Distribution and Interrelationship of Differentiated, Degenerated and Surviving Spikelets on Panicle Branches in Rice (*Oryza sativa*)

T H Ansari[1], T Yoshida[2], Y Yamamoto[2] and A Miyazaki[3]

ABSTRACT

The present investigation evaluated distribution pattern of differentiated, degenerated and surviving spikelet's and interrelationship of spikelet's on the basis of their position on rachis branches in a panicle of both japonica and indica cultivars. Distribution of differentiated spikelets on primary brances (PBs) and secondary brances (SBs) followed 1:1 ratio in the japonica cultivars and 1:2 or more than 2 in the indica ones irrespective of plant types revealed the genetic factor had the more influence on the observed distribution pattern in both japonica and indica cultivars. The percentage of degenerated spikelets to the differentiated ones on PBs was slightly higher in the japonica (4.2%－8.3%) than in the indica (0.5%－6.6%) cultivars. The degenerated percentage of differentiated spikelets on SBs varied more widely in the indica (11.9%－56.2%) than in the japonica (26.1%－48.2%) cultivars, although average was almost the same (37.7% in the japonica and 38.9% in the indica cultivars). Correlation coefficients showed that the increase of differentiated spikelets on PBs strongly increase the number of surviving spikelet per panicle or on PBs per panicle in both cultivar groups. But this was not significantly increase the number of degenerated spikelets on PBs but showed possibility of increase the number of degenerated spikelets on SBs per panicle in both cultivar groups. Increased number of differentiated spikelets on SBs substantially increased the numbers of both surviving and degenerated spikelets on SBs per panicle and showed weak negative (in japonica) and positive (in indica) significant correlation with the percentage of degenerated spikelets on SBs. The number of surviving PBs was highly correlated with the surviving spikelets on PBs per panicle. Therefore, above results imply that the increase of differentiated spikelets on PBs of both cultivar groups and on SBs in the japonica group could sustain the survivility of spikelets with higher number of differentiated PBs per panicle.

Key words: Rice cultivar, degenerated spikelet, differentiated and surviving spikelet, panicle branch.

INTRODUCTION

Rice grain yield is closely related to spikelet number per unit area (Yamamoto et al. 1991, Kato and Takeda 1996) and yield sink size is highly limited by the number of spikelets per unit area in a rice cultivar (Ling et. al. 1994). Higher grain yield in rice has been primarily achieved through the increase of the number of the spikelets per unit area from both genetical and physiological views (Evans et al. 1984, Komatsu et al. 1984, Takeda et al. 1984, Kabaki 1993, Ling et al. 1994). In the yield determining process, the number of spikelet's per square meter contributed 74% and the combined contribution of filled spikelet percentage and grain weight would have 26% among the yield contributing characters indicated the most important yield limiting components is the number of spikelet's (Yoshida, 1981). Therefore developing spikelet differentiation and degeneration in the panicle might have significant role in the development of surviving spikelets in the panicle branches.

[1]Principal Scientific Officer, Bangladesh Rice Research Institute, Gazipur-1701,
[2]Professor and [3]Associate Professor, Faculty of Agriculture, Kochi University, Japan
Corresponding authors' email: tahmidansari@yahoo.com

Differentiated spikelets are composed of surviving and degenerated spikelets. The way to increase the surviving spikelets is either to increase the number of differentiated spikelets or decrease the number of degenerated spikelets (Matsushima 1957). Sasahara et al. (1982) and Yamamoto et al. (1991) reported that indica cultivars bear more spikelets per panicle than japonica ones due to higher number of spikelets on secondary branches (SBs). The number of surviving spikelets per panicle among the cultivars depended primarily on the number of surviving PBs per panicle (Yao et al. 2000). Other reports published yet were not clearly shown the interrelationship of different spikelet components within the same branch and in between the branches elaborately and were based on indica (Saha et al. 1998) or japonica (Matsushima 1957, Wada 1969, Manaka and Matsushima 1971, Fujii et al. 1998) cultivars only.

Yonezawa (1997) reported that short culm panicle number type (PNT) concept is losing its effectiveness for higher yield and has been achieved by increased panicle weight i.e. the number of grains per panicle. High yielding F1 hybrid and modern high yielding homozygous cultivars bred in china recently (Yao et al. 2000, Yamamoto et al 2001) and New Plant Type proposed by IRRI (Khush 1995) tended to increase the number of spikelets through the spikelet number per panicle. Therefore, a changing pattern in these cultivars from the higher number of panicles per unit area (PNT in the Japanese plant type categorization) to higher number of spikelets per panicle (PWT in the Japanese plant type categorization) is observed for increasing the number of spikelets per unit area. Therefore, it is very important to characterize the distribution pattern of differentiated degenerated and surviving spikelets with their interrelationship in a panicle among cultivars belonging to different ecospecies.

This study investigated the cultivars of different origins with a wide range of genetic backgrounds including japonica, high-yielding indica, indica hybrid (F1) and japonica-indica hybrid cultivars (Yamamoto et al. 1991). Analysis of distribution of different spikelet components (differentiated, degenerated and surviving spikelets) and relationship among them has done on the basis of their position on rachis branches with the differences between indica and japonica cultivars. Moreover the influence of the increase in number of differentiated spikelets on the surviving and/or degeneration process of spikelets on PBs and SBs might suggest a new concept of distribution pattern of spikelets on branches in a panicle for new breeding materials.

