

## Response of Spikelet Number per Panicle in Rice Cultivars to Three Transplanting Densities

Binglin Zhang & Junko Yamagishi

To cite this article: Binglin Zhang & Junko Yamagishi (2010) Response of Spikelet Number per Panicle in Rice Cultivars to Three Transplanting Densities, Plant Production Science, 13:3, 279-288, DOI: [10.1626/pp.s.13.279](https://doi.org/10.1626/pp.s.13.279)

To link to this article: <https://doi.org/10.1626/pp.s.13.279>



© 2010 Crop Science Society of Japan



Published online: 03 Dec 2015.



Submit your article to this journal [↗](#)



Article views: 1823



View related articles [↗](#)



Citing articles: 3 View citing articles [↗](#)

# Response of Spikelet Number per Panicle in Rice Cultivars to Three Transplanting Densities

Binglin Zhang and Junko Yamagishi

(Field Production Science Center, Graduate School of Agricultural and Life Sciences, The University of Tokyo, Nishitokyo, Tokyo 188-0002, Japan)

**Abstract:** Spikelet number per panicle (SPP), differentiated spikelet number per panicle (D-SPP), and preflowering aborted spikelet number per panicle (A-SPP) were examined in five rice cultivars at three planting densities (HD; high, MD; medium, LD; low planting density) in the field condition. Rice plants at LD produced a higher panicle number per plant but lower panicle number per unit area, accompanied by higher D-SPP and SPP, on average. A-SPP and the ratio of A-SPP to D-SPP (%A) showed no consistent trends. There was a broader range of D-SPP values at LD than at HD because of larger D-SPP in higher order panicles (panicles with a higher spikelet number). D-SPP was smaller in lower order panicles in all cultivars and years, whereas %A increased. D-SPP and SPP of each panicle were positively correlated with tiller size (tiller height, leaf area, and neck internode diameter). Spikelet production efficiency for D-SPP or for SPP (spikelet number per leaf area) of each tiller was higher in IR65564-44-51 (NPT65) and Akihikari than in the other cultivars, indicating a greater capacity of tillers to produce spikelets or support spikelet growth. In each cultivar except NPT65, spikelet production efficiency for D-SPP increased as panicle order decreased, whereas spikelet production efficiency for SPP remained constant or decreased. This finding indicates that irrespective of planting density, lower order panicles produce more spikelets than they can afford physiologically, but they were regulated downward to a nearly constant value in four cultivars. In NPT65 different from other cultivars, spikelet production efficiency for D-SPP was lower in lower order panicles.

**Key words:** Aborted spikelet, Differentiated spikelet, Panicle number, Planting density, Rice, Spikelet number per panicle.

Planting density is an important determinant of grain yield in rice. The number of grains per unit area is determined by the planting density and spikelet number per plant, which is the sum of the spikelets on each panicle. Studies have shown a large variation in spikelet number per panicle (SPP) in one rice plant. SPP was larger on early-emerging tillers (Counce et al., 1996), and its value decreased from the main stem to primary and secondary stems (Kuroda et al., 1999). Shiratsuchi et al. (2007) reported a strong positive relationship between SPP and tiller dry weight at heading, and Yao et al. (2000) also showed the similar relationship in 32 cultivars. In addition, a negative relationship between panicle number and SPP has been widely reported (Matsushima, 1966; Wells and Faw, 1978; Jones and Snyder, 1987). Therefore, the difference in the numbers of tillers and panicles that results from different planting densities should also affect the SPP (Kuroda et al., 1999). Furthermore, many high-yielding rice cultivars are characterized by markedly large panicles, panicle-weight type, with relatively few tillers

(Maruyama et al., 1988; Yamamoto et al., 1991; Khush, 2000), and the effect of planting density on tiller and panicle numbers may also affect the SPP (Pham et al., 2004a).

SPP is determined by the difference between the differentiated spikelet number per panicle (D-SPP) and the preflowering aborted spikelet number per panicle (A-SPP) (Matsushima, 1966). However, few studies have examined the variation in D-SPP and A-SPP in rice plants. Sheehy et al. (2001) reported that D-SPP was reduced as tiller number increased in spaced cultivation. Ishii and Kumura (1988) found that D-SPP declined and A-SPP increased with the reduction in “shoot vigor” (i.e., smaller shoots) in the cultivar Nipponbare. It is unclear, however, whether genotypic differences exist with regard to the differentiation and abortion of spikelets per panicle in rice plants. Therefore, the effects of cultivars and planting densities on the variation of D-SPP and A-SPP are still not well understood.

Tiller size like leaf area per tiller, and neck internode diameter are closely related to D-SPP and SPP (Yamagishi

Table 1. Panicle characters, panicle number and heading date of five rice cultivars at three transplanting densities in 2007 and 2008.

