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Research article

Combining ability and heritability for yield and its related traits in Thai upland rice (*Oryza sativa* L.)

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Article Info

Abstract

In a rice breeding program, breeders select the best combinations using combining ability analysis while heritability is used to study the degree of variability of the traits transmitted to progenies. Evaluations were studied using a half-diallel mating design of the combining ability and heritability of eight genotypes of Thai upland rice (Hawm Satun, Dawk Pa-yawm, Dawk Kham, Nual Hawm, Dawk Kha, Hawm Mali Doi, Khun Nan and Goo Meuang Luang) which generated 28 F_1 hybrids. A randomized complete block design with two replications was used. Highly significant differences for genotypes, general combining ability (GCA) and specific combining ability (SCA) were noticed for all 10 of the traits under evaluation. The significance of GCA and SCA indicated that both additive and non-additive genetic effects contributed to a trait's inheritance. The parental line Hawm Mali Doi had the highest GCA effect in desired directions for plant height, days to flowering and maturity; Nual Hawm for panicle number; Khun Nan for tiller number, panicle length and 1,000 grain weight; and Dawk Pa-yawm for number of filled grains, spikelet fertility and grain yield. These could be regarded as good general combiners for those characters. Five hybrids were found with a significant positive SCA effect, the highest value was obtained from Nual Hawm × Khun Nan followed by Dawk Pa-yawm × Hawm Mali Doi for grain yield, which could be regarded as good specific combiners for further improvement in the upland rice breeding program. Estimation of narrow sense heritability in response to selection in the next generation was medium to high (35.67–56.72%) for grain yield and its components.

Introduction

Rice (*Oryza sativa* L.) is an essential primary food crop in the world, particularly in Asia. High population growth requires an increase in rice production, but the available area of suitable wetland is decreasing (Papademetriou, 2000). This problem can be solved by cultivating upland rice hybrids in upland (dryland) area and breeding for higher grain yield which has a great potential to increase rice yield (Sari et al., 2019b). On the other hand, it is becoming important to exploit the rice genotypes having the capability

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to tolerate drought stress due to the effects of climate change which is limiting water supply (Pandey and Shukla, 2015). Therefore, the upland rice genotypes used in the current study were comparatively drought resistant (Hussain, 2017) and relatively high yielding (Sari et al., 2019a).

Analysis of combining ability is a powerful tool to estimate the combining ability and gene effects and it also helps in selecting the appropriate parents and crosses for the exploitation of heterosis (Rashid et al., 2007). Various degrees of combining ability and type of gene action in some varieties of rice have been reported by Bagheri and Jelodar (2010), Rahimi et al. (2010), Jarwar et al. (2014) and Veeresha et al. (2015). Assessment of combining ability influencing yield and its components has become progressively important to plant breeders in order to select desirable parents for developing potential hybrids to increase rice yield globally.

There is a need to study various agro-morphological and yield traits to get a better understanding of inheritance and to identify and then select superior genotypes. Values of heritability have been variable depending upon the genetic nature of genotypes for different agro-morphological traits (Vivek et al., 2000; Swati and Ramesh, 2004). Estimation of heritability has been studied by several researchers, such as Bezaweletaw et al. (2006), Saleem et al. (2008) and Chuchert et al. (2018) regarding yield and its components in cereal crops to select superior genotypes and desirable traits in the next generation. Therefore, the objectives of the current study were to evaluate the extent of combining ability and heritability for yield and its related traits in Thai upland rice, to identify and select desirable parental lines and cross combinations, profitable characters and the appropriate breeding method for developing high-yielding upland rice varieties.