MATERIALS AND METHODS

Cultivars and cultivation: Two experiments were conducted in the farm of Kochi University, Japan, during June-October, in 1999 and 2000. Twenty-two cultivars in 1999 and 13 cultivars in 2000 were used in this study under different cultivar groups or ecospecies of different origins i.e. japonica and indica (including japonica-indica hybrid) cultivars with different plant types (Nuruzzaman et al. 2000). Among them, intermediate indica (IMI) and semi-dwarf indica (SDI) cultivars in indica were modern high yielding (Komatsu et al. 1984, Yamamoto et al. 1991). Cultivars approached in both the experiments are mentioned in Table 1. Seedlings were raised following the conventional method of the Faculty Farm except the seeding rate at 100g per box. Seedlings with 3.5-4th leaf stage were transplanted manually at 30cm×15cm plant spacing with two seedlings per hill on June 5 and 2 in 1999 and 2000 respectively. Cultivars were arranged following randomized complete block design (RCBD) with two replications each. Before final puddling, fertilizers for N, P_2O_5 and K_2O were applied at the rate of 10kg/ha from a slow (controlled) release compound fertilizer (Kumiai-hifuku Nyoso iri-fukugo 14-14-14, 140d-E80). Additional 2kg N / 10a was also applied from ammonium chloride to promote the transplanted seedling establishment. Water management, control of weeds, pests and diseases were followed to the conventional agronomic practices.

Differentiation and degeneration of spikelets: At heading, two hills of average number of tillers were selected from the twenty hills counted before sampling. These were collected from every plot in each cultivar for determining the differentiated, degenerated and surviving spikelets. Sampling was done when most of the panicles in a hill headed out and 1/2–3/4th portion of the panicles exerted from the leaf sheath. Samples were dried in an oven first at 95^{0}C for 2 hours and subsequently at 65^{0}C for 48 hours and then preserved in polyethylene bag (Yao et al. 2000). All the panicles in each hill were examined under the stereo binocular microscope (SZH10, Olympus Co. Ltd., Japan) to count the degenerated and surviving spikelets with recording their position on primary rachis branch (PB) and secondary rachis branch (SB).

Data analysis

The sum of the number of surviving and degenerated spikelets was taken as the number of differentiated spikelets (Matsushima 1957, Hoshikawa 1989). The percentage of degenerated spikelets is the number of degenerated spikelets divided by the number of differentiated spikelets×100. The Percentage of surviving spikelets was calculated as the percentage of differentiated spikelets (100%) minus the percentage of degenerated spikelets. Mean comparison was done following the Duncan's Multiple Range Test (DMRT). Both year data was used for correlation analysis separately for japonica and indica. The distribution of spikelet components and branches was described based on the experiment conducted in the year 1999 as both year results showed similar trend.

RESULTS

Distribution of differentiated spikelets and branches in the panicle: The production range of differentiated spikelets number per panicle, on PBs per panicle or on SBs per panicle has shown in Fig. 1A and Fig. 2A. In the japonica cultivars, the distribution of differentiated spikelets on PBs and SBs per panicle ranged from 43.7—53.5% and 41.8—56.3% respectively (Table 1). Average distribution among cultivars was 50.6% on PBs and 49.4% on SBs. In the indica cultivars, the distribution was ranged from 27.9—41.2% and 58.8—72.1% on PBs and SBs per panicle respectively. Average distribution among cultivars was 33.1% on PBs and 66.9% on SBs.

The ratio of differentiated SBs to those PBs was about 2 in the japonica cultivars, while the value was about 3.5 in the indica ones (Table 2). Similar highly significant, strong and positive correlations were observed between the number of the differentiated PBs and SBs per panicle in both japonica (r = 0.787***) and indica (r = 0.807***) cultivars. The number of differentiated spikelets on PBs and SBs was positively and significantly correlated with the numbers of differentiated PBs and SBs respectively in both japonica [r = 0.911***(PB), 0.961***(SB)] and indica cultivars [r =0.979***(PB), 0.935***(SB)] (Table 2).