Cultivar	Density	D-SPP (panicle <sup>-1</sup> )	SPP (panicle <sup>-1</sup> )	A-SPP (panicle <sup>-1</sup> )	% A	PN (hill <sup>-1</sup> )	PN (m <sup>2</sup> )	Heading date (mo/d)
<b>2007</b>								
Akihikari	HD	111 a	98 a	13 a	11.7 a	5.9 c	264 a	8/6
	MD	114 a	102 a	12 a	10.7 a	11.1 b	247 a	8/7
	LD	122 a	110 a	12 a	9.8 a	19.0 a	211 b	8/7
IRAT109	HD	138 a	114 a	24 a	17.2 a	4.0 c	177 a	8/12
	MD	153 a	120 a	33 a	21.7 a	7.2 b	160 ab	8/12
	LD	172 a	139 a	33 a	19.2 a	12.1 a	134 b	8/13
Nipponbare	HD	114 a	95 a	18 a	15.9 b	6.6 c	292 a	8/20
	MD	117 a	91 a	26 a	22.2 a	12.8 b	284 a	8/20
	LD	143 a	108 a	35 a	24.6 a	23.6 a	262 b	8/22
Akenohoshi	HD	169 a	145 a	25 a	14.5 b	6.2 c	277 a	8/23
	MD	164 a	139 a	25 a	15.3 ab	12.3 b	274 a	8/23
	LD	166 a	131 a	36 a	21.4 a	21.9 a	243 b	8/26
NPT65	HD	553 a	323 a	230 a	41.7 a	2.7 c	121 a	8/22
	MD	543 a	339 a	204 a	37.6 a	5.0 b	110 a	8/22
	LD	543 a	322 a	221 a	40.7 a	9.9 a	110 a	8/25
<b>2008</b>								
Akihikari	HD	108 a	93 a	15 a	14.5 a	4.0 c	178 a	8/4
	MD	118 a	98 a	20 a	16.8 a	8.7 b	193 a	8/4
	LD	129 a	116 a	14 a	11.9 a	13.3 a	148 b	8/6
IRAT109	HD	128 a	106 b	22 a	17.1 a	3.2 c	141 a	8/10
	MD	158 a	127 ab	31 a	19.5 a	5.1 b	113 b	8/11
	LD	185 a	146 a	39 a	22.1 a	10.2 a	113 b	8/13
Nipponbare	HD	112 a	96 a	16 a	14.3 a	4.5 c	200 a	8/18
	MD	112 a	96 a	16 a	14.5 a	9.1 b	202 a	8/18
	LD	117 a	96 a	21 a	18.1 a	17.2 a	191 a	8/20
Akenohoshi	HD	123 a	107 a	16 a	13.0 a	4.3 c	193 a	8/21
	MD	145 a	125 a	19 a	13.4 a	8.9 b	198 a	8/21
	LD	146 a	125 a	21 a	14.3 a	14.7 a	163 b	8/23
NPT65	HD	433 c	282 b	151 c	34.8 b	1.9 c	85 a	8/20
	MD	619 a	333 a	286 a	46.2 a	3.8 b	85 a	8/20
	LD	535 b	335 a	199 b	37.3 b	6.2 a	69 a	8/23
Main factor means								
Year	2007	221 a	158 a	63 a	21.6 a	10.69 a	211 a	
	2008	211 a	152 a	59 a	20.5 a	7.67 b	151 b	
Cultivar	Akihikari	117 b	103 b	14 b	12.6 b	10.3 ab	207 ab	
	IRAT109	156 b	125 b	30 b	19.5 b	6.9 bc	140 bc	
	Nipponbare	119 b	97 b	22 b	18.3 b	12.3 a	238 a	
	Akenohoshi	152 b	129 b	24 b	15.3 b	11.4 ab	224 ab	
	NPT65	538 a	322 a	215 a	39.7 a	4.9 c	97 c	
Density	HD	199 b	146 b	53 b	19.5 b	4.3 c	193 a	
	MD	224 a	157 a	67 a	21.8 a	8.4 b	187 a	
	LD	226 a	163 a	63 ab	21.9 a	14.8 a	164 b	
LSD <sub>0.05</sub>								
	Year	ns	ns	ns	ns	0.7	14	
	Cultivar	271	142	129	16.3	4.8	92	
	Density	19	9	14	2.0	0.4	6	
	Y×C	383	201	183	23.0	6.7	131	
	Y×D	27	13	ns	2.8	0.5	9	
	C×D	42	21	32	4.4	0.9	14	
	Y×C×D	60	30	45	6.2	1.2	20	

In each cultivar in each year, the same letters indicate there was no significant difference among densities at the 5% level.

In the means of years, values for cultivars and densities of subplots followed by the same letter are not significantly different at the 5% level.

