

INHERITANCE OF PANICLE EXERTION IN RICE

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ABSTRACT: Incomplete panicle exertion is one of the symptoms of cold injury at the reproductive stage of the rice plant (*Oryza sativa* L.), which damages grain yield and raises disease incidence. For this reason, panicle exertion is a better indicator of cold tolerance under field conditions than spikelet sterility, which may also be affected by other climatic factors. This work studies the variability of degree of panicle exertion in rice, under the Southern Brazilian environmental conditions and determines the inheritance and heritability of this trait. Four rice genotypes of different cool temperature reactions at the reproductive stage were crossed and field evaluated, with the F₂ generation, in relation to the degree of panicle exertion and spikelet fertility. There was variability among the genotypes for panicle exertion. The F₂ generation of the crosses presented continuous distribution and transgressive segregation towards incomplete exertion, indicating that genes controlling this trait may be complementary distributed between the parents. Heritability was moderate, so selection for complete panicle exertion should be applied in advanced generations.

Key words: *Oryza sativa* L., chilling temperature, cold tolerance, complete panicle exertion, heritability

HERANÇA DA EXERÇÃO DA PANÍCULA EM ARROZ

RESUMO: A exerceção incompleta da panícula é um dos sintomas de dano por frio no estágio reprodutivo da planta de arroz (*Oryza sativa* L.), o qual prejudica o rendimento de grãos e aumenta a incidência de doenças. Devido a isso, a exerceção da panícula é um bom indicador da tolerância ao frio sob condições de campo ao invés da esterilidade de espiguetas, que também pode ser afetada por outros fatores climáticos. Este trabalho objetivou estudar a variabilidade do grau de exerceção da panícula de arroz sob as condições ambientais do sul do Brasil e determinar a herança e herdabilidade desta característica. Quatro genótipos de arroz com diferentes reações à temperatura baixa no período reprodutivo foram cruzados e avaliados a campo, juntamente com a geração F₂, quanto ao grau de exerceção da panícula e fertilidade de espiguetas. Houve variabilidade entre os genótipos para exerceção da panícula. A geração F₂ apresentou distribuição contínua e segregação transgressiva na direção da exerceção incompleta, indicando que os genes para exerceção da panícula devem estar distribuídos complementarmente entre os genitores. A herdabilidade foi moderada, portanto seleção para exerceção completa da panícula é recomendada em gerações avançadas.

Palavras-chave: *Oryza sativa* L., temperatura baixa, tolerância ao frio, exerceção completa da panícula, herdabilidade

INTRODUCTION

Rice is very sensitive to cool temperatures during the reproductive period (Yoshida, 1981). Although the main symptom of damage from cold is the high spikelet sterility (Jacobs & Pearson, 1994), incomplete panicle exertion has been cited as a symptom of cold injury in many countries (Chung, 1979; Hamdani, 1979; Alvarado & Grau, 1991).

Cold tolerance at the reproductive period has been associated with the degree of panicle exertion, which could be used as a selection criterion (Nanda & Seshu, 1979). In fact, this trait was suggested as

an indicative of genotype adaptability to cool temperatures (Takahashi, 1984). The inheritance of the degree of panicle exertion under cool temperatures in field conditions was pointed out as having a simple mendelian pattern, with one dominant gene responsible for the complete panicle exertion (Mahishi et al., 1991; Pandey & Gupta, 1993). More recently, 44 QTLs located on 11 of the 12 rice chromosomes were associated with increased panicle exertion and described as major genes with overdominance (Han et al., 2006). In a recombinant inbred line population derived from an Indica × Japonica cross, however, a lower number of QTLs clustered in a few chromosomal blocks

explained a small portion of the variation on this trait (Oh et al., 2004), discarding the involvement of major genes in panicle exertion. In a diallel study, the general combining ability effects were more important than the specific combining ability effects for panicle exertion (Han et al., 2004), showing that inheritance studies are highly dependent on the genetic material.