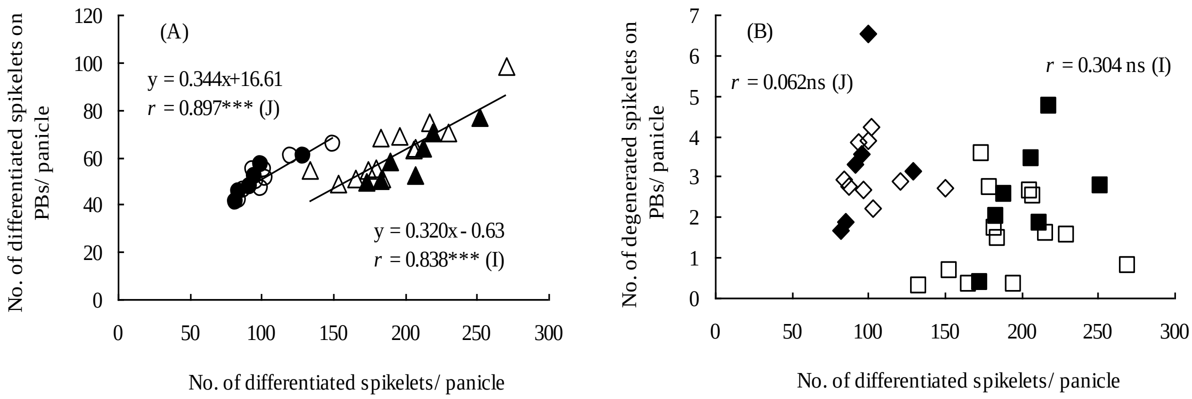

Fig. 1. Relationship between number of differentiated spikelets per panicle and number of differentiated (A) or degenerated (B) spikelets on PBs per panicle. All open symbols represent the cultivars of 1999 and closed for 2000 experiment. * indicates significant at 0.1%, ns= not significant at 5%.**

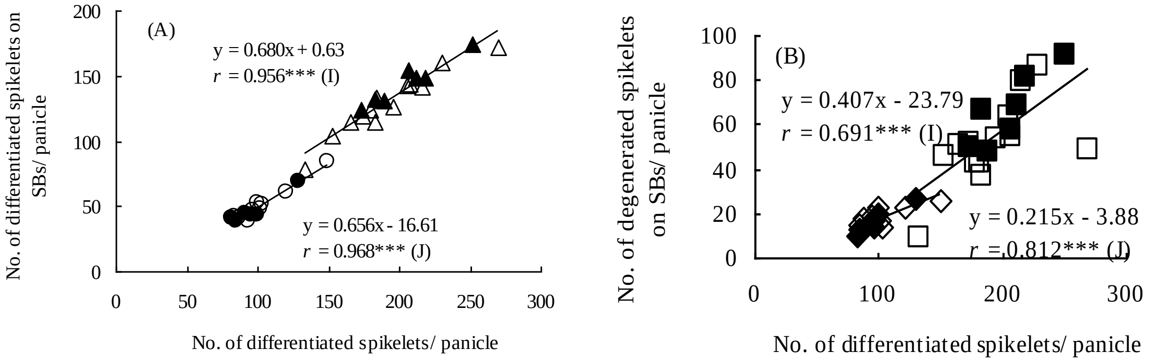

Fig. 2. Relationship between number of differentiated spikelets per panicle and number of differentiated (A) or degenerated (B) spikelets on SBs per panicle. Symbols are same as those in Fig. 1. * indicates significant at 0.1%.**

Distribution of degenerated spikelets and branches in the panicle: The range of degenerated spikelets number per panicle, on PBs per panicle or on SBs per panicle has shown in Fig. 1B and Fig. 2B. The distribution of degenerated spikelets on PBs and SBs per panicle ranged from 9.5—17.0% and 83.0—90.5%, respectively, in the japonica cultivars (Table 2) with an average distribution among cultivars on PBs 14.3% and on SBs 85.7% per panicle. In the indica cultivars, it was ranged from 0.6—6.5% and 93.5—99.4% on PBs and SBs per panicle respectively. While, average distribution among cultivars was 3.0% on PBs and 97.0% on SBs per panicle.

Table 1. Distribution of different spikelet components on primary branches (PBs) and secondary branches (SBs) per panicle in different cultivars in 1999

Plant type	Cultivar[a]	% differentiated spikelets on		% degenerated spikelets on		% surviving spikelets on	
		PBs	SBs	PBs	SBs	PBs	SBs
JPN	Nakateshinsenbon*[1)]	49.5	50.5	16.0	84.0	58.9	41.1
	Kinmaze*[1)]	46.8	53.2	14.5	85.5	58.6	41.4
	Nipponbare[1)]	51.4	48.6	13.8	86.2	61.1	38.9
	Ginnoyume[2]	58.2	41.8	17.0	83.0	71.4	28.6
JPW	Koganenishiki*[1)]	53.5	46.5	19.8	80.2	62.4	37.6
	Omachi[1)]	43.7	56.3	9.5	90.5	51.8	48.2
	Matsuyamamii[1)]	49.6	50.4	14.1	85.9	56.1	43.9
	Yamadanishiki*[1)]	52.7	47.3	13.1	86.9	65.1	34.9
CJ	95-16*[2]	49.8	50.2	11.2	88.8	60.3	39.7
Japonica average[6)]:		50.6A	49.4A	14.3A	85.7B	60.6B	39.4A
TI	Tadukan*[3)]	27.9	72.1	3.8	96.2	34.2	65.8
	Dawn	36.5	63.5	1.6	98.4	44.2	55.8
IMI	Yangdao 4[5)]	30.9	69.1	4.4	95.6	40.8	59.2
	BRRI dhan 28[5)]	30.9	69.1	6.0	94.0	39.3	60.7
	Shanyou 63* (HI)[5)]	30.8	69.2	4.0	96.0	43.5	56.5
SDI	Takanari*[5)]	34.6	65.4	2.0	98.0	54.2	45.8
	Nanjing 11[4)]	37.2	62.8	3.8	96.2	48.1	51.9
	IR 24[4)]	35.4	64.6	0.6	99.4	48.7	51.3
	IR 36*[4)]	32.1	67.9	1.5	98.5	45.6	54.4
	Guichao 2*[4)]	30.6	69.4	1.8	98.2	48.3	51.7
	Akenohoshi* (JI)[5)]	31.4	68.6	6.5	93.5	43.1	56.9
	Milyang 23 (JI)[4)]	41.2	58.8	2.9	97.1	44.1	55.9
	Suweon 258* (JI)[4)]	30.7	69.3	0.7	99.3	43.8	56.2
Indica average[6)]:		33.1A	66.9B	3.0A	97.0B	44.5A	55.5B