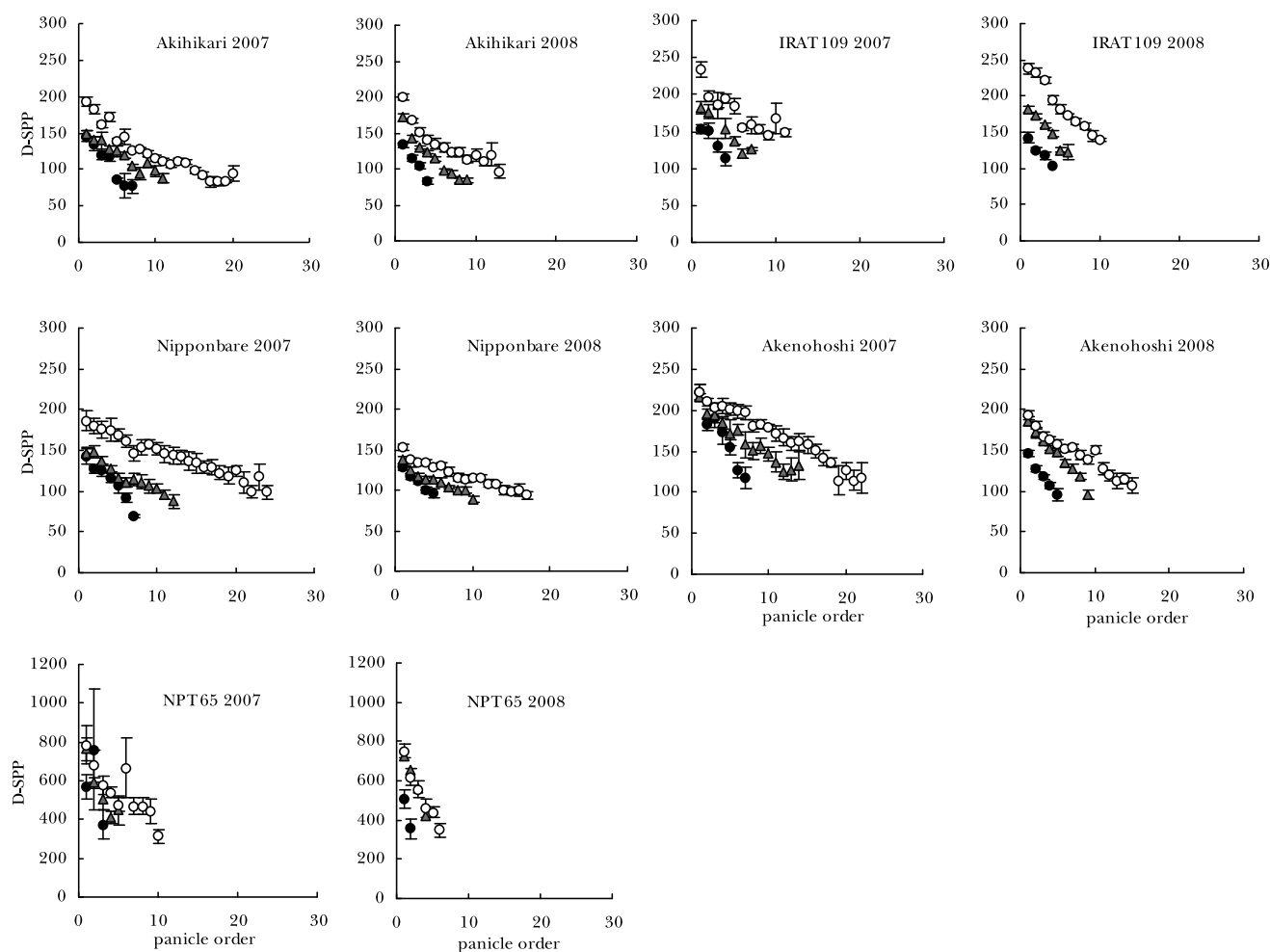


Fig. 1. Differentiated spikelet number per panicle (D-SPP) in five rice cultivars as a function of panicle order at three transplanting densities (●: high density; ▲: medium density; ○: low density) in 2007 and 2008. The standard error was shown.

et al., 1992; Sheehy et al., 2001; Liu et al., 2008). Leaf area per tiller is the important factor influencing the source ability for the panicle development (Sheehy et al., 2001). Both larger neck internode diameter at panicle initiation stage and that at heading are accompanied by the larger spikelet number per panicle (Yamagishi et al., 1992); and the larger neck internode diameter could improve the translocation of assimilates from leaf to panicle (Liu et al., 2008). Tiller height likely plays an important role in the capture of solar radiation when the competition of tillers within plant is intense. Therefore, the leaf area per tiller, neck internode diameter, and tiller height should be involved in the response of D-SPP and A-SPP variation in rice plants to planting density.

In this experiment, the panicle size (SPP), potential panicle size (D-SPP), spikelet abortion before flowering (A-SPP), and ratio of A-SPP to D-SPP (%A) were examined in five cultivars (four with large panicles and Nipponbare) at different planting densities. Tiller size, leaf area per tiller, neck internode diameter and tiller height, were also examined for comparison.

## Materials and Methods

The experiments were conducted at the Field Production Science Center of the Graduate School of Agricultural and Life Science, The University of Tokyo, Nishitokyo, Tokyo, Japan (35°43'N, 139°32'E, 53-m elevation) in 2007 and 2008. Five cultivars, Akihikari, IRAT109, Nipponbare, Akenohoshi, and IR65564-44-51 (NPT65), were planted during the 2 yr. The cultivars other than Nipponbare are regarded as the panicle-weight type, and Nipponbare is the medium type between panicle-number type and panicle-weight type. Three planting distances—15 cm × 15 cm, 15 cm × 30 cm, 30 cm × 30 cm—were designed as three density levels: high, medium and low density. The fields were designated as split-plots with three replications, the cultivar was designated as the main plot (19.8 m<sup>2</sup>), and density as the subplot in both years (high density, 3.51 m<sup>2</sup>; medium density, 8.19 m<sup>2</sup>; low density, 8.1 m<sup>2</sup>).

The seeds were sown on 28 April, and seedlings were transplanted to the paddy field on 28 May in both years.

