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MONOGENIC INHERITANCE OF MULTISPIKELET CLUSTERS IN THE THAI INDIGENOUS UPLAND RICE VARIETY 'NIAW DAM CHAW MAI PAI 49'

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SUMMARY

The Thai indigenous upland rice variety 'Niaw Dam Chaw Mai Pai 49' (NDCMP-49) exhibits two and three spikelet clusters, provides genetically stable panicle development, and produces well-developed fertile seeds. In this study, the inheritance pattern of multispikelet clusters, the minimum number of genes, and the mode of gene actions were investigated over six generations, namely, P_1, P_2, F_1, F_2, BCP_1, and BCP_2 from two different crosses, i.e., NDCMP-49 × 'LLR316' and NDCMP-49 × 'ULR291'. The presence of F1 phenotypes and the segregation of spikelet phenotypic clusters in the F_2, BCP_1, and BCP_2 generations revealed that the multispikelet cluster traits of NDCMP-49 are controlled through monogenic inheritance with incomplete dominance. Therefore, careful selection based on the phenotypic values of the transgressive segregation of these characters in advanced generations would provide a reliable and effective method to determine the prospective grain yield per panicle. The results herein provide new data to clarify and expand the available information on the inheritance of multispikelet cluster characteristics in rice.

Keywords: Generation mean analysis, gene action, number of gene, additive–dominance model, grain yield

Key findings: Multispikelet cluster phenotypes in natural resource variations of Thai rice are monogenically inherited.

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INTRODUCTION

Global food demand is increasing rapidly and is projected to double by 2050 due to population growth, dietary shifts, and biofuel consumption. Rice (*Oryza sativa* L.) is the most important staple food crop in Asia. It has significantly contributed to global food security and will continue to feed approximately half of the global population in the future. Global rice demand is estimated to rise from 676 million tons in 2010 to 763 million tons in 2020 and to further increase to 852 million tons in 2035; these increments represent an overall increase of 26%, or 176 million tons, in the next 25 years (Khush, 2013). However, rice planting areas in major rice-producing countries have been decreasing because of the conversion of land for housing, industry, and highways. As a result, the present rate of crop production on the remaining land is estimated to be inadequate to satisfy future demand. Therefore, research on the enhancement of rice productivity is of increasing concern to rice breeders.

Rice grain yield represents a complex figure that can be determined by several components (Özer *et al*., 1999). According to Sheehy *et al*. (2001), high rice grain yields have a direct correlation with the high potential of spikelet numbers per panicle of plants because rice sets a single grain in each spikelet. Ikeda *et al*. (2005) further demonstrated that rice panicle architecture may be determined by the length of the main panicle axis, length and number of primary branches, number of secondary branches, and number of spikelets distributed on the branches. Additionally, several rice breeders have focused on panicle morphology (spikelet density, branch number, and panicle length) to increase rice yields (Mallik *et al*., 1990; He *et al*., 2010; Wang and Li, 2011; Liu *et al*., 2016). Jiang *et al*. (2014) further reported on novel mutant rice panicles that displayed shortened pedicels via the *sped1-D* gene, which resulted in the rapid shortening of pedicels and the formation of spikelet clusters on secondary branches. However, the presence of spikelet clusters caused by the *sped1-D* mutant gene is negatively correlated with seed fertility and grain filling. Zhang *et al*. (2017) also reported the induction of the lateral floret 1(*lf1*) in three spikelet rice results in the initiation of lateral meristems to generate lateral florets in the axil of sterile lemma. Moreover, the formation of two florets within a single spikelet is characterized by two allelic mutant genes, namely, double *floret1-1* (*df1-1*) and (*df1-2*), that cause a 15%–20% increase in spikelets and result in two florets inside one pair of sterile lemma (Ren *et al*., 2018). Determining lateral floret formation and altering the meristem assist in creating rice cultivars with multifloret spikelets, which increase the number of grains per panicle and potentially improve yield; however, these mutants have floral organ defects, as well as other negative traits that prevent their use in the production of high-yield rice varieties.