*JPN: Japonica panicle number type, JPW: Japonica panicle weight type, CJ: Chinese japonica, TI: Tall indica, IMI: Intermediate indica, SDI: Semi dwarf indica, HI: F_1 hybrid indica, JI: Japonica-indica hybrid. [a]All cultivars used in 1999. *Cultivars including an intermediate japonica cultivar, Hinohikari (bred in 1989) used in 2000.*
[1)] Japonica cultivars bred before 1970, [2)] Japonica cultivars bred after 1980, [3)] Tall and old cultivar, [4)] Old high yielding cultivars bred before 1980, [5)] New high yielding cultivars bred after 1980.
[6)]Means with the same letter in row for PB and SB of different spikelet components are not significantly different at 5% by DMRT.

The Percentage of degenerated spikelets to differentiated spikelets on PBs (i.e., within PBs) varied from 4.2−8.3% and on SBs 26.1−48.2% in the japonica cultivars (Table 3). Similarly percentage of degenerated spikelets to the differentiated ones on PBs varied from 0.5−6.6% and on SBs 11.9-56.2% in the indica cultivars.

Table 2. Distribution percentage of primary branches (PBs) and secondary branches (SBs) per panicle in different cultivars

Plant type	Cultivar	% differentiated branch		% degenerated branch		% surviving branch	
		PBs	SBs	PBs	SBs	PBs	SBs
JPN	Nakateshinsenbon	32.4	67.6	5.04	95.0	40.9	59.1
	Kinmaze	29.9	70.1	6.72	93.3	40.2	59.8
	Nipponbare	33.5	66.5	6.11	93.9	42.5	57.5
	Ginnoyume	36.4	63.6	6.08	93.9	49.1	50.9
	Koganenishiki	34.8	65.2	8.62	91.4	43.5	56.5
JPW	Omachi	26.0	74.0	4.21	95.8	31.9	68.1
	Matsuyamamii	33.0	67.0	6.68	93.3	38.6	61.4
	Yamadanishiki	35.3	64.7	5.05	94.9	46.8	53.2
CJ	95-16	33.4	66.6	5.59	94.4	42.5	57.5
Japonica average:		32.7	67.3	6.0	94.0	41.8	58.2
TI	Tadukan	20.3	79.7	1.60	98.4	24.2	75.8
	Dawn	23.2	76.8	0.67	99.3	28.0	72.0
IMI	Yangdao 4	20.8	79.2	0.92	99.1	27.6	72.4
	BRRI dhan 28	22.1	77.9	0.00	100.0	28.7	71.3
	Shanyou 63 (HI)	21.1	78.9	2.80	97.2	30.1	69.9
SDI	Takanari	23.3	76.7	0.74	99.3	37.8	62.2
	Nanjing 11	23.9	76.1	1.77	98.2	31.3	68.7
	IR 24	24.5	75.5	0.26	99.7	33.6	66.4
	IR 36	24.6	75.4	0.87	99.1	33.7	66.3
	Guichao 2	20.1	79.9	1.09	98.9	30.6	69.4
	Akenohoshi (JI)	22.0	78.0	3.91	96.1	30.1	69.9
	Milyang 23(JI)	28.7	71.3	0.77	99.2	30.9	69.1
	Suweon 258 (JI)	24.0	76.0	0.29	99.7	32.2	67.8
Indica average:		23.0	77.0	1.2	98.8	30.7	69.3

All abbreviations are same as those in Table 1.

The percentage of degenerated PBs to that of differentiated PBs was markedly less than that of the percentage of SBs to its differentiated SBs in each cultivar (Table 3). Percentage of degenerated PBs ranged from 3.4−6.8% in the japonica cultivars and 0.0-5.6% in indica cultivars. Percentage of SBs ranged from 25.3%−43.7% in the japonica cultivars and 10.8%−50.7% in the indica ones with about same average, i.e. 35.1% and 33.0%, respectively (Table 3). The number of degenerated spikelets on SBs showed a highly significant correlation with the number of degenerated SBs, in both japonica (r = 0.962***) and indica cultivars (r = 0.950***). Similarly percentage of degenerated spikelets on SBs showed a highly significant correlation with the degenerated percentage of SBs in both japonica (r = 0.984***) and indica cultivars (r = 0.968***).