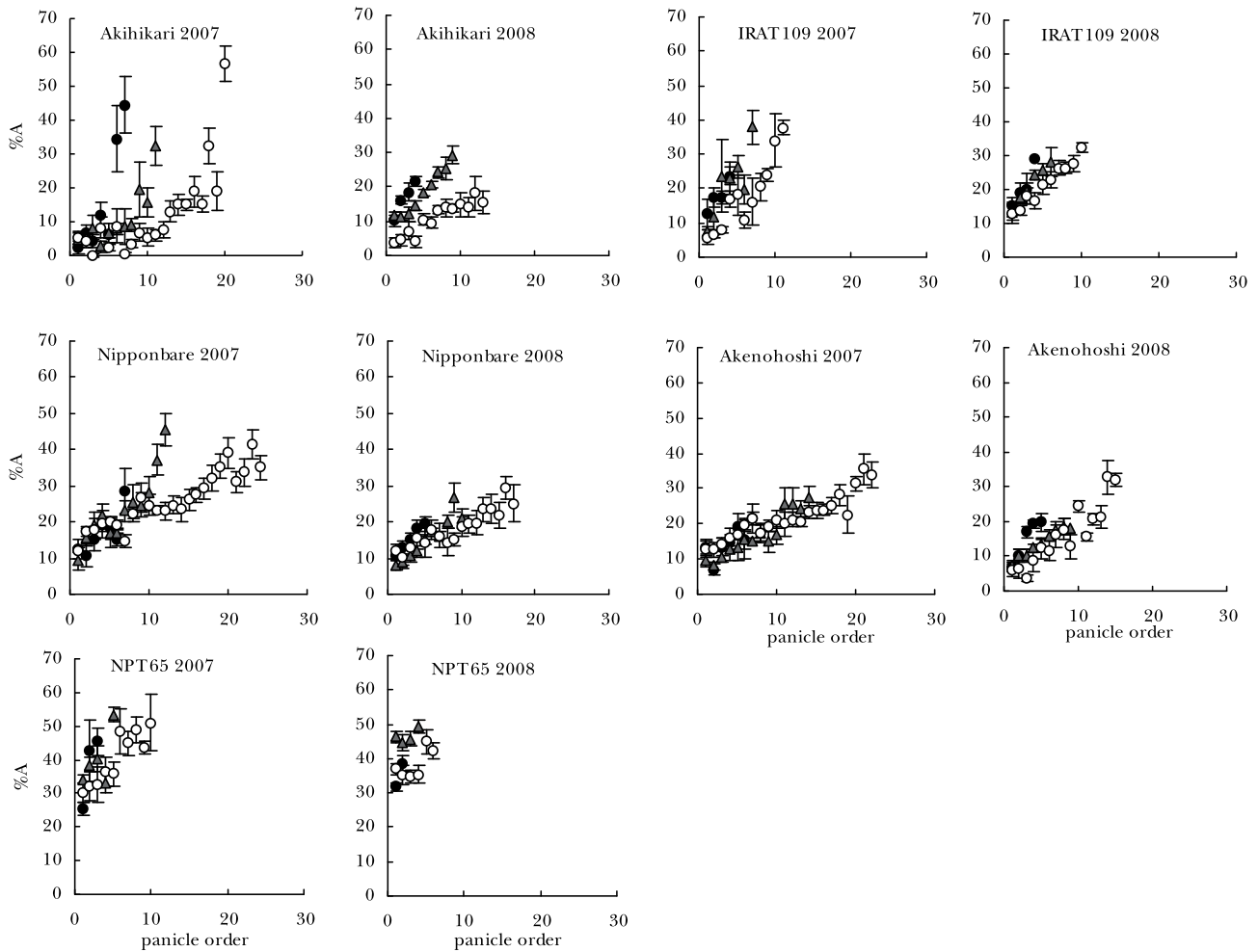


Fig. 2. Ratio of aborted spikelet number per panicle to differentiated spikelet number per panicle (%A) in five rice cultivars as a function of panicle order at three transplanting densities (●: high density; ▲: medium density; ○: low density) in 2007 and 2008. The standard error was shown.

A single seedling per hill was transplanted. In both years, before transplanting, chemical compound fertilizer was applied as N: P<sub>2</sub>O<sub>5</sub>: K<sub>2</sub>O at a rate of 60:90:80 kg ha<sup>-1</sup>. Ammonium sulfate was applied at 2 kg ha<sup>-1</sup> 5 wk after transplanting in 2007; no topdressing was applied in 2008.

Two plants from center of each plot with three replications were collected at the maturity stage (2007) or full heading stage (2008), and panicle number (PN) and SPP for each panicle were counted. Aborted spikelets were counted as the vestiges that remained on the rachis branches following the method reported previously (Ishii and Kumura, 1988); this enabled the measurement of A-SPP. D-SPP was calculated as the sum of SPP and A-SPP. The spikelet abortion percentage (%A) was calculated as the ratio of A-SPP to D-SPP. For comparison of SPP, D-SPP, A-SPP, and %A of all panicles, the panicles in each plant were arranged in descending order from the panicle with the highest SPP to that with the lowest SPP. If the 6 plants (2 plants × 3 replications) of each sample had the different panicle number, the replication should be less than 6 at

the lower order. Therefore, when at least 3 panicles existed in higher order panicles, they were included into analysis. Using these sequences, the responses to the planting densities were examined.

In 2008, the leaf area, tiller height, and neck internode diameter of each productive tiller were measured at heading time after unproductive tillers were removed. Leaf area was measured with an area meter (Li-3100, Li-Cor, Lincoln, NE, USA). Spikelet production efficiency for SPP and D-SPP was calculated as SPP and D-SPP divided by leaf area, respectively. The neck internode diameter was measured by digital vernier caliper (Mitutoyo, Kanagawa, Japan) at the narrowest part 2 cm below the neck node.

Statistical analyses were conducted by the method of Gomez and Gomez (1984).

## Results

### 1. Panicle characters and panicle number

Average D-SPP, SPP, A-SPP, and %A of the panicles in a plant are shown in Table 1. On average, there were no

Table 2. Averages and ranges of leaf area per tiller, tiller height, and neck internode diameter at heading in five rice cultivars under three transplanting densities in 2008.

Cultivar	Density	Leaf area (cm <sup>2</sup> tiller <sup>-1</sup> )			Tiller height (cm)			Neck internode diameter (mm)		
		Mean	Range		Mean	Range		Mean	Range	
Akihikari	HD	65.3 a	34.6	-103.2	73.9 a	55.0	-84.0	1.50 a	1.15	-1.74
	MD	71.5 a	31.9	-116.5	72.9 a	62.0	-92.0	1.50 a	1.15	-1.99
	LD	69.3 a	28.7	-125.7	73.3 a	46.0	-93.0	1.52 a	0.79	-1.96
IRAT109	HD	96.6 b	64.7	-147.3	84.9 b	71.0	-96.0	1.91 b	1.38	-2.24
	MD	103.9 b	55.5	-159.1	90.5 a	69.0	-110.0	2.09 a	1.09	-2.81
	LD	133.3 a	66.9	-213.7	90.2 a	63.0	-123.0	2.15 a	1.39	-2.82
Nipponbare	HD	95.5 a	48.2	-135.1	83.4 a	70.0	-96.0	1.38 a	1.09	-1.59
	MD	102.0 a	49.0	-170.8	81.4 a	61.0	-99.0	1.43 a	1.06	-1.76
	LD	96.7 a	44.6	-176.6	83.3 a	60.0	-100.0	1.41 a	1.01	-1.78
Akenohoshi	HD	126.9 b	47.5	-197.4	87.0 a	54.0	-101.0	1.53 b	0.74	-1.92
	MD	145.9 a	64.0	-253.2	88.2 a	70.0	-102.0	1.62 ab	0.95	-2.16
	LD	142.8 a	72.6	-256.1	88.1 a	70.0	-103.0	1.66 a	1.13	-2.18
NPT65	HD	204.3 b	132.5	-272.1	92.9 a	77.0	-107.0	2.6 b	2.13	-3.12
	MD	215.8 b	135.9	-307.9	93.2 a	48.2	-112.0	2.6 b	1.93	-3.30
	LD	230.2 a	129.0	-337.7	98.4 a	82.0	-116.0	2.8 a	1.71	-3.99
Probability	Cultivar	0.00			0.00			0.00		
	Density	0.00			0.15			0.00		
	C×D	0.00			0.32			0.07		