Materials and Methods

The study was conducted in the experimental field of the Faculty of Natural Resources, Prince of Songkla University, Hat Yai, Thailand ($100°29'46''E$, $7°00'31''N$ and mean annual temperature $24°C$). Thirty-six upland rice genotypes consisting of eight parents (Hawm Satun, Dawk Pa-yawm, Dawk Kham, Nual Hawm, Dawk Kha, Hawm Mali Doi, Khun Nan and Goo Meuang Luang) and their 28 F_1 upland rice hybrids (obtained using a half-diallel mating design of the parents) were replicated twice in a randomized complete block design. The experimental plot was double row (16 plants per row) having a length of 4 m, while 30 cm distance was kept between rows and 25 cm between plants, so there were 32 plants for each genotype per plot. Necessary cultivation techniques followed standard agricultural practice for upland rice (Arraudeau and Vergara, 1988). Weeds were controlled regularly, mainly before applying fertilizer. The fertilizer (15N-15P-15K) was applied at a rate of 20 g per plant before planting and urea (46% N) at a rate of 10 g per plant was applied three times at age 4 wk and 8 wk after planting and at the panicle initiation stages (this application was different, depending on the genotype). During growth, pests and diseases were chemically controlled using 50 mL/L Benfuracarb 20% weight per volume (w/v) effective concentration

(EC) and 20 mL/L cypermethrin 10% w/v EC.

Data were measured on 10 plants per plot which were randomly selected from each genotype per replication for 10 agronomic traits contributing to yield, namely plant height, days to flowering, days to maturity, number of tillers per plant, number of panicles per plant, panicle length, number of filled grains per panicle, spikelet fertility, 1,000 grain weight and grain yield per plant. The data were subjected to analysis of variance for genotypes (Gardner and Eberhart, 1966), combining ability analysis based on Method II of the random model in Griffing (1956) according to Singh and Chaudhary (1979) for the general combining effect (GCA) and the specific combining ability (SCA) using Equation 1 and Equation 2, respectively:

$$\text{GCA effect } = \; g_i = \frac{1}{n+2}\left[\sum(Y_{i.} + Y_{ii}) - \frac{2}{n}Y..\right] \tag{1}$$

$$\text{SCA effect } = \; s_{ij} = Y_{ij} - \frac{1}{n+2}(Y_{i.} + Y_{ii} + Y_{.j} + Y_{jj}) + \frac{2}{(n+1)(n+2)}Y.. \tag{2}$$

where i or j is equal to 1,2, …, n (parents) and Y is the replication mean of observation.

Significance testing for GCA and SCA effects was performed using Student's t test by calculating the critical difference (CD) based on the variances of these effects (Dabholkar, 1992), using Equation 3–5:

$$\text{CD} = \text{SE} \times \text{t (tabulated)} \tag{3}$$

$$\text{GCA variance } = \; \text{Var}(g_i) = \frac{n-1}{n(n+2)}\,\text{MS}_e \tag{4}$$

$$\text{SCA variance } = \; \text{Var}(s_{ij}) = \frac{n^2 + n + 2}{(n+1)(n+2)}\text{MS}_e \tag{5}$$

where SE is the standard error, n is the number of genotypes and MS_e is the error variance $= \sigma^2 e$.

Heritability in the narrow sense and broad sense was calculated according to Singh and Chaudhary (1979) using Equation 6 and Equation 7, respectively:

$$\text{Narrow sense heritability } (h^2_{ns}) = \frac{\sigma^2 a}{\sigma^2 p} \times 100\% \tag{6}$$

$$\text{Broad sense heritability } (h^2_{bs}) = \frac{\sigma^2 a + \sigma^2 d}{\sigma^2 p} \times 100\% \tag{7}$$

where σ^2_a is the additive variance $= 2 \times$ variance of GCA, σ^2_p is the phenotypic variance $= \sigma^2_a + \sigma^2_d + \sigma^2_e$ and σ^2_d is the dominance variance $=$ variance of SCA.

Results and Discussion

Analysis of variance for genotypes and combining ability

Highly significant differences were observed among genotypes for all studied traits as revealed by the analysis of variance (Table 1), which indicated that the genotypes used had different characters and varied significantly from each other. The mean square values of traits were further portioned into parents, hybrids and parents versus hybrids, which revealed highly significant differences except

for plant height, number of filled grains per panicle and 1,000 grain weight for parents versus hybrids. These findings were consistent with Singh and Kumar (2004) and Akter et al. (2010) who also reported significant differences for these characters. This indicated the pair of parents and their hybrids will expose different characters that have significant combining ability effects for those traits.

Similarly, analysis of variance for combining ability (Table 1) revealed that the mean squares due to GCA and SCA were significantly different for all characters. Significant variances of GCA and SCA showed the importance of both the additive and non-additive gene effects which are responsible for the inheritance of the variation observed in the traits under study. Vanaja et al. (2003) and Rahimi et al. (2010) also reported the role of non-additive and additive gene effects in the inheritance of yield and its components for the rice plant. Therefore, any approach that can facilitate the simultaneous exploitation of the additive and non-additive gene actions would be highly desirable for the improvement of these traits.