Table 3. Percentage of degenerated spikelets / branches to the differentiated spikelets/ branches within primary branches (PBs) and secondary branches (SBs)

Plant type	Cultivar	% degenerated spikelets in		% degenerated branch in	
		PBs	SBs	PBs	SBs
JPN	Nakateshinsenbon	7.0	36.2	3.7	33.3
	Kinmaze	8.3	43.0	6.8	40.6
	Nipponbare	5.5	36.2	4.6	35.6
	Ginnoyume	7.1	48.2	5.0	43.7
	Koganenishiki	7.8	36.2	6.2	35.1
JPW	Omachi	4.2	31.9	3.4	27.2
	Matsuyamamii	4.4	26.1	3.7	25.3
	Yamadanishiki	6.0	43.9	3.9	40.1
CJ	95-16	4.8	37.9	4.1	35.0
Japonica average:		6.1 A	37.7 B	4.6 A	35.1 B
TI	Tadukan	2.8	27.5	1.3	20.9
	Dawn	0.8	28.2	0.5	23.0
IMI	Yangdao 4	3.9	37.7	1.1	31.8
	BRRI dhan 28	4.9	34.3	0.0	29.7
	Shanyou 63 (HI)	4.2	44.8	4.4	40.6
SDI	Takanari	2.1	56.2	1.2	50.7
	Nanjing 11	2.5	37.6	1.9	32.8
	IR 24	0.5	42.6	0.3	36.4
	IR 36	1.4	44.3	1.0	36.3
	Guichao 2	2.2	53.9	1.9	43.6
	Akenohoshi (JI)	6.6	43.6	5.6	38.6
	Milyang 23(JI)	0.5	11.9	0.2	10.8
	Suweon 258 (JI)	0.7	43.6	0.3	33.5
Indica average:		2.5 A	38.9 B	1.5 A	33.0 B

Means with the same letter in row for PB and SB of different spikelet components are not significantly different at 5% by DMRT.
All abbreviations are same as those in Table 1.

Distribution of surviving spikelets and branches in the panicle: The range of surviving spikelets number per panicle, on PBs per panicle or on SBs per panicle is the product of number of differentiated spikelets and number of degenerated spikelets per panicle. The distribution of surviving spikelets on PBs and SBs per panicle ranged from 51.8-65.1% and 28.6—48.2%, respectively, in the japonica cultivars (Table 1). Average distribution was 60.6%

on PBs and 39.4% on SBs per panicle. In the indica cultivars, the distribution ranged from 34.2−54.2% and 45.8−65.8% on PBs and SBs per panicle respectively. Average distribution of spikelets was 44.5% on PBs and 55.5% on SBs per panicle respectively. Average percentages of the surviving spikelets to the differentiated ones on PBs and SBs were 93.9% and 62.3% in the japonica cultivars while 97.5% and 61.1% in the indica ones, respectively. Highly and positively significant correlations were observed between the number of surviving PBs or SBs and their surviving spikelets in both japonica [r = 0.914***(PB), 0.967***(SB)] and indica cultivars [r = 0.982***(PB), 0.958***(SB)], respectively. Closer correlation of the number of surviving PBs with the surviving SBs (J: r = 0.693**, I: r = 0.605**) observed which resulted in the significant positive correlation between the number of PBs and spikelets on SBs (J: r = 0.598*, I: r = 0.468*).

Relationship among differentiated, degenerated and surviving spikelet number. PB spikelets and panicle spikelets: On an average of cultivar group, 50.6% and 33.1% of the total differentiated spikelets per panicle was composed of PB spikelets in japonica and indica cultivars, respectively (Table 1). The number of differentiated spikelets per panicle was significantly and positively correlated with the number of differentiated (J: r = 0.897***, I: r = 0.838***) or surviving spikelets (J: r = 0.926***, I: r = 0.807***), but not with the degenerated spikelets (J: r = 0.061ns, I: r = 0.304ns) on PBs per panicle (Fig. 1).

SB spikelets and panicle spikelets: On an average, SB spikelets supported differentiated spikelets per panicle as 49.4% in the japonica and 66.9% in the indica cultivar group (Table 2). The number of differentiated spikelets per panicle was strongly and positively correlated with the number of differentiated, surviving or degenerated spikelets on SBs per panicle (Fig. 2, Table 4). The number of surviving spikelets per panicle and on SBs per panicle was strongly correlated (J: r = 0.945*** I: r = 0.885***). Similarly strong correlation observed between the number of degenerated spikelets per panicle and on SBs per panicle (J: r = 0.979***, I: r = 0.998***) and these correlation values were higher than those correlations of degenerated spikelets between PBs and panicle as mentioned above (Table 4, 5).