The Thai indigenous upland rice variety ‘Niaw Dam Chaw Mai Pai 49’ (NDCMP-49) presents multispikelet clusters on the rachis node in contrast to multifloret spikelets as previously reported by Zhang *et al*. (2017) and Ren *et al*. (2020). This variety is characterized by two and three spikelet cluster phenotypes that develop from each rachis node and display stability. Interestingly, most spikelets produce well-developed fertile seeds in contrast to the *sped1-D* mutant, which shows shortened pedicels and spikelet clusters on secondary branches as previously reported by Jiang *et al*. (2014). Their hypothesis suggested that multispikelet cluster phenotypes may boost the grain yield per plant by increasing multispikelet clusters in each panicle. NDCMP-19 was crossed with rice varieties with normal spikelet phenotypes to evaluate the potential value of multispikelet clusters for rice breeding. We report, for the first time, the genetics of multispikelet cluster phenotypes in natural resource variations. The objective of this study was to investigate the inheritance and gene action of the multispikelet cluster in new resources in the natural genetic variations of multispikelet clusters in rice. We hope that the results of this study can be utilized in future rice breeding programs, thereby increasing the number of grains per panicle and potentially improving rice yield.

MATERIALS AND METHODS

Plant material and population development

Three different Thai indigenous rice varieties, namely, NDCMP-49, ‘LLR316’, and ‘ULR219’, were used in this study.

NDCMP-49, a colored rice variety local to Thailand's southern region, has been collected by the Pattani Rice Research Center since 1996. This variety's distinct traits pose a specific multispikelet cluster phenotype that consists of 2–3 spikelet clusters on a single rachis. 'LLR316' (ssp. *indica*), the lowland rice variety from Phatthalung in Southern Thailand, and 'ULR291' (ssp. *japonica*), the upland rice variety from Chiang Mai in Northern Thailand, exhibit normal spikelets. F_1 seeds (NDCMP-49 × 'LLR316' and NDCMP-49 × ULR219) were crossed during the 2018 summer season under greenhouse conditions. NDCMP-49 was utilized as the female parent to produce F_1 seeds. Later in July, all parents and the F_1 seeds of each cross were grown again in pots to generate the F_2 and to develop backcross seeds. We used the parents of the respective crosses as the female and the F_1 generation as the male parent and performed backcrossing to produce the BCP_1 and BCP_2 generations. The F_1 hybrids were self-pollinated to obtain F_2 seeds.

Evaluation of agronomic traits and data collection

The 30-day-old seedlings of P_1 and P_2 (2 rows × 21 plants/row); F_1, BCP_1, and BCP_2 (4 rows × 21 plants/row); and F_2 (8 rows × 21 plants/row) were transplanted in a completely randomized design with nonreplication in the paddy fields at the Agronomy Field Crop Station at Khon Kaen University to evaluate agronomic traits and grain yield performance. The recommended agronomic practices were followed for fertilization and other plant protection measures. The basic plant characteristics of 10 plants randomly selected from each of the P_1, P_2, and F_1 groups; 40 plants from each of the backcross generations; and 100 plants from the F_2 generation of each cross were recorded. These characteristics included the main panicle, viz., number of spikelets per panicle, number of two- and three spikelet cluster types per panicle, filled grain per panicle, and grain yield per plant (g). The mean value, range, and corresponding standard error (SE) for every single panicle were computed for all six generations of each cross by using Excel software.

Testing of multispikelet cluster inheritance

Observations on multispikelet cluster characteristics were performed in the F_1, F_2, BCP_1, and BCP_2 individual populations and grouped into three classes: (1) nonspikelet clusters; (2) nonspikelet clusters and two spikelet clusters; and (3) nonspikelet clusters with two- and three-spikelet clusters (Figure 1). Data observations on the multispikelet cluster classes were scored (1, 2, and 3) and analyzed by using the χ^2 method to observe the goodness of fit and to obtain the expected classification ratios (Singh and Narayanan, 1993). The following descriptors were applied: Oi = number of observed phenotypes to i; Ei = the number of expected phenotypes; and n = the number of classes. The calculated value of χ^2 was compared with the value in the χ^2 table with the appropriate degree of freedom (*df*). If the value of χ^2 is smaller than the value in the χ^2 table, then the frequency distributions of the F_2 and backcross populations are in accordance with the expected ratio.