The results of the analysis of variance indicated there was worthwhile genetic variability of the Thai upland rice genotypes used in this research and it affected the gene action estimated from the combining ability variances. In addition, there was no doubt in the accuracy of data as the value of the coefficient of variation (CV) was less than 17% for each trait, in the range 1.6–16.3%.

Gene action

The estimations of the GCA and SCA variances (σ^2gca and σ^2sca) and their ratio are given in Table 1. The results clearly suggested that additive and non-additive (dominance) gene actions were equally important for the various variables under evaluation. For plant height, days to flowering and maturity, σ^2gca / σ^2sca > 1, indicating the important role of additive gene action in the inheritance of these traits (Mostofa et al., 2013). These findings conformed with Vanaja

et al. (2003), Akter et al. (2010) and Bagheri and Jelodar (2010) who reported σ^2gca values greater than for σ^2sca with plant height at harvest, second uppermost internodal length, 1,000 grain weight and days to maturity. The values of σ^2gca and σ^2sca for number of tillers per plant were almost equal (σ^2gca / σ^2sca $\approx$ 1), suggesting the equal role of both additive and non-additive genetic expression in the inheritance of this character. A similar result was also reported by Akter et al. (2010) for number of rice panicles per square meter.

For panicle number, panicle length, filled grains number, spikelet fertility, 1,000 grain weight and single plant yield, σ^2gca / σ^2sca < 1, revealing the predominant role of non-additive gene action in the inheritance of these traits. Similar results that implied the existence of the preponderant action of non-additive genes for rice grain yield and its contributing traits were reported by several researchers: Vanaja et al. (2003) and Rashid et al. (2007) for plant height, number of productive tillers, length of panicle, percentage of fertility, 1,000 grain weight and yield per plant; Bagheri and Jelodar (2010) for number of tillers, days to 50% flowering, panicle length, spikelet fertility, number of spikelets per panicle and grain yield per 10 plants; and Akter et al. (2010) for leaf area index, length and weight of panicle, spikelet fertility, spikelets number, 1,000 grain weight and single plant yield.

Reddy et al. (2012) declared a preponderance of additive gene action if σ^2gca / σ^2sca > 1, but the opposite (σ^2gca / σ^2sca < 1) indicated the predominance of non-additive gene action. while σ^2gca / σ^2sca $\approx$ 1 indicated the equal role of both non-additive and additive gene actions in the inheritance of the characters. Both types of these gene actions could be used appropriately to improve the desirable procedure selection in a plant breeding program. Hybridization has been suggested for enhancement of the characters which are mainly dominated by non-additive gene action, whereas for traits showing the prevalence of additive gene action, simple selection can be an option for developing a pure line population which has preferable properties (Tariq et al., 2014).

Table 1 Analysis of variance for genotypes and combining ability, combining ability variances and heritability for studied traits in Thai upland rice

Source	df	Mean square of traits									
		PH	DF	DM	NT	NP	PL	NFG	SF	GW	GY
Replication	1	2631.2**	101.4**	30.5*	950.9**	332.2**	5.6*	2095.6**	131.4**	1.6ns	19.4**
Genotype	35	433.6**	360.4**	333.2**	219.4**	51.2**	14.8**	2928.6**	246.3**	21.8**	10.5**
Parent (P)	7	723.9**	549.7**	458.5**	275.2**	67.8**	15.6**	3854.1**	92.4**	49.5**	11.4**
P vs. H	1	121.6ns	83.1**	26.7*	292.3**	35.2*	32.6**	14.5ns	411.6**	2.7ns	11.5*
Hybrid (H)	27	369.8**	321.5**	312.1**	202.2**	47.5**	13.9**	2796.6**	280.1**	15.3**	10.3**
Error	35	53.5	7.6	5.0	24.4	8.0	1.2	269.9	15.9	1.6	2.3
CV (%)	–	6.2	2.7	1.6	16.3	15.9	3.7	11.4	5.9	4.8	5.2
GCA	7	874.4**	733.9**	696.5**	370.2**	81.3**	10.6**	4786.7**	232.1**	28.9**	12.8**
SCA	28	52.4*	41.7**	34.1**	45.6**	11.6**	6.6**	633.7**	95.9**	6.4**	3.4**
σ^2 gca	–	82.20	69.22	66.24	32.57	6.97	0.40	415.29	13.62	2.25	0.94
σ^2 sca	–	25.63	37.92	31.59	32.37	7.65	6.04	498.80	87.99	5.61	2.25
σ^2 gca / σ^2 sca	–	3.21	1.83	2.10	1.01	0.91	0.07	0.83	0.15	0.40	0.42
h^2_{ns} (%)	–	75.84	76.83	79.53	59.38	54.47	10.71	56.72	22.12	41.17	35.67
h^2_{bs} (%)	–	87.67	97.88	98.49	88.89	84.37	92.20	90.79	93.57	92.60	78.40