The same letters indicate there is no difference among densities at the 5% level.

significant differences in these four characters between 2007 and 2008. Significant differences in panicle characters were noted between NPT65 and the other cultivars; D-SPP, SPP, A-SPP, and %A were highest in NPT65. There were no significant differences in D-SPP and SPP among the other four cultivars, but the values in IRAT109 and Akenohoshi tended to be higher than those in Akihikari and Nipponbare. The values of the four panicle characters were higher at the low and medium planting densities than at the high planting density. There was a significant interaction between year and cultivar, year and planting density, and cultivar and planting density in D-SPP, SPP, A-SPP, and %A, except the interaction between year and planting density for A-SPP. Significant interactions among year, cultivar and planting density was also observed. For each cultivar, there were no significant differences in D-SPP and SPP with the planting density, except for SPP in IRAT109 and D-SPP and SPP in NPT65 in 2008 (Table 1), although D-SPP and SPP tended to be higher at the low planting density. There was no significant difference in A-SPP with the planting density except in NPT65 in 2008, although %A was higher at the low planting density than at the high planting density in Nipponbare and Akenohoshi in 2007.

On average, panicle number per plant and per unit area showed significant differences with the year, cultivar, and

planting density (Table 1). Significant interactions between year and cultivar, year and planting density, and cultivar and planting density for panicle number per plant and per unit area were observed. The smaller panicle number in 2008 than that in 2007 might be due to the lack of nitrogen topdressing in 2008. Among the five cultivars, panicle number was lowest in NPT65, followed by IRAT109 and Akihikari, and higher in Akenohoshi and Nipponbare. Panicle number per plant was significantly larger at the low planting density than at higher densities; however, on a per unit area basis, panicle number was significantly smaller at the low planting density than at a high or medium density. The panicle number per unit area for each cultivar was also significantly larger at the high planting density than at the lower density, except in NPT65 in both years and in Nipponbare in 2008, which showed no difference with the planting density.

## 2. Number and abortion of spikelets in each panicle

The panicles were arranged by descending order of SPP. The panicle orders for D-SPP and %A are shown in Figs. 1, 2, respectively. Generally, the D-SPP values were higher at the low planting density than at higher densities when comparing the same panicle order in the same cultivar and year, and they were lower in higher order panicles in all cultivars and years (Fig. 1). In contrast, %A was higher in

lower order panicles at all planting densities and in all cultivars and years. Therefore, the lower order panicles had fewer SPP because of less spikelet differentiation and a higher percentage of spikelet abortion.

The D-SPP range in plants (i.e., the difference between maximum and minimum D-SPP) was larger at the low planting density than at high and medium densities for all cultivars (Fig. 1). This is because the maximum D-SPP values of the highest order panicles were the greatest at low planting density, followed by medium density, although the minimum D-SPP values of the lowest order panicles showed small differences among the three planting densities. Among the five cultivars, NPT65 had the largest range of D-SPP values, from 314 to 785 at the low planting density in 2007. The narrowest range of D-SPP values, from 96 to 127, was observed in Nipponbare at the high planting density in 2008.

### 3. Relationships of leaf area, tiller height, and neck internode diameter to SPP, D-SPP, and %A

Table 2 shows the average leaf area per tiller, tiller height, and neck internode diameter of tillers. Statistically significant differences among cultivars were observed for all three characters, and significant differences among planting densities were also observed for leaf area and neck internode diameter. Among cultivars, leaf area per tiller was largest in NPT65, followed by Akenohoshi, and lowest in Akihikari. Leaf area per tiller showed significant interaction effects between cultivar and planting density. In IRAT109, Akenohoshi, and NPT65 leaf area per tiller was larger at the low planting density than at the high planting density, although in Akihikari and Nipponbare it did not differ with the planting density. Neck internode diameter showed the same tendency as that of leaf area per tiller. In IRAT109, Akenohoshi, and NPT65, neck internode diameter was higher at the low planting density than at higher densities, although it was not affected by planting density in Akihikari and Nipponbare.

SPP in each tiller showed strong positive linear relationships with leaf area per tiller, tiller height, and neck internode diameter in all cultivars except NPT65 which only showed positive relations to leaf area per tiller (Fig. 3). The slope of the regression lines of SPP to leaf area per tiller were high in Akihikari and NPT65, indicating that more spikelets were produced with the same increase in leaf area in these cultivars.

Fig. 4 shows the spikelet production efficiency for SPP or for D-SPP (SPP or D-SPP divided by leaf area) in each tiller. There were differences in spikelet production efficiencies among cultivars, being high in Akihikari and NPT65, which coincides with the steep slopes of the regression lines of SPP to leaf area per tiller in Fig. 3. In lower order panicles, the spikelet production efficiency for D-SPP tended to increase in most cultivars except NPT65,

whereas spikelet production efficiency for SPP was constant or decreased. Therefore, the difference in spikelet production efficiency between D-SPP and SPP (i.e., spikelet abortion efficiency for A-SPP) was larger in the lower order panicles in all cultivars and planting densities except NPT65. In NPT65, the differences between the spikelet production efficiency for D-SPP and SPP were similar in all panicles at each planting density, although it had fewer panicles than the other cultivars.

## Discussion

### 1. Effects of planting density on average D-SPP, SPP, A-SPP, and %A in rice plants

On average, D-SPP and SPP were higher at low and medium planting densities (Table 1). A negative relationship between panicle number per unit area and SPP has been widely reported (Matsushima, 1966; Wells and Faw, 1978; Jones and Snyder, 1987), and we also found that the average panicle number per unit area was higher at high and medium planting densities. In each cultivar, although the differences in D-SPP and SPP values among planting densities were not statistically significant, D-SPP and SPP tended to be larger at the low planting density than at the high planting density, and, in contrast, panicle number per unit area were smaller at the low planting density than at higher planting densities. No clear planting density effects on A-SPP and %A were observed in Akihikari, IRAT109, Nipponbare or Akenohoshi. In NPT65, %A was much higher than in the other cultivars; this might have been due to a very high A-SPP although D-SPP was also higher in NPT65 than in other cultivars. Kobayasi (1995) reported a strong positive relationship between D-SPP and A-SPP, though in our results the relationships between D-SPP and A-SPP were not always consistent.