In Southern Brazil, in spite of reports on the occurrence of incomplete panicle exertion due to cool temperatures during the reproductive period (Souza, 1990), there are no data concerning the genetics of this trait under field conditions. So, this work aimed at studying the variability for the degree of panicle exertion in four rice genotypes and determining the inheritance and heritability of the trait.

MATERIAL AND METHODS

The rice genotypes studied were Quilla 64117, Diamante, IRGA 417 and BRS Taim. The former two are from Chile, belong to the Japonica subspecies and are cold tolerant, with complete panicle exertion under cool temperatures. The latter two are Brazilian rice cultivars belonging to the Indica subspecies and are cold sensitive, with incomplete panicle exertion under cool temperatures.

In the 1997/98 growing season, the four genotypes were crossed in a partial diallel and the F_1 generation was planted in the next growing season for F_2 seed production. In 1999/2000, a field experiment with the four parents and the F_2 populations was conducted at Santa Vitória do Palmar, State of Rio Grande do Sul, Brazil, (33°31' S and 53°22' W). This location was chosen because it has the highest incidence of cool temperatures during the rice growing season in Southern Brazil.

Sowing time was purposely chosen to be late, on the 2nd of December, 1999, allowing the coincidence between the rice flowering period and the lowest minimum temperatures, which occur at the end of Feb., beginning of March. Experimental units were 9 m² plots with six rows 5 m long and 0.3 m between rows, which were machine sowed using 10 g of seed per plot. Plant emergence occurred 11 days after sowing and N fertilization was applied 35, 50 and 60 days after emergence using 22.5 kg ha⁻¹ of N in each application.

The experiment was conducted using a randomized block design with three replications for each treatment (four genotypes and six F_2 segregating populations). Twenty plants were randomly labeled in parental each plot and 70 plants per F_2 plot. For each labeled plant, the main tiller was individually identified and observed every week as to its flowering stage. The observations started when the earlier genotypes were

at the booting stage and extended until all the labeled plants reached maturity. These weekly observations were used to estimate the flowering period of all the labeled tillers. At maturity, each identified tiller had its panicle harvested and evaluated for degree of exertion. The panicles of the parents were also evaluated for percentage of spikelet fertility. This trait was not evaluated in the F_2 populations due to the high sterility observed in the crosses between Indica and Japonica genotypes, which was attributed to genetic causes, rather than to low temperatures.

Degree of panicle exertion was measured as the distance from the flag leaf ligule to the panicle node, in cm. Positive and negative values indicated complete and incomplete panicle exertion, respectively. Spikelet fertility was obtained by counting the number of filled and empty grains and expressed as the percentage of filled grains by the total number of spikelets of the panicle.

Statistical analysis of the traits measured in the parents was performed considering a randomized block design with subsampling in the plots, with three replications and 20 subsamples per replication. Residual and regression analysis were performed to verify data normality and the need for transformation, respectively. Both degree of panicle exertion and percentage of spikelet fertility were transformed according to $\sqrt{x + 10}$. The traits were submitted to analysis of variance, means comparison by Duncan's Test and calculation of Pearson's correlation coefficients, all performed by the Statistical Analysis System (SAS Institute, 2000).

The inheritance of degree of panicle exertion was studied through an analysis of the distribution of frequencies at the generations P_1 , P_2 and F_2 in each of the crosses, which were obtained by grouping the data into classes, with the class interval corresponding to $\frac{1}{4}$ of the average standard deviation (Steel & Torrie, 1980).