The percentage of spikelet clusters (Classes 2 and 3) per panicle of the parents, F_1, F_2, BCP_1, and BCP_2 were recorded to determine the gene effect, gene action, number of genes, and heritability. We utilized the scaling test outlined by Mather (1949) and Hayman and Mather (1955) to determine the presence or absence of nonallelic interactions. The quantities A, B, C, and D and their respective variances were calculated to test the adequacy of the additive-dominance model in each case. The calculated *t*-values were compared with the tabulated values of *t* at the 5% and 1% levels of probability and *df* of 5 and tested individually for the effect and significance of each gene as delineated in Mather and Jinks (1982). The significance of the A and B scales indicates the

Figure 1. Comparison of the spikelet types of the F_1 and segregated F_2 populations of the parents NDCMP-49 and 'LLR316' (A) and of the parents NDCMP-49 and 'ULR291' (B).

presence of all types of nonallelic gene interactions. The significance of the C scale suggests the [dd] type of epistasis. The significance of the D scale reveals [aa] gene interaction, whereas the significance of the C and D scales indicates the [aa] and [dd] types of gene interaction (Singh and Narayanan, 1993). Generation mean analysis was carried out over six generations by using the mean value of the respective generation (Hayman, 1958). This analysis estimated the gene effects, viz., *m* (mean), *d* (additive effect), *h* (dominant effect), *i* (additive × additive interaction effect), *j* (additive × dominance interaction effect), and *l* (dominance × dominance interaction effect) through the following equations: mean [m] = mean of F_2; the additive gene effect [d] $=BC_1 - BC_2$; dominance gene effect [h] = $F_1 - 4F_2 - 0.5P_1 - 0.5P_2 + 2BC_1 + 2BC_2$; additive × additive gene effect [i] = $2BC_1 + 2BC_2 - 4F_2$; additive × dominance gene effect [j] = $2BC_1 - P_1 - 2BC_2 + P_2$; and the dominance × dominance gene effect [l] = $P_1 + P_2 + 2F_1 + 4F_2 - 4BC_1 - 4BC_2$. The calculated *t*-values were compared with the tabulated values of *t* at the 5% and 1% levels of probability, and the *df* is the sum of the *df* of the various generations involved.

Number of genes

The number of genes contributing to the percentage of spikelet clusters (Classes 2 and 3) per panicle was calculated through the following equation (Poehlman, 1987):

$$N = (M_1 - M_2)^2 / 8(VF_2 - VF_1)$$

where N = number of genes, M_1 = mean value of P_1, M_2 = mean value of P_2,
VF_1 = F_1variance, and VF_2= F_2 variance.

RESULTS

The parental line NDCMP-49 exhibited multispikelet cluster characteristics and produced an average spikelet number per panicle of 153.1, an average filled-grain per panicle of 116.3, and an average grain yield per plant of 9.60 g. By contrast, the parental lines 'LLR316' and 'ULR291' (nonspikelet clusters) produced an average number of spikelets per panicle of 206.9 and 216.3, an average filled grain per panicle of 177.6 and 192.0, and an average grain yield per plant of 13.9 g and 14.6 g, respectively. 'LLR316' and 'ULR291' produced higher grain yield per plant than NDCMP-49. The F_2, BCP_1, and BCP_2 populations derived from the two cross combinations, therefore, segregated for all traits (Table 1).

The mean, range, and standard error for the number of spikelets per panicle, filled grain per panicle, and grain yield per plant of F_1, as well as the different phenotypic classes of F_2, BCP_1, and BCP_2 populations for the cross-combinations of NDCMP-49 × 'LLR316' and NDCMP-49 × 'ULR291' are presented in Table 1. In general, the data exhibited ranges that illustrated the differences among populations and were higher than the data of the parents for all recorded traits. These traits were substantially affected by the presence of multispikelet clusters. The progenies with phenotypic classes similar to the phenotypic classes of F_1 including class 2 of F_2, BCP_1, and BCP_2 displayed the spikelet-cluster ratios of nonclusters (1):two spikelet clusters (2) of 76.4:23.6 (F_2), 77.1:22.9 (BCP_1) and 77.3:22.7 (BCP_2) of the NDCMP-49 × 'LLR316' cross and 70.7:29.3 (F_2), 72.6:27.4 (BCP_1) and 70.6:29.4 (BCP_2) of the NDCMP-49 × 'ULR291' cross (Table 1).. The results indicated that one-fourth of the spikelets within the heterozygous genotype comprised two spikelet clusters. Interestingly, our study created the phenotypic class of F_1 with only two types of nonclusters and two spikelet clusters on the panicle.

In a similar evaluation, the progenies with phenotypic classes similar to the phenotypic class of the NDCMP-49 parent and including the phenotypic class 3 of F_2 and BCP_1 displayed the spikelet-cluster ratio of nonclusters (1):two spikelet clusters (2):three spikelet clusters (3) of 51.5:17.6:30.9 (F_2) and 38.9:19.2:41.9 (BCP_1) in the NDCMP-49 ×

Table 1. Means and ranges with standard error for seed per panicle; filled grain per panicle; and grain yield per plant in the F_1 and different phenotypic classes of F_2, BCP_1, and BCP_2 of NDCMP-49 × 'LLR316' and NDCMP-49 × ULR 219 crosses.