### 2. Effects of planting density on SPP, D-SPP, and A-SPP in each panicle

Plants showed a broader range of D-SPP values at the low planting density than at higher planting densities, mainly because the panicle potential size, D-SPP, on lower order panicles was large at low planting density, but the differences in D-SPP in higher order panicles with planting density were small. Pham et al. (2004b) reported that, in a system with a low planting density with nitrogen topdressing, compared with conventional planting density, the spikelet number per panicle on secondary tillers, which were relatively smaller panicles, were significantly larger, but those on the main stem and primary tillers, which had relatively larger panicles, were not. The effect of a low planting density on spikelet number per panicle was larger in small panicles than in large panicles in a plant. Therefore, these results are inconsistent with our results: We found that D-SPP in higher order panicles, which had relatively larger panicles, was much larger at the low

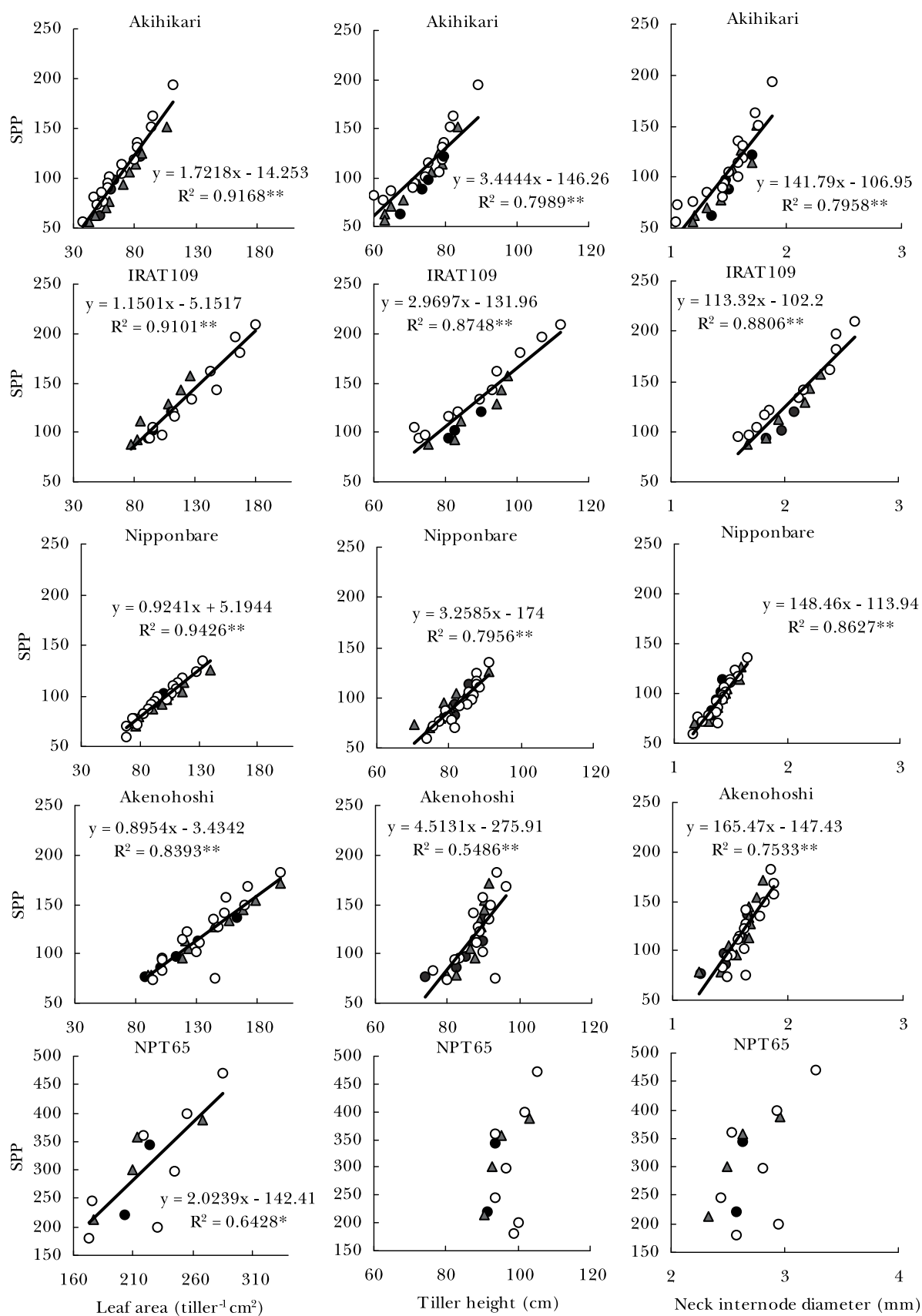


Fig. 3. Relationships between tiller size (leaf area per tiller, tiller height, and neck internode diameter) and spikelet number per panicle (SPP) in five rice cultivars at three transplanting densities (●: high density; ▲: medium density; ○: low density). \*,\*\* showed the coefficient of determinations were significant at the 5%, 1% level.



