proportion of dominant genes to recessive genes is shown by F component and Kd/Kr ratio. The positive value of F component reflects a greater number of dominant genes than recessive genes in the parent (47,49). ~~The~~ ratio of Kd/Kr greater than one ~~indicating~~ more dominant genes in the parent, ~~conversely, the~~ ratio of Kd/Kr smaller than one ~~indicates~~ more recessive genes in the parent (44). The results showed a positive value of F component and a ratio of Kd/Kr greater than one (Table 3.), indicated more dominant genes in the parent for rice length and shape. The same finding was reported by Raju et al. (32).

3.2.8. Number of gene groups

Component of h^2/H_2 ~~indicating~~ number of gene groups that control a trait. The h_2/H_2 values of rice length and shape are -0.03 and 0.22, respectively, lower than one. The ratio smaller than one indicated the involvement of single gene or one group of genes which are responsible for their genetic~~ally~~ control (45). ~~It means~~ rice length and shape are controlled by at least single group of genes.

3.2.9. Direction and order of dominance

The positive value of the correlation between (Wr + Vr) and Y r and close to unity, indicates that dominant alleles have predominantly negative effects, i.e., act in the direction of lower yields (50). A positive value is obtained in the correlation (Wr+Vr) and Yr for rice length and shape (Table 3). That is, in rice length and shape, the dominant genes cause the rice to be short and round.

The direction and order of dominance can be seen in the value (Wr+Vr) component. Based on the value (Wr+Vr) in Table 4 ~~it can be seen that~~ the dominance order of rice grain length and shape was Inpago Unsoed 1, Koshihikari, Tarabas, Basmati Delta 9 and Basmati Pakistan. This is reinforced by the graph of the relationship between the covariance (Wr) and variance (Vr) in Figure 1 and 2.

Distribution of parental array points along the regression line reflected genetic diversity of a trait (51). The array point was scattered along the regression line for rice length and shape, indicating genetic diversity for these traits. The position of the parents on the graph of the relationship between the covariance (Wr) and variance (Vr) reflects the order of dominance. The position of parent which is closer to zero indicating it contains most dominant genes, vice versa farther away a parent position to zero reflecting it contains more recessive genes (47,50). Inpago Unsoed 1 is the closest to zero, reflecting that this parent has the mostly dominant genes for rice length and shape. Basmati Pakistan contain most a recessive gene for the rice length and shape since it is the farthest from zero. Basmati which has extra-long and slender rice contains the most recessive gene, this means that the gene controlling long and slender rice is recessive to the short and round rice gene. This result agreement with finding of Kato (29), Murai & Kinoshita (33) and Ali et al. (52).

Tabel 4. The value (Wr+Vr) of rice length and shape

Genotypes	Rice length	Rice shape
Basmati Delta 9	2,32	1,30
Basmati Pakistan	2,46	1,43
Inpari 31	1,99	0,93
Inpago Unsoed 1	1,00	0,37
Koshihikari	1,75	0,69
Tarabas	1,87	0,73

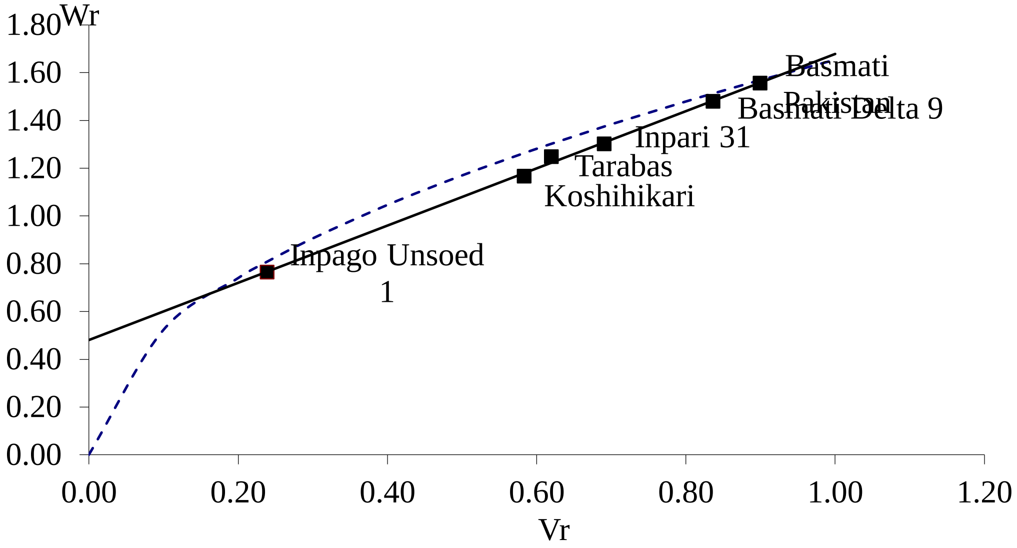

Figure 1. Covariance (Wr) and variance (Vr) graph of rice length.

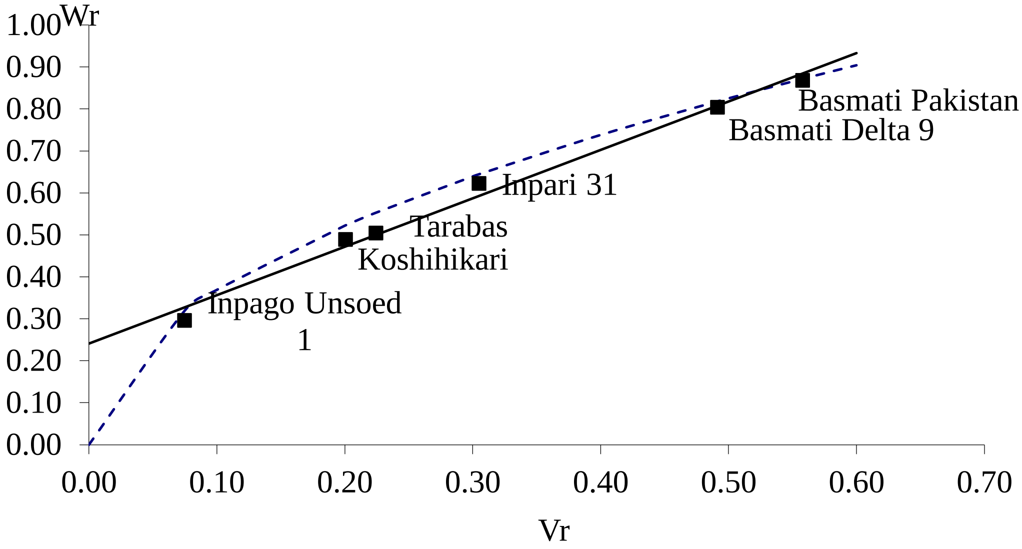

Figure 2. Covariance (Wr) and variance (Vr) graph of rice shape.

The straight line intercepted the vertical axis (Wr) above the origin for rice length and shape (Figure 1 and 2). The straight line intercepted the vertical axis (Wr) above the origin indicated the indicating partial dominance of the genes controlling a trait (21,50,51). This reveals that the rice length and shape was controlled by a partial dominant gene as described previously. Partial dominance results in the appearance of each trait having a tendency to approach the mid parent value and not ~~being~~ having over domina which exceeds the best parent (53). This is reflected in the h^2 value of rice length and shape which is not significantly different so that there is no difference between the F_1 average and the parents' average.

3.2.10. Heritability

Broad sense heritability (h^2_{bs}) estimates for rice length and shape are similar, 0,99. Narrow sense heritability (h^2_{ns}) estimates for these traits is 0.94 and 0.91, respectively (Table 3.). Heritability values more than 0.5 are categorized as high (Stansfield, 1991), thus broad sense heritability (h^2_{bs}) for rice length and shape categorized as high heritability. Similar findings were reported by previous studies (54)

The estimated value of broad sense heritability ~~indicating~~ the relative contribution of genetic factors to variation of observed trait (55). high broad sense heritability value indicates that traits are more influenced by genetic than environmental factors (56). In this study, broad sense heritability estimate of rice length and shape is high, indicating the influence of genetic was greater than environmental factors. Low influence of environmental factors also indicated by not significantly different of environmental variance (E) as described previously (Table 3.).

Narrow sense heritability estimates indicate the role of additive gene action on a trait. High estimated of narrow sense heritability indicates more additive gene action than non-additive gene action (4,57–59). In this study, the narrow sense heritability estimate of rice length and shape was high, meaning that additive gene action played a more important role than non-additive gene action.

Ratio of narrow sense heritability and broad sense heritability reflecting the role of additive and non-additive gene action for a trait. The ratio value closer to one indicates the total genetic variance of a trait is caused by additive gene action (60). Table 3 shows ratio of narrow sense heritability and broad sense heritability ratios are 0.95 for rice length and 0.92 for rice shape respectively. This indicating that additive gene action determines the rice size and shape more than non-additive gene action as previously described. Traits that have high additive variance and heritability in the F_1 population may be selected using individual selection. Individual selection may be applied to traits that have additive variance and high heritability in the F_1 population (21) so that selection of rice length and shape may be carried out using individual selection such as pedigree. This finding agreement with Raju et al. (32).

3.3. Combining ability estimation of rice length and shape

Gene action and ~~influence of cytoplasm female parent~~ for a trait can be predicted through combining ability. ~~Variance~~ of general combining ability (GCA), specific combining ability (SCA), and ~~reciprocal~~ were obtained from diallel analysis of Griffing ~~approach~~ method-1. GCA and SCA variance, ~~which is~~ associated with non-additive and additive gene action, respectively (61–63). Reciprocal variance is useful for knowing the effect of female parent cytoplasm of a trait (64).

General combining ability (GCA) is endorsed to additive gene action and specific combining ability (SCA) ~~usually attributable for~~ non-additive gene action (59,65). This study ~~shows~~ ~~mean square of~~ GCA and SCA of rice length and shape ~~is significantly different~~ (Table 4). The significant GCA and SCA indicated the importance of both additive and non-additive gene actions in the expression of these ~~characters~~ traits. This finding agreement with ~~V.~~ Singh et al. and Soni et al. (66,67).

Table 4. Analysis of variance of combining ability and GCA:SCA ratio of rice length and shape

Source of variance	Degree of freedom	Mean square	
		Rice length	Rice shape
General combining ability (GCA)	5	6,909 *	3,154 *
Specific combining ability (SCA)	15	0,138 *	0,092 *
Reciprocal	15	0,020 ^{ns}	0,006 ^{ns}
Error	70	0,015	0,007
GCA:SCA ratio		50,06	34,28

* = significantly different at the level of 5%, ns = not significantly different

The magnitude of the effect of additive gene action and non-additive gene action on a trait can be determined from GCA:SCA ratio (68). A high GCA:SCA ratio indicates that additive gene action plays a more important role in the expression of a trait than non-additive gene action (69). Ratio of GCA:SCA greater than one indicates that additive gene action has more influence on the expression of a trait and conversely, a GCA:SCA ratio less than one

reflected that non-additive gene action has more influence on the expression of a trait (70). In this study, ratio of GCA:SCA of rice length and shape is greater than one (Table 4), indicating additive gene action is more influential than non-additive gene action on the expression of these traits. These results are in agreement with the estimation of gene action using the Hayman method as described previously. Grain length and shape more influence by additive ~~gen~~ action already reported (66,67). Therefore, the selection for grain length and shape will be effective using pedigree method (71).

Reciprocal mean square of rice length and shape has no significant difference (Table 4). ~~Reciprocal variance was not significantly different, indicating~~ that there was no influence of the female parent cytoplasm ~~of~~ the inheritance of ~~a trait~~ (64,72). So that, the size and shape of the rice are not affected by the female parent cytoplasm.

4. CONCLUSION

Additive and non-additive genes action influencing the rice length and shape are confirmed. The effect of the additive gene action ~~is~~ greater than the non-additive gene action ~~and the heritability value,~~ both broad sense and narrow sense heritability ~~is~~ high, revealed that the selection of these traits at the early generation using the pedigree selection method may be considered. Rice length and shape were ~~characters that~~ not affected by the female parent cytoplasm so that F_2 and $F_{2reciprocal}$ populations might be combined into one population in the next selection generation.

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DIALLEL ANALYSIS OF RICE LENGTH AND SHAPE USING HAYMAN AND GRIFFING METHOD

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Abstract

Rice length and shape are important physical qualities that determine public acceptance of a variety and determine the price. Improvement of rice length and shape requires information on the genetic parameters of these traits. Diallel analysis is one of the methods usually used to estimate the genetic parameters of a trait. The purpose of this study was to estimate the genetic parameters of rice length and shape using full diallel analysis. The plant material used was a full diallel cross population of six rice genotypes, namely Basmati Pakistan, Basmati Delta 9, Inpago Unsoed 1, Inpari 31, Koshihikari and Tarabas. Thirty-six genotypes consisting of parents, F_1 and $F_{1\ \text{reciprocal}}$ were planted using a randomized block design with three replications. The data of rice grain length and length:width ratio was used for diallel analysis using the Hayman and Griffing method-1. The results showed additive and non-additive genes action influencing the rice length and shape. The effect of the additive gene action is greater than the non-additive gene action and the heritability value, both broad sense and narrow sense heritability is high, revealed the selection of these traits at the early generation using the pedigree selection method may be considered. Rice length and shape were not affected by the female parent cytoplasm so that F_2 and $F_{2\text{reciprocal}}$ populations may be combined into one population the next generation.

Keywords: diallel analysis, rice length, rice shape.

1. Introduction

Rice (*Oryza sativa* L.) is one of the major food crops in the world. Nearly 50% of the world population consumes rice as the staple food therefore it has an important role in global

food security (1,2). Indonesia, is the world’s third largest rice producer and it is also one of the world’s main rice consumers (3). More than 80% of Indonesian people consumes rice as a staple food, and it contributes 62.1% of the energy intake (4). It is the main source of income of approximately 18 million household farmers (5). It is also has strategic value from economic, environmental, social and political aspects (6,7). Therefore, rice self-sufficiency in Indonesia is required to fulfil the needs.

The government's program for rice self-sufficiency has four main targets i.e. to increase the national production, to stabilize the domestic prices and reserve stocks, and to minimize imports (8). Improving yield potential of rice varieties through plant breeding plays an important role to increase national production to increase the national production. High yielding rice varieties contributed to 56% of the national rice production (6). Thus, rice breeding in Indonesia aims to develop high yielding varieties that are in accordance with ecosystem conditions, social, cultural, and community interests (9).

Yield still the main target of rice development, however rice grain quality is now getting more attention due to increasing awareness of its importance (10). Rice grain quality determines the market price, consumer acceptability of a variety and consumer acceptability of a variety and becomes the second goal of rice plant breeding after yield (11,12). High yielding varieties with high rice grain quality are easy for farmers to adopted (13).

Grain quality it consists of rice length, rice shape, rice translucency and rice chalkiness. Rice quality directly affects consumer acceptance. Consumers determine the rice quality first from grain quality i.e. rice appearance, rice length and shape, which is followed by cooking quality and taste (14,15). Hence, rice length and shape determine the level of rice market demands and price (16). Therefore, breeding rice varieties that encompass desirable rice length and shape became a major concern for rice breeders in Indonesia.

A rice breeding program begins with increasing genetic diversity by crossing rice genotypes with wide genetic differences, followed by selection of the interest. The effectiveness of plant breeding programs increases in conjunction with scientific research that expands knowledge of plant genetic information (17). An effective and efficient

breeding program is determined by the genetic information that controls the inheritance of traits under study (18,19). Sometimes selection in segregation populations result in low quality progenies to fulfill breeding objectives (20). Hence, it's necessary to know genetic information of traits before determining a breeding and selection method (21). Diallel analysis is one of the manners to obtain genetic information for grain quality traits in rice such as grain length and shape.

Diallel analysis is a mating designs which involves mating a set of parents in all possible combinations, to produce a set of F_1 progeny (22,23). This method is useful to obtain genetic information that controls the inheritance of traits under study in early generation (24,25). It's also as the quickest method for understanding the genetic control of quantitative traits inheritance (26).

Diallel analysis can be carried out using Hayman and Griffing methods. Hayman's method can be used to study of genes action, genetic components and heritability (27). Whereas, Griffing's method (28) is to used estimated general combining ability, specific combining ability and reciprocal effects. It's also can be used to calculate additive and non-additive effects. Hayman and Griffing methods are often used together for complementary data interpretation (21). Hayman and Griffing methods have been used (either one or both) to obtain genetic information of plant traits. It has been widely used to study genetic parameters of length and shape in rice (29,30,39–41,31–38). The results of the study show various conclusions. Furthermore, this research is rarely done in Indonesia (42). The present research was conducted to study genetic components of F_1 population from a cross of six parents with various rice length and shape. The purpose of this study was to estimate the genetic parameters of rice length and shape using full diallel analysis.

