Inheritance of Panicle Types Classified by the Nodal Distribution Pattern of Secondary Spikelets in Rice (*Oryza sativa* L.)

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The inheritance of rice (*Oryza sativa* L.) panicle types classified by the nodal distribution pattern of the number of spikelets on the secondary rachis branches was investigated using four varieties belonging to different ecospecies. Reimei (a modern cultivar from Japan, *japonica*) and Stirpe 136 Anthocyane (a large grain variety from Italy) had a large number of spikelets on their secondary rachis branches at the lower rachis nodes and an extremely small number at the upper rachis nodes. Mao-zu-tao (an old cultivar from China, *indica*) had a large number of spikelets on its secondary rachis branches at the upper rachis nodes and a small number at the lower rachis nodes. Panbila (a modern cultivar from U.S.A., *indica*) had a large number of spikelets on the secondary rachis branches at both the lower and upper rachis nodes. The number of spikelets on the primary rachis branch of each rachis node was about 6.0 and showed little change in the parents, the F_1 and F_2 generations, indicating the existence of genetical similarity among the parents. In the Mao-zu-tao x Reimei cross, the number of spikelets on the secondary rachis branches at the upper rachis nodes was controlled by four independent dominant genes (*Ssp-1*, *Ssp-2*, *Ssp-3* and *Ssp-4*) and that at the lower rachis nodes by a suppressor gene (*Su-1*). The *Su-1* gene was closely linked with *Ssp-3* and controlled by *Ssp-1*, *Ssp-2* and *Ssp-3*. In the Panbila x Stirpe 136 Anthocyane cross, the mode of inheritance of the nodal distribution pattern of the number of spikelets on the secondary rachis branches was very similar to that of the Mao-zu-tao x Reimei cross. However, in this case, three independent dominant genes (*Ssp-1*, *Ssp-2* and *Ssp-3*) controlled the number of spikelets on the secondary rachis branches at the upper rachis nodes. A suppressor (*Su-2*) and an activator (*Act*) genes, which were closely linked with the *Ssp-1* and *Ssp-3* genes, respectively, controlled the number of spikelets on the secondary rachis branches at the lower rachis nodes. The *Su-1*, *Su-2* and *Act* genes were considered to be the regulator genes. It was estimated that they would be stimulated by the *Ssp* genes and control the structural genes which would express the initiation and growth of the secondary spikelets at the lower rachis nodes.

KEY WORDS : *Oryza sativa*, panicle type, secondary spikelet, rice subspecies, filling rate

Introduction

The principal yield components of the rice plant are 1) the number of hills per unit of land area, 2) the number of panicles per hill, 3) the number of spikelets per panicle, 4) the 1000-kernel weight and 5) the percentage of ripened grains. The number of spikelets per panicle seems far beyond genetic control since it largely varies with the planting density and application time and amount of fertilizer (MATSUSHIMA 1957 and KAMBAYASHI *et al.* 1983). The number of spikelets per panicle can be divided into 2 secondary components, 1) the number of primary rachis branches per panicle, and 2) the number of spikelets on the primary and secondary rachis branches per primary rachis branch. MANAKA and MATSUSHIMA (1971) observed that the number of spikelets per primary rachis branch showed little change in a wide range of rice varieties. SASAHARA *et al.* (1982a) observed that the number of spikelets per primary rachis branch ranged

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between 5.0 to 6.0 in rice varieties belonging to three ecospecies, *indica*, *japonica* and *javanica*. Furthermore, they indicated that each ecospecies showed a characteristic nodal distribution pattern of the number of spikelets on the secondary rachis branches. Three basic panicle types were classified by the nodal distribution pattern of the number of spikelets on the secondary rachis branches (SASAHARA *et al.* 1982a), i.e. the relative distribution of the number of spikelets on the secondary rachis branches at the upper, middle and lower rachis nodes. These panicle types remained stable regardless of the level of fertilizer application, planting density and tillering order although the absolute number of spikelets on the secondary rachis branches varied largely at each rachis node (KAMBAYASHI *et al.* 1983).

The present experiment was carried out to analyze the mechanism of genetic control of the panicle types, as classified by the nodal distribution pattern of the number of spikelets on secondary rachis branches.