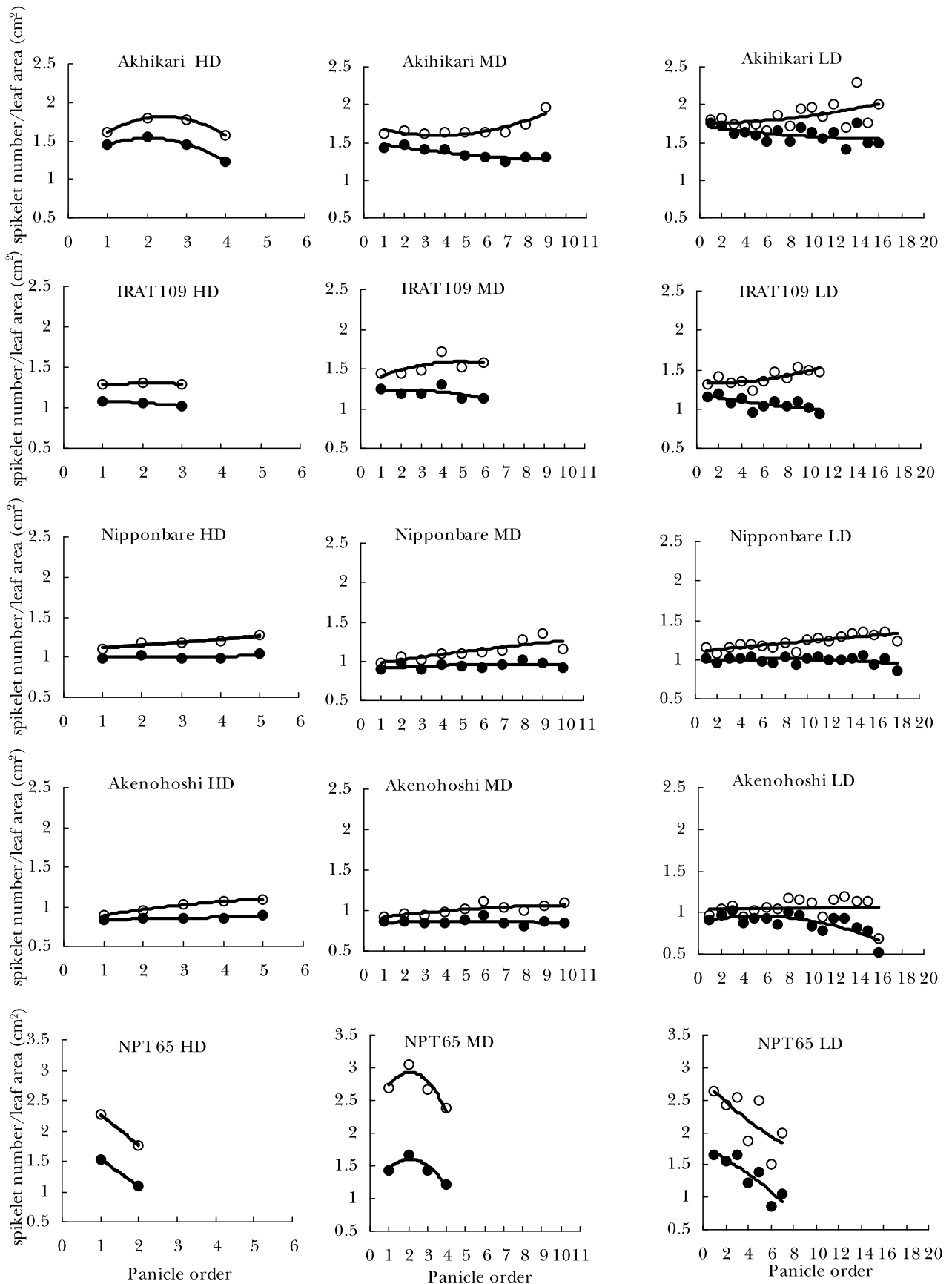


Fig. 4. Spikelet production efficiency of each panicle in five rice cultivars in 2008. ○ : Spikelet production efficiency for D-SPP (cm<sup>2</sup>); ● : Spikelet production efficiency for SPP (cm<sup>2</sup>).

planting density than at high planting density, though D-SPP in lower order panicles were similar at the low and high planting densities. This inconsistency might be caused by the difference in the amount and pattern of the fertilizer application.

SPP decreases with tiller order from the main stem to primary and secondary stems (Kuroda et al., 1999). Ishii et al. (1988) found that D-SPP declined and A-SPP increased with the reduction in “shoot vigor” (i.e., smaller shoots) in the cultivar Nipponbare. SPP is also closely related to tiller size (dry weight per tiller) at heading (Yao et al., 2000; Shiratsuchi et al., 2007) and to dry matter production during panicle formation (Pham et al., 2004a). Our results also showed a close relationship of SPP with tiller height and leaf area per tiller at heading, which could indicate tiller size. Consistent with our results, SPP is also correlated closely with the internode diameter at heading (Yamagishi et al., 1992). Therefore, our results also indicate the importance of a thick culm and dry matter production during panicle formation to produce a heavy tiller dry weight, which results in a high SPP.

Spikelet production efficiency for D-SPP and SPP of each tiller was higher in NPT65 and Akihikari than in the other cultivars, indicating a greater capacity of tillers to produce spikelets or support spikelet growth. However, in lower order panicles, D-SPP decreased and spikelet abortion (%A) increased (Fig. 1), resulting in reduced SPP in all cultivars and at all planting densities. In four cultivars other than NPT65, spikelet production efficiency for D-SPP increased in lower order panicles, especially at the low planting density, whereas spikelet production efficiency for SPP were constant or low in the lower order panicles (Fig. 4). This finding indicates that, irrespective of planting density in the field condition, the lower order panicles produce more spikelets than they can afford physiologically, but they were regulated downward to a nearly constant value in the four cultivars excepting NPT65. This result coincides with the result of Ishii and Kumura (1988) with Nipponbare in pot experiment. Ishii and Kumura (1988) reported that this can be explained by the balance between the source and sink within a plant; lower order tillers obtained assimilates from higher order tillers at the spikelet differentiation stage, but this translocation did not last until heading. In addition, the photosynthetic ability of leaves would also play an important role. Ookawa et al. (1991) reported that the photosynthetic rate of leaves was higher on the main stem than on tillers, even in leaves at a similar position. In the present experiment, the SPAD (Chlorophyll meter reading) of the three top leaves declined with the decrease in panicle order (data not shown). Thus, we may infer that the difference in the photosynthetic ability of leaves on the tillers was related to the high %A and low SPP recorded in lower order panicles. Kobayasi and Shintani (2003)

reported that SPP was closely related to nitrogen content of the shoot at heading. The nitrogen content of a leaf can influence the leaf’s photosynthetic ability; that is, an increase in the nitrogen content can strengthen the source ability of assimilates. On the contrary, in NPT65, different from other cultivars, spikelet production efficiency for D-SPP decreased parallel to spikelet production efficiency for SPP with the decrease in panicle order. This may indicate that in NPT65 each tiller is independent of the photosynthetic assimilate from the other tillers, and that the photosynthetic ability of leaves might decline with the decrease of panicle order.

