

Genetic variability and traits association analyses on F₂ generations for determination of selection criteria in Indonesian inland swamp rice breeding

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Abstract

The progress of rice breeding program for better adaptation and extension on inland swamp ecosystem largely depends on the presence of genetic variability and relevant selection criteria. This study was undertaken to estimate the genetic variability parameters in segregating populations of rice and to determine the relationship of grain yield and yield contributing traits of rice to determine selection criteria for yield improvement under inland swamp condition. The F₂ population was generated from 11 crosses involving Bengkulu landraces of swamp rice. Then, the F₂ population was evaluated on the inland swamp for their yield and yield-related traits. The genetic parameter was estimated using variance component analysis. Simple correlation analysis was performed for all observed traits and the resulting matrix of correlation coefficients was subjected to factor analysis and path analysis. Analysis of variance indicated that significant variation present among and within F₂ families for most of the traits studied. Grain yield plant⁻¹ exhibited the highest GCV (40.3 %) and PCV (60.11%). Moderate to high or moderate h²_B with high GAM was obtained on plant height, tiller number, number of productive tiller, spikelet number panicle⁻¹, 100-grain weight, and grain yield plant⁻¹. Positive and significant correlation was found between grain yield plant⁻¹ and plant height, tiller number, spikelet number panicle⁻¹, panicle length, and 100-grain weight. Factor analysis discerned the 9 observed traits into two-factor axes with overall explaining 79.28% of the total variation among traits. The first factor (59.12%) was strongly characterized by yield and yield components (plant height, tiller number, number of productive tillers, spikelet number panicle⁻¹, panicle length, and 100-grain weight), whereas the second factor (20.16%) was mainly associated with heading date. Path analysis revealed that among the yield components, tiller number and 100-grain weight (the grain size) had strong direct effects on grain yield and they can be taken into account as the selection criteria for rice grain yield improvement under inland swamp ecosystem.

Keywords: rice, inland swamp, genetic parameters, factor analysis, path analysis, selection criteria.

Abbreviations: GCV_Genotypic Coefficient of Variation; PCV_Phenotypic Coefficient of Variation, GAM_Genetic Advance as Percent of Population Mean; h²_B_Broad Sense Heritability.

Introduction

Inland swamp is commonly considered as a marginal ecosystem for crop production due to the inherent physicochemical limiting factors in the soil. The seasonal flood resulted from impeded drainage in inland swamp make the cultural practices more laborious compared dry land or irrigated lowland. Similarly, high acidity and nutrients deficiency, that are main characterization of inland swamp, limit the number of crop species can be grown as well as the productivity of the crop (Fitzpatrick et al., 1993; Waluyo and Djahhari, 2011). Rice is probably the most swamp-adapted food crop and exploitation of swampy areas is commonly devoted to rice production (Aselmann and Crutzen, 1989; Zong et al., 2007; Verhoeven and Setter, 2010). However, all rice varieties cannot express their yield potential when grown on the swampy ecosystem (Nassir and Ariyo, 2011). Successful rice production under swampy ecosystem is majorly dependent to the ability of plant genotype to adapt to various environmental abiotic stresses. Aside from high yielding potential, rice varieties for inland swamp production should be devised with complete submergence tolerance (Sakagami and Kawano, 2011), stagnant flooding tolerance

(Singh et al., 2011) and iron toxicity tolerance (Sahrawat, 2010).

Inland swamps of Indonesia covers 13.3 million hectares and most of these areas are less developed and underutilized (Haryono, 2012). Similarly, the availability of a wide range of indigenous rice varieties that traditionally maintained and cultivated by farmers in swampy areas (Silitonga, 2004; Wahdah et al., 2012) can serve as valuable source of stress-tolerant prevalence to be incorporated with superior germplasms. Therefore, the breeding programs may aim at identifying high-yielding rice varieties with improved tolerance to abiotic stresses in swampy ecosystems. The available genetic resources of Indonesian rice can provide a significant contribution in attaining food self-sufficiency for Indonesia's growing population.

Breeding for yield improvement in rice is often tackled by the genetic and physiological natures of rice yield. Like other cereal crops, grain yield of rice is known to be a complex agronomic trait, governed by polygenic inheritance which highly affected by environmental factors (Gravois and McNew, 1993; Wang et al., 2014). Furthermore, grain yield does not act independently and genetically related to yield

component traits (Hsieh, 1985; Fong et al., 2016). Thus, rice yield improvement through direct selection on grain yield *per se* could be unpredictable.