2. Materials and Methods

2.1. Location of the experiment

A field experiment was conducted at the experimental farm of Agriculture Faculty, Jenderal Soedirman University, Purwokerto, Central Java, Indonesia. This location is at

coordinates 7°24'28.7"LS and 109°15'13.3"N and it’s at an altitude of 112 meters above sea level. The experiment was carried out from June 2019 to December 2019.

2.2. Plant material

Six rice genotypes i.e., Basmati Delta 9, Basmati Pakistan, Inpari 31, Inpago Unsoed 1, Koshihikari and Tarabas rice were used as the parents in this study. These parents have different origins and have various grain size and shape (Table 1). The research material used consisted of 36 rice genotypes which were develop from full diallel crosses among six parents. It consists of six parents, 15 F_1 and 15 $F_{1reciprocal}$.

Table 1. Six rice genotypes used for diallel mating design

No.	Genotype	Rice length and shape	Origin
1	Basmati Delta 9	Extra-long, slender	India
2	Basmati Pakistan	Extra-long, slender	Pakistan
3	Inpari 31	Long, medium	Indonesia
4	Inpago Unsoed 1	Medium, medium	Indonesia
5	Koshihikari	Short, round	Japan
6	Tarabas	Short, round	Indonesia

2.3. Experimental design

The experimental design was a randomized complete block design (RCBD) with three replications. Seeds of 36 genotype were sown in a seed box for two weeks, followed with transplanting to 35 cm x 40 cm polybags containing eight kg of inceptisol soil. Each polybag consisted of one plant per genotype. Recommendations for rice cultivation and plant protection was adopted. Fertilizer applications were 0,4 g N/ polybag and 1.0 g N-P-K/polybag was applied. Fertilizer was applied twice i.e., 10 days and 20 days after transplanting.

2.4. Data collection and analysis

At maturity, panicles were harvested from parents and all generations individually. Panicles were subjected as samples of rice length and shape. Rice shape is determined by grain length to width ratio. (43). Therefore, the observed trait in this study is rice length, width and length to width ratio. Digital caliper was used to measure the grain length and

width. Data collected was used for diallel analysis to estimate the genetic parameters of rice length and shape. Diallel analysis was performed using Hayman and Griffing method-1 (44).

1. Analysis of variance for F_1 in full-diallel crosses

Analysis of variance for F_1 in full-diallel crosses for rice length and shape followed as the statistical model $Y_{ijkl} = m + T_{ij} + b_k + (bT)_{ijk} + e_{ijkl}$ (1)

Where m is the general mean, T_{ij} is the effect of *i* x *j*th genotype, b_k is the effect of *k*th block, $(bT)_{ijk}$ is the interaction effect and e_{ijkl} is the error effect.

2. Genetic components of variation estimated

Genetic components of variation were calculated using the following formulas.

Regression coefficient of b(Wr, Vr) = $\frac{\mathrm{Cov(Wr,Vr)}}{\mathrm{Var(Vr)}}$ (2)

Where Wr is the covariance between parents and their off-sping, Vr is the variance of each array, Cov(Wr,Vr) is the covariance of (Wr,Vr) and Var(Vr) is the variance of Vr.

Additive genetic variance (D) = $V_{0L0} – E$ (3)

Where V_{0L0} is the variance of parents and E is the environmental variance

Dominance variance (H_1) = $V_{0L0} – 4W_{0L01} + 4V_{1L1} – (3n-2)E/n$ (4)

Where V_{0L0} is the variance of parents, W_{0L01} is the covariance between the parents and the arrays, V_{1L1} is the mean variance of the arrays, n is the number of parents and E is the environmental variance.

Proportions of positive or negative genes in the parent (H_2) = $4V_{1L1} – 4V_{0L1} – 2E$ (5)

Where V_{1L1} is the mean variance of the arrays, V_{0L1} is the variance of the mean of arrays and E is the environmental variance.

Mean covariance of additive and dominance (F) = $2V_{0L0} – 4W_{0L0} – 2(n-2)E/n$ (6)

Where V_{0L0} is the variance of parents, W_{0L01} is the covariance between the parents and the arrays, n is the number of parents and E is the environmental variance.

Dominance effect (h^2) = $4(M_{L1} – M_{L0})^2 – 4(n-1)E/n^2$ (7)

Where $(M_{L1} – M_{L0})^2$ is the difference between the mean of the parents and the mean og their n^2 progeny, n is the number of parents and E is the environmental variance.

Environmental variance (E) = $1/r$ (Error SS + Rep. SS) / $[((r – 1) + (c – 1)) \times (r – 1)]$ (8)

Where Error SS is the sum square of error, Rep. SS is the sum square of replication, r is the number of replications, and c is the number of errors.

Average degree of dominance = $(H_1/D)^{1/2}$ (9)

Where H_1 is the dominance variance and D is the additive genetic variance.

The proportion of genes with positive and negative effect in the parent = $H_2/4H_1$ (10)

Where H_1 is the dominance variance and H_2 is the Proportions of positive or negative genes in the parent.

The ratio dominant and recessive gene in the parent = $[(4DH_1)^{1/2} + F] / (4DH_1)^{1/2}–F$ (11)

Where D is the additive genetic variance, H_1 is the dominance variance and F is the mean covariance of additive and dominance.

Number of gene groups = h^2/H_2 (13)

Where h^2 is the dominance effect and H_2 is the Proportions of positive or negative genes in the parent.

The coefficient correlation between (Wr+Vr) and Yr (r) = $\frac{\text{Cov (Wr+Vr),Yr}}{\sqrt{\text{Var (Wr+Yr).Var(Yr)}}}$ (15)

Where (Wr+Vr) is the parental order of dominance, Y_r is the parental measurement, Cov(Wr + Vr) is the covariance of (Wr + Vr), Var(Wr + Vr) is the variance of (Wr + Vr) and Var (Y_r) is the variance of Y_r

Broad sense heritability (h^2_{bs}) =
$(^1/_2D+^1/_2H_1–^1/_4H_2–^1/2F) / (^1/_2D+^1/_2H_1–^1/_4H_2–^1/_2F+E)$ (16)

Where D is the additive genetic variance, H_1 is the dominance variance, H_2 is the Proportions of positive or negative genes in the parent, F is the mean covariance of additive and dominance and E is the environmental variance.

Narrow sense heritability (h^2_{ns}) =

$$(^1/_2D+^1/_2H_1-^1/_2H_2-^1/2F)/(^1/_2D+^1/_2H_1-^1/_2H_2-^1/_2F+E) \qquad (17)$$

Where D is the additive genetic variance, H_1 is the dominance variance, H_2 is the Proportions of positive or negative genes in the parent, F is the mean covariance of additive and dominance and E is the environmental variance.

3. Combining ability analysis

The statistical model for analysis variance of combining ability that were used was:

$$Y_{ij} = m + g_i + g_j + S_{ij} + r_{ij} + \frac{1}{bc}\sum\sum e_{ijkl} \qquad (18)$$

Where Y_{ij} is the mean of *i* x *j*th genotype, m is the general mean, gi is the general combing ability (*gca*) effect of *i*th parent, g_j is the general combing ability (*gca*) effect of *j*th parent, S_{ij} is the interaction, *i.e.* specific combining ability effect, r_{ij} is the reciprocal effect, and $\frac{1}{bc}\sum\sum e_{ijkl}$ is the mean error effect.

General combining ability (GCA) variance (g_i) = $\frac{1}{2n}\sum\left(Y_{i.} + Y_{.j}\right) - \frac{1}{n^2}Y^2..$ (19)

Where $Y_{i.}$ is the total of mean value of *i*th genotype cross, $Y_{.j}$ is the total of mean value of *j*th genotype selfing, n is the number of parents and Y is the grand total.

Specific combining ability (SCA) variance (s_{ij}) =

$$\frac{1}{2}\left(Y_{ij} + Y_{ij}\right) - \frac{1}{2n}\left(Y_{i.} + Y_{.i} + Y_{j.} + Y_{.j}\right) + \frac{1}{n^2}Y.. \qquad (20)$$

Where Y_{ij} is the mean of *i* x *j*th genotype, Y_{ji} is the mean of *j* x *i*th genotype, $Y_{i.}$ is the total of mean value of *i*th genotype cross, $Y_{.i}$ is the total of mean value of *i*th genotype selfing, $Y_{j.}$ is the total of mean value of *j*th genotype cross, $Y_{.j}$ is the total of mean value of *j*th genotype selfing , n is the number of parents and Y is the grand total.

Reciprocal variance (r_{ij}) = $\frac{1}{2}$ = $\left(Y_{ij} - Y_{ji}\right)$ (21)

Where Y_{ij} is the mean of *i* x *j*th genotype and Y_{ji} is the mean of *j* x *i*th genotype.

3. Results and discussion

3.1. Analysis of variance for genotypes

Analysis of variance showed significantly different among genotypes for rice grain length and shape (Table 2). Similar findings were also reported by Bano and Singh (39) and Hijam et al. (37). Significantly different analysis of variance among genotypes is a requirement for estimating genetic parameters using diallel analysis (44). Thus, significance differences among the genotypes for rice length and shape indicate that they are suitable for further genetic studies.

Table 2. Analysis of variance for F_1 in a full-diallel cross for rice length and shape

Source of variation	Degrees of freedom	Mean square			
		Rice length (mm)		Rice shape	
Block	2	0.06		0.01	
Genotype	35	3.16	*	1.51	*
Error	70	0.04		0.02	

* = significantly different at the level of 5%.

3.2. Genetic components of variation

3.2.1. Gene interaction

The values of regression coefficient of b (Wr, Vr) for rice length and shape (1.20 and 1.15, respectively) were not significantly different from one (Table 3). Similar result reported by Bano and Singh (39) for kernel length before cooking (rice length) and kernel length/breadth ratio before cooking (rice length). The value of regression of coefficient of b (Wr, Vr) may be used to determine the gene interaction of a trait. Based on t test, a significantly different value of b (Wr, Vr) from one indicates gene interaction, while a non-significantly different value of b (Wr, Vr) from one reflected no gene interaction (44). It means there is no interaction between genes controlling rice length and shape in this study.

3.2.2. Additive (D) and dominance (H1) variance

Additive (D) and dominance (H_1) variance were significantly different for rice length and shape (Table 3). Significant different values of the components D and H_1 indicated the importance of both additive and non-additive gene action in the expression of traits (45). So that, rice length and shape are influenced by both additive and non-additive types of gene action. Similar findings were also observed by Kato (29), Fu et al. (31), Daradjat & Rumanti (42) Kumar et al. (32,33), Rafii et al. (30) and Senthil Kumar & Mudhalvan (38) for rice length and size.

The results showed the value of additive variance (D) for rice length and shape is 2.72 and 1.36, respectively and the value of dominance variance (H_1) for rice length and shape is 0.26 and 0.19, respectively (Table 3). These showed that the influence of additive variance is greater than dominance variance ($D>H_1$) for rice length and shape. Higher magnitude of additive variance (D) indicated the greater role of additive gene action while *vice versa* dominance variance indicated the greater importance of non-additive gene action (40,45). The value of the additive variance which is greater than the dominance variance indicates the increasing importance of additive gene action (32,33). This means that in this study, rice length and shape are more influenced by additive gene action than non-additive gene action. These results are in accordance with the findings of Kato (29) and Thattil and Perera (46) for rice length and size. However, Daradjat & Rumanti (42) and Senthil Kumar & Mudhalvan (38) reported different results that there is an indication that the non-additive gene action was more predominant than additive gene action for rice length and size.

3.2.3. Gene distribution in the parent

Gene distribution in the parents can be were determined by H_2 values. The results showed that the H_2 values for rice length and shape were significantly different (Table 3.) This indicates that the genes determining the inheritance of rice length and shape are not evenly distributed among the parents. Genes controlling rice length and shape that are not evenly distributed in parents have also been reported (38).

Table 3. Estimates of genetic components of variation for rice length and shape

Genetic components	Rice length (mm)	Rice shape
b (Wr, Vr)	1.20^{ns}	1.15^{ns}
D	2.72 *	1.36 *
H_1	0.26 *	0.19 *
H_2	0.25 *	0.17 *
F	0.44 *	0.33 *
h^2	-0.01^{ns}	0.04^{ns}
E	0.01^{ns}	0.01^{ns}
$(H_1/D)^{1/2}$	0.31	0.38
$H_2/4H_1$	0.23	0.22
Kd/Kr	1.71	1.95
h^2/H_2	-0.03	0.22
r [(Wr+Vr),Yr]	0.69	0.89
h^2_{bs}	0.99	0.99
h^2_{ns}	0.94	0.91
Ratio of h^2_{ns}: h^2_{bs}	0.95	0.92

* = significantly different at the level of 5%, ns = not significantly different.

Proportion of positive genes to negative genes is indicated by value of H_1 component against H_2 component. The value of H_1 is greater than the H_2 indicating more positive genes than negative genes, *vice versa* the value of the H_1 is smaller than H_2 reflecting the positive are gene less than the negative genes (21,47). Table 3 showed the value of H_1 is 0.26 and 0.19, respectively and the value of H_2 is 0.27 and 0.17, respectively for rice length and shape. Its shows the value of H_1 is greater than H_2 for rice length and shape, meaning that positive genes are more involved in determining rice length and shape than negative genes. The results were agreement with that Raju et al. (40).

Proportion of positive genes to negative genes in all parents also can be seen from ratio of $H_2/4H_1$. Values lower than 0.25 indicate positive and negative genes are not present in unequal proportions in the parents (45,48). The results showed the value of $H_2/4H_1$ for rice length and shape is 0.23 and 0.22 respectively (Table 3). They were lower than 0.25, reflecting the unequal distribution of positive and negative genes in the parents. Similar findings were reported by previous studies (38–40).

3.2.4. Dominance level

The influence of dominance can be seen from the value of mean degree of dominance as estimated by $(H_1/D)^{1/2}$. A value $(H_1/D)^{1/2}$ more than 1 indicates over dominance, while a value $(H_1/D)^{1/2}$ between 0 and 1 indicates partial dominance (Hayman, 1954). Table 3 showed the value $(H_1/D)^{1/2}$ of the rice length and shape is less than 1 (0.31 and 0.38, respectively) indicated existence of partial dominance in these traits. Rice length controlled by a partial dominance gene was also reported by Kato (29).

3.2.5. Dominance effect

Dominance effect is indicated by the h^2 value. Table 3 showed that h^2 values were not significantly different for rice length and shape. This indicated no difference in average deviation of F_1 from most parents (47).

3.2.6. Environmental variance

Table 3 showed that environmental variance exhibited no significant influence on rice length and shape. This reflected no influence of environmental factor on the expression of the traits studied (45). Therefore, it is known that expression of rice length and shape are more influenced by genetic than environment effects.

3.2.7. Proportion of dominant gene to recessive gene

Proportion of dominant genes to recessive genes is shown by F component and Kd/Kr ratio. The positive value of F component reflects a greater number of dominant genes than recessive genes in the parent (47,49). A ratio of Kd/Kr greater than one indicating more dominant genes in the parent, conversely, the ratio of Kd/Kr smaller than one indicated more recessive genes in the parent (44). The results showed a positive value of F component and a ratio of Kd/Kr of the rice length and shape is greater than one (1.71 and 1.95, respectively) (Table 3.), which indicated more dominant genes in the parent for rice length and shape. The same finding was reported by Raju et al. (40).

3.2.8. Number of gene groups

Component of h^2/H_2 gives an indication of the number of gene groups that control a trait. The h_2/H_2 values of rice length and shape are -0.03 and 0.22, respectively, lower than one. The ratio smaller than one indicated the involvement of single gene or one group of genes which are responsible for their genetic control (45). As a result, rice length and shape are controlled by at least a single group of genes.

3.2.9. Direction and order of dominance

The positive value of the correlation between (Wr + Vr) and Yr and close to unity, indicates that dominant alleles have predominantly negative effects, i.e., act in the direction of lower yields (50). A positive value is obtained in the correlation (Wr+Vr) and Yr for rice length and shape (Table 3). That is, in rice length and shape, the dominant genes cause the rice to be short and round.

The direction and order of dominance can be seen in the value (Wr+Vr) component. Based on the value (Wr+Vr) in Table 4 the dominance order of rice grain length and shape was Inpago Unsoed 1, Koshihikari, Tarabas, Basmati Delta 9 and Basmati Pakistan. This is reinforced by the graph of the relationship between the covariance (Wr) and variance (Vr) in Figure 1 and 2.

Distribution of parental array points along the regression line reflected genetic diversity of a trait (51). The array point was scattered along the regression line for rice length and shape, indicating genetic diversity for these traits. The position of the parents on the graph of the relationship between the covariance (Wr) and variance (Vr) reflects the order of dominance. The position of parent which is closer to zero indicating it contains most dominant genes, vice versa farther away a parent position to zero reflecting it contains more recessive genes (47,50). Inpago Unsoed 1 is the closest to zero, reflecting that this parent has the mostly dominant genes for rice length and shape. Basmati Pakistan contain most a recessive gene for the rice length and shape since it is the farthest from zero. Basmati which has extra-long and slender rice contains the most recessive gene, this means that the gene controlling long and slender rice is recessive to the short and round rice gene. This result agreement with finding of Kato (29), Murai & Kinoshita (41) and Ali et al. (52).