Df = degrees of freedom; CV = coefficient of variation; h^2_{ns}=narrow sense heritability; h^2_{bs}= broad sense heritability; PH = plant height; DF = days to flowering; DM = days to maturity; NT = number of tillers per plant; NP = number of panicles per plant; PL = panicle length; NFG = number of filled grains per panicle; SF = spikelet fertility; GW= 1,000 grain weight; GY = grain yield per plant.
ns, * and ** indicate non-significance, significance at 5% and 1% level probability, respectively.

Furthermore, based on the results of the present study, a simple selection would be recommended for the traits which are dominated by additive gene action such as plant height, days to flowering and maturity, because the effect of genes and inheritance tend to be independent of other genes and the influence of the environment. On the contrary, for the traits showing the prevalence of non-additive (dominant) gene action, such as grain yield and its components which tended to be influenced by other genes and the environment, hybridization is suggested for the improvement of these traits by utilizing transgressive segregation to obtain superior segregates in the next generation.

Heritability

The heritability values for all the studied traits varied from low to high (Table 1) within the ranges 10.71–79.53% for the narrow sense and 78.40–98.49% for the broad sense. Chuchert et al. (2018) reported high broad sense heritability (more than 60%) for plant height, days to flowering, number of tillers per plant, number of panicles per plant, number of spikelets per panicle, 1,000 grain weight and yield per plant. In contrast, Ghara et al. (2014) observed only low heritability (0–7.25%) for rice yield and its components. Heritability in the narrow sense is estimated on a family-mean basis, calculated by comparing the additive variance to the phenotypic variance, while broad sense heritability is the ratio of the total (additive + non-additive) genotypic variance to phenotypic variance. Therefore, the value of narrow sense heritability is usually less than broad sense heritability.

Higher heritability values in most of the traits in the present study indicated the relatively greater selection effectiveness for these important characters. On the contrary, a low heritability value indicated the selection would be relatively less effective because the phenotypic variance appearance of crops is mostly influenced by environmental factors (Poehlman and Sleper, 2006). A breeding program for characters with low heritability is complicated because it indicates the phenotype is highly uncorrelated with the genotype, supposedly because the contribution of the environmental factors is comparatively high in such characters (Singh, 2005). The level of heritability in the trait will affect selection decisions and selection is more effective if there is a high correlation between the genetic variation to environmental variation. Enhancement tends to be sluggish in lowly heritable traits, whereas traits with higher heritability can achieve progress faster due to higher accuracy in selection decisions.

Combining ability effects

General combining ability

This effect was estimated among parental lines to identify and select the superior parents for designing the subsequent rice development program. The estimates of GCA effects for studied traits are shown in Tables 2 and 3. The significant negative GCA effects for plant height, days to flowering and days to maturity were shown by three, two and three parental lines, respectively, where Hawm Mali Doi had the highest significant negative GCA effects for these traits. For panicle number, the maximum value was for Nual Hawm. Khun Nan had the highest significant positive GCA effects for tiller number and panicle length. Three and four parental lines showed highly significant positive GCA effects for number of filled grains per panicle and spikelet fertility, respectively, where the maximum value was for Dawk Pa-yawm. Hawm Mali Doi, Khun Nan and Goo Meuang Luang had highly significant positive values for 1,000 grain weight, while Dawk Pa-yawm, Dawk Kha and Khun Nan had highly significant positive GCA effects for grain yield per plant, with Khun Nan having the maximum value for both these traits (Table 3).