A clear understanding of genetic variation and association of grain yield of rice and its components are crucial for the establishment of selection strategy, especially in segregating populations (Savitha and Kumari, 2015). Correlation analysis is a common method employed to reveal the degree and direction of the association between all possible pair of traits being studied. However, if a large number of traits involved, the analysis will end up with a large correlation matrix. Inspection on every pair of traits in the matrix would be tedious and gives no conclusive picture of the interrelationship among the traits. One way of reducing this complexity is to use factor analysis.

Factor analysis is a multivariate technique designed to simplify a complex intercorrelated variables into a few interpretable underlying factors (Harman, 1976). It can be used to identify the structure of traits association and to classify these traits into different groups (Streiner, 1994). Similarly, the correlation between a pair of traits implies that both traits happen to coincide with each other, not necessarily causally related. Path analysis is an attempt to deal with causal types of relationships by decomposing correlation matrix into direct effect and indirect effects. The relative importance of the traits assigned as predictor variables on a trait assigned to the resultant variable. Thus, in plant breeding, the information gained from both factor analysis and path analysis would be useful to the breeder in determining selection criteria for yield improvement. The objectives of present study were to estimate the genetic variability parameters and to determine the relationship of yield and yield contributing traits in F_2 rice populations to determine selection criteria for grain yield improvement on inland swamp ecosystem.

Results and Discussion

Traits variability observed among and within F_2 families

Table 1 shows the mean-squares of nine traits observed in the study. The significant variations for most of the observed traits in either among and within F_2 families indicated a wide range of plant variation that provide a large scope and flexibility for selection on the basis of phenotypic performances. F_2 generation is an ideal starting point for different methods of selection, in that segregation and recombination are at a maximum level (Savitha and Kumari, 2015). If a pedigree selection is adopted as the method of crop improvement program, as commonly preferred by rice breeder (Guimaraes, 2009), then ability to isolate desired genotypes in F_2 population stands as a critical stage for the success of the entire breeding program.

The overall performance of the F_2 populations is presented in Table 2. Mean and range values along with their variability (CV) indicate the extent of improvement that can affect the corresponding traits. Selection in F_2 populations with a high mean and variability can potentially produce transgressive segregants with superior performance in the later generations (Kumar et al., 2013). In some cases, low mean and high variability are preferred to serve as the basis for selection of promising segregants. In the present study, the highest CV was exhibited by grain yield plant^{-1} , followed by productive tiller number, and 100-grain weight, suggesting that selection of segregants for good performances on these traits can be carried out with less constraint. The scope of selection for the tall plant for better adaptation on a flood-prone swamp

(Vergara and Dikshit, 1982) may be restricted by moderate variability in plant height. Having a wide range of plant height in the population (62.20 to 122.00 cm), the breeder would have opportunity to select individual segregants with desired tallness. Similarly, a relatively low variability in heading date might not be critical, as mean and range for this trait indicated a medium earliness.

Genetic parameter estimates for yield and yield-related traits

The estimate of mean and CV cannot elucidate the genetic merit of variation in the traits studied. Table 3 depicts the estimate of genetic parameters for each trait. As expected, the estimates of the genotypic coefficient of variation (GCV) were lower than their corresponding phenotypic coefficient of variation (PCV). These phenomena have been reported in rice study everywhere, implying that the apparent variations are not singly attributed to the genetic constitution of the traits, but also due to environmental influence. A smaller difference between GCV and PCV indicates greater genetic determination and less environmental influence on the expression of the trait.

The estimates of broad-sense heritability (h^2_B) refer to the relative contribution of the genetic component to the variation of the observable trait. High h^2_B (>0.60) was observed on plant height, heading date, and spikelet number panicle^{-1} , which also had the lower difference between the GCV and PCV, suggesting that expression of these traits was predominantly controlled by a genetic component. The h^2_B for other traits were mostly moderate, leaving the lowest for percentage of filled grain panicle^{-1} . The grain filling in rice is highly related to the crop growing conditions (Yoshida, 1981; Khalifa and El-Rewainy, 2012; Vergara et al., 2014) and its improvement could be carried out by a good cultural management (Fageria, 2014; Azman et al., 2014).