Generation	Phenotypic classes* (no. of plant)	Number of spikelet per panicle				Filled grain per panicle	Grain yield per plant (g)
		Mean	% of spikelet cluster ratio**			Mean	Mean
			1	2	3		
Cross 1 (NDCMP-49 × 'LLR316')							
P_1	3 (8)	153.1 ± 6.4	38.6	7.5	53.9	116.3 ± 3.8	9.6 ± 0.7
P_2	1 (10)	206.9 ± 3.2	100	-	-	177.6 ± 4.2	13.9 ± 1.2
F_1	2 (10)	244.6 ± 7.4	74.3	25.7	-	217.8 ± 7.3	16.4 ± 1.5
F_2	1 (23)	221.4 ± 10.1	100	-	-	196.8 ± 9.7	11.6 ± 1.2
	2 (54)	221.0 ± 5.8	76.4	23.6	-	194.9 ± 5.6	11.2 ± 0.5
	3 (18)	216.4 ± 11.7	51.5	17.6	30.9	181.1± 11.5	10.4 ± 0.7
BCP_1	2 (19)	243.6 ± 10.4	77.1	22.9		217.2 ± 10.8	13.3 ± 1.2
	3 (25)	246.4 ± 11.2	44.2	17.2	38.6	212.1 ± 10.7	11.4 ± 0.7
BCP_2	1 (16)	261.0 ± 10.6	100	-	-	229.8 ± 10.1	11.3 ± 0.7
	2 (25)	269.6 ± 10.3	77.3	22.7	-	237.0 ± 10.6	13.3 ± 1.1
Cross 2 (NDCMP-49 × 'ULR291')							
P_1	3 (8)	153.1 ± 6.4	38.6	7.5	53.9	116.3 ± 3.8	9.6 ± 0.7
P_2	1 (10)	216.3 ± 5.8	100	-	-	192.0 ± 5.34	14.6 ± 1.3
F_1	2 (10)	232.1 ± 7.8	71.1	28.9		207.7 ± 7.01	14.7 ± 0.6
F_2	1 (25)	189.0 ± 7.5	100	-	-	172.2 ± 7.1	14.3 ± 1.4
	2 (50)	180.4 ± 4.4	70.7	29.3		157.2 ± 4.3	13.2 ± 0.8
	3 (23)	194.8 ± 8.9	38.9	19.2	41.9	164.2 ± 7.4	11.8 ± 1.2
BCP_1	2 (21)	207.2 ± 8.1	72.6	27.4	-	178.2 ± 6.8	12.7 ± 1.2
	3 (18)	217.9 ± 7.8	37.6	18.5	43.9	192.6 ± 8.6	13.2 ± 1.1
BCP_2	1 (13)	204.6 ± 11.0	100	-	-	176.9 ± 9.9	11.9 ± 1.2
	2 (12)	186.2 ± 12.9	70.6	29.4	-	161.8 ± 10.6	12.4 ± 1.1

*Phenotypic class means (1) nonspikelet cluster type, (2) nonspikelet cluster and two spikelet cluster types, and (3) nonspikelet cluster with two and three spikelet cluster types in a single panicle.
**(1) noncluster, (2) two spikelet cluster, and (3) three spikelet cluster types on a single panicle.

'LLR316' and 44.2:17.2:38.6 (F_2) and 37.6:18.5:43.9 (BCP_1) in the NDCMP-49 × 'ULR291' cross (Table 1). These results suggested that the backcrossing method may increase the percentage of three spikelet clusters in these populations

The phenotypic Class 3 in the F_2 and BCP_1 populations, therefore, represented an alternative selection for advanced generations. Notably, the phenotypic Class 3 in the F_2 and BCP_1 populations demonstrated a range of transgressive segregation for all traits, indicating the extensive influence of additive gene action on the inheritance of grain yield per plant within this cross. Therefore, a breeder might improve the number of spikelet clusters of rice panicles by selecting the high-performing transgressive phenotype Class 3 of the BCP_1 and then backcrossing with the NDCMP-49 parent.