Tabel 4. The value (Wr+Vr) of rice length and shape

Genotypes	Rice length	Rice shape
Basmati Delta 9	2,32	1,30
Basmati Pakistan	2,46	1,43
Inpari 31	1,99	0,93
Inpago Unsoed 1	1,00	0,37
Koshihikari	1,75	0,69
Tarabas	1,87	0,73

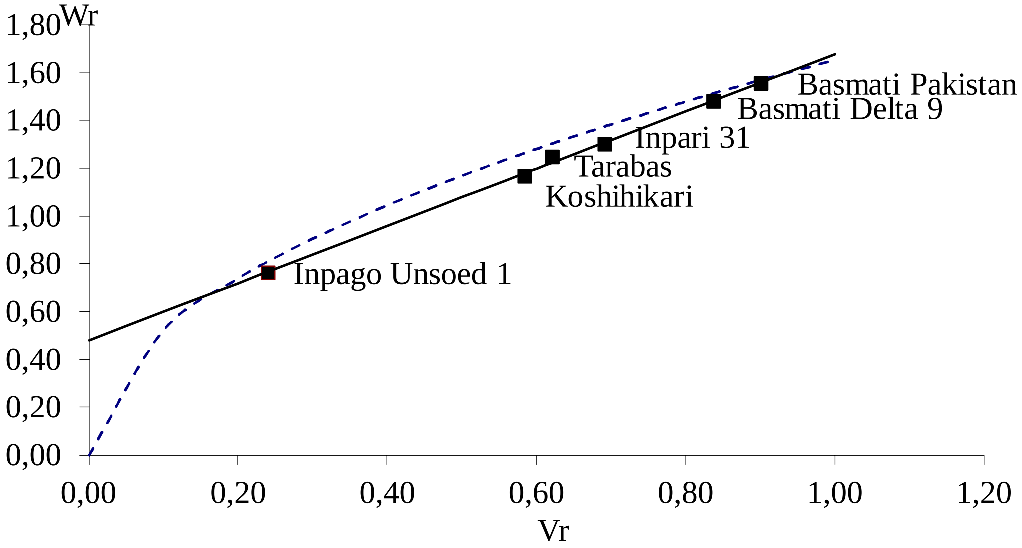

Figure 1. Covariance (Wr) and variance (Vr) graph of rice length.

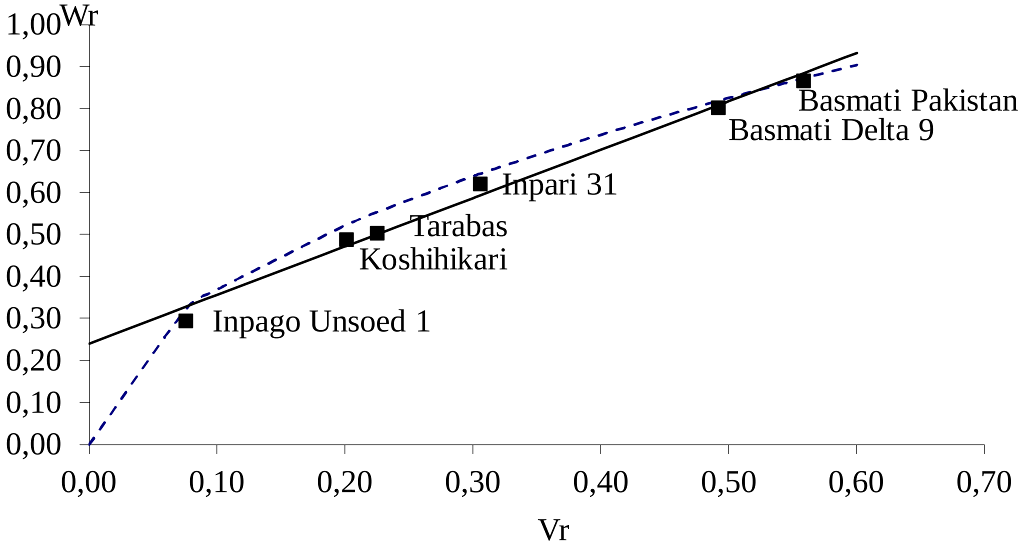

Figure 2. Covariance (Wr) and variance (Vr) graph of rice shape.

The straight line intercepted the vertical axis (Wr) above the origin for rice length and shape (Figure 1 and 2). The straight line intercepted the vertical axis (Wr) above the origin indicated the indicating partial dominance of the genes controlling a trait (21,50,51). This reveals that the rice length and shape was controlled by a partial dominant gene as described previously. Partial dominance results in the appearance of each trait having a tendency to approach the mid parent value and not having over dominance which exceeds the best parent (53). This is reflected in the h^2 value of rice length and shape which is not significantly different so that there is no difference between the F_1 average and the parents' average.

3.2.10. Heritability

Broad sense heritability (h^2_{bs}) estimates for rice length and shape are similar, 0,99. Narrow sense heritability (h^2_{ns}) estimates for these traits is 0.94 and 0.91, respectively (Table 3.). Heritability values more than 0.5 are categorized as high (Stansfield, 1991), thus broad sense heritability (h^2_{bs}) for rice length and shape categorized as high heritability. Similar findings were reported by previous studies (54)

The estimated value of broad sense heritability indicates the relative contribution of genetic factors to variation of the observed trait (55). A high broad sense heritability value indicates that traits are more influenced by genetic than environmental factors (56). In this study, broad sense heritability estimate of rice length and shape is high, indicating the influence of genetic was greater than environmental factors. Low influence of environmental factors were also reflected in the non-significant environmental variance observed in Table 3.

Narrow sense heritability estimates indicate the role of additive gene action on a trait. High estimated of narrow sense heritability indicates more additive gene action than non-additive gene action (4,57–59). In this study, the narrow sense heritability estimate of rice length and shape was high, meaning that additive gene action played a more important role than non-additive gene action.

Ratio of narrow sense heritability and broad sense heritability reflecting the role of additive and non-additive gene action for a trait. The ratio value closer to one indicates the total genetic variance of a trait is caused by additive gene action (60). Table 3 showed ratio of narrow sense heritability and broad sense heritability ratios are 0.95 for rice length and 0.92 for rice shape respectively. This indicating that additive gene action determines the rice size and shape more than non-additive gene action as previously described. Traits that have high additive variance and heritability in the F_1 population may be selected using individual selection. Individual selection may be applied to traits that have additive variance and high heritability in the F_1 population (21) so that selection of rice length and shape may be carried out using individual selection such as pedigree. This finding agreement with Raju et al. (40).

3.3. Combining ability estimation of rice length and shape

Gene action and cytoplasm influence of the female parent for a trait can be predicted through combining ability. Variances of general combining ability (GCA), specific combining ability (SCA), and reciprocals were obtained from diallel analysis of Griffing method-1. GCA and SCA variance are associated with non-additive and additive gene action, respectively (61–63). Reciprocal variance is useful for knowing the effect of female parent cytoplasm of a trait (64).

General combining ability (GCA) is endorsed to additive gene action and specific combining ability (SCA) is mainly attributed to non-additive gene action (59,65). This study showed significant GCA and SCA effects of rice length and shape (Table 4). The significant GCA and SCA indicated the importance of both additive and non-additive gene actions in the expression of these traits. This finding was in agreement with Singh et al. and Soni et al. (66,67).

The magnitude of the effect of additive gene action and non-additive gene action on a trait can be determined from GCA:SCA ratio (68). A high GCA:SCA ratio indicates that additive gene action plays a more important role in the expression of a trait than non-additive gene action (69). Ratio of GCA:SCA greater than one indicates that additive gene action has more influence on the expression of a trait and conversely, a GCA:SCA ratio less than one

reflected that non-additive gene action has more influence on the expression of a trait (70). In this study, ratio of GCA:SCA of rice length and shape is greater than one (50.060 and 32.280, respectively) (Table 4), indicating additive gene action is more influential than non-additive gene action on the expression of these traits. These results agree with the estimation of gene action using the Hayman method as described previously. Additive gene action in grain length and shape has been previously reported (66,67). Therefore, the selection for grain length and shape will be effective using pedigree method (71).

Table 4. Analysis of variance of combining ability and GCA:SCA ratio of rice length and shape

Source of variance	Degree of freedom	Mean square			
		Rice length		Rice shape	
General combining ability (GCA)	5	6.909	*	3.154	*
Specific combining ability (SCA)	15	0.138	*	0.092	*
Reciprocal	15	0.020	ns	0.006	ns
Error	70	0.015		0.007	
GCA:SCA ratio		50.060		34.280	

* = significantly different at the level of 5%, ns = not significantly different

Non-significant reciprocal effects were observed for both rice length and shape (Table 4). This indicated that there was no influence of the female parent cytoplasm on the inheritance of these traits (64,72). So that, the size and shape of the rice are not affected by the female parent cytoplasm.

4. CONCLUSION

The influence of additive and non-additive gene action on rice length and shape were confirmed. The effect of the additive gene action was greater than the non-additive gene action while both broad sense and narrow sense heritability were high. This revealed that that the selection of these traits at the early generation using the pedigree selection method may be considered. Rice length and shape were not affected by the female parent cytoplasm so that F_2 and $F_{2reciprocal}$ populations might be combined into one population in the next selection generation.

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Reviewers' comments:

Reviewer #3:
In this manuscript authors studied genetic parameters of rice length and shape using full diallel analysis. We believe the ideas are clearly and accurately communicated without errors in spelling, grammar, and adequate word choice.
Specific comment:
Line 160, Replace Result and discussion by Results and discussion.
General comment:
In Material and Methods section authors should explain what statistical software was used.

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DIALLEL ANALYSIS OF RICE LENGTH AND SHAPE USING HAYMAN AND GRIFFING METHOD

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Abstract

Rice length and shape are important physical qualities that determine public acceptance of a variety and determine the price. Improvement of rice length and shape requires information on the genetic parameters of these traits. Diallel analysis is one of the methods usually used to estimate the genetic parameters of a trait. The purpose of this study was to estimate the genetic parameters of rice length and shape using full diallel analysis. The plant material used was a full diallel cross population of six rice genotypes, namely Basmati Pakistan, Basmati Delta 9, Inpago Unsoed 1, Inpari 31, Koshihikari and Tarabas. Thirty-six genotypes consisting of parents, F_1 and $F_{1\ \text{reciprocal}}$ were planted using a randomized block design with three replications. The data of rice grain length and length:width ratio was used for diallel analysis using the Hayman and Griffing method-1. The results showed additive and non-additive genes action influencing the rice length and shape. The effect of the additive gene action is greater than the non-additive gene action and the heritability value, both broad sense and narrow sense heritability is high, revealed the selection of these traits at the early generation using the pedigree selection method may be considered. Rice length and shape were not affected by the female parent cytoplasm so that F_2 and $F_{2\text{reciprocal}}$ populations may be combined into one population the next generation.

Keywords: diallel analysis, rice length, rice shape.

1. Introduction

Rice (*Oryza sativa* L.) is one of the major food crops in the world. Nearly 50% of the world population consumes rice as the staple food therefore it has an important role in global

food security (1,2). Indonesia, is the world’s third largest rice producer and it is also one of the world’s main rice consumers (3). More than 80% of Indonesian people consumes rice as a staple food, and it contributes 62.1% of the energy intake (4). It is the main source of income of approximately 18 million household farmers (5). It is also has strategic value from economic, environmental, social and political aspects (6,7). Therefore, rice self-sufficiency in Indonesia is required to fulfil the needs.

The government's program for rice self-sufficiency has four main targets i.e. to increase the national production, to stabilize the domestic prices and reserve stocks, and to minimize imports (8). Improving yield potential of rice varieties through plant breeding plays an important role to increase national production to increase the national production. High yielding rice varieties contributed to 56% of the national rice production (6). Thus, rice breeding in Indonesia aims to develop high yielding varieties that are in accordance with ecosystem conditions, social, cultural, and community interests (9).

Yield still the main target of rice development, however rice grain quality is now getting more attention due to increasing awareness of its importance (10). Rice grain quality determines the market price, consumer acceptability of a variety and consumer acceptability of a variety and becomes the second goal of rice plant breeding after yield (11,12). High yielding varieties with high rice grain quality are easy for farmers to adopted (13).

Grain quality it consists of rice length, rice shape, rice translucency and rice chalkiness. Rice quality directly affects consumer acceptance. Consumers determine the rice quality first from grain quality i.e. rice appearance, rice length and shape, which is followed by cooking quality and taste (14,15). Hence, rice length and shape determine the level of rice market demands and price (16). Therefore, breeding rice varieties that encompass desirable rice length and shape became a major concern for rice breeders in Indonesia.

A rice breeding program begins with increasing genetic diversity by crossing rice genotypes with wide genetic differences, followed by selection of the interest. The effectiveness of plant breeding programs increases in conjunction with scientific research that expands knowledge of plant genetic information (17). An effective and efficient

breeding program is determined by the genetic information that controls the inheritance of traits under study (18,19). Sometimes selection in segregation populations result in low quality progenies to fulfill breeding objectives (20). Hence, it’s necessary to know genetic information of traits before determining a breeding and selection method (21). Diallel analysis is one of the manners to obtain genetic information for grain quality traits in rice such as grain length and shape.

Diallel analysis is a mating designs which involves mating a set of parents in all possible combinations, to produce a set of F_1 progeny (22,23). This method is useful to obtain genetic information that controls the inheritance of traits under study in early generation (24,25). It’s also as the quickest method for understanding the genetic control of quantitative traits inheritance (26).

Diallel analysis can be carried out using Hayman and Griffing methods. Hayman's method can be used to study of genes action, genetic components and heritability (27). Whereas, Griffing’s method (28) is to used estimated general combining ability, specific combining ability and reciprocal effects. It’s also can be used to calculate additive and non-additive effects. Hayman and Griffing methods are often used together for complementary data interpretation (21). Hayman and Griffing methods have been used (either one or both) to obtain genetic information of plant traits. It has been widely used to study genetic parameters of length and shape in rice (29,30,39–41,31–38). The results of the study show various conclusions. Furthermore, this research is rarely done in Indonesia (42). The present research was conducted to study genetic components of F_1 population from a cross of six parents with various rice length and shape. The purpose of this study was to estimate the genetic parameters of rice length and shape using full diallel analysis.

2. Materials and Methods

2.1. Location of the experiment

A field experiment was conducted at the experimental farm of Agriculture Faculty, Jenderal Soedirman University, Purwokerto, Central Java, Indonesia. This location is at

coordinates 7°24'28.7"LS and 109°15'13.3"N and it's at an altitude of 112 meters above sea level. The experiment was carried out from June 2019 to December 2019.

2.2. Plant material

Six rice genotypes i.e., Basmati Delta 9, Basmati Pakistan, Inpari 31, Inpago Unsoed 1, Koshihikari and Tarabas rice were used as the parents in this study. These parents have different origins and have various grain size and shape (Table 1). The research material used consisted of 36 rice genotypes which were develop from full diallel crosses among six parents. It consists of six parents, 15 F_1 and 15 $F_{1reciprocal}$.

Table 1. Six rice genotypes used for diallel mating design

No.	Genotype	Rice length and shape	Origin
1	Basmati Delta 9	Extra-long, slender	India
2	Basmati Pakistan	Extra-long, slender	Pakistan
3	Inpari 31	Long, medium	Indonesia
4	Inpago Unsoed 1	Medium, medium	Indonesia
5	Koshihikari	Short, round	Japan
6	Tarabas	Short, round	Indonesia

2.3. Experimental design

The experimental design was a randomized complete block design (RCBD) with three replications. Seeds of 36 genotype were sown in a seed box for two weeks, followed with transplanting to 35 cm x 40 cm polybags containing eight kg of inceptisol soil. Each polybag consisted of one plant per genotype. Recommendations for rice cultivation and plant protection was adopted. Fertilizer applications were 0,4 g N/ polybag and 1.0 g N-P-K/polybag was applied. Fertilizer was applied twice i.e., 10 days and 20 days after transplanting.

2.4. Data collection and analysis

At maturity, panicles were harvested from parents and all generations individually. Panicles were subjected as samples of rice length and shape. Rice shape is determined by grain length to width ratio. (43). Therefore, the observed trait in this study is rice length, width and length to width ratio. Digital caliper was used to measure the grain length and

width. Data collected was used for diallel analysis to estimate the genetic parameters of rice length and shape. Diallel analysis was performed using Hayman and Griffing method-1 (44) were performed using the software Microsoft® Excel.

1. Analysis of variance for F_1 in full-diallel crosses

Analysis of variance for F_1 in full-diallel crosses for rice length and shape followed as the statistical model $Y_{ijkl} = m + T_{ij} + b_k + (bT)_{ijk} + e_{ijkl}$ (1)

Where m is the general mean, T_{ij} is the effect of *i* x *j*th genotype, b_k is the effect of *k*th block, $(bT)_{ijk}$ is the interaction effect and e_{ijkl} is the error effect.