The estimate of genetic advance (GA) measures the gain that can be expected from selecting the best performance genotypes for a given trait (Allard, 1999). However, to facilitate comparison in the selection gain among traits, the genetic advance is commonly expressed as percent of the population mean (GAM). Results of the present study implied that selecting the top 5% of the segregants could result in substantial improvement in tiller number, number of productive tiller, spikelet number panicle^{-1} , 100-grain weight, and grain yield plant^{-1} ; moderate improvement on heading date and filled grain panicle^{-1} and minor improvement on panicle length. Furthermore, the type of gene action governing these traits and, hence, the method of selection can be deduced by considering magnitudes of their heritability and genetic advances. High or moderate h^2_B coupled with high GAM, which was obtained on plant height, tiller number, productive tiller number, spikelet number panicle^{-1} , 100-grain weight, and grain yield plant^{-1} . This indicates that these traits were predominantly controlled by additive gene action. Similar findings were also reported by Ahmadikhan (2010) and Dutta et al. (2013). Accordingly, simple selection favoring superior segregants for these traits will be effective and bred true in the next generation (Acquaah, 2012). High h^2_B accompanied by moderate GAM was found on heading date, suggesting the involvement of non-additive gene actions in controlling the inheritance of this trait, as reported by Lingaiah et al. (2014). Therefore, improvement in heading date through simple selection would

Table 1. Mean squares for 9 agronomic traits of F₂ rice populations, grown on inland swamp.

Source of variation	Degree of freedom	Plant height	Heading date	Tiller number	Productive tiller number	Panicle length	Spikelet number panicle ⁻¹	% filled grain panicle ⁻¹	100-grain weight	Grain yield plant ⁻¹
Block	2	5365.40 **	5.94 ns	114.20 ns	127.11 ns	102.04 *	6325.56 ns	406.39 ns	3.06 ns	2364.21 **
Among F ₂ family	10	4973.17 **	171.42 **	239.40 **	248.99 **	60.37 *	28455.82 **	2898.36 ns	12.28 **	1070.56 *
Within F ₂ family	20	484.81 **	16.21	48.51 **	53.07 **	19.86 **	3202.30 **	1328.51 **	2.27 **	323.69 **
Error	297	61.79	–	12.18	12.22	5.44	598.54	280.45	0.25	37.72

ns Non significant at P ≤ 0,05; *, ** Significant at P ≤ 0.05 and P ≤ 0.01, respectively

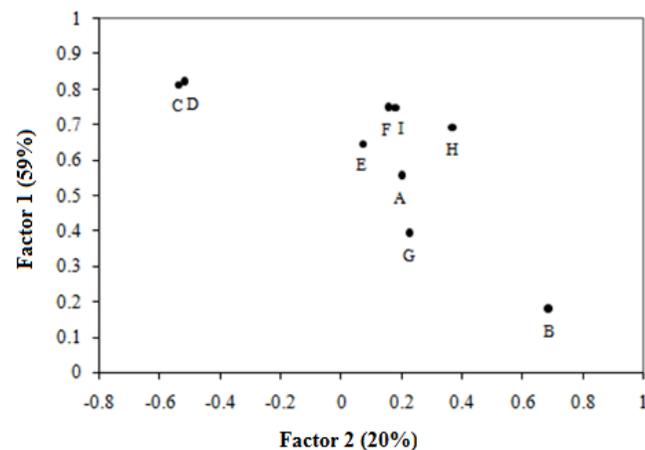


Fig 1. Plot values of 9 agronomic traits of an F₂ population of rice on two principal axes, grown on an inland swamp. A: plant height; B: heading date; C: tiller number; D: productive tiller number; E: panicle length; F: Spikelet number panicle⁻¹; G: percentage of filled grain panicle⁻¹; H: 100-grain weight; and I: grain yield plant⁻¹. Factor 1 axis represent a single plant productivity factor and Factor 2 axis represent plant developmental factor. Dot positions on the chart indicate the degree of association between the traits and the corresponding axes.

Table 2. Plant performances of F₂ rice populations grown on inland swamp in respect to 9 agronomic traits.

Trait	Mean	Range	SD	CV (%)
Plant height (cm)	89.31	65.20 – 122.00	14.81	16.58
Heading date (DAP)	73.2	56.0 – 90.0	8.00	10.94
Tiller number	10.1	4.8 – 19.5	3.35	33.19
Productive tiller number	9.9	4.4 – 19.5	3.45	34.89
Panicle length (cm)	22.39	17.35 – 26.40	1.94	8.68
Spikelet number panicle ⁻¹	106.06	46.1 – 184.2	33.60	31.68
% filled grain panicle ⁻¹	60.57	36.41– 88.22	13.10	21.63
100-grain weight (g)	2.07	0.96 – 3.50	0.72	34.75
Grain yield plant ⁻¹ (g)	12.38	3.12 – 34.12	8.27	66.83

Table 3. Estimates of genetic parameter for 9 agronomic traits in F₂ populations of rice, grown on inland swamp.