Materials and Methods

Four rice (*Oryza sativa* L.) varieties belonging to different ecospecies, which differed

Fig.1. Panicle types of the parents and F_1 , F_2 generations in a cross between Mao-zu-tao and Reimei.

- : Number of spikelets on primary rachis branches.
-● : Number of secondary rachis branches.
- : Number of spikelets on secondary rachis branches.

The horizontal bars across the symbols indicate the standard errors, and the standard errors are within the symbol size in the symbols without horizontal bars.

Ordinates : Rachis node numbered from panicle base (=zero) upwards. Interval of the primary rachis nodes on the figures is the ratio of average panicle length to average number of primary rachis branches per panicle.

Abscissae : Number of grains or secondary rachis branches.

in the nodal distribution pattern of the number of spikelets on the secondary rachis branches, were selected, viz. Mao-zu-tao (an old cultivar from China, *indica*), Panbila (a modern cultivar from U.S.A., *indica*), Reimei (a modern cultivar from Japan, *japonica*) and Stirpe 136 Anthocyane (a large grain variety from Italy, *javanica*). The number of spikelets on the secondary rachis branches was large at the upper rachis nodes but very small at the lower ones in Mao-zu-tao, large at both the upper and lower rachis nodes in Panbila, very small at the upper rachis nodes but large at the lower rachis nodes in Reimei and Stirpe 136 Anthocyane (SASAHARA *et al.* 1982a).

Mao-zu-tao and Reimei were crossed in August, 1979. The F_1 plants were grown, and the F_2 seeds were harvested in the same year by the method of rapid generation advancement at the Shonai Branch Station of Yamagata Agriculture Research Institute. Ten plants of each parent, ten F_1 plants and 1533 F_2 plants were grown at the Yamagata University farm in 1980. Stirpe 136 Anthocyane and Panbila were crossed in August, 1980, and the F_2 seeds were harvested by the same method as that described above. Ten plants of each parent, ten F_1 plants, and 292 F_2 plants were also grown in 1981.

Fully ripened panicles were sampled from the longest culm in the hills. The primary rachis branches were numbered from the panicle base (=zero) upwards. The number of spikelets on the primary and secondary rachis branches, and the number of secondary rachis branches per primary rachis branch were determined. After recording these values, the panicles were classified into three types which have a large number of the spikelets on the secondary rachis branches at the upper, middle and lower rachis nodes (SASAHARA *et al.* 1982a). They are denoted as the upper-node large number type, middle-node large number type and lower-node large number type for convenience hereafter, respectively.

Fig. 2. Panicle types of the parents and F_1 and F_2 generations in a cross between Panbila and Stirpe 136 Anthocyane. See Fig.1 for other symbols and comments.

Results and Discussion

The panicle types of Mao-zu-tao, Reimei and their F_1 and F_2 plants, and of Panbila, Stirpe 136 Anthocyane and their F_1 and F_2 plants are shown in Fig. 1 and 2, respectively.

Table 1. Mode of inheritance of panicle types in a cross between Mao-zu-tao and Reimei

Genetic control of number of grains on the secondary rachis branches at the upper rachis nodes				
Genotype of parents	Mao-zu-tao <i>Ssp-1, Ssp-2, Ssp-3-Su-1, Ssp-4</i>		×	Reimei <i>ssp-1, ssp-2, ssp-3-su-1, ssp-4</i>
Genotype of F_1 plants	<i>Ssp-1, Ssp-2, Ssp-3-Su-1, Ssp-4</i> (Heterozygote)			
Genotype of F_2 Plants and segregation ratio	Mao-zu-tao type <i>Ssp-1, Ssp-2, Ssp-3-Su-1, Ssp-4</i>	Intermediate type	Reimei type	
	<i>Ssp-1, Ssp-2, Ssp-3-Su-1, Ssp-4</i>	81		
	<i>Ssp-1, Ssp-2, Ssp-3-Su-1, ssp-4</i>	27	<i>ssp-1, Ssp-2, Ssp-3-Su-1, Ssp-4</i>	27
	<i>Ssp-1, Ssp-2, ssp-3-su-1, Ssp-4</i>	27	<i>Ssp-1, ssp-2, Ssp-3-Su-1, ssp-4</i>	9
	<i>Ssp-1, ssp-2, Ssp-3-Su-1, Ssp-4</i>	27	<i>ssp-1, Ssp-2, ssp-3-su-1, Ssp-4</i>	9
	<i>Ssp-1, Ssp-2, ssp-3-su-1, Ssp-4</i>	9	<i>ssp-1, ssp-2, Ssp-3-Su-1, ssp-4</i>	9
	<i>Ssp-1, ssp-2, ssp-3-su-1, Ssp-4</i>	9	<i>ssp-1, ssp-2, ssp-3-su-1, Ssp-4</i>	9
		180		63
Observed (total=1533)	1089 ¹⁾		367	
Expected	1078		377	
Chi-square test	0.8 < p < 0.9			