2. Genetic components of variation estimated

Genetic components of variation were calculated using the following formulas.

Regression coefficient of b(Wr, Vr) = $\frac{\mathrm{Cov(Wr,Vr)}}{\mathrm{Var(Vr)}}$ (2)

Where Wr is the covariance between parents and their off-sping, Vr is the variance of each array, Cov(Wr,Vr) is the covariance of (Wr,Vr) and Var(Vr) is the variance of Vr.

Additive genetic variance (D) = $V_{0L0} – E$ (3)

Where V_{0L0} is the variance of parents and E is the environmental variance

Dominance variance (H_1) = $V_{0L0} – 4W_{0L01} + 4V_{1L1} – (3n-2)E/n$ (4)

Where V_{0L0} is the variance of parents, W_{0L01} is the covariance between the parents and the arrays, V_{1L1} is the mean variance of the arrays, n is the number of parents and E is the environmental variance.

Proportions of positive or negative genes in the parent (H_2) = $4V_{1L1} – 4V_{0L1} – 2E$ (5)

Where V_{1L1} is the mean variance of the arrays, V_{0L1} is the variance of the mean of arrays and E is the environmental variance.

Mean covariance of additive and dominance (F) = $2V_{0L0} – 4W_{0L0} – 2(n-2)E/n$ (6)

Where V_{0L0} is the variance of parents, W_{0L01} is the covariance between the parents and the arrays, n is the number of parents and E is the environmental variance.

Dominance effect (h^2) = $4(M_{L1} – M_{L0})^2 – 4(n-1)E/n^2$ (7)

Where $(M_{L1} – M_{L0})^2$ is the difference between the mean of the parents and the mean og their n^2 progeny, n is the number of parents and E is the environmental variance.

Environmental variance (E) = $1/r$ (Error SS + Rep. SS) / $[((r – 1) + (c – 1)) \times (r – 1)]$ (8)

Where Error SS is the sum square of error, Rep. SS is the sum square of replication, r is the number of replications, and c is the number of errors.

Average degree of dominance = $(H_1/D)^{1/2}$ (9)

Where H_1 is the dominance variance and D is the additive genetic variance.

The proportion of genes with positive and negative effect in the parent = $H_2/4H_1$ (10)

Where H_1 is the dominance variance and H_2 is the Proportions of positive or negative genes in the parent.

The ratio dominant and recessive gene in the parent = $[(4DH_1)^{1/2} + F] / (4DH_1)^{1/2}–F$ (11)

Where D is the additive genetic variance, H_1 is the dominance variance and F is the mean covariance of additive and dominance.

Number of gene groups = h^2/H_2 (13)

Where h^2 is the dominance effect and H_2 is the Proportions of positive or negative genes in the parent.

The coefficient correlation between (Wr+Vr) and Yr (r) = $\frac{\text{Cov (Wr+Vr),Yr}}{\sqrt{\text{Var (Wr+Yr).Var(Yr)}}}$ (15)

Where (Wr+Vr) is the parental order of dominance, Y_r is the parental measurement, Cov(Wr + Vr) is the covariance of (Wr + Vr), Var(Wr + Vr) is the variance of (Wr + Vr) and Var (Y_r) is the variance of Y_r

Broad sense heritability (h^2_{bs}) =

$({}^{1}/_{2}D+{}^{1}/_{2}H_1–{}^{1}/_{4}H_2–{}^{1}/2F)/({}^{1}/_{2}D+{}^{1}/_{2}H_1–{}^{1}/_{4}H_2–{}^{1}/_{2}F+E)$ (16)

Where D is the additive genetic variance, H_1 is the dominance variance, H_2 is the Proportions of positive or negative genes in the parent, F is the mean covariance of additive and dominance and E is the environmental variance.

Narrow sense heritability (h^2_{ns}) =

$({}^1/_2D+{}^1/_2H_1–{}^1/_2H_2–{}^1/2F)/({}^1/_2D+{}^1/_2H_1–{}^1/_2H_2–{}^1/_2F+E)$ (17)

Where D is the additive genetic variance, H_1 is the dominance variance, H_2 is the Proportions of positive or negative genes in the parent, F is the mean covariance of additive and dominance and E is the environmental variance.

3. Combining ability analysis

The statistical model for analysis variance of combining ability that were used was:

$$Y_{ij} = m + g_i + g_j + S_{ij} + r_{ij} + \frac{1}{bc}\sum\sum e_{ijkl} \quad (18)$$

Where Y_{ij} is the mean of *i* x *j*th genotype, m is the general mean, gi is the general combing ability (*gca*) effect of *i*th parent, g_j is the general combing ability (*gca*) effect of *j*th parent, S_{ij} is the interaction, *i.e.* specific combining ability effect, r_{ij} is the reciprocal effect, and $\frac{1}{bc}\sum\sum e_{ijkl}$ is the mean error effect.

General combining ability (GCA) variance (g_i) = $\frac{1}{2n}\sum(Y_{i.} + Y_{.j}) - \frac{1}{n^2}Y^2..$ (19)

Where $Y_{i.}$ is the total of mean value of *i*th genotype cross, $Y_{.j}$ is the total of mean value of *j*th genotype selfing, n is the number of parents and Y is the grand total.

Specific combining ability (SCA) variance (s_{ij}) =

$\frac{1}{2}(Y_{ij} + Y_{ij}) - \frac{1}{2n}(Y_{i.} + Y_{.i} + Y_{j.} + Y_{.j}) + \frac{1}{n^2}Y_{..}$ (20)

Where Y_{ij} is the mean of *i* x *j*th genotype, Y_{ji} is the mean of *j* x *i*th genotype, $Y_{i.}$ is the total of mean value of *i*th genotype cross, $Y_{.i}$ is the total of mean value of *i*th genotype selfing, $Y_{j.}$ is the total of mean value of *j*th genotype cross, $Y_{.j}$ is the total of mean value of *j*th genotype selfing , n is the number of parents and Y is the grand total.

Reciprocal variance (r_{ij}) = $\frac{1}{2} = (Y_{ij} - Y_{ji})$ (21)

Where Y_{ij} is the mean of *i* x *j*th genotype and Y_{ji} is the mean of *j* x *i*th genotype.

3. Results and discussion

3.1. Analysis of variance for genotypes

Analysis of variance showed significantly different among genotypes for rice grain length and shape (Table 2). Similar findings were also reported by Bano and Singh (39) and Hijam et al. (37). Significantly different analysis of variance among genotypes is a requirement for estimating genetic parameters using diallel analysis (44). Thus, significance differences among the genotypes for rice length and shape indicate that they are suitable for further genetic studies.

Table 2. Analysis of variance for F_1 in a full-diallel cross for rice length and shape

Source of variation	Degrees of freedom	Mean square	
		Rice length (mm)	Rice shape
Block	2	0.06	0.01
Genotype	35	3.16 *	1.51 *
Error	70	0.04	0.02

* = significantly different at the level of 5%.

3.2. Genetic components of variation

3.2.1. Gene interaction

The values of regression coefficient of b (Wr, Vr) for rice length and shape (1.20 and 1.15, respectively) were not significantly different from one (Table 3). Similar result reported by Bano and Singh (39) for kernel length before cooking (rice length) and kernel length/breadth ratio before cooking (rice length). The value of regression of coefficient of b (Wr, Vr) may be used to determine the gene interaction of a trait. Based on t test, a significantly different value of b (Wr, Vr) from one indicates gene interaction, while a non-significantly different value of b (Wr, Vr) from one reflected no gene interaction (44). It means there is no interaction between genes controlling rice length and shape in this study.

3.2.2. Additive (D) and dominance (H1) variance

Additive (D) and dominance (H_1) variance were significantly different for rice length and shape (Table 3). Significant different values of the components D and H_1 indicated the importance of both additive and non-additive gene action in the expression of traits (45). So that, rice length and shape are influenced by both additive and non-additive types of gene action. Similar findings were also observed by Kato (29), Fu et al. (31), Daradjat & Rumanti (42) Kumar et al. (32,33), Rafii et al. (30) and Senthil Kumar & Mudhalvan (38) for rice length and size.

The results showed the value of additive variance (D) for rice length and shape is 2.72 and 1.36, respectively and the value of dominance variance (H_1) for rice length and shape is 0.26 and 0.19, respectively (Table 3). These showed that the influence of additive variance is greater than dominance variance ($D>H_1$) for rice length and shape. Higher magnitude of additive variance (D) indicated the greater role of additive gene action while *vice versa* dominance variance indicated the greater importance of non-additive gene action (40,45). The value of the additive variance which is greater than the dominance variance indicates the increasing importance of additive gene action (32,33). This means that in this study, rice length and shape are more influenced by additive gene action than non-additive gene action. These results are in accordance with the findings of Kato (29) and Thattil and Perera (46) for rice length and size. However, Daradjat & Rumanti (42) and Senthil Kumar & Mudhalvan (38) reported different results that there is an indication that the non-additive gene action was more predominant than additive gene action for rice length and size.

3.2.3. Gene distribution in the parent

Gene distribution in the parents can be were determined by H_2 values. The results showed that the H_2 values for rice length and shape were significantly different (Table 3.) This indicates that the genes determining the inheritance of rice length and shape are not evenly distributed among the parents. Genes controlling rice length and shape that are not evenly distributed in parents have also been reported (38).

Table 3. Estimates of genetic components of variation for rice length and shape

Genetic components	Rice length (mm)		Rice shape	
b (Wr, Vr)	1.20	ns	1.15	ns
D	2.72	*	1.36	*
H_1	0.26	*	0.19	*
H_2	0.25	*	0.17	*
F	0.44	*	0.33	*
h^2	-0.01	ns	0.04	ns
E	0.01	ns	0.01	ns
$(H_1/D)^{1/2}$	0.31		0.38	
$H_2/4H_1$	0.23		0.22	
Kd/Kr	1.71		1.95	
h^2/H_2	-0.03		0.22	
r [(Wr+Vr),Yr]	0.69		0.89	
h^2_{bs}	0.99		0.99	
h^2_{ns}	0.94		0.91	
Ratio of h^2_{ns}: h^2_{bs}	0.95		0.92	

* = significantly different at the level of 5%, ns = not significantly different.

Proportion of positive genes to negative genes is indicated by value of H_1 component against H_2 component. The value of H_1 is greater than the H_2 indicating more positive genes than negative genes, *vice versa* the value of the H_1 is smaller than H_2 reflecting the positive are gene less than the negative genes (21,47). Table 3 showed the value of H_1 is 0.26 and 0.19, respectively and the value of H_2 is 0.27 and 0.17, respectively for rice length and shape. Its shows the value of H_1 is greater than H_2 for rice length and shape, meaning that positive genes are more involved in determining rice length and shape than negative genes. The results were agreement with that Raju et al. (40).

Proportion of positive genes to negative genes in all parents also can be seen from ratio of $H_2/4H_1$. Values lower than 0.25 indicate positive and negative genes are not present in unequal proportions in the parents (45,48). The results showed the value of $H_2/4H_1$ for rice length and shape is 0.23 and 0.22 respectively (Table 3). They were lower than 0.25, reflecting the unequal distribution of positive and negative genes in the parents. Similar findings were reported by previous studies (38–40).

3.2.4. Dominance level

The influence of dominance can be seen from the value of mean degree of dominance as estimated by $(H_1/D)^{1/2}$. A value $(H_1/D)^{1/2}$ more than 1 indicates over dominance, while a value $(H_1/D)^{1/2}$ between 0 and 1 indicates partial dominance (Hayman, 1954). Table 3 showed the value $(H_1/D)^{1/2}$ of the rice length and shape is less than 1 (0.31 and 0.38, respectively) indicated existence of partial dominance in these traits. Rice length controlled by a partial dominance gene was also reported by Kato (29).

3.2.5. Dominance effect

Dominance effect is indicated by the h^2 value. Table 3 showed that h^2 values were not significantly different for rice length and shape. This indicated no difference in average deviation of F_1 from most parents (47).

3.2.6. Environmental variance

Table 3 showed that environmental variance exhibited no significant influence on rice length and shape. This reflected no influence of environmental factor on the expression of the traits studied (45). Therefore, it is known that expression of rice length and shape are more influenced by genetic than environment effects.

3.2.7. Proportion of dominant gene to recessive gene

Proportion of dominant genes to recessive genes is shown by F component and Kd/Kr ratio. The positive value of F component reflects a greater number of dominant genes than recessive genes in the parent (47,49). A ratio of Kd/Kr greater than one indicating more dominant genes in the parent, conversely, the ratio of Kd/Kr smaller than one indicated more recessive genes in the parent (44). The results showed a positive value of F component and a ratio of Kd/Kr of the rice length and shape is greater than one (1.71 and 1.95, respectively) (Table 3.), which indicated more dominant genes in the parent for rice length and shape. The same finding was reported by Raju et al. (40).

3.2.8. Number of gene groups

Component of h^2/H_2 gives an indication of the number of gene groups that control a trait. The h_2/H_2 values of rice length and shape are -0.03 and 0.22, respectively, lower than one. The ratio smaller than one indicated the involvement of single gene or one group of genes which are responsible for their genetic control (45). As a result, rice length and shape are controlled by at least a single group of genes.

3.2.9. Direction and order of dominance

The positive value of the correlation between (Wr + Vr) and Yr and close to unity, indicates that dominant alleles have predominantly negative effects, i.e., act in the direction of lower yields (50). A positive value is obtained in the correlation (Wr+Vr) and Yr for rice length and shape (Table 3). That is, in rice length and shape, the dominant genes cause the rice to be short and round.

The direction and order of dominance can be seen in the value (Wr+Vr) component. Based on the value (Wr+Vr) in Table 4 the dominance order of rice grain length and shape was Inpago Unsoed 1, Koshihikari, Tarabas, Basmati Delta 9 and Basmati Pakistan. This is reinforced by the graph of the relationship between the covariance (Wr) and variance (Vr) in Figure 1 and 2.

Distribution of parental array points along the regression line reflected genetic diversity of a trait (51). The array point was scattered along the regression line for rice length and shape, indicating genetic diversity for these traits. The position of the parents on the graph of the relationship between the covariance (Wr) and variance (Vr) reflects the order of dominance. The position of parent which is closer to zero indicating it contains most dominant genes, vice versa farther away a parent position to zero reflecting it contains more recessive genes (47,50). Inpago Unsoed 1 is the closest to zero, reflecting that this parent has the mostly dominant genes for rice length and shape. Basmati Pakistan contain most a recessive gene for the rice length and shape since it is the farthest from zero. Basmati which has extra-long and slender rice contains the most recessive gene, this means that the gene controlling long and slender rice is recessive to the short and round rice gene. This result agreement with finding of Kato (29), Murai & Kinoshita (41) and Ali et al. (52).

Tabel 4. The value (Wr+Vr) of rice length and shape

Genotypes	Rice length	Rice shape
Basmati Delta 9	2,32	1,30
Basmati Pakistan	2,46	1,43
Inpari 31	1,99	0,93
Inpago Unsoed 1	1,00	0,37
Koshihikari	1,75	0,69
Tarabas	1,87	0,73

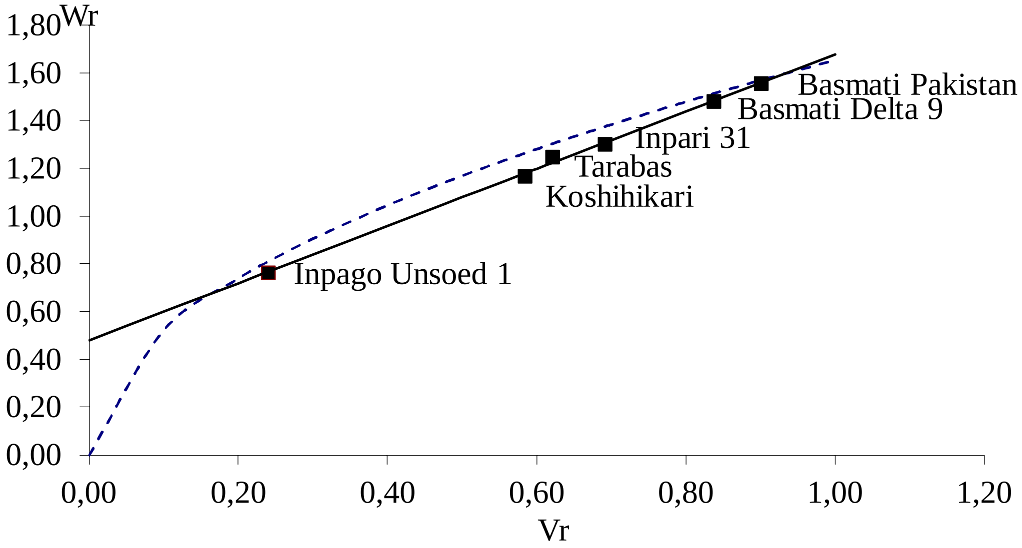

Figure 1. Covariance (Wr) and variance (Vr) graph of rice length.