The phenotypic classes of panicle spikelet clusters may be categorized into three classes: 1) nonspikelet clusters, 2) nonspikelet and two spikelet clusters, and 3) nonspikelet clusters with two and three spikelet clusters. The segregation of the phenotypic classes in the F_2 population was consistent with that of NDCMP-49 × 'LLR316' and NDCMP-49 × 'ULR291'. They segregated at a ratio of one nonspikelet cluster:two nonspikelet clusters and two spikelet clusters:one nonspikelet cluster with two and three spikelet clusters or into 1 [Class1]:2 [Class 2]:1 [Class3]. This segregation pattern indicated that the spikelet clusters were controlled by a monogenic gene (Table 2).

The mode of inheritance in the F_2 population was confirmed on the basis of the backcross populations. The progenies that were derived from backcrossing to the NDCMP-49 parent segregated at a ratio of one nonspikelet cluster and two spikelet clusters [Class 2]:one nonspikelet cluster with two and three spikelet clusters [Class 3]. Moreover, the progenies derived from backcrossing with the 'LLR316' and 'ULR291' parents segregated at a ratio of one nonspikelet cluster [Class 1]:one nonspikelet cluster and two spikelet clusters [Class 2] (Table 2). This result again confirmed the monogenic governance of the spikelet cluster. The phenotypes of the F_1 and heterozygous genotypes, such as the phenotypic Class 2 in the F_2, BCP_1, and BCP_2 populations, produced only noncluster spikelets and two spikelet clusters in each panicle in contrast to the phenotypes of the NDCMP-49 parent. These results indicated that the gene controlling the spikelet clusters exhibits monogenic inheritance with the incomplete dominant action of the three

Table 2. χ^2 tests of segregation and the minimum number of genes estimated for the multispikelet cluster phenotype in F_2, BCP_1, and BCP_2 populations derived from crosses between NDCMP-49 × 'LLR316' and between NDCMP-49 × 'ULR291'.

Crosses	Populations	Phenotypic classes*			Total	χ^2 test**	*P - value*	Number of genes of phenotypic classes 2 and 3
		1	2	3				
NDCMP-49 × 'LLR316'	F_2	23	54	18	95	2.33	0.312	1.65
	BCP_1	-	19	25	44	0.82	0.365	
	BCP_2	16	25	-	41	1.97	0.161	
NDCMP-49 × 'ULR291'	F_2	25	50	23	98	0.12	0.941	0.86
	BCP_1	-	21	18	39	0.23	0.632	
	BCP_2	13	12	-	25	0.04	0.842	

*Phenotypic class means (1) nonspikelet clusters, (2) nonspikelet clusters and two spikelet clusters, and (3) nonspikelet clusters with two- and three spikelet clusters in a single panicle.

** χ^2 tests for the pinnacle ratio in each population: 1 (phenotypic class 1):2 (phenotypic class 2):1 (phenotypic class 3) in the F_2 population; 1 (phenotypic class 2):1 (phenotypic class 3) in the BCP_1 population; and 1 (phenotypic class 1):1 (phenotypic class 2) in the BCP_2 population.

Table 3. Scaling tests and estimation of gene action for panicle spikelet cluster types in rice over two different crosses.

Components	Cross 1 (NDCMP-49 × 'LLR316')	Cross 2 (NDCMP-49 × 'ULR291')
A	3.21 ± 6.39	3.27 ± 6.74
B	−2.00 ± 3.87	0.77 ± 6.39
C	22.34 ± 7.55*	0.81 ± 9.94
D	−10.56 ± 4.95	1.61 ± 6.52
m	22.63 ± 1.75**	29.63 ± 2.38**
d	28.09 ± 3.50**	29.45 ± 4.46**
h	16.15 ± 10.00	−4.96 ± 13.12
i	21.13 ± 9.90	−3.23 ± 13.05
j	−5.21 ± 7.39	−2.49 ± 9.22
l	−19.91 ± 15.91	7.26 ± 20.41

m = mean; [m] = additive; [h] = dominance; [i] = additive × additive; [j] = additive × dominance; [l] = dominance × dominance.*,**indicate that the value was significant by the t-test at the 0.05 and 0.01 probability level, respectively.

spikelet cluster type over the nonspikelet cluster type.

The minimum number of genes estimated for the control of the multispikelet cluster phenotypes of both crosses and the combined phenotypic Classes 2 and 3 were 1.65 and 0.86 genes in the crosses of NDCMP-49 × 'LLR316' and NDCMP-49 × 'ULR291', respectively. The results presented in Table 2 indicate that the heritable characters for the spikelet cluster traits were represented by a very large genetic component with a small environmental proportion.