Table 4. Correlation coefficients (*r*s) among the numbers of differentiated (dif), degenerated (deg), surviving (sur) spikelets, and the percentage of degenerated spikelets on panicle and on primary branches (PBs)

	Spikelet no. / %	Panicle dif	Panicle deg	Panicle sur	Panicle % deg
		Among japonica cultivars (n=16)			
PB	dif	0.897***	0.765	0.839	0.195
	deg	0.061	0.503	-0.105	0.699
	sur	0.926***	0.714	0.894***	0.085
	% deg	-0.225	0.303	-0.389	0.711
		Among indica cultivars (n=20)			
PB	dif	0.838***	0.392	0.823***	0.057
	deg	0.304	0.493*	0.006	0.466*
	sur	0.807***	0.342	0.821***	0.010
	% deg	0.152	0.363	-0.094	0.400

, *: Significant at 1% and 0.1% respectively.*

Table 5. Correlation coefficients (*r*s) among the numbers of differentiated (dif), degenerated (deg), surviving (sur) spikelets, and the percentage of degenerated spikelets on panicle and on secondary branches (SBs)

	Spikelet no. / %	Panicle			
		dif	deg	sur	% deg
		Among japonica cultivars (n=16)			
SB	dif	0.968***	0.678**	0.959***	0.001
	deg	0.812***	0.979***	0.657**	0.613*
	sur	0.875***	0.398	0.945***	-0.321
	% deg	0.0001	0.618*	-0.223	0.939***
		Among indica cultivars (n=20)			
SB	dif	0.956***	0.759***	0.679***	0.502*
	deg	0.691***	0.998***	0.115	0.908***
	sur	0.581**	-0.105	0.885***	-0.381
	% deg	0.394	0.905***	-0.215	0.981***

, **, *: Significant at 5%, 1% and 0.1% respectively.*

Table 6. Correlation coefficients (*r*s) among the numbers of differentiated (dif), degenerated (deg), surviving (sur) spikelets, and the percentage of degenerated spikelets on primary branches (PBs)

Branch		differentiated	degenerated	survival	% degenerated
		Among japonica cultivars (n=16)			
Primary branches (PB)	dif	1			
	deg	0.337	1		
	sur	0.987***	0.181	1	
	% deg	0.0077	0.939***	-0.152	1
		Among indica cultivars (n=20)			
Primary branches (PB)	dif	1			
	deg	0.040	1		
	sur	0.995***	-0.06	1	
	% deg	-0.147	0.968***	-0.244	1

****: Significant at 0.1%.*

Table 7. Correlation coefficients (*r*s) among the numbers of differentiated (dif), degenerated (deg), surviving (sur) spikelets, and the percentage of degenerated spikelets on srecondary branches (SBs)

		SB			
		dif	deg	sur	% deg
		Among japonica cultivars (n=16)			
SB	dif	1			
	deg	0.768***	1		
	sur	0.942***	0.508*	1	
	% deg	-0.123	0.527*	-0.442	1
		Among indica cultivars (n=20)			
SB	dif	1			
	deg	0.756***	1		
	sur	0.566**	-0.112	1	
	% deg	0.469*	0.910***	-0.432	1

, **, *: Significant at 5%, 1% and 0.1% respectively.*

Table 8. Correlation coefficients (*r*s) among the numbers of differentiated (dif), degenerated (deg), surviving (sur) spikelets, and the percentage of degenerated spikelets on primary branches (PBs) and secondary branches (SBs)

		PB			
		dif	deg	sur	% deg
		Among japonica cultivars (n=16)			
SB	dif	0.757***	-0.1	0.808***	-0.336
	deg	0.761***	0.315	0.741**	0.111
	sur	0.619*	-0.301	0.697*	-0.511
	% deg	0.216	0.638*	0.118	0.621
		Among indica cultivars (n=20)			
SB	dif	0.641**	0.406	0.6	0.293
	deg	0.402	0.443	0.357	0.311
	sur	0.467*	0.058	0.461*	0.053
	% deg	0.156	0.360	0.12	0.269

, **, *: Significant at 5%, 1% and 0.1% respectively.*

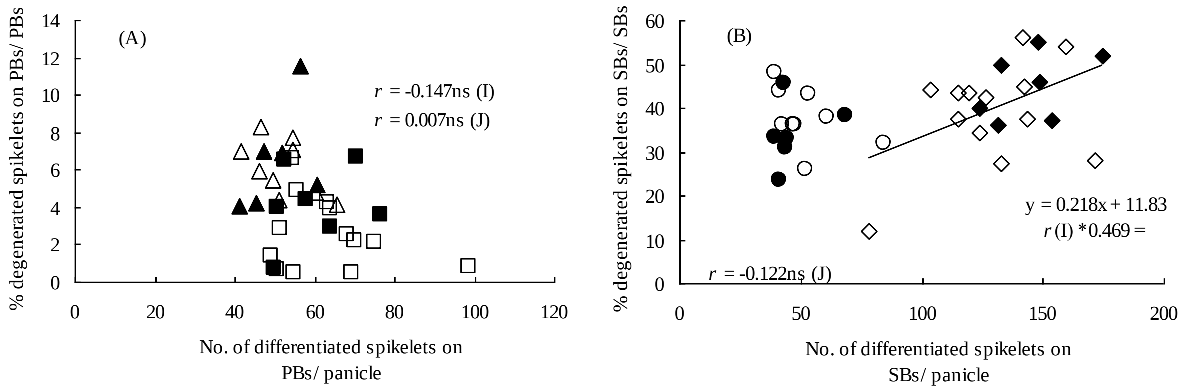

Fig. 3. Relationship between (A). number of differentiated spikelets on PBs per panicle and percentage of degenerated spikelets PBs. (B). number of differentiated spikelets on SBs per panicle and percentage of degenerated spikelets on SBs. All open symbols represent the cultivars of 1999 and closed for 2000. Symbols are same as those in Fig 1. * indicates significant at 5%, ns = not significant at 5%. I- indica, J- japonica.