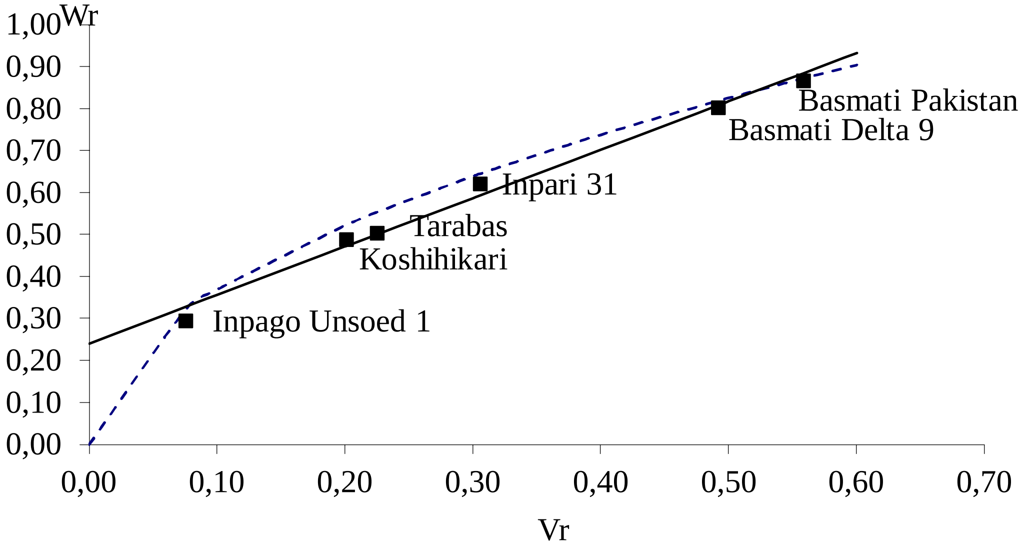

Figure 2. Covariance (Wr) and variance (Vr) graph of rice shape.

The straight line intercepted the vertical axis (Wr) above the origin for rice length and shape (Figure 1 and 2). The straight line intercepted the vertical axis (Wr) above the origin indicated the indicating partial dominance of the genes controlling a trait (21,50,51). This reveals that the rice length and shape was controlled by a partial dominant gene as described previously. Partial dominance results in the appearance of each trait having a tendency to approach the mid parent value and not having over dominance which exceeds the best parent (53). This is reflected in the h^2 value of rice length and shape which is not significantly different so that there is no difference between the F_1 average and the parents' average.

3.2.10. Heritability

Broad sense heritability (h^2_{bs}) estimates for rice length and shape are similar, 0,99. Narrow sense heritability (h^2_{ns}) estimates for these traits is 0.94 and 0.91, respectively (Table 3.). Heritability values more than 0.5 are categorized as high (Stansfield, 1991), thus broad sense heritability (h^2_{bs}) for rice length and shape categorized as high heritability. Similar findings were reported by previous studies (54)

The estimated value of broad sense heritability indicates the relative contribution of genetic factors to variation of the observed trait (55). A high broad sense heritability value indicates that traits are more influenced by genetic than environmental factors (56). In this study, broad sense heritability estimate of rice length and shape is high, indicating the influence of genetic was greater than environmental factors. Low influence of environmental factors were also reflected in the non-significant environmental variance observed in Table 3.

Narrow sense heritability estimates indicate the role of additive gene action on a trait. High estimated of narrow sense heritability indicates more additive gene action than non-additive gene action (4,57–59). In this study, the narrow sense heritability estimate of rice length and shape was high, meaning that additive gene action played a more important role than non-additive gene action.

Ratio of narrow sense heritability and broad sense heritability reflecting the role of additive and non-additive gene action for a trait. The ratio value closer to one indicates the total genetic variance of a trait is caused by additive gene action (60). Table 3 showed ratio of narrow sense heritability and broad sense heritability ratios are 0.95 for rice length and 0.92 for rice shape respectively. This indicating that additive gene action determines the rice size and shape more than non-additive gene action as previously described. Traits that have high additive variance and heritability in the F_1 population may be selected using individual selection. Individual selection may be applied to traits that have additive variance and high heritability in the F_1 population (21) so that selection of rice length and shape may be carried out using individual selection such as pedigree. This finding agreement with Raju et al. (40).

3.3. Combining ability estimation of rice length and shape

Gene action and cytoplasm influence of the female parent for a trait can be predicted through combining ability. Variances of general combining ability (GCA), specific combining ability (SCA), and reciprocals were obtained from diallel analysis of Griffing method-1. GCA and SCA variance are associated with non-additive and additive gene action, respectively (61–63). Reciprocal variance is useful for knowing the effect of female parent cytoplasm of a trait (64).

General combining ability (GCA) is endorsed to additive gene action and specific combining ability (SCA) is mainly attributed to non-additive gene action (59,65). This study showed significant GCA and SCA effects of rice length and shape (Table 4). The significant GCA and SCA indicated the importance of both additive and non-additive gene actions in the expression of these traits. This finding was in agreement with Singh et al. and Soni et al. (66,67).

The magnitude of the effect of additive gene action and non-additive gene action on a trait can be determined from GCA:SCA ratio (68). A high GCA:SCA ratio indicates that additive gene action plays a more important role in the expression of a trait than non-additive gene action (69). Ratio of GCA:SCA greater than one indicates that additive gene action has more influence on the expression of a trait and conversely, a GCA:SCA ratio less than one

reflected that non-additive gene action has more influence on the expression of a trait (70). In this study, ratio of GCA:SCA of rice length and shape is greater than one (50.060 and 32.280, respectively) (Table 4), indicating additive gene action is more influential than non-additive gene action on the expression of these traits. These results agree with the estimation of gene action using the Hayman method as described previously. Additive gene action in grain length and shape has been previously reported (66,67). Therefore, the selection for grain length and shape will be effective using pedigree method (71).

Table 4. Analysis of variance of combining ability and GCA:SCA ratio of rice length and shape

Source of variance	Degree of freedom	Mean square	
		Rice length	Rice shape
General combining ability (GCA)	5	6.909 *	3.154 *
Specific combining ability (SCA)	15	0.138 *	0.092 *
Reciprocal	15	0.020 ^{ns}	0.006 ^{ns}
Error	70	0.015	0.007
GCA:SCA ratio		50.060	34.280

* = significantly different at the level of 5%, ns = not significantly different

Non-significant reciprocal effects were observed for both rice length and shape (Table 4). This indicated that there was no influence of the female parent cytoplasm on the inheritance of these traits (64,72). So that, the size and shape of the rice are not affected by the female parent cytoplasm.

4. CONCLUSION

The influence of additive and non-additive gene action on rice length and shape were confirmed. The effect of the additive gene action was greater than the non-additive gene action while both broad sense and narrow sense heritability were high. This revealed that that the selection of these traits at the early generation using the pedigree selection method may be considered. Rice length and shape were not affected by the female parent cytoplasm so that F_2 and $F_{2reciprocal}$ populations might be combined into one population in the next selection generation.

5. ACKNOWLEDGEMENT

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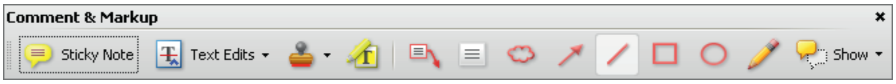

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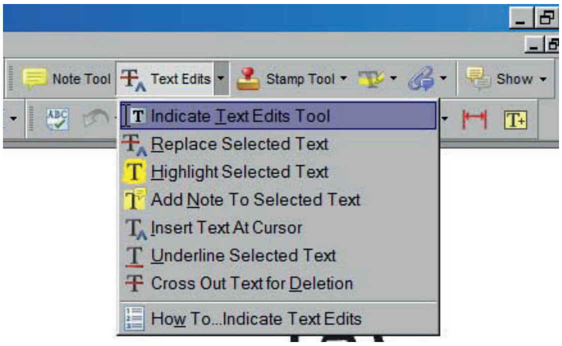

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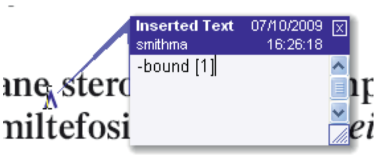

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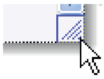

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Research Article

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Diallel analysis of length and shape of rice using Hayman and Griffing method

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Abstract: Length and shape of rice are important physical qualities that determine public acceptance of a variety and determine the price. Improvement of length and shape of rice requires information on the genetic parameters of these traits. Diallel analysis is one of the methods usually used to estimate the genetic parameters of a trait. The purpose of this study was to estimate the genetic parameters of length and shape of rice using full diallel analysis. The plant material used was a full diallel cross-population of six rice genotypes, namely, Basmati Pakistan, Basmati Delta 9, Inpago Unsoed 1, Inpari 31, Koshihikari, and Tarabas. Thirty-six genotypes consisting of parents, F_1 and $F_{1\text{reciprocal}}$, were planted using a randomized block design with three replications. The data of rice grain length and length:width ratio were used for diallel analysis using the Hayman and Griffing method-1. The results showed additive and non-additive gene action influencing the length and shape of rice. The effect of the additive gene action is greater than the non-additive gene action and the heritability value, both broad sense and narrow sense heritability is high, revealed the selection of these traits at the early generation using the pedigree selection method may be considered. Length and shape of rice were not affected by the female parent cytoplasm so that F_2 and $F_{2\text{reciprocal}}$ populations may be combined into one population the next generation.

Keywords: diallel analysis, rice length, rice shape

1 Introduction

Rice (*Oryza sativa* L.) is one of the major food crops in the world. Nearly 50% of the world population consumes rice as the staple food; therefore, it has an important role in global food security [1,2]. Indonesia is the world's third largest rice producer, and it is also one of the world's main rice consumers [3]. More than 80% of Indonesian people consume rice as a staple food, and it contributes 62.1% of the energy intake [4]. It is the main source of income of approximately 18 million household farmers [5]. It also has strategic value from economic, environmental, social, and political aspects [6,7]. Therefore, rice self-sufficiency in Indonesia is required to fulfill the needs.

The government's program for rice self-sufficiency has four main targets, that is, to increase the national production, to stabilize the domestic prices and reserve stocks, and to minimize imports [8]. Improving yield potential of rice varieties through plant breeding plays an important role to increase the national production. High yielding rice varieties contributed to 56% of the national rice production [6]. Thus, rice breeding in Indonesia aims to develop high yielding varieties that are in accordance with ecosystem conditions, social, cultural, and community interests [9].

Yield still is the main target of rice development; however, rice grain quality is now getting more attention due to increasing awareness of its importance [10]. Rice grain quality determines the market price, consumer acceptability of a variety, and consumer acceptability of a variety and becomes the second goal of rice plant breeding after yield [11,12]. High yielding varieties with high rice grain quality are easy for farmers to adopt [13].

Grain quality consists of rice length, rice shape, rice translucency, and rice chalkiness. Rice quality directly affects consumer acceptance. Consumers determine the rice quality first from grain quality, that is, rice appearance, ~~rice length, and shape,~~ which is followed by cooking quality and taste [14,15]. Hence, length and shape of rice determine the level of rice market demands and price [16].

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Therefore, breeding rice varieties that encompass desirable length and shape of rice became a major concern for rice breeders in Indonesia.

A rice breeding program begins with increasing genetic diversity by crossing rice genotypes with wide genetic differences, followed by the selection of interest. The effectiveness of plant breeding programs increases in conjunction with scientific research that expands knowledge of plant genetic information [17]. An effective and efficient breeding program is determined by the genetic information that controls the inheritance of traits under study [18,19]. Sometimes selection in segregation populations results in low-quality progenies to fulfill breeding objectives [20]. Hence, it is necessary to know genetic information of traits before determining a breeding and selection method [21]. Diallel analysis is one of the manners to obtain genetic information for grain quality traits in rice such as length and shape of grain.

Diallel analysis is a mating design, which involves mating a set of parents in all possible combinations, to produce a set of F_1 progeny [22,23]. This method is useful to obtain genetic information that controls the inheritance of traits under study in early generation [24,25]. It is also the quickest method for understanding the genetic control of the inheritance of quantitative traits [26].

Diallel analysis can be carried out using Hayman and Griffing methods. Hayman's method can be used to study gene action, genetic components, and heritability [27], whereas Griffing's method [28] is used to estimate general combining ability (GCA), specific combining ability (SCA), and reciprocal effects. Also, it can be used to calculate additive and non-additive effects. Hayman and Griffing methods are often used together for interpretation of complementary data [21]. Hayman and Griffing methods have been used (either one or both) to obtain genetic information of plant traits. It has been widely used to study genetic parameters of length and shape of rice [29–41]. The results of the study show various conclusions. Furthermore, this research is rarely performed in Indonesia [42]. The present research was conducted to study genetic components of F_1 population from a cross of six parents with various lengths and shapes of rice. The purpose of this study was to estimate the genetic parameters of length and shape of rice using the full diallel analysis.

2 Materials and methods

2.1 Location of the experiment

A field experiment was conducted at the experimental farm of Agriculture Faculty, Jenderal Soedirman University, Purwokerto, Central Java, Indonesia. This location is at coordinates 7°24′28.7″LS and 109°15′13.3″N, and it is at an altitude of 112 m above the sea level. The experiment was carried out from June 2019 to December 2019.

2.2 Plant material

Six rice genotypes, i.e., Basmati Delta 9, Basmati Pakistan, Inpari 31, Inpago Unsoed 1, Koshihikari, and Tarabas rice, were used as the parents in this study. These parents have different origins and have various ~~grain sizes and shapes~~ (Table 1). The research material used consisted of 36 rice genotypes, which were developed from full diallel crosses among six parents. It consists of 6 parents, 15$F_{1,}$ and 15$F_{1\text{reciprocal}}$.

2.3 Experimental design

The experimental design was a randomized complete block design with three replications. Seeds of 36 genotypes were sown in a seed box for 2 weeks, followed by transplanting to 35 cm × 40 cm polybags containing 8 kg of inceptisol soil. Each polybag consisted of one plant per genotype. Recommendations for rice cultivation and plant protection were adopted. Fertilizer applications were 0.4 g N/polybag and 1.0 g N-P-K/polybag was applied. Fertilizer was applied twice, i.e., 10 and 20 days after transplanting.

2.4 Data collection and analysis

At maturity, panicles were harvested from parents and all generations individually. Panicles were subjected as samples of length and shape of rice. The shape of rice is determined by ~~grain~~ length-to-width ratio [43]. Therefore, the observed trait in this study is rice length, width, and

Table 1: Six rice genotypes used for diallel mating design

No.	Genotype	Length and shape of rice	Origin
1	Basmati Delta 9	Extra-long, slender	India
2	Basmati Pakistan	Extra-long, slender	Pakistan
3	Inpari 31	Long, medium	Indonesia
4	Inpago Unsoed 1	Medium, medium	Indonesia
5	Koshihikari	Short, round	Japan
6	Tarabas	Short, round	Indonesia

length-to-width ratio. Digital caliper was used to measure the ~~grain length and width~~. Data collected were used for diallel analysis to estimate the genetic parameters of length and shape of rice. Q7 Diallel analysis was performed using Hayman and Griffing method-1 [44] were performed using the software Microsoft® Excel.

1. Analysis of variance for F_1 in full diallel crosses

   Analysis of variance for F_1 in full diallel crosses for length and shape of rice followed the statistical model

$$Y_{ijkl} = m + T_{ij} + b_k + (bT)_{ijk} + e_{ijkl}, \tag{1}$$

where m is the general mean, T_{ij} is the effect of $i \times j$th genotype, b_k is the effect of kth block, $(bT)_{ijk}$ is the interaction effect, and e_{ijkl} is the error effect.