¹⁾ See Table 2 for segregation.

Table 2. Mode of inheritance of panicle types in a cross between Mao-zu-tao and Reimei

Genetic control of number of grains on the secondary rachis branches at the lower rachis nodes of Mao-zu-tao type panicles				
Genotype and segregation ratio	Type I <i>Ssp-1, Ssp-2, Ssp-3-Su-1, ssp-4</i>	27	Type II and III	
	<i>Ssp-1, Ssp-2, ssp-3-su-1, Ssp-4</i>	27		
	<i>Ssp-1, Ssp-2, ssp-3-su-1, ssp-4</i>	9	<i>Ssp-1, Ssp-2, Ssp-3-Su-1, Ssp-4</i>	81
	<i>Ssp-1, ssp-2, ssp-3-su-1, Ssp-4</i>	9	<i>Ssp-1, ssp-2, Ssp-3-Su-1, Ssp-4</i>	27
		72		108
Observed (total=1089)	449		640	
Expected	436		653	
Chi-square test	0.3 < p < 0.5			

The panicle type of the F_1 plants was similar to that of the parents, corresponding to the upper-node large type in both cases. However, the number of spikelets on the secondary rachis branches in the F_1 plants resulting from crosses between Panbila and Stirpe 136 Anthocyane was lower by about eight units for all the rachis nodes than in Panbila. In the Mao-zu-tao and Reimei cross, five panicle types appeared in the F_2 generation, i. e. the upper and lower-node large number type, 2 upper-node large number types, middle-node large number type, and lower-node large number type, and in the

Table 3. Mode of inheritance of panicle types in a cross between Panbila and Stirpe 136 Anthocyane

Genetic control of number of grains on the secondary rachis branches at the upper rachis nodes				
Genotype of parents	Panbila <i>Ssp-1-Su-2, Ssp-2, Ssp-3-Act</i>		×	Stirpe 136 Anthocyane <i>ssp-1-su-2, ssp-2, ssp-3-act</i>
Genotype of F_1 plants			<i>Ssp-1-Su-2, Ssp-2, Ssp-3-Act</i> (Heterozygote)	
Genotype of F_2 plants and segregation ratio	Panbila type	Intermediate type		Stirpe 136 Anthocyane type
				<i>Ssp-1-Su-2, ssp-2, ssp-3-act</i> 3
				<i>ssp-1-su-2, Ssp-2, ssp-3-act</i> 3
	<i>Ssp-1-Su-2, Ssp-2, Ssp-3-Act</i> 27	<i>Ssp-1-Su-2, ssp-2, Ssp-3-Act</i> 9		<i>ssp-1-su-2, ssp-2, Ssp-3-Act</i> 3
	<i>Ssp-1-Su-2, Ssp-2, ssp-3-act</i> 9	<i>ssp-1-su-2, Ssp-2, Ssp-3-Act</i> 9		<i>ssp-1-su-2, ssp-2, ssp-3-act</i> 1
Observed (total=292)	36	18		10
Expected	157 ¹⁾	89		46
Chi-square test	164	82		46
		0.5 < p < 0.8		

¹⁾ See Table 4 for segregation.