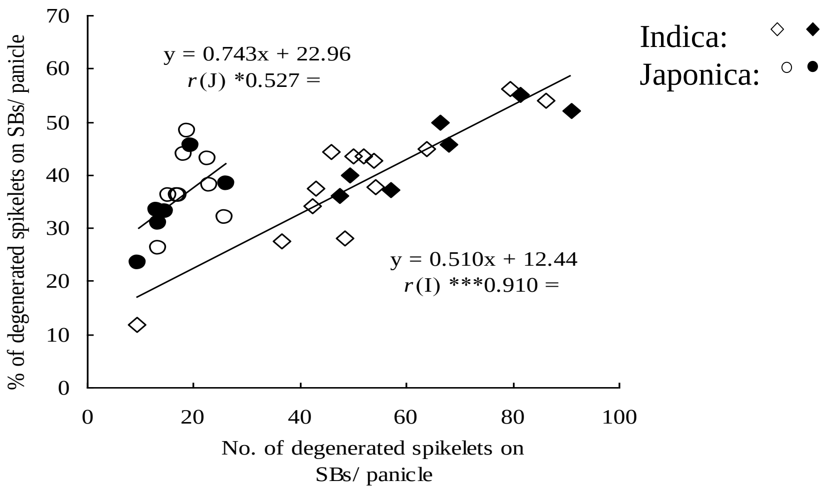

Fig. 4. Relationship between number of differentiated spikelets on secondary branches (SBs) and percentage of degenerated spikelets on the same SBs for both japonica (J) and indica (I) cultivars. All open symbols represent the cultivars of 1999 and closed for 2000. * and * indicate significant at 5% and 0.1% respectively.**

PB spikelets and/or SB spikelets: The number of differentiated spikelets on PBs was strongly and positively correlated with the surviving spikelets on PBs per panicle (J: r = 0.987***, I: r = 0.995***) but very weakly correlated with that of degenerated spikelets in both cultivar group (J: r = 0.337ns, I: r = 0.040ns) (Table 6). Again the number of differentiated spikelets on PBs per panicle was insignificantly correlated with the percentage of degenerated spikelets on PBs per PBs (Fig. 3A). Increase of the number of differentiated spikelets on SBs increased the number of surviving spikelets significantly on the same branch (J: r = 0.942***, I: r = 0.566**) where the number of degenerated spikelets also significantly increased in both japonica and indica cultivars (J: r = 0.768***, I: r = 0.756***) (Table 7). Further, the number of differentiated spikelets on SBs per panicle was insignificantly correlated with the percentage of degenerated spikelets on SBs per SBs (Fig. 3B). The correlations between the number of surviving and degenerated spikelet on PBs or SBs per panicle were not so high in both cultivar groups and only significant correlation at 5% was observed in SBs spikelets in japonica cultivars (r = 0.508*).

The number of differentiated spikelet on PBs showed positive significant effect on the number of differentiated and surviving spikelet on SBs per panicle (J: r = 0.757*** and r = 0.619*, I: r = 0.641** and r = 0.467*) (Table 8). Whereas increase of the number of differentiated spikelets on PBs per panicle increased the number of degenerated spikelets on SBs per panicle in the japonica cultivars (r = 0.761***) but not in the indica ones (r = 0.402ns). Significant relation was also true for indica cultivars (r = 0.696**) in case of excluding two cultivars, Dawn and Milyang 23 which produced lower percentage of degenerated spikelets in a panicle (both on PBs and on SBs) among the cultivars (Table 3).

Relationship between percentage of degenerated spikelets and its related factors: The number of degenerated spikelets composed of two factors, i.e. the number of differentiated spikelets and the percentage of degenerated spikelets. Therefore, the percentage of degenerated spikelets plays important role to reduce the number of degenerated spikelets and to increase the surviving ones after their differentiation. Correlation between the number of degenerated spikelets and the percentage of degenerated spikelets was significant on PBs per panicle [r = 0.939***(J), r = 0.968***(I)] or on SBs per panicle [r = 0.527*(J), r = 0.910***(I)] in both cultivar groups, while the number of differentiated spikelets was not significantly correlated with the number of degenerated spikelets in case of spikelets on PB as mentioned above.

Correlation between the percentage of degenerated spikelets and the number of differentiated spikelets was generally low, but a significant positive relation was observed in case of spikelets on SBs in the indica cultivars (r = 0.469*), while the relation was weak and negative in the japonica cultivars (r = −0.123) (Table 7).