2. Genetic components of variation

Genetic components of variation were calculated using the following formulas:

$$\text{Regression coefficient of } b\ (W_r, V_r) = \frac{\text{Cov}(W_r, V_r)}{\text{Var}(V_r)}, \tag{2}$$

Q8 where W_r is the covariance between parents and their offspring, V_r is the variance of each array, $\text{Cov}(W_r,V_r)$ is the covariance of (W_r,V_r), and $\text{Var}(V_r)$ is the variance of V_r.

$$\text{Additive genetic variance } (D) = V_{0L0} - E, \tag{3}$$

where V_{0L0} is the variance of parents and E is the environmental variance.

$$\text{Dominance variance } (H_1) = V_{0L0} - 4W_{0L01} + 4V_{1L1} - (3n - 2)E/n, \tag{4}$$

where V_{0L0} is the variance of parents, W_{0L01} is the covariance between the parents and the arrays, V_{1L1} is the mean variance of the arrays, n is the number of parents, and E is the environmental variance.

$$\text{Proportions of positive or negative genes in the parent } (H_2) = 4V_{1L1} - 4V_{0L1} - 2E, \tag{5}$$

where V_{1L1} is the mean variance of the arrays, V_{0L1} is the variance of the mean of arrays, and E is the environmental variance.

$$\text{Mean covariance of additive and dominance } (F) = 2V_{0L0} - 4W_{0L0} - 2(n - 2)E/n, \tag{6}$$

where V_{0L0} is the variance of parents, W_{0L01} is the covariance between the parents and the arrays, n is the number of parents, and E is the environmental variance.

$$\text{Dominance effect } (h^2) = 4(M_{L1} - M_{L0})^2 - 4(n - 1)E/n^2, \tag{7}$$

where $(M_{L1} - M_{L0})^2$ is the difference between the mean of the parents and the mean of their n^2 progeny, n is the number of parents, and E is the environmental variance.

$$\text{Environmental variance } (E) = 1/r(\text{Error SS} + \text{Rep. SS}) / [((r-1) + (c - 1)) \times (r - 1)], \tag{8}$$

where Error SS is the sum square of error, Rep. SS is the sum square of replication, r is the number of replications, and c is the number of errors.

$$\text{Average degree of dominance} = (H_1/D)^{1/2}, \tag{9}$$

where H_1 is the dominance variance and D is the additive genetic variance. Q9

$$\text{The proportion of genes with positive and negative effects in the parent} = H_2/4H_1, \tag{10}$$

where H_1 is the dominance variance and H_2 is the proportion of positive or negative genes in the parent.

$$\text{The ratio dominant and recessive gene in the parent} = [(4DH_1)^{1/2} + F]/(4DH_1)^{1/2} - F, \tag{11}$$

where D is the additive genetic variance, H_1 is the dominance variance, and F is the mean covariance of additive and dominance.

$$\text{Number of gene groups} = h^2/H_2, \tag{12}$$

where h^2 is the dominance effect and H_2 is the proportion of positive or negative genes in the parent.

$$\text{The coefficient correlation between } (W_r + V_r) \text{ and } Y_r(r) = \frac{\text{Cov}\ (W_r + V_r),\ Y_r}{\sqrt{\text{Var}\ (W_r + Y_r) \cdot \text{Var}(Y_r)}}, \tag{13}$$

where $(W_r + V_r)$ is the parental order of dominance, Y_r is the parental measurement, $\text{Cov}(W_r + V_r)$ is the covariance of $(W_r + V_r)$, $\text{Var}(W_r + V_r)$ is the variance of $(W_r + V_r)$, and Var (Y_r) is the variance of Y_r.

$$\text{Broad-sense heritability } (h^2_{bs}) = (1/2D + 1/2H_1 - 1/4H_2 - 1/2F)/(1/2D + 1/2H_1 - 1/4H_2 - 1/2F + E), \tag{14}$$

where D is the additive genetic variance, H_1 is the dominance variance, H_2 is the proportion of positive or negative genes in the parent, F is the mean covariance of additive and dominance, and E is the environmental variance.

$$\text{Narrow-sense heritability } (h^2_{ns}) = (1/2D + 1/2H_1 - 1/2H_2 - 1/2F) / (1/2D + 1/2H_1 - 1/2H_2 - 1/2F + E), \tag{15}$$

where D is the additive genetic variance, H_1 is the dominance variance, H_2 is the proportion of positive or negative genes in the parent, F is the mean covariance of additive and dominance, and E is the environmental variance.

2.5 Combining ability analysis

The statistical model for the analysis variance of combining ability that was used was as follows:

$$Y_{ij} = m + g_i + g_j + S_{ij} + r_{ij} + \frac{1}{bc}\sum\sum e_{ijkl}, \qquad (16)$$

where Y_{ij} is the mean of $i \times j$th genotype, m is the general mean, g_i is the general combing ability (gca) effect of ith parent, g_j is the general combing ability (gca) effect of jth parent, S_{ij} is the interaction, i.e., SCA effect, r_{ij} is the reciprocal effect, and $\frac{1}{bc}\sum\sum e_{ijkl}$ is the mean error effect.

$$\text{GCA variance } (g_i) = \frac{1}{2n}\sum(Y_{i.} + Y_{.j}) - \frac{1}{n^2}Y^2, \qquad (17)$$

Q10 where $Y_{i.}$ is the total mean value of ith genotype cross, $Y_{.j}$ is the total mean value of jth genotype selfing, n is the number of parents, and Y is the grand total.

$$\text{SCA variance } (s_{ij}) = \frac{1}{2}(Y_{ij} + Y_{ij}) - \frac{1}{2n}(Y_{i.} + Y_{.i} + Y_{j.} + Y_{.j}) + \frac{1}{n^2}Y, \qquad (18)$$

where Y_{ij} is the mean of $i \times j$th genotype, Y_{ji} is the mean of $j \times i$th genotype, $Y_{i.}$ is the total of mean value of ith genotype cross, $Y_{.i}$ is the total of mean value of ith genotype selfing, $Y_{j.}$ is the total of mean value of jth genotype cross, $Y_{.j}$ is the total of mean value of jth genotype selfing, n is the number of parents, and Y is the grand total.

$$\text{Reciprocal variance } (r_{ij}) = \frac{1}{2} = (Y_{ij} - Y_{ji}), \qquad (19)$$

where Y_{ij} is the mean of $i \times j$th genotype and Y_{ji} is the mean of $j \times i$th genotype.

3 Results and discussion

3.1 Analysis of variance for genotypes

Analysis of variance showed significant difference among genotypes for length and shape of rice grain (Table 2). Similar findings were also reported by Bano and Singh [39] and Hijam et al. [37]. Significantly different in the analysis of variance among genotypes is a requirement for estimating genetic parameters using diallel analysis [44]. Thus, significant differences among the genotypes for length and shape of rice indicate that they are suitable for further genetic studies.

Table 2: Analysis of variance for F_1 in a full diallel cross for length and shape of rice Q11

Source of variation	Degrees of freedom	Mean square	
		Rice length (mm)	Rice shape
Block	2	0.06	0.01
Genotype	35	3.16*	1.51*
Error	70	0.04	0.02

*Significantly different at the level of 5%.

3.2 Genetic components of variation

3.2.1 Gene interaction

The values of regression coefficient of $b(W_r, V_r)$ for length and shape of rice (1.20 and 1.15, respectively) were not significantly different from one (Table 3). Similar results reported by Bano and Singh [39] for kernel length before cooking (rice length) and kernel length/breadth ratio before cooking (rice length). The value of regression of coefficient of $b(W_r, V_r)$ may be used to determine the gene

Table 3: Estimates of genetic components of variation for length and shape of rice

Genetic components	Rice length (mm)	Rice shape
$b(W_r, V_r)$	1.20ns	1.15ns
D	2.72*	1.36*
H_1	0.26*	0.19*
H_2	0.25*	0.17*
F	0.44*	0.33*
h^2	−0.01ns	0.04ns
E	0.01ns	0.01ns
$(H_1/D)^{1/2}$	0.31	0.38
$H_2/4H_1$	0.23	0.22
Kd/Kr	1.71	1.95
h^2/H_2	−0.03	0.22
$r[(W_r + V_r),Y_r]$	0.69	0.89
h^2_{bs}	0.99	0.99
h^2_{ns}	0.94	0.91
Ratio of $h^2_{ns}:h^2_{bs}$	0.95	0.92

*Significantly different at the level of 5%, ns = not significantly different.

interaction of a trait. Based on *t* test, a significantly different value of $b(W_r, V_r)$ from one indicates gene interaction, while a non-significantly different value of $b(W_r, V_r)$ from one reflected no gene interaction [44]. It means that there is no interaction between genes controlling length and shape of rice in this study.

3.2.2 Additive (*D*) and dominance (H_1) variance

Additive (D) and dominance (H_1) variance were significantly different for length and shape of rice (Table 3). Significantly different values of the components D and H_1 indicated the importance of both additive and non-additive gene action in the expression of traits [45], so that length and shape of rice are influenced by both additive and non-additive types of gene action. Similar findings were also observed by Kato [29], Fu et al. [31], Daradjat and Rumanti [42], Kumar et al. [32,33], Rafii et al. [30], and Senthil Kumar and Mudhalvan [38] for length and size of rice.

The results showed the value of additive variance (D) for length and shape of rice is 2.72 and 1.36, respectively, and the value of dominance variance (H_1) for length and shape of rice is 0.26 and 0.19, respectively (Table 3). These showed that the influence of additive variance is greater than dominance variance ($D > H_1$) for length and shape of rice. Higher magnitude of additive variance (D) indicated the greater role of additive gene action, while dominance variance indicated the greater importance of non-additive gene action *vice versa* [40,45]. The value of the additive variance, which is greater than the dominance variance, indicates the increasing importance of additive gene action [32,33]. This means that in this study, length and shape of rice are more influenced by additive gene action than non-additive gene action. These results are in accordance with the findings of Kato [29] and Thattil and Perera [46] for length and size of rice. However, Daradjat and Rumanti [42] and Senthil Kumar and Mudhalvan [38] reported that different results are an indication that the non-additive gene action was more predominant than additive gene action for length and size of rice.

3.2.3 Gene distribution in the parents

Gene distribution in the parents can be determined by H_2 values. The results showed that the H_2 values for length and shape of rice were significantly different (Table 3). This indicates that the genes determining the inheritance of length and shape of rice are not evenly distributed among the parents. Genes controlling length and shape of rice that are not evenly distributed in parents have also been reported [38].

Proportion of positive genes to negative genes is indicated by the value of H_1 component against H_2 component. The value of H_1 is greater than the H_2 indicating more positive genes than negative genes, *vice versa* the value of the H_1 is smaller than H_2 reflecting the positive are gene less than the negative genes [21,47]. Table 3 shows that the value of H_1 is 0.26 and 0.19, respectively, and the value of H_2 is 0.27 and 0.17, respectively, for length and shape of rice. It shows that the value of H_1 is greater than H_2 for length and shape of rice, meaning that positive genes are more involved in determining length and shape of rice than negative genes. The results were in agreement with those of Raju et al. [40].

Proportion of positive genes to negative genes in all parents also can be seen from ratio of $H_2/4H_1$. Values lower than 0.25 indicate that positive and negative genes are not present in unequal proportions in the parents [45,48]. The results showed the value of $H_2/4H_1$ for length and shape of rice is 0.23 and 0.22, respectively (Table 3). They were lower than 0.25, reflecting the unequal distribution of positive and negative genes in the parents. Similar findings were reported by previous studies [38–40].

3.2.4 Dominance level

The influence of dominance can be seen from the value of mean degree of dominance as estimated by $(H_1/D)^{1/2}$. A value $(H_1/D)^{1/2}$ more than 1 indicates over dominance, while a value $(H_1/D)^{1/2}$ between 0 and 1 indicates partial dominance (Hayman, 1954). Table 3 shows the value $(H_1/D)^{1/2}$ of length and shape of rice is less than 1 (0.31 and 0.38, respectively), which indicated the existence of partial dominance in these traits. Rice length controlled by a partial dominance gene was also reported by Kato [29].

3.2.5 Dominance effect

Dominance effect is indicated by the h^2 value. Table 3 shows that h^2 values were not significantly different for length and shape of rice. This indicated no difference in average deviation of F_1 from most parents [47].

3.2.6 Environmental variance

Table 3 shows that environmental variance exhibited no significant influence on length and shape of rice. This

reflected no influence of environmental factor on the expression of the traits studied [45]. Therefore, it is known that the expression of length and shape of rice is more influenced by genetic than environment effects.

3.2.7 Proportion of dominant gene to recessive gene

Proportion of dominant genes to recessive genes is shown by F component and Kd/Kr ratio. The positive value of F component reflects a greater number of dominant genes than recessive genes in the parent [47,49]. A ratio of Kd/Kr greater than one indicates more dominant genes in the parent; conversely, the ratio of Kd/Kr smaller than one indicated more recessive genes in the parent [44]. The results showed a positive value of F component, and a ratio of Kd/Kr of the length and shape of rice is greater than one (1.71 and 1.95, respectively) (Table 3), which indicated more dominant genes in the parent for length and shape of rice. The same finding was reported by Raju et al. [40].

3.2.8 Number of gene groups

Component of h^2/H_2 gives an indication of the number of gene groups that control a trait. The h_2/H_2 values of length and shape of rice are −0.03 and 0.22, respectively, lower than one. The ratio smaller than one indicated the involvement of single gene or one group of genes, which are responsible for their genetic control [45]. As a result, length and shape of rice are controlled by at least a single group of genes.

3.2.9 Direction and order of dominance

The positive value of the correlation between $(W_r + V_r)$ and Y_r and close to unity indicates that dominant alleles have predominantly negative effects, i.e., acting in the direction of lower yields [50]. A positive value is obtained in the correlation $(W_r + V_r)$ and Y_r for length and shape of rice (Table 3). That is, in length and shape of rice, the dominant genes cause the rice to be short and round.

The direction and order of dominance can be seen in the value $(W_r + V_r)$ component. Based on the value $(W_r + V_r)$ in Table 4, the dominance order of length and shape of ~~rice grain was~~ Inpago Unsoed 1, Koshihikari, Tarabas, Basmati Delta 9, and Basmati Pakistan. This is reinforced by the graph of the relationship between the covariance (W_r) and variance (V_r) in Figures 1 and 2.

Table 4: Value $(W_r + V_r)$ of length and shape of rice Q14

Genotypes	Rice length	Rice shape
Basmati Delta 9	2.32	1.30
Basmati Pakistan	2.46	1.43
Inpari 31	1.99	0.93
Inpago Unsoed 1	1.00	0.37
Koshihikari	1.75	0.69
Tarabas	1.87	0.73

Distribution of parental array points along the regression line reflected genetic diversity of a trait [51]. The array point was scattered along the regression line for length and shape of rice, indicating genetic diversity for these traits. The position of the parents on the graph of the relationship between the covariance (W_r) and variance (V_r) reflects the order of dominance. The position of parent which is closer to zero indicating it contains most dominant genes, *vice versa* farther away a parent position to zero reflecting it contains more recessive genes [47,50]. Q15 Inpago Unsoed 1 is the closest to zero, reflecting that this parent has the mostly dominant genes for length and shape of rice. Mostly, Basmati Pakistan contains a recessive gene for length and shape of rice since it is the farthest from zero. Basmati, which has extra-long and slender rice, contains the most recessive gene, and this means that the gene controlling long and slender rice is recessive to the short and round rice gene. This result is in agreement with the findings of Kato [29], Murai and Kinoshita [41], and Ali et al. [52].

The straight line intercepted the vertical axis (W_r) above the origin for length and shape of rice (Figures 1 and 2). The straight line that intercepted the vertical axis (W_r) above the origin indicated partial dominance of the genes controlling a trait [21,50,51]. This reveals that length and shape of rice were controlled by a partial dominant gene as described previously. Partial dominance results in the appearance of each trait having a tendency to approach the mid-parent value and not having overdominance, which exceeds the best parent [53]. This is reflected in the h^2 value of length and shape of rice, which is not significantly different, so that there is no difference between the F_1 average and the parents' average.

3.2.10 Heritability

Broad sense heritability (h^2_{bs}) estimates for length and shape of rice are similar to 0.99. Narrow sense heritability (h^2_{ns}) estimates for these traits are 0.94 and 0.91,

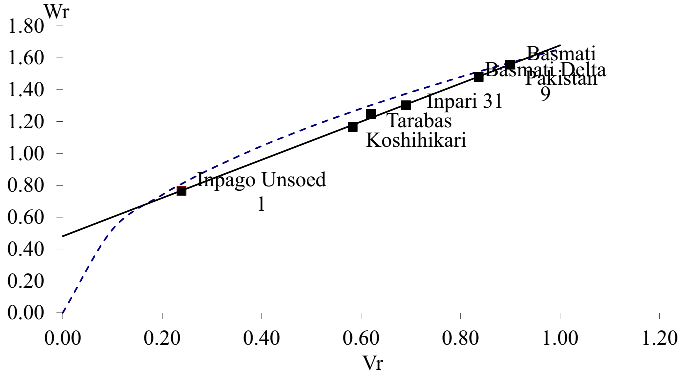

Figure 1: Covariance (W_r) and variance (V_r) graph of rice length.

respectively (Table 3). Values of heritability more than 0.5 are categorized as high (Stansfield, 1991); thus, broad-sense heritability (h^2_{bs}) for length and shape of rice is categorized as high heritability. Similar findings were reported by previous studies [54].

The estimated value of broad-sense heritability indicates the relative contribution of genetic factors to the variation of the observed trait [55]. A high broad-sense heritability value indicates that traits are more influenced by genetic than environmental factors [56]. In this study, broad-sense heritability estimate of length and shape of rice is high, indicating the influence of genetic was greater than environmental factors. Low influence of environmental factors was also reflected in the non-significant environmental variance observed in Table 3.

Narrow sense heritability estimates indicate the role of additive gene action in a trait. Estimates of narrow-sense heritability indicate more additive gene action than non-additive gene action [4,57–59]. In this study, the narrow sense heritability estimate of length and shape of rice was high, meaning that additive gene action played a more important role than non-additive gene action.