Therefore, it is suggested that an optimum value of spikelet production efficiency for SPP might exist for each cultivar apart from spikelet production efficiency for D-SPP, reflecting the balance of assimilate availability, which must be explained by differences in leaf characters related to photosynthetic ability and the resulting capacity of tillers to support spikelet growth.

#### Acknowledgments

We are grateful to Noboru Washizu, Kenichiro Ichikawa, Ryuichi Soga, and Keisuke Yatsuda (Field Production Science Center, the University of Tokyo) for their technical assistance in field management.

#### References

- Counce, P.A., Siebenmorgen, T.J., Poag, M.A., Holloway, G.E., Kocher, M.F. and Lu, R. 1996. Panicle emergence of tiller types and grain yield of tiller order for direct-seeded rice cultivars. *Field Crops Res.* 47: 235-242.
- Gomez, K.A. and Gomez, A.A. 1984. *In* Statistical Procedures for Agricultural Research. 2nd ed. John Wiley & Sons, New York, 680.
- Ishii, Y. and Kumura, A. 1988. The yield formation process viewed from the development of the sink and source of individual shoots in the rice plant. I. The determining process of the sink size and the sink / source ratio of individual shoots of a plant in relation to their vigor. *Jpn. J. Crop Sci.* 57: 146-156\*.
- Jones, D.B. and Snyder, G.H. 1987. Seeding rate and row spacing effects on yield and yield components of drill-seeded rice. *Agron. J.* 79: 623-626.
- Khush, G.S. 2000. New plant types of rice for increasing the genetic yield potential. *In* J.S. Nanda, Ed. Rice Breeding and Genetics. Science Publishers, Enfield, New Hampshire, 99-108.
- Kobayasi, K. 1995. Comparison of spikelet number between Akenohoshi and Nipponbare. *Jpn. J. Crop Sci.* 64 (Extra issue 1): 170-171\*\*.
- Kobayasi, K. and Shintani, K. 2003. Analysis for spikelet production efficiency among several rice varieties. *Jpn. J. Crop Sci.* 72 (Extra issue 2): 82-83\*\*.
- Kuroda, E., Abe, S., Ishibashi, F., Hirano, M. and Murata, T. 1999. Varietal difference in the relationship between the number of panicles per hill and the number of spikelets per panicle on the main stems and on primary and secondary tillers of rice. *Jpn. J. Crop Sci.* 68: 385-389\*.

- Liu, G.L., Mei, H.W., Zou, G.H., Liu, H.Y., Hu, S.P., Li, M.S., Wu, J.H., Chen, L. and Luo, L.J. 2008. QTL analysis of panicle neck diameter, a trait highly correlated with panicle size, under well-watered and drought conditions in rice. *Plant Sci.* 174: 71-77.
- Maruyama, S., Kabaki, N. and Tajima, K. 1988. Growth response to nitrogen in *japonica* and *indica* rice varieties. *Jpn. J. Crop Sci.* 57: 470-475\*.
- Matsushima, S. 1966. *In Crop Science in Rice: Theory of Yield Determination and Its Application.* Fuji, Tokyo. 365.
- Ookawa, T., Kuroda, E. and Ishihara, K. 1991. Difference of photosynthetic rates among the leaves at the equivalent positions on the main stem and its tillers in rice plants. *Jpn. J. Crop Sci.* 60: 413-420\*.
- Pham, Q.D., Hirano, M., Sagawa, S. and Kuroda, E. 2004a. Analysis of the dry matter production process relating to yield and yield components of rice plants grown under the practice of nitrogen-free basal dressing accompanied with sparse planting density. *Plant Prod. Sci.* 7: 155-164.
- Pham, Q.D., Tanaka, D., Abe, A., Sagawa, S. and Kuroda, E. 2004b. Analysis of the number of spikelets per panicle on the main stems, primary and secondary tillers of different rice genotypes grown under the conventional and nitrogen-free basal dressing accompanied with sparse planting density practices. *Plant Prod. Sci.* 7: 456-462.
- Sheehy, J.E., Dionora, M.J.A. and Mitchell, P.L. 2001. Spikelet numbers, sink size and potential yield in rice. *Field Crops Res.* 71: 77-85.
- Shiratsuchi, H., Ohdaira, Y. and Takanashi, J. 2007. Relationship between dry weight at heading and the number of spikelets on individual rice tillers. *Plant. Prod. Sci.* 10: 430-441.
- Wells, B.E. and Faw, W.F. 1978. Short-statured rice response to seeding and N rates. *Agron. J.* 70: 477-480.
- Yamagishi, J., Yajima, T., Etoh, K., Suzuki, H. and Inanaga, S. 1992. Relation of number of spikelets per panicle to the characteristics of shoot and the size around growing point at panicle initiation stage in rice varieties. *Jpn. J. Crop Sci.* 61: 568-575\*.
- Yamamoto, Y., Yoshiad, T., Enomoto, T. and Yoshikawa, G. 1991. Characteristics for the efficiency of spikelet production and ripening in high-yielding *japonica-indica* hybrids and semidwarf *indica* rice varieties. *Jpn. J. Crop Sci.* 60: 365-372\*.
- Yao, Y., Yamamoto, Y., Wang Y., Miyazaki, A. and Cai, J. 2000. Numbers of degenerated and surviving spikelets associated with the number of differentiated spikelets among various rice cultivars. *Jpn. J. Trop. Agric.* 44: 51-60.

---

\* In Japanese with English abstract.

\*\* In Japanese.