Trait	GCV (%)	PCV (%)	h ² _B	GA	GAM (%)
Plant height (cm)	13.70	15.76	0.76	22.28	24.55
Heading date (DAP)	9.83	11.99	0.76	12.95	16.63
Tiller number	24.98	33.17	0.57	4.15	38.82
Productive tiller number	25.85	34.81	0.55	4.14	39.61
Panicle length (cm)	5.21	8.16	0.41	1.67	6.86
Spikelet number panicle ⁻¹	27.36	32.14	0.72	52.31	48.04
% filled grain panicle ⁻¹	11.41	22.13	0.27	8.61	12.13
100-grain weight (g)	27.27	35.43	0.59	0.94	43.31
Grain yield plant ⁻¹ (g)	40.30	61.11	0.43	7.02	54.83

Table 4. Simple correlation coefficient for 9 agronomic traits in F₂ populations of rice, grown on inland swamp.

Trait	Heading date	Tiller number	Productive tiller number	Panicle length	Spikelet number panicle ⁻¹	% filled grain panicle ⁻¹	100-grain weight	Grain yield plant ⁻¹
Plant height	0.41*	0.40*	0.41*	0.35*	0.34	0.05	0.35*	0.49**
Heading date		-0.17	-0.14	0.01	0.19	0.12	0.38*	0.19ns
Tiller number			0.99**	0.37*	0.46**	0.20	0.40*	0.52**
Productive tiller number				0.37*	0.47**	0.18	0.41*	0.53**
Panicle length					0.83**	0.19	0.31	0.40*
Spikelet number panicle ⁻¹						0.36*	0.43*	0.44*
% filled grain panicle ⁻¹							0.48**	0.34ns
100-grain weight								0.75**

Values with * or ** are significant at P=0.05 or 0.01; value with ns are not significant at P=0.05.

Table 5. Total variance explained by each factor based on 9 agronomic traits in F₂ populations of rice, grown on inland swamp.

Factor	Eigenvalue	Variance proportion	Cumulative (%)
1	3.870	0.591	59.12
2	1.320	0.202	79.28
3	0.867	0.132	92.52
4	0.594	0.091	101.59
5	0.196	0.030	104.59
6	0.011	0.002	104.77
7	-0.023	-0.004	104.41
8	-0.107	-0.016	102.77
9	-0.181	-0.028	100.00

Table 6. Loading of the two important principal factors of 11 traits 9 agronomic traits in F₂ populations of rice, grown on inland swamp.

Trait	Factor 1	Factor 2	Communality
Plant height	0.556	0.196	0.348
Heading date	0.179	0.685	0.502
Tiller number	0.816	-0.542	0.960
Productive tiller number	0.822	-0.521	0.947
Panicle length	0.650	0.068	0.427
Spikelet number panicle ⁻¹	0.749	0.152	0.584
% filled grain panicle ⁻¹	0.394	0.223	0.205
100-grain weight	0.695	0.369	0.620
Grain yield plant ⁻¹	0.752	0.180	0.597

Table 7. The direct effect (diagonal and bold) and indirect effect (off-diagonal) of 8 agronomic traits on grain yield in F₂ populations of rice, grown on inland swamp.

Trait	Plant height	Heading date	Tiller number	Productive tiller number	Panicle length	Spikelet number panicle ⁻¹	% filled grain panicle ⁻¹	100-grain weight	Total effect to Grain yield plant ⁻¹
Plant height	0.227	-0.040	0.287	-0.235	0.035	-0.012	-0.001	0.230	0.489
Heading date	0.094	-0.097	-0.121	0.077	0.001	-0.007	-0.003	0.248	0.192
Tiller number	0.092	0.016	0.709	-0.569	0.037	-0.017	-0.005	0.260	0.523
Productive tiller number	0.094	0.013	0.706	-0.571	0.037	-0.017	-0.004	0.269	0.526
Panicle length	0.079	-0.001	0.262	-0.213	0.099	-0.031	-0.004	0.205	0.395
Spikelet number panicle ⁻¹	0.076	-0.018	0.325	-0.268	0.083	-0.037	-0.008	0.283	0.436
% filled grain panicle ⁻¹	0.012	-0.011	0.142	-0.103	0.019	-0.013	-0.023	0.318	0.341
100 grain weight	0.079	-0.036	0.281	-0.234	0.031	-0.016	-0.011	0.656	0.750
								Residual effect =	0.181

possibly be slowing down by these non-additive gene effects.