Ratio of narrow-sense heritability and broad-sense heritability reflects the role of additive and non-additive gene action in a trait. The ratio value closer to one indicates the total genetic variance of a trait is caused by additive gene action [60]. Table 3 shows that the ratio of narrow-sense heritability and broad-sense heritability is 0.95 for rice length and 0.92 for rice shape, respectively. This indicates that additive gene action determines size and shape of rice more than non-additive gene action as previously described. Traits that have high additive variance and heritability in the F_1 population may be selected using individual selection. Individual selection may be applied to traits that have additive variance and high heritability in the F_1 population [21] so that the selection of length and shape of rice may be carried out using individual selection such as pedigree. This finding was in agreement with that of Raju et al. [40].

3.3 Combining ability estimation of length and shape of rice

Gene action and cytoplasm influence of the female parent for a trait can be predicted through combining ability. Variances of GCA, SCA, and reciprocals were obtained from diallel analysis of Griffing method-1. Variances of

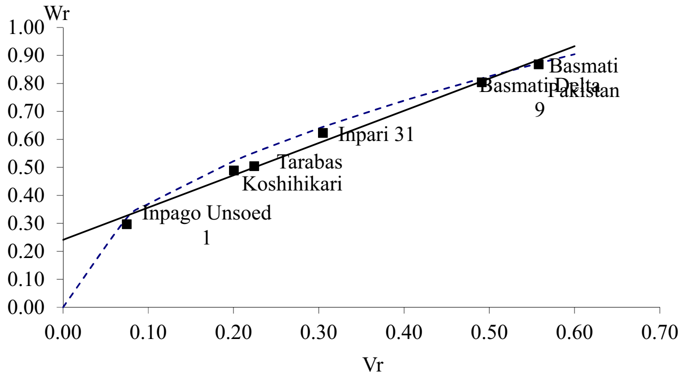

Figure 2: Covariance (W_r) and variance (V_r) graph of rice shape.

Table 5: Analysis of variance of combining ability and GCA:SCA ratio of length and shape of rice

Source of variance	Degree of freedom	Mean square	
		Rice length	Rice shape
GCA	5	6.909*	3.154*
SCA	15	0.138*	0.092*
Reciprocal	15	0.020^{ns}	0.006^{ns}
Error	70	0.015	0.007
GCA:SCA ratio		50.060	34.280

*Significantly different at the level of 5%, ns = not significantly different.

GCA and SCA are associated with non-additive and additive gene actions, respectively [61–63]. Reciprocal variance is useful for knowing the effect of female parent cytoplasm of a trait [64].

GCA is endorsed to additive gene action, and SCA is mainly attributed to non-additive gene action [59,65]. This study shows significant effects of GCA and SCA on length and shape of rice (Table 5). The significant GCA and SCA indicated the importance of both additive and non-additive gene actions in the expression of these traits. This finding was in agreement with that of Singh et al. and Soni et al. [66,67].

The magnitude of the effect of additive gene action and non-additive gene action on a trait can be determined from GCA:SCA ratio [68]. A high GCA:SCA ratio indicates that additive gene action plays a more important role in the expression of a trait than non-additive gene action [69]. Ratio of GCA:SCA greater than one indicates that additive gene action has more influence on the expression of a trait, and conversely, a GCA:SCA ratio less than one reflected that non-additive gene action has more influence on the expression of a trait [70]. In this study, ratio of GCA:SCA of length and shape of rice is greater than one (50.060 and 32.280, respectively) (Table 5), indicating that additive gene action is more influential than non-additive gene action on the expression of these traits. These results agree with the estimation of gene action using the Hayman method as described previously. Additive gene action in length and shape of grain has been previously reported [66,67]. Therefore, the selection of length and shape of grain will be effective using pedigree method [71].

Non-significant reciprocal effects were observed for both length and shape of rice (Table 5). This indicated that there was no influence of the female parent cytoplasm on the inheritance of these traits [64,72] so that the size and shape of the rice are not affected by the female parent cytoplasm.

4 Conclusion

The influence of additive and non-additive gene actions on length and shape of rice was confirmed. The effect of the additive gene action was greater than the non-additive gene action, while both broad-sense heritability and narrow-sense heritability were high. This revealed that the selection of these traits at the early generation using the pedigree selection method may be considered. Length and shape of rice were not affected by the female parent cytoplasm so that F_2 and $F_{2\text{reciprocal}}$ populations might be combined into one population in the next selection generation.

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Research Article

Agus Riyanto, Ponendi Hidayat, Y. Suprayogi, Totok Agung Dwi Haryanto*

Diallel analysis of length and shape of rice using Hayman and Griffing method

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Abstract: Length and shape of rice are important physical qualities that determine public acceptance of a variety and determine the price. Improvement of length and shape of rice requires information on the genetic parameters of these traits. Diallel analysis is one of the methods usually used to estimate the genetic parameters of a trait. The purpose of this study was to estimate the genetic parameters of length and shape of rice using full diallel analysis. The plant material used was a full diallel cross-population of six rice genotypes, namely, Basmati Pakistan, Basmati Delta 9, Inpago Unsoed 1, Inpari 31, Koshihikari, and Tarabas. Thirty-six genotypes consisting of parents, F_1 and $F_{1\text{reciprocal}}$, were planted using a randomized block design with three replications. The data of rice grain length and length:width ratio were used for diallel analysis using the Hayman and Griffing method-1. The results showed additive and non-additive gene action influencing the length and shape of rice. The effect of the additive gene action was greater than the non-additive gene action, while both broad-sense heritability and narrow-sense heritability were high, revealed that the selection of these traits at the early generation using the pedigree selection method may be considered. Length and shape of rice were not affected by the female parent cytoplasm so that F_2 and $F_{2\text{reciprocal}}$ populations may be combined into one population the next generation.

Keywords: diallel analysis, rice length, rice shape

1 Introduction

Rice (*Oryza sativa* L.) is one of the major food crops in the world. Nearly 50% of the world population consumes rice as the staple food; therefore, it has an important role in global food security [1,2]. Indonesia is the world's third largest rice producer, and it is also one of the world's main rice consumers [3]. More than 80% of Indonesian people consume rice as a staple food, and it contributes 62.1% of the energy intake [4]. It is the main source of income of approximately 18 million household farmers [5]. It also has strategic value from economic, environmental, social, and political aspects [6,7]. Therefore, rice self-sufficiency in Indonesia is required to fulfill the needs.

The government's program for rice self-sufficiency has four main targets, that is, to increase the national production, to stabilize the domestic prices and reserve stocks, and to minimize imports [8]. Improving yield potential of rice varieties through plant breeding plays an important role to increase the national production. High yielding rice varieties contributed to 56% of the national rice production [6]. Thus, rice breeding in Indonesia aims to develop high yielding varieties that are in accordance with ecosystem conditions, social, cultural, and community interests [9].

Yield still is the main target of rice development; however, rice grain quality is now getting more attention due to increasing awareness of its importance [10]. Rice grain quality determines the market price, consumer acceptability of a variety, and consumer acceptability of a variety and becomes the second goal of rice plant breeding after yield [11,12]. High yielding varieties with high rice grain quality are easy for farmers to adopt [13].

Grain quality consists of rice length, rice shape, rice translucency, and rice chalkiness. Rice quality directly affects consumer acceptance. Consumers determine the rice quality first from grain quality, that is, rice appearance, length and shape of rice, which is followed by cooking quality and taste [14,15]. Hence, length and shape of rice determine the level of rice market demands and

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price [16]. Therefore, breeding rice varieties that encompass desirable length and shape of rice became a major concern for rice breeders in Indonesia.

A rice breeding program begins with increasing genetic diversity by crossing rice genotypes with wide genetic differences, followed by the traits selection of interest. The effectiveness of plant breeding programs increases in conjunction with scientific research that expands knowledge of plant genetic information [17]. An effective and efficient breeding program is determined by the genetic information that controls the inheritance of traits under study [18,19]. Sometimes selection in segregation populations results in low-quality progenies to fulfill breeding objectives [20]. Hence, it is necessary to know genetic information of traits before determining a breeding and selection method [21]. Diallel analysis is one of the manners to obtain genetic information for grain quality traits in rice such as length and shape of grain.

Diallel analysis is a mating design, which involves mating a set of parents in all possible combinations, to produce a set of F_1 progeny [22,23]. This method is useful to obtain genetic information that controls the inheritance of traits under study in early generation [24,25]. It is also the quickest method for understanding the genetic control of the inheritance of quantitative traits [26].

Diallel analysis can be carried out using Hayman and Griffing methods. Hayman's method can be used to study gene action, genetic components, and heritability [27], whereas Griffing's method [28] is used to estimate general combining ability (GCA), specific combining ability (SCA), and reciprocal effects. Also, it can be used to calculate additive and non-additive effects. Hayman and Griffing methods are often used together for interpretation of complementary data [21]. Hayman and Griffing methods have been used (either one or both) to obtain genetic information of plant traits. It has been widely used to study genetic parameters of length and shape of rice [29–41]. The results of the study show various conclusions. Furthermore, this research is rarely performed in Indonesia [42]. The present research was conducted to study genetic components of F_1 population from a cross of six parents with various lengths and shapes of rice. The purpose of this study was to estimate the genetic parameters of length and shape of rice using the full diallel analysis.

2 Materials and methods

2.1 Location of the experiment

A field experiment was conducted at the experimental farm of Agriculture Faculty, Jenderal Soedirman University, Purwokerto, Central Java, Indonesia. This location is at coordinates 7°24′28.7″LS and 109°15′13.3″N, and it is at an altitude of 112 m above the sea level. The experiment was carried out from June 2019 to December 2019.

2.2 Plant material

Six rice genotypes, i.e., Basmati Delta 9, Basmati Pakistan, Inpari 31, Inpago Unsoed 1, Koshihikari, and Tarabas rice, were used as the parents in this study. These parents have different origins and have various length and shape of rice (Table 1). The research material used consisted of 36 rice genotypes, which were developed from full diallel crosses among six parents. It consists of 6 parents, 15$F_{1,}$ and 15$F_{1\text{reciprocal}}$.

2.3 Experimental design

The experimental design was a randomized complete block design with three replications. Seeds of 36 genotypes were sown in a seed box for 2 weeks, followed by transplanting to 35 cm × 40 cm polybags containing 8 kg of inceptisol soil. Each polybag consisted of one plant per genotype. Recommendations for rice cultivation and plant protection were adopted. Fertilizer applications of 0.4 g N/polybag and 1.0 g N-P-K/polybag was applied twice i.e., 10 days and 20 days after transplanting.

2.4 Data collection and analysis

At maturity, panicles were harvested from parents and all generations individually. Panicles were subjected as samples of length and shape of rice. The shape of rice is determined by rice length-to-width ratio [43]. Therefore, the observed trait in this study is rice length, width, and

Table 1: Six rice genotypes used for diallel mating design

No.	Genotype	Length and shape of rice	Origin
1	Basmati Delta 9	Extra-long, slender	India
2	Basmati Pakistan	Extra-long, slender	Pakistan
3	Inpari 31	Long, medium	Indonesia
4	Inpago Unsoed 1	Medium, medium	Indonesia
5	Koshihikari	Short, round	Japan
6	Tarabas	Short, round	Indonesia

length-to-width ratio measured with help of digital caliper. Data collected were used for diallel analysis to estimate the genetic parameters of length and shape of rice. Diallel analysis was perfomed according to Hayman and Griffing method-1 [44] and the results were calculated using the software Microsoft® Excel.

1. Analysis of variance for F_1 in full diallel crosses

   Analysis of variance for F_1 in full diallel crosses for length and shape of rice followed the statistical model

$$Y_{ijkl} = m + T_{ij} + b_k + (bT)_{ijk} + e_{ijkl}, \tag{1}$$

where m is the general mean, T_{ij} is the effect of $i \times j$th genotype, b_k is the effect of kth block, $(bT)_{ijk}$ is the interaction effect, and e_{ijkl} is the error effect.

2. Genetic components of variation

Genetic components of variation were calculated using the following formulas:

$$\text{Regression coefficient of } b\ (W_r, V_r) = \frac{\text{Cov}(W_r, V_r)}{\text{Var}(V_r)}, \tag{2}$$

where W_r is the covariance between parents and their offspring, V_r is the variance of each array, $\text{Cov}(W_r,V_r)$ is the covariance of (W_r,V_r), and $\text{Var}(V_r)$ is the variance of V_r.

$$\text{Additive genetic variance } (D) = V_{0L0} - E, \tag{3}$$

where V_{0L0} is the variance of parents and E is the environmental variance.

Dominance variance

$$H_1 = V_{0L0} - 4W_{0L01} + 4V_{1L1} - (3n-2)E/n, \tag{4}$$

where V_{0L0} is the variance of parents, W_{0L01} is the covariance between the parents and the arrays, V_{1L1} is the mean variance of the arrays, n is the number of parents, and E is the environmental variance.

Proportions of positive or negative genes in the parent

$$H_2 = 4V_{1L1} - 4V_{0L1} - 2E, \tag{5}$$

where V_{1L1} is the mean variance of the arrays, V_{0L1} is the variance of the mean of arrays, and E is the environmental variance.

Mean covariance of additive and dominance

$$F = 2V_{0L0} - 4W_{0L0} - 2(n-2)E/n, \tag{6}$$

where V_{0L0} is the variance of parents, W_{0L01} is the covariance between the parents and the arrays, n is the number of parents, and E is the environmental variance.

Dominance effect

$$h^2 = 4(M_{L1} - M_{L0})^2 - 4(n-1)E/n^2, \tag{7}$$

where $(M_{L1} - M_{L0})^2$ is the difference between the mean of the parents and the mean of their n^2 progeny, n is the number of parents, and E is the environmental variance.

Environmental variance

$$E = 1/r(\text{Error SS} + \text{Rep. SS})/[((r-1) + (c-1)) \times (r-1)], \tag{8}$$

where Error SS is the sum square of error, Rep. SS is the sum square of replication, r is the number of replications, and c is the number of errors.

$$\text{Average degree of dominance} = (H_1/D)^{1/2}, \tag{9}$$

where H_1 is the dominance variance and D is the additive genetic variance.

$$\text{The proportion of genes with positive and negative effects in the parent} = H_2/4H_1, \tag{10}$$

where H_1 is the dominance variance and H_2 is the proportion of positive or negative genes in the parent.

$$\text{The ratio dominant and recessive gene in the parent} = [(4DH_1)^{1/2} + F]/(4DH_1)^{1/2} - F, \tag{11}$$

where D is the additive genetic variance, H_1 is the dominance variance, and F is the mean covariance of additive and dominance.

$$\text{Number of gene groups} = h^2/H_2, \tag{12}$$

where h^2 is the dominance effect and H_2 is the proportion of positive or negative genes in the parent.

The coefficient correlation between

$$(W_r + V_r) \text{ and } Y_r(r) = \frac{\text{Cov}\,(W_r + V_r),\, Y_r}{\sqrt{\text{Var}\,(W_r + Y_r) \cdot \text{Var}(Y_r)}}, \tag{13}$$

where $(W_r + V_r)$ is the parental order of dominance, Y_r is the parental measurement, $\text{Cov}(W_r + V_r)$ is the covariance of $(W_r + V_r)$, $\text{Var}(W_r + V_r)$ is the variance of $(W_r + V_r)$, and $\text{Var}(Y_r)$ is the variance of Y_r.

Broad-sense heritability

$$h^2_{\text{bs}} = (1/2D + 1/2H_1 - 1/4H_2 - 1/2F)/(1/2D + 1/2H_1 - 1/4H_2 - 1/2F + E), \tag{14}$$

where D is the additive genetic variance, H_1 is the dominance variance, H_2 is the proportion of positive or negative genes in the parent, F is the mean covariance of additive and dominance, and E is the environmental variance.

Narrow-sense heritability

$$h^2_{\text{ns}} = (1/2D + 1/2H_1 - 1/2H_2 - 1/2F)/(1/2D + 1/2H_1 - 1/2H_2 - 1/2F + E), \tag{15}$$

where D is the additive genetic variance, H_1 is the dominance variance, H_2 is the proportion of positive or negative genes in the parent, F is the mean covariance of additive and dominance, and E is the environmental variance.