Table 2 Estimates of general combining ability for plant height (PH), days to flowering (DF), days to maturity (DM), number of tillers per plant (NT) and number of panicles per plant (NP) based on random model of Griffing's approach

Genotype	General combining ability				
	PH	DF	DM	NT	NP
Hawm Satun	-1.98	7.31**	6.00**	-10.20**	-4.73**
Dawk Pa-yawm	**-5.60****	4.13**	4.47**	-3.68**	-0.20
Dawk Kham	-2.83	5.24**	4.48**	**5.54****	**1.93****
Nual Hawm	-1.37	-1.00	**-1.12***	6.33**	**_4.79_******
Dawk Kha	**-3.44***	5.84**	6.15**	1.56	**1.54****
Hawm Mali Doi	**_-11.77_******	**_-15.47_******	**_-14.92_******	-3.89**	-0.39
Khun Nan	8.38**	-10.87**	-10.81**	**_6.85_******	-2.19**
Goo Meuang Luang	18.61**	4.82**	5.74**	-2.51*	-0.76
SE (g$_i$)	1.53	0.58	0.47	1.03	0.59
SE (g$_i$ - g$_j$)	2.31	0.87	0.71	1.56	0.89

* and ** indicate significance at 5% and 1% level probability, respectively.
Bold and **_bold_** indicate significance and highest significance in desirable direction, respectively.

Table 3 Estimates of general combining ability for panicle length (PL), number of filled grains per panicle (NFG), spikelet fertility (SF), 1,000 grain weight (GW) and grain yield per plant (GY) based on random model of Griffing's approach

Genotype	General combining ability				
	PL	NFG	SF	GW	GY
Hawm Satun	-1.52**	**18.75****	-2.64**	-3.09**	-1.84**
Dawk Pa-yawm	-0.13	**<u>39.50</u>****	**<u>5.67</u>****	-1.12**	1.44**
Dawk Kham	**0.49***	**11.45****	3.39**	-0.13	0.02
Nual Hawm	-1.18**	-1.67	**2.76****	-0.27	-0.44
Dawk Kha	-0.60**	-17.86**	-0.71	-0.55**	**0.90****
Hawm Mali Doi	**1.03****	-12.08**	**2.00***	**1.78****	-0.43
Khun Nan	**<u>1.29</u>****	-11.49**	-0.50	**<u>1.93</u>****	**<u>1.23</u>****
Goo Meuang Luang	**0.62****	-26.60**	-9.98**	1.45**	-0.89**
SE (g_i)	0.22	3.44	0.83	0.27	0.32
SE (g_i - g_j)	0.34	5.19	1.26	0.40	0.48

* and ** indicate significance at 5% and 1% level probability, respectively.
Bold and **<u>bold</u>** indicate significance and highest significance in desirable direction, respectively.

The genotype Hawm Mali Doi was a great general combiner due having the highest significant negative GCA effects for plant height (-11.77), days to flowering (-15.47) and days to maturity (-14.92) as shown in Table 2. For the earliness characters, such as days to flowering and maturity and plant height, the negative combining ability effect is highly desirable, but for yield attributes, positive combining ability effects are desirable. For example, Vanaja et al. (2003) and Akter et al. (2010) mentioned that significant negative GCA effects for growth duration and plant height are worthwhile for the development of the early semi-dwarf variety. On the other hand, maximum significant positive GCA effects for yield components (number of tillers, number of panicles, panicle length, number of filled grains, spikelet fertility, 1,000 grain weight and grain yield per plant) were identified in Dawk Pa-yawm, Nual Hawm and Khun Nan, indicating they are good general combiners for these traits. The results were in agreement with the findings of Rashid et al. (2007), Jampatong et al. (2010) and Rahimi et al. (2010) who reported the desirable positive direction of GCA effects for grain yield and its components which was expected to increase the yield of cereal crops.