Scaling tests were conducted to determine the presence or absence of nonallelic interactions. The results of scaling tests A, B, C, and D revealed nonsignificant values ($P < 0.05$) for the NDCMP-49 × 'ULR291' cross, and scaling test C provided significant results ($P < 0.05$) only for the NDCMP-49 × 'LLR316' cross (Table 3). The results further indicated the adequacy of an additive-dominance model for the inheritance of the multispikelet cluster phenotypes in rice. Genetic components, which were estimated via generation means analyses for the multispikelet cluster type index by using a six-parametric model, were significant ($P < 0.01$) for only the additive effects of both cross combinations, stressing the importance of an additive mode of gene action to regulate the multispikelet cluster phenotype. This result was further confirmed by the increase in the percentage of three spikelet cluster types in the BCP_1 population through cross-breeding and the effective selection of phenotypic values. The selection of the cluster traits can only be conducted on early generations; however, the diversity of grain yields per plant trait suggests that selection may be conducted on advanced generations to avoid gene segregation. The selection of superior genotypes based on the phenotypic performance for this trait may be effective.

DISCUSSION

Spikelet number per panicle is one of the major components of rice yield (Zhou *et al*., 2015). Normally, rice breeders have focused on the improvement of spikelet number per panicle by increasing the length of the main panicle axis, the length and number of primary branches, the number of secondary branches, the number of spikelets distributed on the branches, and the density of spikelets instead of focusing on the number of florets because almost all rice varieties produce one seed per florets. In this study, we report the genetics of the Thai indigenous rice variety 'NDCMP-49', the only indigenous Thai rice germplasm that exhibits three fertile spikelets per florets.

The results for the spikelet phonotypes of six populations demonstrated that the spikelet character differed among populations and segregated within populations (Table 1, Figure 1). The results revealed that one-fourth of the spikelets within the heterozygous genotype comprised two spikelet clusters. Interestingly, in contrast to the study of Jiang *et al*. (2014), wherein the F_1 class presented variations in clustered spikelets, our study created the phenotypic class of F_1 with only two types of nonclusters and two spikelet clusters per panicle.

The F_1 population of both crosses produced the highest grain yield per plant due to the heterosis phenomena of hybrid populations (Hwa and Yang, 2008; Sharma *et al*., 2013). However, the expression of spikelet clusters in the F_1 was unlike that in the NDCMP-49 parent. Moreover, the percentage of the three spikelet clusters in the F_2 and BCP_1 populations was lower than that of NDCMP-49, implying that backcrossing is needed to generate three spikelet clusters. The increase to two and three spikelet clusters per panicle appeared to increase the number of spikelets per panicle, filled grain per panicle, and grain yield per plant (Table 1), indicating a balance in the ratio between the sink and source for filled fertile grains, which increases the number of spikelet clusters per panicle.

Notably, the phenotypic Class 3 of the F_2 and BCP_1 populations demonstrated a range of transgressive segregation for all traits, indicating the extensive influence of additive gene action on the inheritance of grain yield per plant within this cross. Similar findings were also reported by Thirugnanakumar *et al.* (2011) and Banumathy *et al*. (2017).

The results verified that multispikelet characters in rice were controlled by the monogenic incomplete-dominance gene. Furthermore, previous studies have found that in wheat, the multispikelet trait might be a dominantly or partially dominantly inherited trait that is controlled by one or two genes (Chapman and McNeal, 1971; Dencic, 1988; Sun *et al*., 2000; Sun *et al*., 2009). Jiang *et al*. (2014) reported that the cluster spikelet phenotype is controlled by an incompletely dominant gene that is designated *sped1-D*. The fertility of the *sped1-D* mutant was negatively correlated with the presence of spikelet clusters. In this study, most spikelets produced from NDCMP-49 and their progenies presented well-developed fertile seeds (Table 1, Figure 1). We hypothesized that the gene that controls the multispikelet cluster of NDCMP-49 would differ from the *sped1-D* reported by Jiang *et al*., 2014. Therefore, the functional map-based cloning of the gene that controls the multispikelet cluster phenotype of NDCMP-49 warrants future study.

CONCLUSIONS

Our research focused on the inheritance and gene action of multispikelet clusters in the NDCMP-49 variety. Monogenic inheritance with incomplete dominance represents a new resource for the natural genetic variation of multispikelet clusters in rice. The new genetic information proved that the multispikelet cluster phenotype is a suitable trait for the breeding of high-yielding rice. We further identified the need to study the functional map-based cloning of genes that control multispikelet clusters in NDCMP-49 in future work.

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