Table 4. Mode of inheritance of panicle types in a cross between Panbila and Stirpe 136 Anthocyane

Genetic control of number of grains on the secondary rachis branches at the lower rachis nodes of Panbila type panicles				
Genotype and segregation ratio	<i>Ssp-1-Su-2, Ssp-2, Ssp-3-Act</i> 27		<i>Ssp-1-Su-2, ssp-3-act, Ssp-2,</i> 9	
	Type		Type	
Observed (total=157)	I 53	II 41	III 26	IV 37
	120			
Expected	118		39	
Chi-square test			0.5 < p < 0.8	

Panbila and Stirpe 136 Anthocyane cross, six panicle types, i.e. the upper and lower-node large number type, three upper-node large number types, middle-node large number type, and lower-node large number type. The number of spikelets on the primary rachis branch of each rachis node varied little in the parents and their descendants in both crosses.

The following hypothesis can be put forward with regard to the mode of inheritance and gene expression of the panicle types shown in Table 1 and 2 for the Mao-zu-tao and Reimei cross.

1) The dominant gene *Ssp-1* may express the number of spikelets at the upper rachis nodes of the Mao-zu-tao type panicles. The *Ssp-1* gene may be strongly stimulated by the *Ssp-2* and *Ssp-4* genes, and weakly by *Ssp-3*.

2) The *Ssp-2* and *Ssp-4* genes, which act in synergy, along with the contribution of the *Ssp-3* gene may take part in the control of the intermediate distribution of the secondary spikelets at the upper rachis nodes.

3) The dominant gene *Su-1*, which is closely linked with the *Ssp-3* gene, may inhibit the increase in the number of secondary spikelets at the lower rachis nodes of the Mao-zu-tao type panicles. However, the *Su-1* gene may act only when the *Ssp-3*, *Ssp-4* and *Ssp-1* genes exist.

4) The *Ssp-1* gene without the contribution of *Ssp-2* and *Ssp-4* genes may fail to express the character manifested by the upper-node large number type in the Reimei type panicles, resulting in the lower-node large number type in the Reimei type panicles because the *Su-1* gene did not express itself. The Reimei type panicles of the F_2 generation bore a few spikelets at the uppermost rachis nodes. This indicates that modifiers may control the growth of the secondary spikelets at the uppermost rachis nodes.

The mode of inheritance and gene expression of the panicle types in the Panbila and Stirpe 136 Anthocyane cross (Table 3 and 4) are essentially similar to those of the Mao-zu-tao x Reimei group. However, in this case, the *Ssp-4* gene is absent, and hence the *Su-1* gene would not be able to express itself. In turn, the dominant gene *Act*, which is closely linked with the *Ssp-3* gene, may promote the large number of secondary spikelets at the lower rachis nodes in the Panbila type panicles. Furthermore, the dominant gene *Su-2*, which is closely linked with the *Ssp-1* gene and whose expression is enhanced by the *Ssp-1* and *Ssp-2* genes, may depress the bearing capacity and growth of the secondary spikelets at the lower rachis nodes. Expression of the *Su-2* gene may be blocked by the *Ssp-3* gene. As in the Reimei type panicles, failure of expression of the upper-node large number type in the Stirpe 136 Anthocyane type panicles would bring about a lower-node large number type in spite of the inactivation of the *Act* gene which expresses the lower-node large number type in the Panbila type panicles. Therefore, the lower-node large number type in the Reimei and Stirpe 136 Anthocyane type panicles may be ascribed to a recessive epistatic effect.

The *Su-1*, *Su-2* and *Act* genes may be regulator genes, and they may be stimulated by the *Ssp* genes and control the structural genes which express the initiation and growth of the secondary spikelets at the lower rachis nodes.

It is well known that the spikelets on the primary rachis branches show a higher

growth rate, heavier final dry weight (NAGATO 1964 and ARAI and KONO 1978), and higher percentage of ripened grains (OTA *et al.* 1958 and WADA 1969) than spikelets on the secondary rachis branches. Therefore, it would be important to increase the number of spikelets on the primary rachis branches in order to increase grain yield. However, it was demonstrated that the number of spikelets per primary rachis branch does not show appreciable changes in a wide range of rice varieties (MANAKA and MATSUSHIMA 1971), and among different ecospecies regardless of the level of fertilizer application and planting density (SASAHARA *et al.* 1981a and KAMBAYASHI *et al.* 1983). The present results indicate that the number of spikelets per primary rachis branch may be regulated by genetic factors. In turn, the number of primary rachis branches per panicle appears to be the main factor responsible for the increase in the number of spikelets per panicle on the primary rachis branches.