Variances were estimated as follows (Allard, 1960): $VP = VF_2$; $VE = (VP_1 + VP_2) / 2$; $VG = VP - VE$

where: VP_1 and VP_2 represent the variances of the parents and VF_2 represent the variance of the F_2 generation. Heritability estimates in the broad sense were calculated according to the formula (Allard, 1960):

$$h_b^2 = (VP - VE) / VP$$

RESULTS AND DISCUSSION

Flowering in the parents and in the F_2 progenies began in the second half of Feb. and extended until the end of March (data not presented). The cold tol-

erant genotypes Quilla 64117 and Diamante flowered approximately 20 days before the sensitive ones, BRS Taim and IRGA 417. As a consequence, there was a large segregation for growth duration in the F₂ generation derived from the crosses between sensitive and tolerant genotypes. This makes selection for cold tolerance under field conditions very imprecise, once the plants were exposed to different air temperatures at flowering. To avoid this effect, only plants that flowered between Feb. 19th and March 18th were considered for evaluating the parents and for the inheritance study. Average temperature and average minimum temperature did not vary considerably within this period. Average temperature was 22°C (±1.5) and the average minimum temperature was 17°C (±2.0), which is below the critical limit of 20°C for cold damage (Fepagro, 2000).

Differences were observed among the parents for panicle exertion and percentage of spikelet fertility, indicating variability among them for these traits. The cold tolerant genotypes Quilla 64117 and Diamante had a better performance than the sensitive parents, presenting complete panicle exertion (positive values) and higher percentage of spikelet fertility (Table 1).

The F₁ and F₂ generations derived from the crosses between sensitive and tolerant genotypes presented a high degree of sterility (data not shown), as they resulted from an Indica × Japonica combination. High sterility has been often observed in this type of cross and has genetic causes (Oka & Morishima, 1997; Kubo & Yoshimura, 1999; Kubo et al., 2000). In fact, in the F₂ generation, segregation for spikelet fertility was clearly observed, and due to its genetic origin, evaluation of this trait as a cold tolerance parameter was not performed. So, panicle exertion was chosen as a cold tolerance indicator because complete panicle exertion has been associated with cold tolerance (Chung, 1979; Han et al., 2006). A moderate and posi-

tive phenotypic correlation ($r = 0.43^{**}$) between panicle exertion and spikelet fertility was found based on parental data obtained in the field experiment, demonstrating that larger the panicle exertion, higher the percentage of spikelet fertility. This is in accordance with data that shows a positive correlation between panicle exertion and seed setting in rice under cold water conditions (Han et al., 2004).

The distributions of frequency for the degree of panicle exertion in the six crosses are presented in Figure 1. The two cold tolerant genotypes had very similar distributions, which was expected since they did not differ to degree of panicle exertion (Table 1). In the case of the cold sensitive genotypes, although there was a certain similarity, the genotype IRGA 417 presented lower values of panicle exertion than BRS Taim, as shown by Duncan's Test (Table 1).

Distinction between the parents could be observed in the four sensitive × tolerant crosses in which the cold sensitive parent presented predominantly negative values (incomplete panicle exertion) and the cold tolerant parent mostly positive values (complete panicle exertion). Panicle exertion data for the F₂ generation of these crosses revealed a continuous distribution, but the average was negative, indicating predominance of incomplete panicle exertion such as the cold sensitive parent (Figure 1). A continuous distribution for panicle exertion has also been reported (Bardhan Roy et al., 1982), but other studies have related that complete panicle exertion is controlled by a dominant gene (Mahishi et al., 1991; Pandey & Gupta, 1993). In both of these studies, however, panicle exertion was treated as a discrete variable with data computed in one of the two classes: complete vs. incomplete exertion and analyzed by the Chi-Square Test.

There are also two other differences between those studies and the present one. First, in both studies the tolerant × sensitive type of cross was between Indica genotypes, while here they involved an Indica versus a Japonica genotype. Second, despite being also conducted under field conditions, they were performed in India, which presents environmental differences in relation to the Brazilian irrigated rice region. So the different results between this study and the ones by Mahishi et al. (1991) and Pandey & Gupta (1993) may be attributed to different genotypes and environmental conditions.