Association between traits using correlation analysis

The matrix of simple correlation coefficient presented in Table 4 indicates the degree and direction of the association between each pair of the nine agronomic traits studied. A maximum positive correlation was revealed on the association between tiller number and productive tiller number, followed by the association between panicle length and spikelet number panicle⁻¹. As expected, the number of tillers bearing panicle is largely determined by the number of tillers produced by the plant. Similarly, spikelet number panicle⁻¹ is profoundly dictated by panicle length. Grain yield exhibited moderate to strong and positive association with plant height, tiller number, productive tiller number, panicle length, spikelet number panicle⁻¹, and 100-grain weight. Sravan et al. (2012) reported that grain yield plant⁻¹ had significant and positive correlations with plant height, tiller number, productive tiller, and spikelet number panicle⁻¹. Similarly, Ranawake and Amarasinghe (2014) reported a significant and positive correlation between grain yield plant⁻¹ and 100-grain weight.

Structure of traits association using factor analysis

The factor analysis was performed to explore deeply into the structure of trait associations in order to detect underlying shared components of the complex traits, which potentially represent pleiotropic phenomena (Lange, 2002; Wang et al., 2009). Based on the rule of Eigenvalue greater than unity (Kaiser, 1960), only the first two factors which accounted for 79.28% of the existent variation among the traits were retained and considered as important factors (Table 5). The two principal factors along with their loadings and communality of each trait are presented in Table 6. The value of loading indicates the strength of association between the trait and its corresponding factors. The value of communality indicates the proportion of trait variance explained by the both retained factors. Factor 1, which accounted for about 60% of the total variation, can be regarded as a single plant productivity factor since it was strongly associated (loading > 0.50) with plant height, tiller number, productive tiller number, panicle length, spikelet number panicle⁻¹, 100-grain weight, and grain yield plant⁻¹. The positive loading of these traits indicates the positive direction of the association between the factors. Factor 2, which accounted for 20% of the total variation, was composed of heading date, tiller number, and productive tiller number. This factor seemed to be a measure of plant development, so it can be deemed as plant developmental factor. It can be noted that tiller number and productive tiller number had negative loadings in Factor

2. Fig 1 depicts the structure of association among the observed traits as plotted on two principal axes. It became clear that a productive genotype was characterized by medium earliness and high tillering ability when it grew on inland swamp ecosystem.

Causal association between grain yield and its related traits using path analysis

As far as grain yield is the main concern in rice breeding for inland swamp ecosystem, elucidation of the causal relationship between grain yield and all contributing traits would be the central issue in determining the key traits that can beneficially be exploited to achieve the desired level of grain yield improvement. Path analysis is an effective method of partitioning the correlation coefficient into direct and indirect effects of yield contributing traits on grain yield. Table 7. shows the direct and indirect effect values from path analysis. The highest positive direct effect on grain yield was exhibited by tiller number (0.709), followed by 100-grain weight (0.656), and plant height (0.227). Productive tiller number had the high negative direct effect on grain yield (-0.571) but it had the high positive indirect effect on grain yield through tiller number (0.706). In all cases, 100-grain weight, and to some extent the tiller number, served as intermediate traits for the indirect effect of other traits on grain yield. It was revealed that traits showed strong association with grain yield did not necessarily have high direct effects on the grain yield, and vice versa. Similar features were reported in various rice researches (Ekka et al., 2011; Haider et al., 2012; Seyoum et al., 2012; Ketan and Sarkar, 2014). The residual effect was 0.181, indicated there were other traits contributed to rice grain yield and was not yet considered in this experiment.

Materials and Methods

Characteristics of the experimental site

The study was conducted in 2014 at the inland swamp of the Agronomy Experimental Orchard, University of Bengkulu, Indonesia (5 m above sea level). The soil of the experimental field was inceptisol with peat thickness < 75 cm and submerged during the growing season with a maximum height of 50 cm from the soil surface.