DISCUSSION

The distribution and interrelations of the number of differentiated, degenerated and surviving spikelets might be very important to reveal the characteristic phenomenon of developing different kinds of spikelets with the surviving or degeneration process in the panicles of cultivars belonging to japonica and indica ecospecies. The distribution percentage of differentiated spikelets between PBs and SBs per panicle indicated that Japonica cultivars produced their spikelets almost equally on PBs and SBs and indica cultivars produced as PB:SB = 1:2 or more in both years. Also higher ratio of differentiated SBs to PBs in indica cultivars made the clear significant difference of producing differentiated spikelets on SB in the japonica cultivars. Finally these resulted in higher numbers of differentiated spikelets per panicle and on SBs in the indica cultivars than in the japonica cultivars. Komatsu et al. (1984) also reported that the higher number of differentiated spikelets in the indica cultivars than the japonica ones mainly due to the greater number of spikelets on the SBs. However, the distribution pattern of differentiated spikelets on PBs and SBs and the ratio of PBs and SBs in a panicle of both ecospecies suggested that these were controlled genetical rather than environmental factors associated. Distribution of degenerated spikelets was very low on PBs compared to SBs per panicle. Again percentage of degenerated spikelet within the PBs was also very low compared to the degenerated percentage of spikelets within SBs. So, the degenerated percentage of differentiated spikelets in a panicle was controlled mainly by degenerated spikelets on SBs (Xu and Vergara 1986, Yao et al. 2000). On the other hand, distribution of surviving spikelets in the japonica cultivars was more on PBs than SBs. Whilst this was opposite in the indica cultivars with a small difference. Higher percentage of surviving spikelets on SBs in the indica cultivars were due to its higher (double or more) differentiated spikelets. It indicates that the survivility percentage of spikelets would be more on PBs under equal distribution of differentiated spikelets on PBs and SBs in a panicle. The number of surviving SB spikelets played a more important role in the total number of surviving spikelets in the cultivars with larger panicles than those with smaller panicles (Yao et al 2000). Differentiation, degeneration and surviving of spikelets in rice plant were affected by cultural conditions such as nitrogen absorption and carbohydrate production during young panicle development stage as well as genetic backgrounds (Matsushima 1957, Wada 1969, Motomatsu et al. 1988, Kobayasi and Horie 1994, Fujii et al. 1998,). Yao et al. (2000) reported that the percentage of degenerated spikelets was significantly and negatively correlated with the shoot dry weight per differentiated spikelet at heading in the experiment using wide range of indica cultivars in relation to spikelet number.

The results showed that the number of surviving and degenerated spikelets per panicle increased with the increase of the differentiated ones in both cultivar groups (Yao et al.

2000). Therefore, the cultivar which differentiated more spikelets, produced more surviving spikelets as well as more degenerated ones. The number of surviving spikelets significantly correlated with that of degenerated ones in the japonica cultivars, but not in the indica ones. This might be caused by the difference in the range of survival rate of spikelets in the cultivars belonging to japonica and indica used in the experiments and the range was smaller in the japonica than in the indica cultivars.

The spikelets of panicle are composed of the spikelets on PBs and those on SBs. Close correlations were observed between the numbers of differentiated, degenerated and surviving spikelets per panicle and the respective spikelets on SBs than those on PBs per panicle. These results showed that spikelets on SBs were the main determinant of the total spikelet per panicle, not only the surviving spikelets (Matsushima 1957, Maruyama et al. 1988, Yamamoto et al. 1991) but also the differentiated and degenerated ones, irrespective of the cultivars belonging to both ecospecies.

Harvestable surviving spikelets is determined as a result of the degenerated percentage of differentiated spikelets. Therefore, the degenerated percentage of spikelets played a very important role to determine the number of surviving spikelets in a panicle. The percentage of degenerated spikelets was closely and positively correlated with the number of degenerated spikelets on SBs per panicle in both japonica and indica cultivars (Fig. 4). But the correlations were closer in indica than in japonica cultivars, and especially for the spikelets on SB, r value was 0.910*** in the indica group compared with 0.527* in the japonica group in which the number of differentiated spikelets showed comparatively higher correlation with the number of degenerated ones (r = 0.768***). The observed difference in the cultivar groups might be brought about by the different association between the numbers of differentiated spikelets and the degenerated percentage of spikelet on SBs per panicle, i.e. the association was significant and positive in indica cultivars (r = 0.469*), but very weak and negative in japonica cultivars (r = −0.123).

CONCLUSION

Therefore, the effective way to increase the number of surviving spikelets in indica should be based on the increase of spikelets on PBs having lower degeneration, because the increase of spikelets on SBs resulted in the parallel increase of the degeneration percentage of these spikelets. On the other hand, in the japonica cultivars, a possibility to increase the surviving spikelets depending on the increase of differentiated spikelets on SBs to some extent was suggested due to the negative tendency of the relation between the differentiated spikelets and the degenerated percentage of these spikelets. However, the difference observed in the association between the number of differentiated spikelets on SBs and the degenerated percentage of these spikelets in this study might be related with the different range in the number of spikelets on SBs in the japonica and indica cultivars used in the experiments. So, further study should be carried out to examine the interrelations among the numbers of differentiated, degenerated and surviving spikelets as well as the degenerated percentage of spikelets under the condition of about the same range in number of spikelets per panicle and on SBs in both japonica and indica cultivars.

ACKNOWLEDGEMENTS

We thank Dr. Yao Youli, Mr. Masaaki Yamamoto and Mr. Hironori Kobayashi, members of Laboratory of Crop Science and Laboratory of Soil and Plant Nutrition, Kochi University for technical assistance. Also thank to Mr. Yasuo Takemura and Mr. Koji Urabe, members of Faculty Farm, Kochi University, for their assistance during cultivation.

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