Griffing (1956) noted that high GCA effects could be attributed to the additive or additive × additive gene actions, which represent the improved genetic components of variance. In the current study, the performance of beneficial GCA effects were identified as great general combiners for particular traits related to additive or additive × additive gene actions. The parental lines (Hawm Mali Doi, Dawk Pa-yawm, Nual Hawm and Khun Nan) which had the highest significant GCA effects in a desirable direction for the traits of interest could be exploited in multiple crossing programs for isolating desired lines and then they could be developed for release as superior conventional varieties or utilized as improved parents for evaluation and further hybridization in upland rice breeding programs.

Specific combining ability

Estimates of the SCA effects of 28 Thai upland rice hybrids are presented in Tables 4 and 5. Two of the hybrids, namely Hawm Mali Doi × Goo Meuang Luang (HMD × GML) and Khun Nan × Goo Meuang Luang (KN × GML) had significant negative SCA effects for plant height. Shortening plant height is a desirable trait in rice crop cultivation as it enhances resistance to lodging and increases tillering ability (Saleem et al., 2008). Similarly, a negative SCA value is desired for days to flowering and maturity to develop an early-maturing hybrid. Five and eight hybrids had significant negative SCA effects for plant height and days to flowering and maturity, with Nual Hawm × Khun Nan (NH × KN) having the highest significant negative values (-16.49 and -14.60, respectively) as shown in Table 4. These results were in agreement with Bagheri and Jelodar (2010) and Rahimi et al. (2010) who recorded the significant negative SCA effects for these traits in several rice plant crosses.

An increase in productive tillers will encourage the presence of more panicles; therefore, it is also a desirable trait in rice hybrids because it can increase grains yield. This was supported by the findings of Sari et al. (2019a) that the heterosis values for both of these traits were positively correlated with each other and normally the number of tillers was greater than the number of panicles. In the current study, there were significant positive SCA effects observed for the number of tillers and panicles in eight and five crosses, respectively, with Nual Hawm × Dawk Kha (NH × DK) producing the greatest SCA effects for both these traits (11.62 and 6.20, respectively). This was in accordance with Rashid et al. (2007) and Akter et al. (2010) who also found significant positive SCA effects in some crosses for tiller and panicle numbers.

Table 4 Estimates of specific combining ability for plant height (PH), days to flowering (DF), days to maturity (DM), number of tillers per plant (NT) and number of panicles per plant (NP) based on random model of Griffing's approach

Genotype	Specific combining ability				
	PH	DF	DM	NT	NP
HS × DP	10.33*	-1.02	-1.29	-2.09	-0.98
HS × DM	-2.15	-4.51*	0.60	-5.54	-2.48
HS × NH	-4.23	3.23	2.99*	-2.83	-0.33
HS × DK	4.63	0.51	-0.63	-3.46	-2.29
HS × HMD	-3.89	0.90	-1.67	-1.11	-0.32
HS × KN	0.93	-2.04	**-4.94****	**7.10***	3.05
HS × GML	7.45	-4.53*	**-2.91***	**10.52****	2.96
DP × DM	1.21	3.47	2.23	-0.16	0.29
DP × NH	-1.11	2.71	3.17*	-6.29*	-3.27
DP × DK	3.61	4.25*	2.40	2.03	0.74
DP × HMD	-7.80	-12.00**	-9.67**	9.78**	5.91**
DP × KN	-6.37	5.40**	7.86**	2.03	-0.58
DP × GML	4.63	6.69**	4.73**	-0.43	1.05
DM × NH	0.10	4.66**	3.56*	-8.40**	-7.16**
DM × DK	-3.97	-2.22	**-4.51****	-1.63	-0.58
DM × HMD	5.88	**-7.15****	**-4.68****	**8.91****	**4.51***
DM × KN	-3.06	-2.67	**-6.29****	**8.12***	3.19
DM × GML	8.95	4.25*	2.36	3.06	1.91
NH × DK	5.82	7.09**	7.09**	<u>**11.62**</u>**	<u>**6.20**</u>**
NH × HMD	8.82	-3.43	**-3.39***	**7.70***	1.33
NH × KN	-6.36	-16.49**	<u>**-14.60**</u>**	8.32**	4.66*
NH × GML	7.38	2.03	0.95	4.99	4.26*
DK × HMD	-3.88	4.48*	7.24**	0.78	0.87
DK × KN	-0.51	2.62	4.23**	-8.61**	-4.12*
DK × GML	11.16*	1.94	2.43	-5.49	-3.71*
HMD × KN	2.87	13.61**	6.51**	-1.65	-0.69
HMD × GML	<u>**-11.43**</u>*	0.88	-0.49	-6.79*	-3.63*
KN × GML	**-9.58***	3.40	5.64**	-0.33	-0.32
SE (s$_{ij}$)	4.08	1.54	1.25	2.75	1.58
SE (s$_{ij}$ - s$_{ik}$)	6.94	2.62	2.13	4.68	2.68
SE (s$_{ij}$ - s$_{kl}$)	6.54	2.47	2.01	4.42	2.53