2.5 Combining ability analysis

The statistical model for the analysis variance of combining ability that was used was as follows:

$$Y_{ij} = m + g_i + g_j + S_{ij} + r_{ij} + \frac{1}{bc}\sum\sum e_{ijkl}, \tag{16}$$

where Y_{ij} is the mean of $i \times j$th genotype, m is the general mean, g_i is the general combing ability (gca) effect of ith parent, g_j is the general combing ability (gca) effect of jth parent, S_{ij} is the interaction, i.e., SCA effect, r_{ij} is the reciprocal effect, and $\frac{1}{bc}\sum\sum e_{ijkl}$ is the mean error effect.

$$\text{GCA variance } (g_i) = \frac{1}{2n}\sum(Y_{i.} + Y_{.j}) - \frac{1}{n^2}Y^2, \tag{17}$$

where $Y_{i.}$ is the total mean value of ith genotype cross, $Y_{.j}$ is the total mean value of jth genotype selfing, n is the number of parents, and Y is the grand total.

$$\begin{aligned} \text{SCA variance } (s_{ij}) = {} & \frac{1}{2}(Y_{ij} + Y_{ij}) - \frac{1}{2n}(Y_{i.} + Y_{.i} + Y_{j.} \\ & + Y_{.j}) + \frac{1}{n^2}Y, \end{aligned} \tag{18}$$

where Y_{ij} is the mean of $i \times j$th genotype, Y_{ji} is the mean of $j \times i$th genotype, $Y_{i.}$ is the total of mean value of ith genotype cross, $Y_{.i}$ is the total of mean value of ith genotype selfing, $Y_{j.}$ is the total of mean value of jth genotype cross, $Y_{.j}$ is the total of mean value of jth genotype selfing, n is the number of parents, and Y is the grand total.

$$\text{Reciprocal variance } (r_{ij}) = \frac{1}{2} = (Y_{ij} - Y_{ji}), \tag{19}$$

where Y_{ij} is the mean of $i \times j$th genotype and Y_{ji} is the mean of $j \times i$th genotype.

3 Results and discussion

3.1 Analysis of variance for genotypes

Analysis of variance showed significant difference among genotypes for length and shape of rice grain (Table 2). Similar findings were also reported by Bano and Singh [39] and Hijam et al. [37]. Significantly different in the analysis of variance among genotypes is a requirement for estimating genetic parameters using diallel analysis [44]. Thus, significant differences among the genotypes for length and shape of rice indicate that they are suitable for further genetic studies.

Table 2: Analysis of variance for F_1 in a full diallel cross for length and shape of rice

Source of variation	Degrees of freedom	Mean square	
		Rice length (mm)	Rice shape
Block	2	0.06	0.01
Genotype	35	3.16*	1.51*
Error	70	0.04	0.02

*Significantly different at the level of 5%.

3.2 Genetic components of variation

3.2.1 Gene interaction

The values of regression coefficient of $b(W_r, V_r)$ for length and shape of rice (1.20 and 1.15, respectively) were not significantly different from one (Table 3). Similar results reported by Bano and Singh [39] for kernel length before cooking (rice length) and kernel length/breadth ratio before cooking (rice length). The value of regression of coefficient of $b(W_r, V_r)$ may be used to determine the gene

Table 3: Estimates of genetic components of variation for length and shape of rice

Genetic components	Rice length (mm)	Rice shape
$b(W_r, V_r)$	1.20ns	1.15ns
D	2.72*	1.36*
H_1	0.26*	0.19*
H_2	0.25*	0.17*
F	0.44*	0.33*
h^2	−0.01ns	0.04ns
E	0.01ns	0.01ns
$(H_1/D)^{1/2}$	0.31	0.38
$H_2/4H_1$	0.23	0.22
Kd/Kr	1.71	1.95
h^2/H_2	−0.03	0.22
$r[(W_r + V_r), Y_r]$	0.69	0.89
h^2_{bs}	0.99	0.99
h^2_{ns}	0.94	0.91
Ratio of h^2_{ns}:h^2_{bs}	0.95	0.92

*Significantly different at the level of 5%, ns = not significantly different.

interaction of a trait. Based on t test, a significantly different value of $b(W_r, V_r)$ from one indicates gene interaction, while a non-significantly different value of $b(W_r, V_r)$ from one reflected no gene interaction [44]. It means that there is no interaction between genes controlling length and shape of rice in this study.

3.2.2 Additive (D) and dominance (H_1) variance

Additive (D) and dominance (H_1) variance were significantly different for length and shape of rice (Table 3). Significantly different values of the components D and H_1 indicated the importance of both additive and non-additive gene action in the expression of traits [45], so that length and shape of rice are influenced by both additive and non-additive types of gene action. Similar findings were also observed by Kato [29], Fu et al. [31], Daradjat and Rumanti [42], Kumar et al. [32,33], Rafii et al. [30], and Senthil Kumar and Mudhalvan [38] for length and size of rice.

The results showed the value of additive variance (D) for length and shape of rice is 2.72 and 1.36, respectively, and the value of dominance variance (H_1) for length and shape of rice is 0.26 and 0.19, respectively (Table 3). These showed that the influence of additive variance is greater than dominance variance ($D > H_1$) for length and shape of rice. Higher magnitude of additive variance (D) indicated the greater role of additive gene action, while dominance variance indicated the greater importance of non-additive gene action *vice versa* [40,45]. The value of the additive variance, which is greater than the dominance variance, indicates the increasing importance of additive gene action [32,33]. This means that in this study, length and shape of rice are more influenced by additive gene action than non-additive gene action. These results are in accordance with the findings of Kato [29] and Thattil and Perera [46] for length and size of rice. However, Daradjat and Rumanti [42] and Senthil Kumar and Mudhalvan [38] reported that the non-additive gene action dominated over additive gene action for length and size of rice.

3.2.3 Gene distribution in the parents

Gene distribution in the parents can be determined by H_2 values. The results showed that the H_2 values for length and shape of rice were significantly different (Table 3). This indicates that the genes determining the inheritance of length and shape of rice are not evenly distributed among the parents. Genes controlling length and shape of rice that are not evenly distributed in parents have also been reported [38].

Proportion of positive genes to negative genes is indicated by the value of H_1 component against H_2 component. The value of H_1 is greater than the H_2 indicating the number of positive genes would be higher than negative genes. On contrary, the value of the H_1 is smaller than H_2 reflecting that the number of positive genes would be fewer than the negative genes [21,47]. Table 3 shows that the value of H_1 is 0.26 and 0.19, respectively, and the value of H_2 is 0.27 and 0.17, respectively, for length and shape of rice. It shows that the value of H_1 is greater than H_2 for length and shape of rice, meaning that positive genes are more involved in determining length and shape of rice than negative genes. The results were in agreement with those of Raju et al. [40].

Proportion of positive genes to negative genes in all parents also can be seen from ratio of $H_2/4H_1$. Values lower than 0.25 indicate that positive and negative genes are not present in unequal proportions in the parents [45,48]. The results showed the value of $H_2/4H_1$ for length and shape of rice is 0.23 and 0.22, respectively (Table 3). They were lower than 0.25, reflecting the unequal distribution of positive and negative genes in the parents. Similar findings were reported by previous studies [38–40].

3.2.4 Dominance level

The influence of dominance can be seen from the value of mean degree of dominance as estimated by $(H_1/D)^{1/2}$. A value $(H_1/D)^{1/2}$ more than 1 indicates over dominance, while a value $(H_1/D)^{1/2}$ between 0 and 1 indicates partial dominance (Hayman, 1954). Table 3 shows the value $(H_1/D)^{1/2}$ of length and shape of rice is less than 1 (0.31 and 0.38, respectively), which indicated the existence of partial dominance in these traits. Rice length controlled by a partial dominance gene was also reported by Kato [29].

3.2.5 Dominance effect

Dominance effect is indicated by the h^2 value. Table 3 shows that h^2 values were not significantly different for length and shape of rice. This indicated no difference in average deviation of F_1 from most parents [47].

3.2.6 Environmental variance

Table 3 shows that environmental variance exhibited no significant influence on length and shape of rice. This

reflected no influence of environmental factor on the expression of the traits studied [45]. Therefore, it is known that the expression of length and shape of rice is more influenced by genetic than environment effects.

3.2.7 Proportion of dominant gene to recessive gene

Proportion of dominant genes to recessive genes is shown by F component and Kd/Kr ratio. The positive value of F component reflects a greater number of dominant genes than recessive genes in the parent [47,49]. A ratio of Kd/Kr greater than one indicates more dominant genes in the parent; conversely, the ratio of Kd/Kr smaller than one indicated more recessive genes in the parent [44]. The results showed a positive value of F component, and a ratio of Kd/Kr of the length and shape of rice is greater than one (1.71 and 1.95, respectively) (Table 3), which indicated more dominant genes in the parent for length and shape of rice. The same finding was reported by Raju et al. [40].

3.2.8 Number of gene groups

Component of h^2/H_2 gives an indication of the number of gene groups that control a trait. The h_2/H_2 values of length and shape of rice are −0.03 and 0.22, respectively, lower than one. The ratio smaller than one indicated the involvement of single gene or one group of genes, which are responsible for their genetic control [45]. As a result, length and shape of rice are controlled by at least a single group of genes.

3.2.9 Direction and order of dominance

The positive value of the correlation between $(W_r + V_r)$ and Y_r and close to unity indicates that dominant alleles have predominantly negative effects, i.e., acting in the direction of lower yields [50]. A positive value is obtained in the correlation $(W_r + V_r)$ and Y_r for length and shape of rice (Table 3). That is, in length and shape of rice, the dominant genes cause the rice to be short and round.

The direction and order of dominance can be seen in the value $(W_r + V_r)$ component. Based on the value $(W_r + V_r)$ in Table 4, the dominance order of length and shape of rice was Inpago Unsoed 1, Koshihikari, Tarabas, Basmati Delta 9, and Basmati Pakistan. This is reinforced by the graph of the relationship between the covariance (W_r) and variance (V_r) in Figures 1 and 2.

Table 4: Value $(W_r + V_r)$ of length and shape of rice

Genotypes	Rice length	Rice shape
Basmati Delta 9	2.32	1.30
Basmati Pakistan	2.46	1.43
Inpari 31	1.99	0.93
Inpago Unsoed 1	1.00	0.37
Koshihikari	1.75	0.69
Tarabas	1.87	0.73

Distribution of parental array points along the regression line reflected genetic diversity of a trait [51]. The array point was scattered along the regression line for length and shape of rice, indicating genetic diversity for these traits. The position of the parents on the graph of the relationship between the covariance (W_r) and variance (V_r) reflects the order of dominance. The position of parent which is closer to zero point indicating it is the most dominant genes [47,50]. Inpago Unsoed 1 is the closest to zero, reflecting that this parent has the mostly dominant genes for length and shape of rice. Mostly, Basmati Pakistan contains a recessive gene for length and shape of rice since it is the farthest from zero. Basmati, which has extra-long and slender rice, contains the most recessive gene, and this means that the gene controlling long and slender rice is recessive to the short and round rice gene. This result is in agreement with the findings of Kato [29], Murai and Kinoshita [41], and Ali et al. [52].

The straight line intercepted the vertical axis (W_r) above the origin for length and shape of rice (Figures 1 and 2). The straight line that intercepted the vertical axis (W_r) above the origin indicated partial dominance of the genes controlling a trait [21,50,51]. This reveals that length and shape of rice were controlled by a partial dominant gene as described previously. Partial dominance results in the appearance of each trait having a tendency to approach the mid-parent value and not having overdominance, which exceeds the best parent [53]. This is reflected in the h^2 value of length and shape of rice, which is not significantly different, so that there is no difference between the F_1 average and the parents' average.

3.2.10 Heritability

Broad sense heritability (h^2_{bs}) estimates for length and shape of rice are similar to 0.99. Narrow sense heritability (h^2_{ns}) estimates for these traits are 0.94 and 0.91,

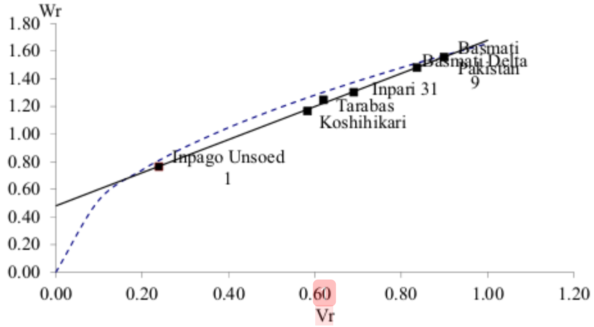

Figure 1: Covariance (W_r) and variance (V_r) graph of rice length.

respectively (Table 3). Values of heritability more than 0.5 are categorized as high (Stansfield, 1991); thus, broad-sense heritability (h^2_{bs}) for length and shape of rice is categorized as high heritability. Similar findings were reported by previous studies [54].

The estimated value of broad-sense heritability indicates the relative contribution of genetic factors to the variation of the observed trait [55]. A high broad-sense heritability value indicates that traits are more influenced by genetic than environmental factors [56]. In this study, broad-sense heritability estimate of length and shape of rice is high, indicating the influence of genetic was greater than environmental factors. Low influence of environmental factors was also reflected in the non-significant environmental variance observed in Table 3.

Narrow sense heritability estimates indicate the role of additive gene action in a trait. Estimates of narrow-sense heritability indicate more additive gene action than non-additive gene action [4,57–59]. In this study, the narrow sense heritability estimate of length and shape of rice was high, meaning that additive gene action played a more important role than non-additive gene action.

Ratio of narrow-sense heritability and broad-sense heritability reflects the role of additive and non-additive gene action in a trait. The ratio value closer to one indicates the total genetic variance of a trait is caused by additive gene action [60]. Table 3 shows that the ratio of narrow-sense heritability and broad-sense heritability is 0.95 for rice length and 0.92 for rice shape, respectively. This indicates that additive gene action determines size and shape of rice more than non-additive gene action as previously described. Traits that have high additive variance and heritability in the F_1 population may be selected using individual selection. Individual selection may be applied to traits that have additive variance and high heritability in the F_1 population [21] so that the selection of length and shape of rice may be carried out using individual selection such as pedigree. This finding was in agreement with that of Raju et al. [40].

3.3 Combining ability estimation of length and shape of rice

Gene action and cytoplasm influence of the female parent for a trait can be predicted through combining ability. Variances of GCA, SCA, and reciprocals were obtained from diallel analysis of Griffing method-1. Variances of

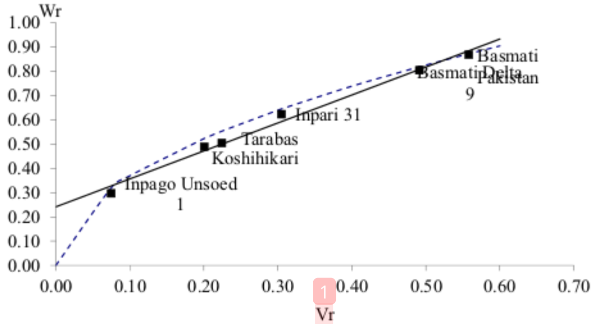

Figure 2: Covariance (W_r) and variance (V_r) graph of rice shape.

Table 5: Analysis of variance of combining ability and GCA:SCA ratio of length and shape of rice

Source of variance	Degree of freedom	Mean square	
		Rice length	Rice shape
GCA	5	6.909*	3.154*
SCA	15	0.138*	0.092*
Reciprocal	15	0.020^{ns}	0.006^{ns}
Error	70	0.015	0.007
GCA:SCA ratio		50.060	34.280

*Significantly different at the level of 5%, ns = not significantly different.

GCA and SCA are associated with non-additive and additive gene actions, respectively [61–63]. Reciprocal variance is useful for knowing the effect of female parent cytoplasm of a trait [64].

GCA is endorsed to additive gene action, and SCA is mainly attributed to non-additive gene action [59,65]. This study shows significant effects of GCA and SCA on length and shape of rice (Table 5). The significant GCA and SCA indicated the importance of both additive and non-additive gene actions in the expression of these traits. This finding was in agreement with that of Singh et al. and Soni et al. [66,67].

The magnitude of the effect of additive gene action and non-additive gene action on a trait can be determined from GCA:SCA ratio [68]. A high GCA:SCA ratio indicates that additive gene action plays a more important role in the expression of a trait than non-additive gene action [69]. Ratio of GCA:SCA greater than one indicates that additive gene action has more influence on the expression of a trait, and conversely, a GCA:SCA ratio less than one reflected that non-additive gene action has more influence on the expression of a trait [70]. In this study, ratio of GCA:SCA of length and shape of rice is greater than one (50.060 and 32.280, respectively) (Table 5), indicating that additive gene action is more influential than non-additive gene action on the expression of these traits. These results agree with the estimation of gene action using the Hayman method as described previously. Additive gene action in length and shape of grain has been previously reported [66,67]. Therefore, the selection of length and shape of grain will be effective using pedigree method [71].

Non-significant reciprocal effects were observed for both length and shape of rice (Table 5). This indicated that there was no influence of the female parent cytoplasm on the inheritance of these traits [64,72] so that the size and shape of the rice are not affected by the female parent cytoplasm.

4 Conclusion

The influence of additive and non-additive gene actions on length and shape of rice was confirmed. The effect of the additive gene action was greater than the non-additive gene action, while both broad-sense heritability and narrow-sense heritability were high. This revealed that the selection of these traits at the early generation using the pedigree selection method may be considered. Length and shape of rice were not affected by the female parent cytoplasm so that F_2 and $F_{2\text{reciprocal}}$ populations might be combined into one population in the next selection generation.

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