Besides the continuous distribution, the transgressive segregation observed for panicle exertion in the F₂ generation points to genes complementary distributed between the parents. This transgressive segregation was towards incomplete exertion, which was clearly dominant over complete exertion in the crosses between sensitive and tolerant genotypes. A similar re-

Table 1 - Panicle exertion and spikelet fertility means for the parents under field conditions in Santa Vitória do Palmar, RS.

Genotype	Panicle exertion cm	Spikelet fertility %
Quilla 64117	1.9 a	91.4 a
Diamante	2.4 a	87.9 b
BRS Taim	-1.8 b	81.7 c
IRGA 417	-3.7 c	76.8 d
CV(%)	11.3	3.9
R ²	0.69	0.59

Means followed by the same letter in each column do not differ (Duncan's Test $p < 0.05$).

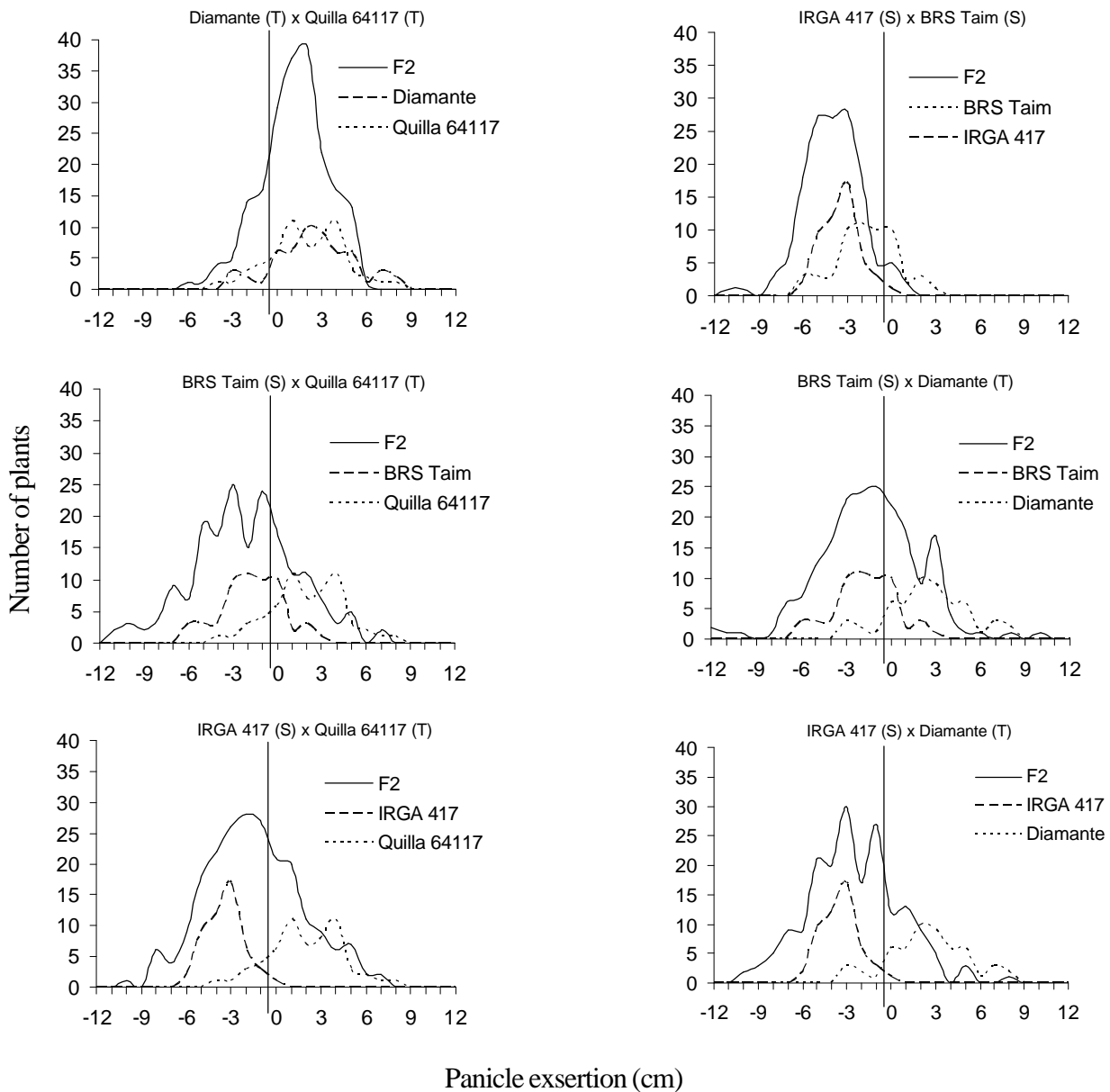


Figure 1 - Frequency distributions for the parents and the F_2 generation of six rice crosses involving two cold tolerant (T) and two cold sensitive (S) genotypes evaluated for panicle exertion under field conditions in Santa Vitória do Palmar, RS.

sult was reported in a diallel analysis, where it was verified that the alleles that increased panicle exertion were, in their majority, recessives (Acharya, 1987).

Broad sense heritabilities for the crosses between cold sensitive and cold tolerant genotypes were moderate (Table 2), and the crosses involving Quilla 64117 presented slightly higher heritabilities than the ones in which Diamante was the cold tolerant parent.

In the process of breeding for cold tolerant rice genotypes at the reproductive period, under the Southern Brazilian field conditions, selection for complete panicle exertion is recommended as an indicative of cold tolerance, once it increases spikelet ferti-

lity (Chung, 1979). However, considering the results here obtained, temperature variation in the field and the fact that plants do not flower at the same time in a segregating population, it is advisable to select for panicle exertion in more advanced generations of the breeding program. In this case, plants will have already been selected for adequate growth duration and so they will flower mostly at the same period, lowering the environmental variance. An association between plant stature and panicle exertion has been reported (Bardhan Roy et al., 1982) and should also be taken into account, with selection for taller plants recommended in order to get better panicle exertion. In the present study, the two genotypes with complete