Experimental materials and setup

Eleven F₂ families of rice generated from crosses involving 5 landrace varieties (Hanafi Putih, Tigotigo, Harum Curup, Batubara, and Lubuk Durian) and 3 improved varieties (Sidenuk, Diahsuci, and Bestari) were used in this study

(Suppl Table 1). The landrace varieties were collected in 2012 from farmers' fields and traditionally grown in swampy areas in Bengkulu Province, while the improved varieties were developed by National Nuclear Energy Agency of Indonesia (BATAN) for lowland irrigated cultivation and procured as foundation seeds (Suppl Table 2).

A half diallel crossing scheme amongst the parental was implemented in 2013 to produce F₁ seeds under a greenhouse environment. The resulting F₁ seeds from each cross were grown in the same year on inland swamp soil. The selection was applied to the survival and general performances of the resulting plants. The F₂ seeds generated from the selected 11 crosses were grown separately on the experimental arranged in a randomized complete block design with three replications. Each family of F₂ occupied a plot of 3 m width and 5 m length.

Crop management and data collection

A no-tillage system was applied for land preparation, but the existing weeds were controlled using a herbicide 15 days prior transplanting. The rice transplants of 21-day-old from each family were arranged at 25 cm x 25 cm planting space in the assigned plot. Urea (75 kg ha⁻¹), SP-36 (100 kg ha⁻¹) and KCl (100 kg ha⁻¹) were used as basal fertilizers and applied following transplanting. Additional urea (75 kg ha⁻¹) was implemented at heading stage. Weed and pest controls were carried out as necessary.

At maturity, 10 samples of the plant on each plot were observed for plant height, tiller number, productive tiller number, panicle length, spikelet number panicle⁻¹, the percentage of filled grain panicle⁻¹, 100-grain weight, and grain yield plant⁻¹. Heading date was recorded on plot basis as days to 50 % flowering. The trait measurements were made based on the standard evaluation system for rice (IRRI, 1996).

Data analysis

Analysis of variance was employed to determine the significance of variations among and within 11 F₂ families. The genetic parameters, including within-family variance (σ^2_E), genotypic variance among F₂ families (σ^2_G), phenotypic variance (σ^2_P), and broad sense heritability were estimated from the resulting mean-squares and expected mean squares (Becker, 1992), where $\sigma^2_E = \frac{MS_{Within F_2 \text{ family}}}{3}$, $\sigma^2_G = \frac{MS_{Among F_2 \text{ family}} - MS_{Within F_2 \text{ family}}}{\sigma^2_P}$

$= \sigma^2_G + \sigma^2_E$, and $h^2_B = \frac{\sigma^2_G}{\sigma^2_P}$. Both phenotypic and genotypic coefficient of variations were estimated as $PCV = \frac{\sigma_P}{\bar{x}}$ and

$GCV = \frac{\sigma_G}{\bar{x}}$, respectively, where \bar{x} is the general mean of

the corresponding trait. Genetic advance for a given trait was estimated as $GA = i \cdot \sigma_P \cdot h^2_B$, where $i = 2.06$ for 5% selection intensity (Allard, 1999) and as percentage of the trait grand mean, i.e. $GAM = \frac{GA}{\bar{x}} \times 100\%$ (Johnson et al., 1955). Degree

and direction of traits association were as estimated as the simple correlation coefficient. The structure of traits association was identified using factor analysis with principal factor analysis as the method for factor extraction. Path analysis was carried out with grain yield plant⁻¹ as the

resultant variable and other traits as the causal variables. Direct and indirect effects of yield contributing traits to grain yield were identified by matrix operation, as suggested by Singh and Choudhary (1976). Analysis of variance, correlation analysis, and factor analysis was performed using SAS version 9 (SAS Institute Inc., 2004), whereas path analysis was carried out using MS-Excel 2007.

Conclusion

An overall consideration of findings revealed that wide range of variations exist for most of the traits, which provide information that progress of rice breeding program for better adaption to inland swamp ecosystem could be expected from the current populations. The estimates of heritability and genetic advance for plant height, tiller number, productive tiller number, spikelet number panicle⁻¹, 100-grain weight, and grain yield plant⁻¹ indicated that these traits were mainly controlled by additive gene actions and; therefore, simple selection would be brought about a worthwhile improvement. With respect to efficiency of selection, correlation analysis, factor analysis, and path analysis gave complementary information on the most suitable selection criteria for yield improvement. Correlation analysis and factor analysis indicated that tall plant, high tiller number and productive tiller number, long panicle, high spikelet number, and large grain significantly contributed on rice grain yield. However, path analysis revealed that tiller number and 100-grain weight, instead of many traits, should firstly be used in selection to improve rice grain yield grown on inland swamp environment.

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