HS = Hawm Satun; DP =Dawk Pa-yawm; DM = Dawk Kham; NH = Nual Hawm; DK = Dawk Kha; HMD = Hawm Mali Doi; KN = Khun Nan; GML = Goo Meuang Luang.
* and ** indicate significance at 5% and 1% level probability, respectively.
Bold and <u>**bold**</u> indicate significance and highest significance in desirable direction, respectively.

Grain yield is the final objective of breeding and development programs of rice breeders. In the current study, positive and significant SCA effects were observed in five crosses for grain yield per plant and its components, such as panicle length (10 crosses), number of filled grains per panicle (4 crosses), spikelet fertility (6 crosses), and 1,000 grain weight (6 crosses), with the hybrid Nual Hawm × Khun Nan (NH × KN) having the maximum SCA effects for these traits (3.89, 6.44, 56.56, 16.40 and 4.09, respectively), as shown in Table 5. The results were confirmed by Rashid et al. (2007), Saleem et al. (2008), Bagheri and Jelodar (2010) and Rahimi et al. (2010) who reported significant positive SCA effects for rice grain yield and its related traits.

The specific combining ability of a cross is an indicator for the selection of a hybrid combination because it is the estimation and cognition of the effect of non-additive gene action for a character. Thus, a highly significant SCA effect is desired for an effective hybrid breeding program. The great specific combiners are recommended for heterosis breeding because they have the maximum significant SCA effects in a preferable direction which might be caused by non-additive gene actions in controlling these traits as Reddy et al. (2012) stated that the best specific combiners having the dominant

gene action in controlling traits should be used for heterosis breeding. This provides a very good opportunity for hybrid breeding through the exploitation of non-additive genetic variation for certain characters and represents the greater importance of non-additive gene effects on their expression (Annadurai and Nadarajan, 2001).

The presence of significant SCA effects in the desired direction involved additive × additive (high × high), additive × dominance (high × low), and dominance × dominance (low × low) general combiners as parental lines which produced great specific cross combinations. For example, in the present study, the hybrid Nual Hawm × Khun Nan had the highest significant positive SCA effect for single plant yield; it was derived from the combination of additive (high: Khun Nan) × dominance (low: Nual Hawm) as general combiners in grain yield per plant (Table 3), indicating that the best specific combiners are not only gained from the combination of high × high general combiners but also from the combination of low × low and high × low general combiners. The superiority of the cross combinations involving low × low or high × low general combiners as parental lines was probably associated with the number of heterozygous loci of the parents involved in the cross combinations which represented the

genetic diversity (Kumar et al., 2006).

Out the top five promising specific combiners identified for yield and its contributing traits, two crosses (Nual Hawm × Khun Nan and Dawk Pa-yawm × Hawm Mali Doi) had one parent with high (additive) GCA effects in each trait. These can be utilized in recombination breeding by the selection of a single plant in the next generations to develop lines or varieties with higher grain yield and its related components. This was supported by Reddy et al. (2012) who stated that for a hybrid from parental lines contained low and high GCA effects, the parent with the low GCA effect could provide the desired transgressive segregates giving rise to a favourable population. This would only be possible if there were an additive genetic system in the great general combiner accompanied by an epistatic effect in the crosses acting in a complementary manner to maximize the desired plant characters which could be exploited in further breeding programs.

Furthermore, it could be further exploited by utilizing the tendency of quantitative inheritance for several of the progeny to go beyond the scope of the parents, which is known as transgressive segregation (Rick and Smith, 1953). Breeders rely on this to obtain superior segregates compared to parental lines for characters inherited in a quantitative manner. Crops which represent the results of transgressive segregation might be selected from the second filial (F_2) generation progeny that contain new combinations of several genes for greater yield and other desired quantitative characters than were present in either parent (Poehlman and Sleper, 2006).