Table 2 - Phenotypic (VP), genetic (VG) and environmental (VE) variances and broad sense heritabilities (h^2_b) for degree of panicle exertion in four rice crosses.

Cross	VP	VG	VE	h^2_b
BRS Taim × Quilla 64117	12.22	7.21	5.01	0.59
BRS Taim × Diamante	11.06	5.54	5.52	0.50
IRGA 417 × Quilla 64117	10.33	6.62	3.71	0.64
IRGA 417 × Diamante	9.64	5.41	4.23	0.56

panicle exertion are indeed taller than the other two genotypes, which was already expected as they are Japonicas.

In fact, panicle exertion seems to be related to many other traits in rice as demonstrated by the clustering of QTLs for panicle exertion, plant height, panicle number, panicle length and biomass production at the same marker intervals (Hittalmani et al., 2002). Pleiotropism and/or tight linkage were suggested as the plausible reasons for the congruence of all these QTLs. If these arguments are confirmed, selection for better panicle exertion will have a direct effect on many other traits or will be affected by selection on these traits. Also, the reported relationship between the last internode and panicle development (Sunohara et al., 1999) indicates that the genes responsible for complete panicle exertion under low temperature are probably internode elongation genes less sensitive to chilling. The recessive *eui1* gene, which controls elongation of the uppermost internode in rice and was produced by mutagenesis (Ma et al., 2004), proves the relationship among internode elongation, plant stature and panicle exertion in rice. When compared with the wild type, plant height, internode elongation and panicle exertion were increased significantly in the mutated genotype. QTL for culm length and affecting cold tolerance have been mapped in a Japonica population (Takeuchi et al., 2001). These results make the study of panicle exertion more complex as an individual trait, but as mapping efforts advance, more about the genetic control of plant stature, internode elongation and panicle exertion will be revealed, which will contribute to our knowledge of the relationship among them.

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