The number of spikelets on the secondary rachis branches is also a very important factor in determining yield components and it can account for more than fifty percent of the total number of spikelets per panicle (SASAHARA *et al.* 1982a and b). However, the increase in the number of spikelets on the secondary rachis branches has been found to reduce the percentage of ripened grains (MATSUSHIMA 1957 and WADA 1969). This finding indicates that the number of spikelets per panicle on the secondary rachis branches should be well compensated by the source activity.

SASAHARA *et al.* (1982b) observed that the increment in panicle weight was larger in *indica* and *javanica* than in *japonica* varieties. They indicated that the large increment in panicle weight in *indica* varieties could be ascribed to the fact that the number of spikelets on the secondary rachis branches in *indica* varieties was large at the upper rachis nodes where the secondary spikelets benefitted from the effect of apical dominance. On the other hand, in spite of the lower-node large number type, the *javanica* varieties showed a larger increment in panicle weight compared to *japonica* varieties. However, SOFIELD *et al.* (1977) in wheat, EGLI *et al.* (1978) in soybean, JONES *et al.* (1979) in rice, CARR and PONELEIT (1973) and PONELEIT *et al.* (1980) in corn observed that the varieties with heavier grain weight had a higher grain filling rate. Therefore, the large increment in panicle weight recorded in *javanica* varieties may be ascribed to their heavier grain weight. Thus, it may be concluded that since the genetic factors appear to be involved in the control of the number of secondary spikelets at the upper rachis nodes and/or grain weight, genetic manipulation could contribute to the improvement of grain filling rate of the secondary spikelets.

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穂軸節位の二次枝梗着生の差異によって分類された穂型の遺伝

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穂軸節位によって二次枝梗の着生数の異なる水稻品種を用いて異なる穂軸節位における二次枝梗着生の遺伝を検討した。材料は上位穂軸節位に二次枝梗が多く着生する品種（以下、二次枝梗着生上位優勢型とする）の帽子頭と Panbila（ともに *indica*）、下位穂軸節位に二次枝梗が多く着生する品種（以下、二次枝梗着生下位優勢型とする）のレイメイと Stirpe 136 Anthocyane (*javanica*) を用いた。ただし、Panbila は疎植などの条件下では、二次枝梗を下位穂軸節位にも多く着生する品種である。

二次枝梗着生上位および下位優勢型の遺伝を検討するため、帽子頭×レイメイ、Panbila×Stirpe 136 Anthocyane の交配を行なった。穂は、両親、 F_1 および F_2 植物の株の最長茎から採取した。穂首節位を零とし、上位に向って一次枝梗に番号を付し、穂当たりの一次枝梗数、各穂軸節位の一次枝梗数、二次枝梗数、二次枝梗数を調査した。これらの値を穂ごとに図示したのち、二次枝梗着生上位、中位、下位優勢型などに分類した。

帽子頭の二次枝梗着生上位優勢型の発現には4つの優性遺伝子 (*Ssp-1*, *Ssp-2*, *Ssp-3*, *Ssp-4*) が関与し、また帽子頭の下位穂軸節位の二次枝梗着生の抑制には上記優性遺伝子の1つ (*Ssp-3*) と連鎖した1優性遺伝子 (*Su-1*) が関与していると推定された。

一方、Panbila の二次枝梗着生上位優性型の発現には3つの優性遺伝子 (*Ssp-1*, *Ssp-2*, *Ssp-3*) が関与し、また Panbila の下位穂軸節位の二次枝梗の着生を上記の1優性遺伝子 (*Ssp-1*) に連鎖した1抑制遺伝子 (*Su-2*) と上記の他の1優性遺伝子 (*Ssp-3*) に連鎖した1促進遺伝子 (*Act*) が関係していると推定された。

他方、レイメイと Stirpe 136 Anthocyane の二次枝梗着生下位優勢型は、劣性上位によって発現されるものと推定された。