In conclusion, the study revealed that both GCA and SCA effects were significant along with high heritability for grain yield and its associated traits that were assessed. The importance of both additive and non-additive gene actions contributed to the inheritance of quantitative traits, with the predominance of non-additive gene action for most of the yield components. The parental lines Dawk Pa-yawm, Nual Hawm, Hawm Mali Doi and Khun Nan were more controlled by additive gene action resulting in them being great general combiners and could be utilized as the most promising parental lines in the upland rice hybridization program. In addition, this may generate an elite population for the selection of high yielding lines in advanced generations. The F_1 hybrids from Nual Hawm × Khun Nan and Dawk Pa-yawm × Hawm Mali Doi were more controlled by non-additive (dominance) gene action, suggesting them as the most promising cross combinations in the selection of favourable segregants for developing high yielding upland rice hybrid varieties.

Table 5 Estimates of specific combining ability for panicle length (PL), number of filled grains per panicle (NFG), spikelet fertility (SF), 1,000 grain weight (GW) and grain yield per plant (GY) based on random model of Griffing's approach

Genotype	Specific combining ability				
	PL	NFG	SF	GW	GY
HS × DP	-0.01	-11.45	0.99	1.33	1.23
HS × DM	3.43**	18.75	5.00	-1.35	-0.89
HS × NH	-2.36**	-21.67*	-4.34	-0.56	-0.88
HS × DK	-0.08	12.94	**5.55***	0.27	1.06
HS × HMD	-0.05	13.90	3.79	-0.62	0.10
HS × KN	**1.82**	**21.36***	3.13	**2.94**	**2.27*
HS × GML	-0.12	-40.24**	-10.75**	0.62	-1.08
DP × DM	-0.33	-10.57	-3.47	-0.97	0.77
DP × NH	1.18	0.09	-11.37**	-2.36**	-1.38
DP × DK	**1.86**	15.60	4.10	0.24	0.48
DP × HMD	3.88**	53.30**	13.57**	2.92**	3.18**
DP × KN	-2.47**	-26.05*	1.07	-0.34	-1.43
DP × GML	-2.80**	-9.46	-7.54**	-0.56	-0.49
DM × NH	-3.33**	-33.31**	-6.13*	-0.86	-1.11
DM × DK	-2.99**	-18.47	-4.79	0.26	-1.14
DM × HMD	**2.03**	7.13	-2.54	**1.77*	1.69
DM × KN	0.76	14.23	-1.94	**2.14**	**2.29*
DM × GML	-1.38*	-0.91	4.11	0.44	-1.07
NH × DK	0.94	**25.01***	**5.04***	-0.08	1.08
NH × HMD	**1.82**	20.41	**7.76**	**2.50**	**2.78**
NH × KN	6.44**	56.56**	16.40**	4.09**	3.89**
NH × GML	**2.07**	4.59	**5.31***	0.33	0.34
DK × HMD	2.32**	-7.99	-2.94	1.11	0.74
DK × KN	-0.59	-21.50*	2.23	-0.52	-1.21
DK × GML	0.13	0.47	-14.33**	-0.54	0.30
HMD × KN	-3.89**	36.99**	-18.63**	-6.39**	-3.53**
HMD × GML	**1.47*	-7.70	-13.63**	-2.13**	1.65
KN × GML	0.31	-11.33	-11.41**	-6.60**	0.38
SE (s_{ij})	0.60	9.16	2.22	0.71	0.84
SE ($s_{ij} - s_{ik}$)	1.02	15.58	3.78	1.21	1.43
SE ($s_{ij} - s_{kl}$)	0.96	14.69	3.56	1.14	1.35

HS = Hawm Satun; DP =Dawk Pa-yawm; DM = Dawk Kham; NH = Nual Hawm; DK = Dawk Kha; HMD = Hawm Mali Doi; KN = Khun Nan; GML = Goo Meuang Luang.

* and ** indicate significance at 5% and 1% level probability, respectively.

Bold and **bold** indicate significance and highest significance in desirable direction, respectively.

Conflict of Interest

The authors declare that there are no conflicts of interest.

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